MY LIFE-LONG SEARCH FOR THE "SELF" IN OURSELVES

Personal memories given to my daughter Mary

By

SIR JOHN CAREW ECCLES

Annotated and extended with supplementary family & biographical information by Mary R. Mennis & James P. Chalcroft

Prefaced by Dr. John Carmody

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Sir John Eccles' Search for the "Self"

Frontispiece: Portrait of Sir John Eccles (pastel on paper by Pam Macfarlane, dated 1959).

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Sir John Eccles' Search for the "Self"

Foreword

" Nothing in Biology Makes Sense except in the Light of Evolution "

Theodosius Dobzhansky[1] (1937)

I first met Dr John Eccles[2] in the 1960s and, even then (for reasons which, as a yet unformed physiologist, I would not have been able to articulate), I *knew* that I was in the presence of greatness.

I had come from Brisbane to Sydney to join the young School of Physiology at UNSW early in 1965 and, a year or so later, my professor, the wonderful Paul Korner[3], invited Eccles to come up from the ANU in Canberra to deliver a lecture. Its subject was his recent research on the neuronal circuitry of the cerebellum (work which, I believe, has never been surpassed or invalidated) and, when it had been delivered, a colleague (who was not a neurophysiologist) exclaimed with awe that it had been "as if Eccles had run a 'Hoover'[A] over the brain and extracted his elegant maps which he then simply displayed on the screen of the lecture theatre." He was correct in his assessment, though I accept that he hadn't understood their real significance any more than I had, myself.

Afterwards, the academic staff of the School assembled in Paul's office and drank the Angove's "Fino" dry-sherry which he so greatly favoured, and I had the marvelous experience of a conversation with Jack Eccles, of which I remember nothing at all apart from that powerful and enduring sense of true greatness which I, then a mere proto-physiologist, indelibly felt. It did not come simply from his magnificent lecture which had preceded it, nor from my certain knowledge that Jack Eccles had won the Nobel Prize a few years earlier and that I had never previously been even in the same room as such a Laureate. It was far more than any of those reasons.

It was only years later that I had so much a glimpse of the reason. It was, to a significant degree, because here was not just an enormous and wide-ranging philosophical intellect but, even more, because it was one which could fight so tenaciously for a major physiological concept yet could also recognise that *his own* research had unequivocally falsified that concept. Such behaviour called for the noblest strength of character.

Eccles had long, even abrasively, argued that the available evidence just as strongly supported his view that it was an *electrical* mechanism which effected the

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1 Dobzhansky, Theodosius Grigorievich (25.01.1900 18.12.1975) UA/US geneticist & evolutionary biologist.

2 Eccles, John Carew (27.01.1903 06.05.1997) AU neurophysiologist/teacher/writer/philosopher. (NP 1963).

3 Korner, Paul Ivan (18.11.1925 – 03.10.2012) CZ(J) Sydney Univ. physiologist. "Essential hypertension".

linkage of discrete neuronal entities (not to mention nerve cells and their target muscles and glands) rather than the increasingly popular view that it was a *chemical* process. Working, initially, on feline α-motor neurones and using the powerful (but intensely demanding) technique of recording intracellularly with tiny electrolyte-filled glass micro-electrodes, he and his colleagues showed, irrefutably, that inhibition was a real and independent process (not merely the scaling-back of excitation but that, on an Ohmic basis, quite distinct forces were driving discrete ionic currents into those cells (with individual "null-potentials" *i.e.* conditions of zero flow of current) whenever excitation and inhibition were induced. [**see:** JS. Coombs, JC Eccles & P Fatt (1955) "The specific ionic conductances and the ionic movements across the motoneuronal membrane that produce the inhibitory post-synaptic potential", *Journal of Physiology* 130, 326-373 (in particular Figure 1). *Cf* JS Coombs, JC Eccles & P Fatt (1955) "Excitatory synaptic action in motoneurones", *Journal of Physiology* 130, 374-395 (specifically Figure 1)].

These observations (here combined together in the following figure) were incompatible with a purely electrical mechanism and Eccles immediately recognised what he had achieved. Later, he acknowledged that the philosopher of science, Karl Popper, noted that, all along, his had been the rigorously correct approach and had, thereby, saved Eccles' intellectual life and reputation.

In his retirement from the experimental laboratory, Eccles, unsurprisingly moved back into philosophy, thereby reuniting his deep undergraduate concerns with those of his mature self. Like a few of his great contemporaries, he had been impelled into medical research and the asking of truly major questions by his student reading of such monumental books as Darwin's (1859) "*On the origin of species"*.

Will we Australians ever know his like again?

John Carmody, December 2023.

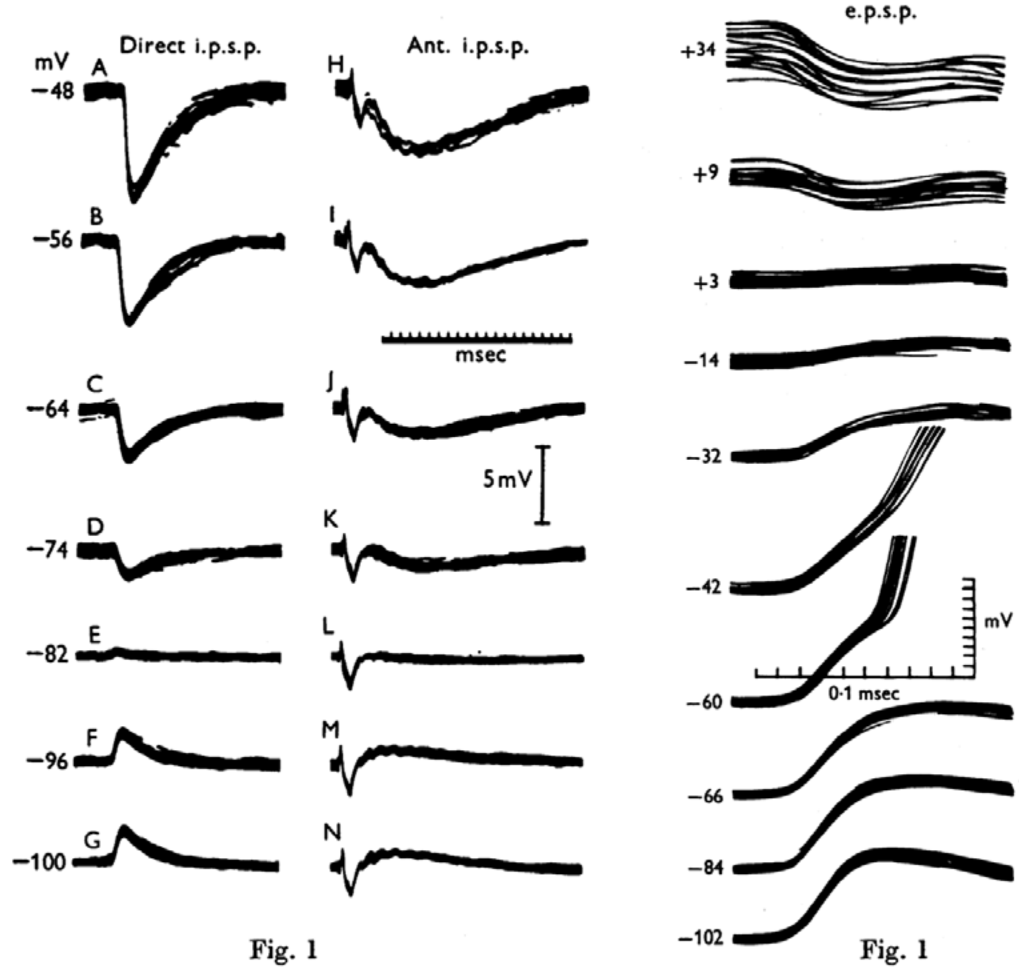

Fig. 0. Intracellular potential behaviours with i.p.s.p. and e.p.s.p. actions. [Foreword]

Left two columns (i.p.s.p.'s): Records **A** to **G** show i.p.s.p. intracellular potentials set up by direct inhibitory action, whereas records **H** to **N** show i.p.s.p. inhibitory action exerted by an antidromic volley. The membrane potential was set in the range – **48** mV to – **100** mV by means of a steady background current through one barrel of a double microelectrode. Without application of this current, the membrane "resting" potential was – **74** mV.
From Coombs, Eccles & Fatt (1955) [1A-126], p. 329, fig.1.

Right column (e.p.s.p.'s): Here, the e.p.s.p. intracellular potentials were recorded with membrane potentials set between + **34** mV and – **102** mV (the resting potential was – **66** mV).
From Coombs, Eccles & Fatt (1955) [1A-127], p. 377, fig. 1.
In all these experiments, *biceps-semitendinosus* motoneurones were used. Each record was formed by superimposing multiple sweeps.

Editorial comments and acknowledgements

The history of this Autobiography

The autobiography typescript of 171 pages (plus 25 pages of photocopied research publication figures) given to Mary Mennis by her father in 1991 is the only extant version discovered to date. Unfortunately, it covers only the period prior to John Eccles' move from Dunedin to Canberra. Although it has been claimed by his Swiss physician that Eccles continued writing his autobiography until the time of his death in 1997 (Mombelli & Monotti, 2000) neither a copy of Mary Mennis' text pages nor the completed work appeared in his estate of publications, donated by Lady Helena Eccles and presently archived in Düsseldorf.

Original autobiography text of 1991

The original typewritten text, scanned as pdf file, was converted by optical character recognition to searchable text and carefully compared with the scanned pages to remove character recognition errors and to correct spelling and typographic errors.

Eccles' division of his text into alphabetically-labelled sections (from **A** to **BU**) has been retained and these have been additionally grouped into STAGES (1 to 4), corresponding to the first four geographical stages of his worldwide odyssey. These stages cover only part of Eccles' professional life; from his first physiology experimental research with C. S. Sherrington until the last meeting with his dying mentor.

Additional autobiography text from 1957

To achieve continuity and completeness, it was deemed necessary to extend Eccles' unfinished autobiography to cover the remaining stages of his life. It is fortunate that this period has been covered (albeit in less detail) in an earlier publication. Thanks to its publishers, the required missing information has been transferred verbatim into this book, viz:

On behalf of Annual Reviews and the Annual Review of Physiology, we grant Mrs. Mary Mennis permission to reuse any portion of the article "My Scientific Odyssey" by John C. Eccles. We ask that the following attribution be included: "Portions of text reproduced and adapted with permission from the Annual Review of Physiology, Volume 39 © 1977 by Annual Reviews. https://www.annualreviews.org/".

Dated: Tues 19.01.2021

A. Introduction

My aim is to tell the story of my life as a neuroscientist with the linked philosophy. I want to convey my dedication to the greatest rroblem, which is the mystery of the human person, as experienced by each of us. In my autobiography I am of necessity the narrator and the central actor. I am fortunate to have a clear and vivid memory and I have an immense store of letters and documents, tens of thousands. My misfortune is that there are almost no survivors from my Oxford years. Ragnar Granit has just died and so has John Wolfenden, my Exeter College associate. Prof. J.Z.Young remains as my last Oxford contemporary. We matriculated together as Magdalen College students in October 1925. We have even published a paper together in 1932, and we review one another's books. The next stage of my Odyssean journey was Sydney. Bernard Katz and Archie Macintyre can share my memories. When I moved to Dunedin there are several living associates, most notably Sir Karl Popper, but also Dr Mariane Fillenz, a student in Dunedin, is now a distinguished Oxford physiologist. At my most important Odyssean stage at Canberra, my associates flourish all over the civilized world, and so on for my later 2 American stages.

B. Memories of early life

I was an extrovert with great academic successes and also I was good in sport, athletics and tennis. My father, a wise teacher, warned me that despite my successes at country schools, there would be much greater competition as I moved into the world. However, I rejoiced in the competition. I always have. And so it was when at the age of 16 I moved from 4 years in a country high School to Melbourne High School, one of the top 2 or 3 schools in Melbourne. It was not a religiously based school, but had very dedicated and religious boys and girls that were kept segregated at school! I was happy at the cultural and friendly atmosphere and did not hear one "dirty" story in the whole year. They were

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discredited myograph away in a cupboard and published nothing! I had the advantage of having one of the old myographs to compare with the new. So a solution was immediately presented to me by superimposed recordings as in Fig.5.

John Fulton had already left the study of muscle contraction and had begun at Oxford his great investigations on the brain that distinguished his Yale laboratory with the study of brain lesions by a wide variety of electrical and behavioural testing. We remained very good friends and I often visited him at Yale and stayed at his magnificent home above New Haven.

K. The synapse

As I try to survey in retrospect what was known on the histology of neurons and synapses, it is difficult to appreciate the inadequacy of our vision in those days before electronmicroscopy, which transformed our vision in 1955. From the time of Ramón y Cajal, in the 1890's nerve terminals were recognized as making a close contact with the surfaces of neurones by an expansion called various names, but I choose to use bouton.. It was this close contact that Sherrington had termed a synapse in 1897. In the typical silver stained preparation this bouton was often seen as a loop lying within about 1 µm of the neuronal surface. Fig.6a illustrates the best picture and displays an unusual density of boutons on the surface. Fig.6b displays a single terminal loop or bouton. Electronmicroscopy transformed the anatomical situation, but that was not to come until 1955. It has to be realized that the whole controversy on synaptic mechanisms and transmission was carried out on the basis of a quite inadequately understood structure (Fig.7), in contrast to Fig. that is based on electronmicroscopy (EM).Fig.7 is interesting because it illustrates how the silver staining of neurofibrils gave a picture of a loop up to 1 µm from the neuronal surface (Fig.6b) whereas the EM picture shows a synaptic cleft only 0.02 µm across. Furthermore with silver staining only the small number of boutons that have neurofibrils are recognized. Fig.6a is exceptional because it was of degenerating nerve terminals, where apparently neurofibrils are hypertrophied. The ultimate picture

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intracellular recording from motoneurons. Two more techniques were required and my two associates, Jack Coombs and Lawrence Brock soon provided them. Jack Coombs built the cathode-follower amplifier and all the ancillary equipment and Lawrence Brock meticulously solved the production of micropipettes with a tip diameter of 0,5 um. When filled with 3 M KCl the resistance was 5 to 10 MΩ, as was to be expected. The microelectrode track for insertion has been illustrated in Fig.42, 51A which give some picture of the problem of inserting the microelectrode into a motoneurone without seriously damaging it. An important guide for the insertion was to have antidromic stimulation every second of these motoneurons that were the targets, sometimes the antidromic stimulation was switched sequentially from one motor nerve to another, e.g. from quadriceps to hamstring to gastrocnemius nerves.
So in the experiments the completely blind insertion was guided by the antidromic responses extracellularly recorded as in Fig.42 track B Penetration was signalled by the appearance of a negativity of about 70 mV in the continuously running DC record, and by the reversal of the antidromic spike potential. However, the situation was usually quite complex with partial insertion and surface membrane damage. It was like fishing - one had to play with the neuron with the most clever micromovements guided by the DC potential and the antidromic responses. Sometimes the microelectrode would just graze a neuron without penetration. In imagination one conceived of neurons as coyly swaying to avoid penetration by the approaching microelectrode! An American, Marmont, wrote of his microelectrode penetrations of giant nerve fibres as being micro-rapes! There was great satisfaction when one eventually achieved a stable penetration, as shown by a steady membrane potential of about -70 mV, and steady synaptic potentials and spike potentials.

It has to be appreciated that in those far-away days in Dunedin we had to make everything in the laboratory with our technicians and ourselves. The only bought equipment was the film camera in Archie's laboratory. Now that Jack Coombs had taken over the electronics design and manufacture with Annand, mechanical problems were our chief concern - the fixation of the spinal cord of the cat, despite the respiratory and circulatory movements, and control of the microelectrode insertion. But we did succeed far better than anybody else in the world as I recognized in my world tour.

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BR. Review of my 8 years in Dunedin from age 41 to 48

These years were the most strenuous of my life, but I was able to rise to the challenge, and even to introduce what could be regarded as my most important scientific contribution - intracellular recording from neurons of the central nervous system.

I had the advantage of very good colleagues. My association with Karl Popper gave me the inestimable advantage of understanding the philosophy of science. Consequently I was much more flexible and creative idealogically. So with Popper's encouragement I set up neural models for synaptic excitation and inhibition as illustrated in Sections BG and BJ, and these formed the basis of experimental tests in Sections BI, BK and BQ. However, the testing procedures even by sophisticated extracellular recording were not discriminative enough. The final solution that it was chemical transmission came with intracellular recording towards the end of my Dunedin life (Section BQ). Nevertheless all those earlier investigations gave valuable insights into the simpler neuronal mechanisms in the spinal cord.

I had concentrated through all the Dunedin period on the simplest level of the central nervous system, the spinal cord of the anaesthetized cat. This preparation had two great advantages. I could use group Ia inputs (Figs 35A,53) from muscles that monosynaptically excited homologous motoneurons, i.e. the motoneurons of the muscle of origin and of its synergists (Sections BI, BD); and these same group Ia afferents produced the simplest inhibitory action, so-called direct, on antagonist motoneurons (Sections BK,BQ). As illustrated in Fig.53 it was possible to excite a large Ia response without contamination by group Ib impulses that have a quite different synaptic action.

I had studied the response induced by firing an impulse from the motor axon into the motoneuron as described in several sections Q,T, BE,BK. However, the final understanding came with intracellular recording in Section BQ as shown in Figs 47,51B, 52 with the recognition of the IS and SD components of the neuronal spike potentials.

Fig. A00. Page samples from Sir John Eccles' original typescript. [Editorial comments]

Four pages from the 171-page (uncompleted) manuscript, as given by him personally to daughter Mary Mennis during her visit to Contra in 1991.

This additional text has been subdivided into alphabetically ordered sections (**CA** to **EB**) corresponding to geographical STAGES (5 to 7), thus continuing the section-labelling scheme already established by Eccles in his autobiography of 1991. It is however, a poor substitute for Eccles' forthright comments and detailed observations which dominate Mary's rescued text; more resembling a lizard's meagrely regrown tail following loss of the original by mishap or sacrifice to enable escape from an enemy.

Family reminiscences

These notes and photographs from the married life of John and Rene are mostly derived from the two books by Mary Mennis:

1. (Mennis, 2000) *Hullo Eccles: The Eccles Family 1850 to 2000.*
2. (Mennis, 2003) *The Book of Eccles: A Portrait of Sir John Eccles, Australian Nobel Laureate and Scientist. 1903 – 1997.*

Her books reveal interesting aspects of domestic life of Sir John's family, the houses they lived in and travels they made during his long "Odyssey".

In the present book, mention is also made of John's second (almost 30 year-long) married life with Helena Táboriková.

These family reminiscences in sections (**FA** to **FM)** have been included to illuminate John Eccles' life via the unavoidably close human relationships where intimate views into his character can often be discovered.

Biographical notes

Notes referring to Eccles' career are provided after his autobiography and family reminiscences. These are keyed into his alphabetically-labelled sections by means of superscript letters so that the reader can move quickly between the main text and the notes.

Some notes are provided merely to provide essential background history, explaining the experimental methods and techniques employed by Eccles in his experimental work. Other notes are intended to provide yet an extra dimension of richness to his prosaic style, and to give yet more valuable insight into the personality of the author. Many personal reminiscences are included from his associates and some of these have been quoted at length where it is felt that important information complements Eccles' text, or assists the reader to comprehend scientific knowledge and techniques already discovered by his predecessors. The incorporation of these quoted reminiscences should reduce the need for the readers to undertake time-consuming, and often expensive, searches through original technical publications.

Extra figures, which were not specified in Eccles' autobiography, have been provided to further illustrate the career notes. The biographical notes are in sections (**GA** to **GF**) and amplify the text in the earlier sections (**A** to **EB**).

Footnotes

The one-line page footnotes, provided copiously in the autobiography sections and also elsewhere, are intended to assist readers who may wish to acquaint themselves with the lives of the many (often famous) personages Eccles encountered during his lifetime. Some persons mentioned may seem to be far *too* well-known to require such entries, nevertheless it is assumed here that even today only a minority of readers are well versed in the history of European/British culture and that this percentage could continuously decrease in the future. Most of these personages also appear as separate entries in reference works, such as the Internet resource, Wikipedia, where greater detail can be found.

Footnote lines include (if known) full name, birth and death dates, country of birth (as IBAN Alpha-2 code, ISO 3166 standard) supplemented with (J) if known to be of Jewish parentage/Jewish diaspora, followed by condensed fact(s) of special interest. Nobel Prize laureates are indicated at line-end thus: (NP year).

Figures

All figures are included in the contents list: **Figures, Photographs and Tables**. They have been organized to follow *en bloc* the texts of the Autobiography and Biography notes sections, whereas in the Family Reminiscences section they have been inserted within the text to enhance readability. To assist navigation the figure numbers associated with the three sections have been prefixed by **A** (for the autobiography), **F** (for the family notes) and **X** (for biographical notes and background information).

Internet link texts and QR-codes

Where https texts are supplied, these lines can be manually entered directly into the Internet via a browser (note that line endings appearing within the link do not indicate carriage returns; simply type in the complete blue-coloured link text without any breaks). In many cases, associated square-format QR code images are additionally provided to enable immediate access to the Internet links by means of "smartphone" scanning with a QR code reader.

Glossary

This chapter is provided to assist the reader comprehend the numerous abbreviations and specialized technical terms which appear in the autobiography.

The title given to the autobiography

Arriving at our choice was not difficult: From youth onwards and throughout his entire life, the question of "Self" seems to have remained prominent in John Eccles's thoughts. The word "Self" can often be substituted by similar English words, such as "Character" "Ego", "Identity", "Individuality", "Personality", "Soul", etc., and could perhaps be adequately described here as the set of behavioural features which describe completely the reaction spectrum of a human being to life's experiences. "Self-ness" is possessed uniquely by each person. Associated with "Self" is a sometimes-experienced awareness of a mysterious invisible entity, outside our constraints of space and time, which judges, and to some extent regulates, our behaviour. This "Spiritual" interaction, believed to extend even beyond the end of mortal life, is the basis of organized religious faiths where, in Christianity it is associated with a God above the heavens, in other faiths with idolatry, or with an environmental entity such as the forest God, “Tane” of the Māori.

John Eccles described at length his personal concept of the “Self” in chapter IV and of the “Soul” in chapter X of his book “Facing Reality”, (Eccles, 1970), which also contains many examples of his experiences and mature wisdom as student, scientist university lecturer and philosopher; thus, providing a fitting companion to the present work - his Autobiography.

Reasons for the publication of this autobiography

Criticism of its publication has been encountered in the form: Why publish when Sir John explicitly forbade this in a strangely-worded letter posted to his family members some weeks after daughter Mary brought the copy back to Australia?

The answer from Mary is that she was handed the rapidly copied notes personally without the knowledge of his second wife and instructed to “take it because of its importance”. She contends that her father definitely wished to have his autobiography published, but had to resort to smuggling the text and figures out surreptitiously because his wife Helena could otherwise manage to prevent its publication.

Other criticism encountered by us is that this book’s complex compendium-like style attempts too much: Should not its constituent material preferably appear in two or more books in order to be more attractive to prospective readers and hence sell better?

The editor defends the adopted layout with the argument that achievement of popularity was never the purpose adopted by us, but rather the hope that our readership would appreciate the wide illumination from multiple perspectives presented here of Sir John’s life - without the need to search much further. We would be greatly contented if this hope can become reality.

Acknowledgements

The authors thank the following figure and photo owners listed below for permissions granted for the use of their illustrations as figures in this autobiography:

ABIE, *ETN Communications Pty Ltd* (fig. X09)
Alexander Turnbull Library (fig. X16
ANU E Press, Allen & Unwin Pty Ltd. (fig. X24right)
American Physiol. Soc. (figs. 0, A05A, A05B, A15, A16A, A16B, A18A, A18B, A19, A20A, A20B, A24left, A24right, A25, A26, A28A, A29, A30, A31A, A31B, A32, A33, A36, A37, A40, A42, A43, A46, A49upper, A51, A52, A53, X04, X23, X24left)
Annual Reviews (text used from "My Scientific Odyssey" in Stages 6 and 7.)
Aust. National University (fig. F21, X21)
Cambridge Instruments catalogue (fig. X08)
Christchurch City Library (fig. X16left)
Churchill, London (fig. A49lower)
Eccles family (figs. A54, A55, A56, F01, F02, F03, F04, F05, F07, F09, F12, F13, F14, F18, F20, F22, F23, F24, F25, F26, F27, F28, F29, F30, F31, F33, F34, F35, F36, F37, F38, F39, F40, X20, X26right)
FT Press Science, New Jersey (figs. A27a, A27b)
Google Maps (fig. F41)
Jaques Cattell Press (fig. A28B)
Kanematsu Fund (fig. A21, X10)
Knopf Doubleday Publishing Group (fig. A22L)
Misc. adverts (fig. F08)
Nature (fig. A41)
New York Academy of Science (figs. A38, A39, A48)
Otago Univ. Hocken Library (figs. A34, A47, X13, X14, X15, X16r, X17, X18, X19)
Oxford Univ. Press (figs. A01A, A01B, A02, A06a, A06b, A09, A12, A13A, A13B, A14A, A14B, A14C, A23)
Palmer Catalogue (fig. X01)
Pinterest (fig. X26left)
Plenum Press: (figs. A03, A08C)
Proc. Physiolog. Soc. (fig. X03)
Quart. J. Exp. Neurol. (fig. X03)
Routledge, London (fig. A35)
Royal Society, London (figs. A04A, A04B, A07, A08A, A08B, A44, A45, A50)
Smith RN "Aussi Airlines" (fig. F17)
Society for Neuroscience SfN (fig. A17)
Springer (fig. A10)
State Library of Queensland (fig. F10)
Taylor and Francis (fig X11, X12)

Thomas Nelson, London (fig. A11)
Toronto Univ. Press (fig. X06)
Trends Neuroscience (figs. X01, X02, X05)
Universitetsforlaget Oslo (fig. X07)
Voodg, (fig. F32)
Wikimedia Commons (figs. A22Right, F06, F11, F15, F16, X01lower left)
Wilson Lythgoe Collection (fig. X16above)
Zimmermann (fig. X01)

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Am Klopferspitz 18, D82152 Planegg/Martinsried, Germany.

STAGE 1: Childhood & Youth in Australia: 1903-1927
(Sections A to H)

"If the human brain were so simple that we could understand it, we would be so simple that we couldn't."

Emerson M. Pugh[4] (ca. 1938)

A. Introduction (written in 1991)

My aim is to tell the story of my life as a neuroscientist with the linked philosophy. I want to convey my dedication to the greatest problem, which is the mystery of the human person, as experienced by each of us. In my autobiography I am of necessity the narrator and the central actor. I am fortunate to have a clear and vivid memory and I have an immense store of letters and documents, tens of thousands. My misfortune is that there are almost no survivors from my Oxford years. Ragnar Granit[5] has just died and so has John Wolfenden[6], my Exeter College associate. Prof. J. Z. Young[7] remains as my last Oxford contemporary.[A] We matriculated together as Magdalen College students in October 1925. We have even published a paper together in 1932, and we review one another's books. The next stage of my Odyssean journey was Sydney. Bernard Katz[8] and Archie McIntyre[9] can share my memories. When I moved to Dunedin there are several living associates, most notably Sir Karl Popper[10], but also Dr. Marianne Fillenz[11], a student in Dunedin, now a distinguished Oxford physiologist. At my most important Odyssean stage at Canberra, my associates flourish all over the civilized world, and so on for my later two American stages.

B. Memories of early life

I was an extrovert with great academic successes and also, I was good in sport, athletics and tennis. My father, a wise teacher, warned me that despite my successes in sport, athletics and tennis at country schools, there would be much greater competition

4 Pugh, Emerson Martindale (19.07.1896 – 01.07.1981) US physicist/teacher/author. "Hall effect".

5 Granit, Ragnar Arthur (30.10.1900 – 12.03.1991) SE Prof. Neurophysiology Karolinska Inst. (NP 1967).

6 Wolfenden, John Hulton (1902 – 1989) UK Professor of Chemistry, Dartmouth College. Pioneer alpinist.

7 Young, John Zachary "JZ" (18.03.1907 – 04.07.1997) UK zoologist & neurophysiologist. Textbook author.

8 Katz, Bernard (26.03.1911 – 20.04.2003) AT(J) UK physician & neurophysiologist. (NP 1970).

9 McIntyre, Archibald Keverall (01.05.1913 – 20.07.2002) UK Scottish/Tasmanian neurophysiologist & lecturer.

10 Popper, Karl Raimund (28.07.1902 – 17.09.1994) AT(J) UK philosopher/writer, "empirical falsification".

11 Fillenz, Marianne (1924 – 2012) RO(J) NZ/UK neurophysiologist. "Voltammetry; catecholamine/dopamine".

as I moved into the world. However, I rejoiced in the competition. I always have. And so it was, when at the age of sixteen I moved from four years in a country high school[A] to Melbourne High School, one of the top two or three schools in Melbourne. It was not a religiously based school, but had very dedicated and religious boys and girls that were kept segregated at school! I was happy at the cultural and friendly atmosphere and did not hear one "dirty" story in the whole year. They were lovely young people going on to distinguished careers at the university and thereafter.

I was doing Science and Mathematics and had an extraordinary geometry teacher, Mr Nesbitt[12] (Nessy) who had been an Oxford mathematician and a musical critic. He appreciated me and always called me "The ***Eccles***iastical gentleman" to the amusement of the class. He gave out homework which he corrected with witty comments. I still remember vividly my success on one geometrical problem that with much line construction turned out to be solved by the linear arrangement of the three midpoints on the diagonals of a complete quadrilateral. Nessy gave the standard complex solution to the class and then said "here is what the Ecclesiastical gentleman elegantly proposes", remarking that it was an original solution.[B] My geometrical imagination thus exhibited has been of great value in providing me with creative ideas in neuroscience. In the final state examinations, I shared the geometry prize and was second in the Senior Scholarship list. I had the top performance for Melbourne High School. This story leads on to the most significant turning point in my career.

I had no one to consult about my future course at the university. I had just turned seventeen. I told my parents that it could be Mathematics or Medicine, but they did not care to choose for me, leaving me to decide. Mathematics appealed to my imagination and I had my recent successes in the examinations, but it might not lead beyond being a secondary school teacher; whereas with Medicine I could have an independent useful life. My dilemma was simply solved when I discovered at the Registrar's office where one enrolled that the Mathematics course had already started one week before, and that I was just in time for Medicine, so I chose Medicine and kept my mathematical love for enjoyment and private study. It was a real turning point because in those days in Australia a mathematician never would have become a neuroscientist.

I rejoiced in the intellectual challenges in the Medical course with dedicated teachers in Zoology (Agar[13]), and Chemistry (Rivett[14]). In my academic courses I had great successes and was given special attention by my professors, being singled out even in the large classes of over 200, by Osborne[15] (Physiology), Berry[16] (Anatomy) and Apperly[17] (Pathology). In retrospect I realise they gave just[C] competent teaching!

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12 Nesbitt, Alfred Mortimer (27.12.1854 – 03.07.1926) UK composer/mathematician/music reviewer.

13 Agar, Wilfred Eade (27.04.1882 – 14.07.1951) UK university lecturer, "marsupial chromosomes & genetics".

14 Rivett, Albert Cherbury David (04.12.1885 – 1961) AU Univ. Melbourne Professor of Chemistry 1924-1927.

15 Osborne, William Alexander (26.08.1873 – 28.08.1967) IE professor of Physiology & Histology 1903-1938.

16 Berry, Richard James Arthur (30.05.1867 – 30.09.1962) UK Professor of Anatomy 1905-1929 (& psychiatrist).

17 Apperly, Frank Longstaff (26.07.1888 – 24.10.1961) AU senior lecturer in Pathology 1920-1931, later in US.

Fortunately, I was excitedly moving alone into the world of culture, widely reading in literature and trying to understand and appreciate the thoughts of poets, essayists, novelists and dramatists. Of special interest for me were the poems of Robert Browning[18] with his robust Christian philosophy. Eventually I bought his complete works to take on the ship to England. My father had a large collection of poetry - Shakespeare[19], Milton[20], Shelley[21], Keats[22] etc. Illustrated books of the works of the great artists specially appealed to me. I longed for the time when I could travel in order to experience classical and European works of art. My cultural interests rather separated me from my fellow medical students, but in 1923, my sister and I were fortunate to be invited into a wonderful group of religious young people who were seriously dedicated to music. That opened a new world for me. It was immersion into joyous and thoughtful living that seems to be quite different from that which occurs today. We all loved each other, but not in a sexual manner. That could come later on the way to a hoped-for marriage, but we meanwhile enjoyed our country walks and our music under the expert leadership of a young lawyer, Ted Mulvaney[23], who was musical critic for the leading newspaper. We had many musical evenings with gramophone recordings in his parent's home.

C. My early philosophical interests

As I try to look back on my formative years in scholarship, I find no great landmark except at age 17 (1920) in my first year at Melbourne University. I had been brought up as a practising Catholic.[A] I did not take dogma very seriously. I had a general biblical belief. Then at age seventeen in my study of Zoology I came to read Darwin's[24] Origin of Species that my father had in his library at home.[B] The full impact of this was to convert me to Agnosticism, as I confessed to my dear younger sister, who was my confidant. However, in a few weeks of anguished reading and thinking I came to realise that Darwinian evolution had no explanation for me as an experiencing self.[C] So, I embarked on a study of what the great thinkers of the past had written on this, to me the very urgent problem of brain and mind. I was surprised to find that even up to recent times the brain had been almost universally ignored or misunderstood. The philosophers and psychologists that I read were very deficient in their knowledge of the brain that would have been helped them discuss the problem of the unique experiencing self. Of course, my field of enquiry was very limited, but I had an excellent encyclopaedia in which there were scholarly accounts of the Pre-Socratics

18 Browning, Robert (07.05.1812 – 12.12.1889) UK philosopher-poet & playwright. A critic of spiritualism.

19 Shakespeare, William (23.04.1564 – 23.04.1616) UK dramatist, playwright/poet/actor. "Bard of Avon".

20 Milton, John (09.12.1608 – 08.11.1674) UK poet. Epic poem "Paradise Lost". Defended freedom of speech.

21 Shelley, Percy Bysshe (04.08.1792 – 08.07.1822) UK romantic/philosophical poet. "Prometheus Unbound".

22 Keats, John (31.19.1795 – 23.02.1821) UK Romantic poet. Sensual style. "Ode to a Nightingale".

23 Mulvaney, Edward C. "Ted" (?–?) AU Melbourne lawyer and (Church-) music critic.

24 Darwin, Charles Robert (12.02.1809 – 19.04.1882) UK biologist/evolutionist "On the Origin of Species".

with Greek philosophy all the way to Plato.[25] I did come to appreciate Descartes[26], though his knowledge of the brain was very deficient. So, I decided as a medical student to devote myself especially to a study of the brain.**[D]**

D. My medical course and Rhodes Scholarship

I worked very hard on all the diverse subjects of my medical course, but I always had before me the vision of a life dedicated to the brain. I got to know Sherrington's great book "The integrative action of the nervous system".**[A]** Then I heard from my friend, Prof. Frank Apperly that Sherrington[27] was at Oxford. The ideal way to get to Oxford was as a Rhodes Scholar, one being awarded every year to Victoria (Melbourne). Apperly had himself been a Rhodes Scholar so he gave me the best advice. I bought a book [by Crosby[28]] on Oxford University (Oxford of Today) with fascinating pictures and descriptions. I still treasure the book.

I had the qualifications for a Rhodes Scholarship with First Class Honours and the exhibition in eight of the ten subjects of the Medical Course of over 200 students. Also, I had success in sport with a full blue in Athletics and was active in university societies. However, the selection committee had to be specially impressed because up to that time the Rhodes always went to students from the Greater Public Schools and the three residential University Colleges, and I was merely in High School, living at home! I had good help in my application from Prof. Apperly (Pathology) and Prof. Osborne (Physiology) and amazingly I was elected on my first try (1924).

The award was made after a stylish luncheon at Government House and I was seated on the right side of a charming English lady, the wife of the Governor. There I was able to make good use of my cultural knowledge with sparkling conversation to offset my deficiency in social polish! That came later to me at Oxford!

The award was in November 1924 and I was due at Oxford in early October 1925, having been accepted by my college of choice, Magdalen, where Sherrington was a Fellow. I completed my Medical Course in February 1925 [aged 22], with First Class Honours and First Place and several clinical prizes. Then I had almost six months as a Resident and Registrar, so ending my clinical life.**[B]** Meanwhile I was preparing for Oxford. Never in my life had such a transcendent opportunity appeared. In retrospect I cannot imagine how my life would have developed without this magnificent Oxford opportunity. I am eternally grateful to Cecil Rhodes[29] for his great foundation. In my life I have been blessed by two great benefactions created by idealistic rich men who never married and who were rather similar, Cecil Rhodes and Alfred Nobel[30].

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25 Plato, (Plátōn) (~425 BC – ~348 BC): GR ancient Athenian philosopher. “Platonist school of thought”.

26 Descartes, René (31.03.1596 – 11.02.1650) FR philosopher “I think, therefore I am”. “Cartesian dualism”.

27 Sherrington, Charles Scott “Sherrie” (27.11.1857 – 04.03.1952) UK Electrophysiology – reflexes. (NP 1932).

28 Crosby, Laurence Alden (1892 – 1980) UK “Oxford of Today: Manual for Prospective Rhodes Scholars”.

29 Rhodes, Cecil John (05.07.1853 –26.03.1902) UK mining magnate in South Africa. "Rhodes scholarship”.

30 Nobel, Alfred Bernhard (21.10.1833 –10.12.1896) SE chemist/inventor. “Dynamite”. (NP benefactor).

E. Travel to Oxford

My great adventure in life started at the end of August 1925, when the Australian ship "Jervis Bay" left Melbourne and I was fare welled by my mother and father and my dear sister Rosamond, who had been my loving companion for 20 years. I had good friends on the voyage, particularly Ivan Turner[31], a mathematician from Sydney, on the way to a two-year scholarship at Trinity College Cambridge. There was a nice cultural, religious group on the ship, so it was a happy trip with an excursion to Cairo and the Pyramids on the way. We arrived at Southampton in early October and then by train to London to Oxford on the same day.

It was a very emotional journey down High Street in an open horse carriage exactly as I remembered it from a picture, and so to Magdalen College with the tower that originally attracted me to choose Magdalen College as my academic home. I had high and cold rooms on the ground floor of new Buildings (staircase three) with a view over the deer park, to the North. It was an exciting new world which I enjoyed accepting and learning, so as to become as English as possible, as my father would have liked. I had to make up for my early life in the relative isolation of Australia. I had come over with my medical scientific books and some literature, but I soon found my way to Blackwell and opened an account that I still have. So, I was gradually filling up the book case in my room. I soon went to London to the National Gallery, the British Museum, the Tate Gallery and bought prints that I had framed for hanging, just as my father had done in the home I grew up in with pictures of Greek sculptures and of Raphael[32], Leonardo[33], Titian[34], Michelangelo[35], Turner[36] etc.

F. Early life at Oxford

After this cultural and medical introduction, I come to my scientific life with the ideal before me of trying to understand the brain so that philosophy of the mind could be given a scientific base.[A] It was a vision that lured me on in my effort to transcend the materialism that was so dominant in philosophy and science. I had studied Sherrington's great book "The integrative action of the Nervous System" on the ship and also Bayliss[37]'s great work "Principles of General Physiology" 1924 that I still have with its more than 2000 references. I had also studied in Melbourne the psychology

31 Turner, Ivan Stewart (1918 – 25.03.1984) AU Mathematician. Principal of Sydney Teachers College.

32 Raphael, Raffaello Sanzio de Urbino (1483 – 06.04.1520) IT painter, Renaissance architect.

33 Leonardo, "Lionardo di ser Piero da Vinci" (15.04.1452 –02.05.1519) IT Renaissance painter, universal genius.

34 Titian, "Tiziano Vecelli" (ca. 1490 –27.08.1576) IT Renaissance painter.

35 Michelangelo, "di Lodovico Buonarroti Simoni" (06.03.1475 –18.02.1564) IT Renaissance sculptor, painter.

36 Turner, Joseph Mallord William (23.04.1775 –19.12.1851) UK painter, printmaker, watercolourist.

37 Bayliss, William Maddock (02.05.1860 – 27.08.1924) UK physiologist "water-regulating hormone; secretin".

book by McDougal[38], two books by Freud[39], that I rejected as too materialistic, and many more, that I still have.

I had hoped to start research for a D.Phil. as soon as I arrived at Oxford, but my Magdalen tutor MacKeith[40] insisted that I become on matriculation a senior student and study for the Final Honour School in Physiology and Biochemistry for two years and then qualify to do my D.Phil. course in two more years. I had to agree and recognised later that at that time the only way to progress in the Collegiate system of Oxford was via the Final Honour School with First Class Honours. There were good teachers in the course, Sherrington, Douglas[41] (Respiration) and Peters[42] (Biochemistry), but I had to repeat it in 1926-7. There were also visiting lecturers.

Now I return to my overwhelming personal experiences at Oxford. I had a letter of introduction to Sherrington written by Prof. W. A. Osborne, the Physiology Professor at Melbourne, who was a personal friend of Sherrington. So, in early October 1925 I knocked on Sherrington's door and came in to present my letter. I was received most cordially, and was invited to afternoon tea on the next Sunday afternoon at 3.30 PM in his home at 9 Chadlington Road. It was a large house in grounds, even with a tennis court. In the party there were Denny-Brown[43] who became the famous Neurologist and Bob Aitken[44], eventually a Medical Professor and then Vice-Chancellor at Dunedin and Birmingham. Both were medical graduates from Dunedin, New Zealand, and became my most intimate friends for the whole of our lifetimes. It was a wonderful new experience for me with Lady Sherrington[45] taking a special interest in these young men from overseas and also several other young men and women were there; several from South Africa. As was his custom, Sir Charles came down from his study-library upstairs to join us before we moved to the dining room where tea was served by Lady Sherrie and servants to us seated around the large dining table.**[B]** Conversation always seemed to sparkle with Sherrie enjoying the company and modestly displaying his enormous wisdom. He was no narrow scientist, but had immense knowledge of European culture from Greek times to the present and was learned in the plastic arts, especially of the great Italian ages and in literature of many European countries and the classics. He had started at Cambridge as a classical scholar. He had just published a book of poems "The Assaying of Brabantius and other Verse". I was overwhelmed by

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38 McDougall, William (22.06.1871 – 28.11.1938) UK parapsychologist/writer: “Outline of Psychology, 1923”.

39 Freud, Sigismund Schlomo (06.05.1856 – 23.09.1939) AT(J) neurologist and founder of psychoanalysis.

40 MacKeith, Malcolm Henry (14.04.1895 – 05.02.1942) UK Fellow and Tutor in Medicine, Magdalen College.

41 Douglas, Claude Gordon (26.02.1882 – 23.03.1963) UK inventor of “Douglas bag” for indirect calorimetry.

42 Peters, Rudolph Albert (13.04.1889 – 29.01.1982) UK developed BAL as antidote to warfare agent, lewisite.

43 Denny-Brown, Derek Ernest (1901 – 20.04.1981) NZ director of Harvard Neurological Unit, Boston Hosp.

44 Aitken, Robert Stevenson (16.04.1901 – 10.04.1997) NZ physician. Otago Univ. Vice-chancellor 1948-53.

45 Sherrington, Ethel Mary née Wright (1869 – 13.05.1933) UK “Lady Sherrie”, wife of Sir Charles Sherrington.

the experience that I had arrived at an earthly Paradise that I fitted into naturally after my years of cultural studies during the medical course at Melbourne.

So, Denny-Brown, Bob Aitken and I walked back in what to me was a kind of ecstasy. And it was to be repeated indefinitely because we were told to come without invitation for any Sunday in Term time, and also to bring friends. Lady Sherrie was most hospitable and enjoyed the company of young people, inviting me and others to dinner at the North-gate and then to the New Theatre for plays or operas or to concerts on many occasions. Sir Charles never came. He had no feeling for music or drama, though a great Shakespearean scholar. I think John Keats was his poetic love and I have a fine present from him, Keats and Shakespeare by Middleton Murry[46], 1926. I can remember the great excitement in the department when Robert Bridges'[47] epic "The Testament of Beauty" was published in 1930. We were reading it and quoting from it in the laboratory. I have reread it twice since and it has given me my lifelong dedication to beauty as can be seen at the end of my last book. So, life had come to scintillate with beauty.

I had realised that my ambition to provide the neuroscience for the brain-mind problem of philosophy was to be literally a life-long dedication and not to be accomplished in a few years. So, for many years I put aside this ambition in order to become a well-informed neuroscientist broadly based on all the relevant sciences. I was dedicated to both religion and to science, and I did not feel the antinomy as did many scientists who had not the philosophic and religious background that I had. All this time I was reading widely and thinking deeply, believing that there would be resolution of the mind-matter enigmas as we achieved a deeper scientific knowledge of the brain. I was closely associated with the scholars in several Catholic Oxford foundations, which included famous philosophers and theologians such as Father Martin D'Arcy[48] and Father Martindale.[49] I got to know especially well Father Ronald Knox[50], the Catholic Chaplain, who was a fascinating and amusing scholar, famous in Oxford as a wit. His book on Enthusiasm is a classic.

G. My Scientific Studies in 1925-1927.

I was studying most week nights in the Radcliffe Library and making notes on all my reading. I filled many notebooks with my abstracts. I learned scientific German by reading the great Rudolf Magnus[51] book "Körperstellung" (1924), which I still have, with all the translated words. Besides Sherrington's publications I read the literature of

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46 Murry, John Middleton (06.08.1889 – 12.03.1957) UK writer. Married NZ author Katherine Mansfield 1918.

47 Bridges, Robert Seymour (23.10.1844 – 21.04.1930) UK Poet laurate: "The Testament of Beauty", 1929.

48 D'Arcy, Martin Cyril (1888 – 20.11.1976) UK Jesuit teacher/philosopher/author. "The mind & heart of love".

49 Martindale, Cyril Charles (25.05.1879 – 18.03.1963) UK Jesuit scholar & preacher.

50 Knox, Ronald Arbuthnott (17.02.1888 – 24.08.1957) UK Catholic priest & detective author. "Decalogue".

51 Magnus, Rudolf (02.09.1873 – 25.07.1927) DE pharmacologist/physiologist/writer. Book: "Body Posture".

Lucas[52] and Adrian[53] (Cambridge) and the critical study and rejection of their decremental theory by Genichi Kato[54] of Kyoto in his 1924 and 1926 books that described his study with single nerve fibres. Adrian had fortunately left that impulse conduction study for his great work on receptor organ discharge and then later to the central nervous system. Other studies I was making on the nervous system were by Gasser[55] and Erlanger[56], using for the first time the cathode-ray oscilloscope. I studied Forbes[57] and Davis[58] also of America, Ramón y Cajal[59] of Spain, Pavlov[60] of Russia, A. V. Hill[61], Biedermann[62], Lapicque[63] and countless others. My aim was to have knowledge of a wide range of science as a basis for my Final Honour School examination and for my later planned research. So, I read widely in biophysics, physiology and biochemistry.

In the spring of 1927, I sat the examination for the Christopher Welch Scholarship that was open to all biological sciences. I had by then a very wide biological knowledge and could reply well in the oral examination by Professor Peters, so I succeeded. The £150 a year for three years would help when my Rhodes scholarship terminated in three years in June 1928. But the great event was the Final Honour School examination in June 1927 with Peters and Adrian as examiners. I was fully prepared and apparently impressed the examiners, obtaining a First. I also got a Gotch Prize, in a separate examination. All of this was important in building a scientific future in Oxford. I was relieved to have finished my undergraduate career so well. For me those two years were too long a probation for research. Denny-Brown had a two-year start in research, though we came up to Magdalen College together in 1925 and he was no better qualified than I. However, I also noticed that his research suffered in some detail because he did not have sufficient basic physiology.

H. Undergraduate life at Oxford and vacations.

At Magdalen College I was inducted into rowing, which gave me excessive exercise in 3 terms. However, I became an expert, participating in the Magdalen second Eight

52 Lucas, Keith (08.03.1879 – 05.10.1916) UK pioneering neurophysiologist & Cambridge Instruments designer.

53 Adrian, Edgar Douglas (30.11.1889 – 04.08.1977) UK Cambridge electrophysiologist. (NP 1932).

54 Kato, Genichi (11.02.1890 –01.05.1979) JP Keio University Japan Professor. Neurophysiologist.

55 Gasser, Herbert Spencer (05.07.1888 – 11.05.1963) US neurophysiologist. (NP 1944).

56 Erlanger, Joseph (05.01.1874 – 05.12.1965) US(J) physiologist. (NP 1944).

57 Forbes, Alexander (14.05.1882 – 27.05.1965) US pioneer electrophysiologist with Lucas, Sherrington & Davis.

58 Davis, Hallowell (31.08.1896 – 22.08.1992) US electrophysiologist with Adrian, later pioneer in audiology.

59 Cajal, Ramón y Santiago (01.05.1852 – 17.10.1934) ES pioneering neuroscientist/pathologist/histologist.

60 Pavlov, Ivan Petrovich (26.09.1849 – 27.02.1936) RU physiologist/neurologist, “conditioned reflex”.

61 Hill, Archibald Vivian (26.09.1886 – 03.06.1977) UK physiologist; studied muscle heat production. (NP 1922).

62 Biedermann, Wilhelm (14.01.1852 – 27.11.1929) DE. physiologist/writer “Electrophysiology” in 1898.

63 Lapicque, Louis Édouard (01.08.1866 – 06.12.1952) FR neurologist. “integrate & fire”, neuron model.

in June 1927 just before the final Honour examination. We had already worked our way up in the First Eight list in 1926 and now went on to great success bumping First Eights every night in less than 60 seconds.[A] So, we earned a bump supper despite a debacle on the last night when the stroke [number 8] and number 6 both caught crabs, for we still had a net of four bumps. We each got an oar, mine travelled the whole world with me and now is in my study looking at me from the wall. I rowed at number five as the heaviest man in the boat (12st. 3lb. [77.56 kg]). The London Times report said that we were the fastest boat on the river. I [found] rowing gave good fellowship, but was not distinguished for culture! However, I did have at Magdalen good friends who had cultural interests. One became a Canon of York Minster, another [J. H. Whitfield[64]?], Professor of Italian at Birmingham, and another, Mervyn [Alan?] Griffiths[65], then an Atheist, became a Benedictine and Abbott of Farnborough, and later left for an Ashram College in India. Another good friend was a Rhodes Scholar from Queensland, Jack Barry[66], reading Philosophy in Balliol College. He was a brilliant and turbulent Catholic flirting with Communism. He had a motorcycle and side car and we travelled together to The Vosges, but the trip was very stressful with accidents. I stayed on at Gérardmer in the spring daffodils and then went home from Mainz to Koln in a ship, down the Rhine, as my father had done 30 years before. In 1941 Jack Barry died in a bomber over Berlin - gallant to the end!

When one was an undergraduate at Oxford, there was the problem of how to spend the long summer vacation when the College was closed down. I was keen to see more of Britain rather than the Continent because of problems with language. So, my good friend Ivan Turner and I drove for many weeks in a car I had bought and on which we loaded a tent and camping facilities and even a gramophone. So, we travelled over much of England visiting the cathedral cities and Wales and right up through the mountains to North Scotland. At times we would recover from camping by hospitality at stately mansions to which we had been invited, thanks to the organization of Lady Frances Ryder[67] that was devoted to students from the Dominions. We were most grateful. We of course carried a good dinner jacket outfit, so we would drive up with our jalopy to some mansion in our camping clothes and then appear a half hour later in full dinner costume. Also, we were most proper in our behaviour and conversation, in contrast to some Australians! I am sure our visits were appreciated by our kind hosts as much as we did. Lady Frances Ryder thought well of them. One visit was to her parents' home, Lord Harrowby at Sandon Hall, Staff.

In another spring vacation trip, Ivan Turner and I went to the Tirol. I was very interested in visiting an isolated Tyrolese valley to see how good religious people lived, and I chose the Lech valley where there would be crocuses in April. So, we walked

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64 Whitfield, John Humphreys (02.10.1906 – 20.02.1995) UK. Prof. of Italian at Birmingham Univ. 1946-1974.

65 Griffiths, Alan Richard (17.12.1906 – 13.05.1993) UK Monastic name "Bede" later yogi, "Swami Dayananda".

66 Barry, John Edmund (01.06.1904 – 18.11.1942) AU League of Nations, Geneva. Killed in action over Berlin.

67 Ryder, Lady Frances (07.08.1888 – 1965) UK organiser of Dominion Services & Students Hospitality Scheme.

enjoyably for several days and stayed at the local inns, but alas at the end we had to cope with heavy snow at Warth village, where we stayed the night, having bought skis and then learned a bit so that we could go over Flexen Pass and down to Langen for the train home. It was most strenuous for 20 km, much in deep snow. I have never skied again!

STAGE 2: Research in Oxford: 1927-1937.
(Sections I to AF)

I. Fellowship at Exeter College.

In the autumn of 1927 on arrival back from a long vacation visit to Australia, I found in Magdalen College Lodge a notice about a Junior Research Fellowship at Exeter College, Oxford. It was the opening that I had been longing for, as it would give me 5 more years at Oxford with £250 a year, free rooms and dinners at High Table. So, I applied and Sherrie wrote me a wonderful testimonial. However, I did not see it till long afterwards. I had of course a good record and this justified my two undergraduate years, because such Fellowships were only given at that time to those with First Class distinctions in the Final Honour School. There were several candidates, some with lists of published research and I had not even started research! At the interview I spoke with enthusiasm about my research plans. The interview went very well and that night I received a note from the Rector, Dr. Lewis Farnell of my appointment. I had achieved much general culture that was valuable in my interview. I also had a good research program developing from what Sherrington had done, so my future at Oxford was assured, and research started immediately, firstly with Liddell[68] and Denny-Brown on the cerebellum.

Immediately after my election to the Exeter Fellowship I moved to my suite of rooms (3) in the front quadrangle that I furnished very modestly! Dacre Balsdon[69] (Classics) and John Wolfenden (Chemistry) were elected to Exeter Fellowships simultaneously with me, and became my life-long friends. In the Christmas vacation I stayed on in College alone with Henderson[70], an austere old classicist. I was told by him to select reading during meals, so we rarely spoke for day after day. I was careful not to infringe his privacy! Fortunately, I was due to visit a nice family for Christmas, thanks again to Lady Frances Ryder. Then I returned to Henderson with other Fellows slowly returning. Exeter had at that time surprisingly few Fellows, much of the teaching being done by appointed Lecturers.

As a Junior Fellow I was on probation for one year and did not attend College meetings or participate in tutorials. So, during 1928 I concentrated on research and writing. I was especially concerned to become a good writer with a simple and lucid style. I am told that I have succeeded! I bought the great 2-volume Shorter Oxford English Dictionary and the King's English by the Fowler[71]'s, all of which I still have. Later, when discussing punctuation with my good friend Tolkien[72], Professor of

68 Liddell, Edward George Tandy "Pat" (25.03.1895 – 17.08.1981) UK became Waynflete professor 1940.

69 Balsdon, John Percy Vyvian Dacre (04.11.1901 – 18.09.1977) UK ancient historian.

70 Henderson, Bernard William (1872 – 1929) UK Oxford historian. Roman history writer.

71 Fowler, Henry Watson (10.03.1858 – 26.12.1933) UK lexicographer. Book: "The King's English", 1906.

72 Tolkien, John Ronald Reuel (03.01.1892 – 02.09.1973) UK writer. Author of "The Hobbit".

English at Oxford, I confessed that I was modelling my punctuation on The King's English, and he surprised me by saying- "so do I". I continued throughout life to read English classics, so that good English seeps into my mind despite my environment in foreign countries.

My life at Exeter College was very happy with a wide variety of scholars, who were Fellows or associates. The first Rector, Lewis Farnell[73], a world-renowned Greek scholar invited me for strenuous country walks and good conversation. The next Rector, R. R. Marett[74], was a world-famous anthropologist, the Professor of Spanish was Madariaga[75], the famous writer, who was plotting the overthrow of King Alphonsus XIII and left for Spain when this happened, but later returned during the Civil war. Professor Soddy[76] had shared a Nobel Prize for Chemistry with Rutherford[77] on isotopes, but now had become an eccentric in finance and geometrical form. Richard Dawkins[78] was an old bachelor Greek scholar and was a great entertainer and an after-dinner attraction in his rooms, next to mine. Atkinson[79], Fellow in history, was an amusing and eccentric woman hater! Of younger Fellows there was Barber[80], a classicist, and my golf companion. Nevill Coghill[81] from Irish aristocracy taught English and was a beloved human person. He became a famous producer of plays and a Chaucerian Scholar. Cheshire[82] taught law and entertained us to tennis parties on his estate. Finally, there were those selected with me, particularly John Wolfenden, who became my dearest companion in tennis at Oxford and in mountaineering in the English Lake District. Jim Bezzant[83] was the theologian, an Anglican modernist and an authority on modern literature, from whom I learned to appreciate Hardie's[84] (sic) novels. He died in the Japanese attack on his ship "Repulse" near Singapore. Later Bill Kneale[85] was appointed to Philosophy and fortunately was not a materialist. He wrote well on the mind. I give this list to illustrate that we were an interesting and happy family of scholars at Exeter College, to which I owe so much for over 6 years at Oxford.

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73 Farnell, Lewis Richard (10.01.1856 – 1934) UK classical scholar. Exeter College Rector 1913-1928.

74 Marett, Robert Ranulph (13.06.1866 – 18.02.1943) UK. anthropologist. Exeter College Rector 1928-1943.

75 Madariaga, Salvador de (23.07.1886 – 14.12.1978) ES diplomat. Book: “Englishmen, Frenchmen, Spaniards”.

76 Soddy, Frederick (02.09.1877 – 22.09.1956) UK radiochemist. Book: “The Role of Money”. (NP 1921).

77 Rutherford, Ernest (30.08.1871 – 19.10.1937) NZ pioneer nuclear physicist. Radioactivity. (NP 1908).

78 Dawkins, Richard MacGillivray (24.10.1871 – 04.05.1955) UK archaeologist and Greek language scholar.

79 Atkinson, Christopher Thomas (1880 – 08.02.1964) UK military historian. Book: “A History of Germany”.

80 Barber, Eric Arthur (08.10.1888 – 24.05.1965) UK tutor & lecturer in Classics. Later rector at Exeter College.

81 Coghill, Nevill Henry Kendal Aylmer (19.04.1899 – 06.11.1980) UK literary scholar. “Canterbury tales”.

82 Cheshire, Geoffrey Chevalier (27.06.1886 – 27.10.1978) UK barrister. Book: “Modern law of real property”.

83 Bezzant, James Stanley (14.05.1897 – 1967) UK chaplain (who actually survived the sinking of the Repulse!).

84 Hardy, Thomas (02.06.1840 – 11.01.1928) UK poet & novelist. The so-called “Wessex novels”.

85 Kneale, William Calvert (22.06.1906 – 24.06.1990) UK philosopher/logician. Bk: “The development of logic”.

In 1931 I was appointed to the Staines Medical Fellowship at a stipend of £400, replacing my Junior Research Fellowship. However, it was also limited to 5 years. The College tried to get it extended, but failed, so I was limited to 5 years, retiring in 1936.

J. Onset of Research at Oxford

My Exeter Fellowship was of great value as a status symbol at Oxford. For example, Creed[86], a Fellow of New College, immediately asked me to join him on a research project he had planned on the distribution of inhibition to the motor units of a flexor muscle.**[A]** Our conjoint paper was published in the Journal of Physiology in 1928. It was my first scientific publication. Then Creed very kindly gave his research room over to me as he was changing to visual physiology in another room. The room I had inherited from him had the basic equipment for recording reflex contractions by an isometric mirror myograph and falling plate camera with ancillary stimulating equipment [sundry induction coils].**[B]** I retained and developed this room and added adjacent rooms during the 10 years that I was to remain at Oxford. It was this research room that Ragnar Granit and I shared when he came from Tigerstedt[87]'s Institute at Helsingfors [Helsinki] to work under Sherrington. Granit took over my rooms in Rose Lane near Magdalen and thus saved me from financial trouble with my land-lady who was concerned at my departure for my rooms in Exeter.

As a consequence of my two study years at Oxford in the Final Honour School, I had some basic ideas on what experiments could be done with Granit using the limited equipment I had inherited from Creed. So, in 1928 on the same conceptual framework that had been used by Cooper[88], Denny-Brown and Sherrington in the preceding years (diagrammed in Fig. A01B) with tetanic stimulations evoking ipsilateral flexor reflexes, we concentrated on the crossed extensor reflex. This study was focussed on the manner in which extensor reflex contractions were composed of the responses of the individual motor units. In the Sherringtonian concept each such unit was a motoneuron with the muscle fibres that it innervated almost exclusively. The different reflexes could be shown often to activate the same motor units, which resulted in occlusion of the two reflexes, the combined response being much less than the sum of the individual reflexes. In a complementary study it was found that weak reflexes when superimposed resulted in a reflex much larger than the arithmetical sum. There had been reflex facilitation bringing in additional motor units. Similar investigations with Ragnar Granit on the more complex deafferented crossed extensor reflex into deafferented muscles also revealed occlusion and facilitation but with more enduring after-effects.

All results could be satisfactorily accounted for on the motor unit hypothesis. However, the facilitation effects were often more prominent than with flexor reflexes

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86 Creed, Richard Stephen (20.12.1898 – 07.07.1964) UK long-term Oxford physiology demonstrator & lecturer.

87 Tigerstedt, Robert Adolph Armand (28.02.1853 – 12.02.1923) FI circulation physiologist. Discoverer of renin.

88 Cooper, Sybil (Jan. 1900 – 1970) UK demonstrator in anatomy at Oxford; later lecturer at St. Hilda's College.

and there were sometimes complications by reflex inhibition. I wrote up our experimental results and their interpretations. There was publication in the Journal of Physiology in 1929.

The physiology department was really run by George Cox[89], brought from Liverpool by Sherrie. He supervised the animal procurement and accommodation.**C** He was a martinet, dominating even Sherrie. I have heard him attacking Sherrie violently on some minor happening in the department and Sherrie saying "Please, George, forgive me I promise I won't do that again - I promise". He was a tyrant over the young technicians that he selected from schools. In this regime some succeeded. I selected Chapman[90] to come with me when I left for Sydney in 1937 and he stayed with me through Dunedin to Canberra where I left him in 1965. Fulton[91] took Kerby[92] to Yale, Giles[93] stayed on to succeed Cox as head technician. Another was Meadows[94], a sensitive boy, that I first noticed when he was sobbing in a dark corner in the department, having been mercilessly scolded by Cox. I comforted him and in the end he succeeded well. He became well educated, was the technicians' union representative in labour politics and become an Alderman in Oxford City. He remained as a good technician in the department, but was given special privileges, being valuable to the University in its relations with the unions. Finally, he became for many years Lord Mayor of Oxford, while still a technician.**D** His ultimate success was to entertain the Physiological Society of Great Britain at a reception in the Oxford City Hall with many good speeches. I was there at the Physiological meeting, but I did not tell him of our first encounter! The great success of Meadows reminds me of the story of Dick Whittington![95]

In my first year (1928), there were 5 of us research workers, sitting with minimum privacy in the old mammalian research room. We each had an old laboratory table covered by a cloth, 2 chairs and a pseudo-privacy provided by folded screens that kept on falling over. Sherrington and the more senior staff, Liddell, Douglas, Priestley[96], Creed and Sybil Cooper had their own rooms, and I was rapidly acquiring a room. Denny-Brown, Granit, Olmsted[97] (US), Marcu[98] (Romania) and myself were the five.**E** There was no office in the Department, no secretary – and not even a typewriter! We

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89 Cox, George (? – ?) UK Sherrington's first technician and long-serving laboratory manager.

90 Chapman, Arthur Stanley (07.04.1878 – 15.09.1980) UK technician; with Eccles to Australia & New Zealand.

91 Fulton, John Farquhar (01.11.1899 – 29.05.1960) US neurophysiologist and science writer/historian.

92 Kerby, Frank (?–?) UK Oxford technician, later accompanied Fulton to Yale. (Wall, 2001, p.485).

93 Giles, ? (? – ?) UK Oxford technician, was also working with HM Carleton in histology.

94 Meadows, Thomas James (25.05.1916 – 1982) UK Oxford technician and Lord Mayor of Oxford 1971-1972.

95 Whittington, Richard "Dick" (c. 1354 – 1423) UK Lord Mayor of London & subject of famous English legend.

96 Priestley, John Gillies (1880 – 09.02.1941) UK physiologist with JS Haldane. Studied role of CO_2.

97 Olmsted, James Montrose Duncan (21.05.1886 – 26.05.1956) US physiologist & historian Univ. of California.

98 Marcu, I (?–?) RO cardiologist. Later worked with Danielopolu at Kliniko Medical Institute, Bucharest.

had to buy our own typewriter and use it at home. Sherrington wrote by hand his letters and did the filing himself. Official letters were sent out for typing. There was a workshop with a lathe etc. run by O'Neill[99], a very good mechanical man.

Those were the days when you constructed and serviced your own equipment. It was the same everywhere in those simple days before the great instrument companies took over. A good friend from my earliest days at Oxford was Pat Liddell,[F] who was Sherrington's right-hand man and associate in research (1920-1924). He was a very good scholar and teacher and wrote an excellent historical book "Discovery of Reflexes".[G] He and his wife Joan were always helpful. In 1930-1932 he was the editor of the 5-author book that will be described later. It was always a pleasure to meet him with his knowledge, charm and his wit. Richard Creed has already been mentioned. Sybil Cooper who had worked with me on the muscle contraction research was a good biological scientist who had come from Adrian of Cambridge. She and Creed were very good friends of Ragnar Granit when he came for his second stay of 2 years as a Rockefeller Scholar. We recognised that Creed and Sybil should marry. They were obviously fond of each other, but they were too shy in those far-off days! So, what could we do? It was Ragnar who got the solution: He set up a visual experiment in which they had to remain together in a dark room for 30 minutes of dark adaptation. I can now still remember the benign expression on Ragnar's face as he was smoking a cigar outside the adaptation room and thinking that his strategy was working, as indeed it did. They were married, set up a nice home and had 4 children. I tell these stories to give some concept of the loving society that we had in the laboratory. Ragnar and I were very close friends and in his second visit he came with his young wife Daisy and a baby son Mikey [Michael] to live just opposite our house at 1 Staverton Road, North Oxford. We regularly walked home together so that we could enjoy our conversation.

K. Time course of c.e.s. - central excitatory states

In June 1928 Sir Charles (Sherrie) asked me to join him in experiments. I was much elated and suggested that we could study the time course of the central excitatory states c.e.s. that he had postulated in 1925 (Sherrington, 1925, p. 520 and p. 525, fig. 1 as **E**) as being the enduring neuronal process leading on to a reflex discharge. The experimental idea appealed to me because it was an effective test of his c.e.s. hypothesis of a reflex response. We showed that small inputs into the spinal cord by converging pathways could evoke a reflex discharge when either one alone was ineffective. So, it could be concluded that c.e.s.'s could summate to evoke a reflex discharge of some motoneurons. The simplest time course of this summation showed a maximum with simultaneous inputs and declined to zero facilitation when the interval was increased to 15 msec. as in Fig. A02. So, the duration of the c.e.s. was about 15 msec. However, there were in many experiments, complex curves, often with a maximum facilitation at about 12 msec. interval. This could be accounted for by after-discharge through complex neural pathways. It was wrongly assumed at that time that the simplest central

99 O'Neill, C. J. (? – ?) UK constructor of Sherrington's torsion wire interrupter, myograph & fall-table.

pathway for the flexor reflex was monosynaptic. The great Spanish neuroanatomist [Ramón y Cajal] had diagrammed this pathway as illustrated in Fig. A03A with dorsal root fibres directly acting on motoneurons and Fig. A03B showed the connections of the pathway to and from the muscle that was set up for recording the muscle contraction by a myograph, and also for electrical recording by a string galvanometer as was done in 1930.

I was very pleased with the assumed monosynaptic experiments and wrote it up for publication.[A] For the first time, it had been shown that synaptic excitation set up an enduring process of about 15 msec. duration, the central excitatory state (c.e.s.) postulated by Sherrington in 1925 (but called first **E**), and that the c.e.s.'s produced synaptically by different converging inputs on a motoneuron could sum to evoke a reflex discharge. The concept of neuron threshold had now been demonstrated, namely that several impulses converging on a motoneuron were required to generate the c.e.s. adequate for setting up a discharge. However, this initial study failed in details because there was an interneuron on the pathway drawn as in Fig. A01B. Moreover, electrical recording was necessary for precise studies and that came in 1930, with the string galvanometer, as illustrated in Fig. A03B and the series of publications in 1931.

There are two memories that I have on this study. One is that, when setting up the demonstration to the Physiological Society at Oxford this reflex summation from two ineffective inputs, the flexor muscle commenced spontaneous twitching, which would spoil the demonstration. Everything was tried to eliminate the cause in some injured focus. Then Sherrie got the bright idea of squeezing the cat's tail. It was a decerebrated spinal cat, unanaesthetised.[B] It worked wonderfully in quietening the twitching. So, we gave the demonstration of reflex summation of two subliminal inputs with Sherrie sitting behind the cat with his hand squeezing the tail covered by a cloth. All went excellently in this first demonstration ever given of summation of two reflexly subliminal inputs. But we kept our secret of the tail squeezing and enjoyed our success like two conspirators. The second story is that I was so enthusiastic about my first significant experimental study, that I wrote it up for publication, of course conjointly with Sir Charles, but without having his permission. So, I invited him to dinner with me at Exeter College on a Sunday night festive dinner, and afterwards showed him the manuscript, reading extracts from it. He was a little surprised, but very kind, criticising some of the language and told me that I would be helped in word choice by Roget's Thesaurus, which he gave me the next day with the dedication J.C. Eccles -"My joke" Aug. 21 1930. I still use it. So, this complex paper with some rewriting was eventually published in 1930. As we sent it in for publication, Sherrie told me that it was the first of his published papers that he did not personally write! So, the dinner was a success!

L. The motor unit

In those early years the mechanical recording of reflexes with isometric optical myographs was the key technique of the Sherrington school, and the results were discussed in terms of motor units, as already described. So, Sherrington planned to measure the size of contraction of average motor units. To do that all one had to do was to divide the maximum tetanic and twitch contractions of a muscle by the number of motor fibres innervating that muscle. It was a simple idea and Sherrie asked me to join him in measuring the muscle contractions and in counting the motor nerve fibres. He had already prepared muscles in which all the afferent innervation had been degenerated by aseptically operating on the nerve roots going from the spinal cord to the muscle and excising the dorsal root ganglia some weeks before. Then we recorded the contractions of the selected muscles.**[A]** They were not deteriorated by the deafferentation as compared with the other side. After the motor recording, Sherrie excised the nerves to the muscle and prepared them by osmic acid [OsO_4] staining so that in transverse sections the motor nerve fibres could be seen as black rings in his excellent staining procedures. Such pure motor nerves had never been examined before, and we expected a simple statistical distribution of fibre sizes matching the range of electrical stimulation thresholds for the muscle contraction. I can still remember my great astonishment as soon as I looked at the sections. There were two distinct fibre sizes. I was alone in the weekend and measured and plotted histograms of the "motor" fibre sizes for nerve after nerve. About 30% were in the small fibre range, the γ fibres, 2 to 8μ, being completely separate from the large α fibres, 10 to 20μ. Next morning Sherrie was also amazed at this double population distribution (Fig. A04A, A04B). In our published paper there can be seen the various attempts to account for this α, γ motor innervation.

While we were working together on the motor units the XIII International Physiological Congress was being held in Boston on 19th – 23rd August 1929. Sherrie sent a cable to the President of the Congress, Prof. W. Howell[100], wishing them every success and signed it Sherrington and Eccles - Eccles was then a quite unknown name, but he insisted!

I tell this story of the alpha and gamma fibres because both of us missed the obvious explanation that had to await discovery by Granit's pupil Leksell[101] many years later (1945). The explanation was simply that the γ-fibres were motor to the muscle fibres of the specialised receptor organs, the muscle spindles in the muscle.**[B]** That discovery led to a whole field of important studies by Granit, Kuffler[102], Hunt[103], Lloyd[104] and at Canberra. The irony of the situation was that in his Linacre Lecture of 1924.**[C]** Sherrington had considered a separate motor innervation for muscle spindles. I did not see Sherrie again from 1937 until just before his death in 1952, and I tried to tell him of our mistake, but mercifully he did not understand. His thoughts were, in a different world, on the mystery of our spiritual Self!

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100 Howell, William Henry (20.02.1860 – 06.02.1945) US physiologist. "Heparin as blood anticoagulant".

101 Leksell, Lars Gustaf Fritiof (23.11.1907 – 12.01.1986) SE physician/neurosurgeon Karolinska. "radiosurgery".

102 Kuffler, Stephen William (24.08.1913 – 11.19.1980) AT(J) AU/US neurophysiologist. "Endplate" GABA.

103 Hunt, Carlton C. (11.08.1918 –08.02.2008) US research pioneer studying innervation of mammalian muscle.

104 Lloyd, David P. Caradoc (23.09.1911 –20.04.1985) US/CA neurophysiologist. "Spinal-cord/muscle reflexes".

M. Frictionless myographs, viscoelasticity and the “angle”.

At the time before oscilloscopes, electrical recording from the central nervous system was rather imprecise, even with string galvanometers. I was tempted to follow Sherrington with an effort to perfect the recording of muscle contractions. Moreover, I was looking for an opportunity for my mathematical interest. I achieved an unintended success when I turned my attention to the extraordinary time course of a muscle twitch that had been revealed with recording by the isometric mirror myographs developed by Sherrington at Oxford in the early 1920's. The twitch contraction was evoked by a single volley of motor impulses. The twitch rose up sharply to a plateau which declined abruptly at an "angle" (Fig. A05A, A05B). Fulton described a detailed investigation of the angle in his D.Phil. thesis in 1925, and in the first part of his great book "Muscular contraction and the reflex control of movement" (1926). I of course accepted its validity. Because of the high reputation of the Oxford Laboratory the "angle" was generally regarded as a criterion for the excellence of motor recording.

There was the problem of how the "angle" was generated in the muscle twitch. I planned to discover this by applying a fast, oscillatory stress along the length of the muscle during the twitch so as to study the viscoelasticity of the muscle at all stages of the twitch, much as had been done by Gasser & Hill [1924], but with more finesse and at much higher frequencies. Hitherto, the optical myograph was by torsion applied to a steel rod fixed at one end and supported at the free end in a V-shaped slot. It looked crude, but was accepted because it gave twitches with such good "angles"! I recognised that for my precise oscillatory study the free end of the torsion rod should have an axial knife-edge resting on a steel plate so that the applied oscillations would be unimpeded.[A] This was well constructed by O'Neill in the workshop. The oscillations were started by a magnetically releasing device and beautiful sine waves were recorded, both in free oscillations and in oscillations damped by two long rubber cylinders attached symmetrically as models for muscle in preliminary tests.

Unfortunately, when the very accurate measurements of amplitude and frequency of the oscillations were applied to the standard Rayleigh equations for viscoelasticity, there were systematic deviations when the frequency and amplitude of the oscillations were varied. Evidently there was some defect in the viscoelasticity equations that introduced errors in the calculations for the coefficient of viscosity. My testing arrangements were far superior to any preceding investigations. I was at that time in the informal lecture course of Prof. E. A. Milne[105] on the dynamic structure of stars, so I mentioned my viscoelasticity problem to him. He was the professor of Applied Mathematics at Oxford, and quickly recognised that in the standard equations derived by W. Thompson[106] (Lord Kelvin) in 1865, it was assumed that the applied stress travelled instantaneously along the rod. Milne's research student J. H. C. Thompson[107]

105 Milne, Edward Arthur (14.02.1896 – 21.09.1950) UK astrophysicist/mathematician. “Kinematic relativity”.

106 Thompson, William (26.06.1824 – 17.12.1907) UK, 1st Baron Kelvin, mathematician “thermodynamics”.

107 Thompson, John Harold Crossley “Jack” (1909 – 1975) UK, with Creed. “The after-image of black”, 1931.

carried out the immense mathematical task of setting up equations for viscoelasticity with allowance for the longitudinal velocity of the stresses. From the equations so set up, a true coefficient of viscosity could be calculated for the first time. Thompson was awarded a D.Phil. for his great thesis (Thompson, 1933), and we published a conjoint paper with the derived coefficients of viscosity for two types of rubber.**B** We never tried to study the viscoelastic properties of muscle at rest and contraction, which was the original goal of this study. Insurmountable complications were introduced for muscle because two quite different structures, muscle and tendon, were necessarily in series.

However, at an early stage the newly designed myograph was used to record muscle contractions, but to my chagrin the muscle twitches displayed no angle. I was thunderstruck and immediately tried the same muscle on the old myograph where its twitch had a good angle! Superposition of the two twitches (Fig. A05A, A05B) immediately gave me the solution that the angle was caused by friction that impeded the rotation of the torsion rod on its V-shaped support. We had thought that the angle guaranteed a good ic recording, but it was the reverse! My problem to study the angle by the refined oscillation study had disappeared in a flash!**C**

But now I had the great emotional problem of how I, as a very junior person, could break the news, because Sherrington's Oxford Laboratory was famous for the excellence of the optical myographic recording with the "angle". So, that very afternoon I broke the news to Sherrie. He looked at my demonstration of the superimposed records and was convinced, but made no further comment. Next day he was so happy. He told me that he had looked through that night all his publications and he had not mentioned the angle once - though of course he had believed ever since it was revealed in Fulton's detailed study! He suggested a wise solution. He and I would present a joint communication to the Physiological Society on the redesign of the myograph to avoid the friction artefact of the angle.**D** Then I, with Sybil Cooper, would illustrate the superimposed muscle twitches to show the friction artefact. Sybil had been working with me on muscle contractions, but was away on the day I made the discovery.

I was keen not to cause pain to my dear friend John Fulton when so much of his work on the angle had thus disappeared, so there was no reference to his work in our immediate publications. For me the Physiological Society, Dec. 14th 1929, meeting was my first success story, as my good friend, Brian McSwiney[108] delighted to tell me. The angle disappeared from the literature with the introduction of frictionless myographs.

Sybil Cooper and I now had the attractive task of studying muscle contractions with our frictionless myographs. We chose a wide range of cat muscles, the slow *soleus*, the medium *gastrocnemius* and *extensor digitorum longus* and the very fast eye muscle, the *internal rectus*.**E** We used maximal stimuli applied singly for twitches, doubly for summation over a whole range of intervals, and tetanically at a range of frequencies up to tetanic fusion at 350/sec for the eye muscles, 100/sec for the *gastrocnemius* and 30/sec for *soleus*. The significant discovery was that muscle contractions varying over

108 McSwiney, Bryan Austin (20.05.1894 – 08.03.1947) US, UK physiology prof. "Smooth muscle function".

more than 10 to 1 in speed were similar when scaled for the respective speed. The wide range of stimulus frequencies was provided by a neon tube stimulator that A.V. Hill and his technician Downing[109] gave as a present to Sherrie. They came from London by car without prior notice. With great excitement we set it up and it worked perfectly, so it immediately was applied to our muscle stimulations. Everybody was so happy, and I realised that scientists were dedicated to help each other with generosity. The neon stimulator was a great improvement on the repetitive break shock machine that we were using.[F]

There are some good stories relating to the angle. Forbes and Davis had constructed at Harvard an excellent myograph that was frictionless, but it gave smooth curves for muscle twitches as in Fig. A05A, A05B, with no trace of the expected angle. So, they put their discredited myograph away in a cupboard and published nothing! I had the advantage of having one of the old myographs to compare with the new, so a solution was immediately presented to me by superimposed recordings, as in Fig. A05B.

John Fulton had already left the study of muscle contraction and had begun at Oxford his great investigations on the brain that distinguished his Yale laboratory with the study of brain lesions by a wide variety of electrical and behavioural testing. We remained very good friends and I often visited him at Yale and stayed at his magnificent home above New Haven.[G]

N. The synapse

As I try to survey in retrospect what was known on the histology of neurons and synapses, it is difficult to appreciate the inadequacy of our vision in those days before electron microscopy, which transformed our vision in 1955. From the time of Ramón y Cajal, in the 1890's nerve terminals were recognised as making a close contact with the surfaces of neurones by an expansion called various names but I choose to use "bouton". It was this close contact that Sherrington had termed a "synapse" in 1897.[A] In the typical silver-stained preparation this "bouton" was often seen as a loop lying within about 1 μm of the neuronal surface. Fig. A06A illustrates the best picture and displays an unusual density of boutons on the surface. Fig. A06B displays a single terminal loop or "bouton".

Electron microscopy transformed the anatomical situation, but that was not to come until 1955. It has to be realised that the whole controversy on synaptic mechanisms and transmission was carried out on the basis of a quite inadequately understood structure, Fig. A06 – in contrast to Fig. A07, that is based on electron microscopy (EM). Fig. A07 is interesting because it illustrates how the silver staining of neurofibrils gave a picture of a loop up to 1 μm from the neuronal surface (Fig. A06B) whereas the EM picture shows a synaptic cleft only·0.02 μm across. Furthermore, with silver staining only the small number of "boutons" that have neurofibrils are recognised. Fig. A06A is exceptional because it was of degenerating nerve terminals, where apparently neurofibrils are hypertrophied. The ultimate picture is by the freeze-fracture technique

109 Downing, A. C. (?-?) UK Galvanometer designer. Measured heat production of muscles and nerves.

of Konrad Akert[110] and his associates with EM technique, but that will come much later in my story.**B**

O. The last Sherrington experiments 1930-1931

With the arrival of the string galvanometer and the frictionless myograph we planned a comprehensive study of the "simplest" spinal reflexes. There was still the limitation of the falling plate speed of the camera, 450 mm/sec, but it was not serious. We had also a Lucas pendulum, used for giving three induction shocks with an accuracy of 0.1 msec.**A**

Sherrie and I decided to use the flexor reflex in order to study further the hypothesis of c.e.s. that he had proposed in 1925. This comprehensive study was in the mistaken belief that the flexor reflex was monosynaptic. At that time, we, at Oxford, regrettably had not known that Paul Hoffmann[111] had in 1921 shown that the tension receptors of muscle provided the monosynaptic input to that muscle, and that it was exhibited in tendon reflexes such as the knee jerks.**B**

We could investigate that monosynaptic reflex only when there had been developed electrical recording by amplifiers feeding into oscilloscopes, but for that we had to wait for two more years. Our first results on true monosynaptic reflexes were not published until 1937 in a short paper **C** with Pritchard.[112]

Despite this mistaken belief that the flexor reflex was monosynaptic there were valuable findings on flexor reflexes. For example, facilitation by two successive volleys resulted in a more direct synaptic connection, probably down to two synapses in sequence, with the summed c.e.s. causing an earlier motoneuron discharge. I was particularly concerned with the effects produced by antidromic invasion of motoneurons.**D** This technique could be understood by reference to the diagram of Fig. A03B. In Fig. A03B, stimulation by an electrode on the motor nerve would set up impulses travelling to the muscle and also antidromically to the motoneuron, the afferent fibres having being cut. The testing flexor reflex is set up by stimulation through electrode **c**.

The antidromic impulse does not stop at the axon hillock (Fig. A07), but invades the surface of the motoneuron, setting up there a refractory period much longer than with the motor axon, and it also appears to destroy any preformed c.e.s. of the motoneuron. Denny-Brown was the first to study the antidromic invasion of the motoneuron (1927) and found evidence for these same results. The antidromic testing showed that in the flexor reflex there were often repetitive discharges from motoneurons and this was due to repetitive bombardments of the synapses on the motoneuron even in the response to a single afferent volley. So, there was some insight into the complexity of the neuronal responses evoked in the spinal cord by a single afferent volley.

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110 Akert, Konrad (21.05.1919 – 10.01.2015) CH brain researcher in US & Zürich. Founder of "Brain Research".

111 Hoffmann, Paul (19.06.1884 – 09.03.1962) DE neurophysiologist and discoverer of the "H-reflex".

112 Pritchard, John Joseph "Jack" (09.02 1916 – 14.04.1979) AU Prof. Anatomy Belfast. "Osteoblasts".

At the time of these investigations, I was hoping to achieve an understanding of synaptic action using for this purpose the flexor reflex of the neurally isolated spinal cord. It proved to be a rather heroic adventure with Sherrie providing much wise advice and experimental help. I set up the experiment usually before he arrived in the morning, and then we worked through without a lunch break, walking down town for a cafe meal in the later afternoon, and returning for a further experimental study. It was of course too arduous for him, as I well realised. During the experiment he took down all the notes and carefully watched the results, and gave critical evaluation.

I was working strenuously, measuring and plotting the results and developing the figures and tables of the five papers that I prepared. Sherrie thought that I should be the sole author of the antidromic paper. He felt that it was beyond his expertise. However, all five were assembled together and Sherrie submitted them in January 1931 for publication in the Proceedings of the Royal Society.[E]

We went together to London to a meeting of the Royal Society in early 1931 that was almost entirely devoted to my hour-long presentation.

This work aroused much interest with an audience of about 200 and a good discussion. It was a time when the principles of synaptic transmission in the central nervous system were an important theme in many laboratories.

Overlapping with this flexor reflex study was the final experimental study with Sherrie on inhibition of flexor reflexes. An excellent model to study was the inhibition of a flexor reflex by a contralateral input into the spinal cord. This investigation was designed to test as far as possible the original concept of Sherrington in 1925 that inhibition was due to an enduring state of synaptic action, the central inhibitory state, c.i.s. (originally called **I state** in Sherrington, 1925, p. 528, that was reciprocal to the **E state**, later c.e.s.).

It was surprising to find that a single contralateral volley produced a long depression of a flexor reflex for over 100 msec. So, c.i.s. would appear to be longer than c.e.s., which could be as brief as 15 msec. (Fig. A02), but this difference was probably due to repetitive discharge in the inhibitory pathway by what are called delay paths. Repetitive stimulation caused an increase and lengthening of the inhibition. There was also evidence that c.i.s. was inactivated by c.e.s. So, in general these last investigations with Sherrie provided good evidence for the 1925 Sherringtonian concepts of c.e.s. and c.i.s. that were oppositely acting and enduring synaptic processes. The complications inevitably introduced by delay paths prevented a precise study of synaptic interaction. However, the alternative theory of inhibition as due to Wedensky[113] blockade by high-frequency discharges, as proposed by Lucas, Adrian and Forbes, had been made untenable.[F]

P. The reflex activity of the Spinal Cord

Sir Charles was one of the Syndics of the Oxford University Press.[A] One morning in late 1930 he came with the story that the night before the Board had asked him if he

113 Wedensky, Nikolai Evenievich (28.04.1852 – 16.09.1922) RU physiologist at St. Petersburg University.

would write a book on his science. He replied that he would only do this if he could be joined by his colleagues, Liddell, Creed, Eccles and his recent colleague, Denny-Brown. I was very excited at this project as I thought that the work on the spinal cord that I have written about in the preceding pages would be valuable for the book. We all agreed that Liddell should be the editor of the book. When we discussed the Chapters, Sir Charles would do the last chapter with the opportunity to write up his final scientific thoughts. Liddell and Denny-Brown would do postural reflexes and reflexes in extensor muscles, Creed the histology of the spinal cord. I was so enthusiastic that I was given 3 Chapters: the introductory, the flexor reflex and central inhibition.

All these subjects filled my mind, so I started to write at once, and in a month or so I had typed out a preliminary draft and submitted it to my colleagues, who read it critically and made valuable comments. So, I composed an amended copy, which in due time was again criticized. So, I had a final copy ready in mid-1931, but my colleagues had still done nothing. However, in the latter part of 1931 there was good progress, Creed and Liddell doing their chapters. Denny-Brown was so occupied as a Neurologist in London that he did nothing until finally, in desperation he managed a chaotic contribution, working all night on a ship taking him to New Zealand that called in at Southampton *en route* from London. Liddell got a stack of writing posted from Southampton. Fortunately, Liddell knew his story very well and could decipher the aggregate and it came out in Chapter 4 and a bit of Chapter 5.

We were concerned that we did not see anything that Sherrie wrote. Later we found out that he was writing his Chapter by hand - there was no secretary in the department. So, he would submit to the Oxford Press successive sections that he had written, without showing them to us. Anyway, we were relieved to see the Proofs in 1932.

Sherrie, as we hoped, had written what was to be the grand finale to his Neuroscience in a Chapter entitled "Lower Reflex Coordination" His great contribution of 56 pages dominated the book of 186 pages, and incorporated his two recent lecture reviews: the Ferrier[114] [Sherrington, 1929] and the Hughlings Jackson[115] [Sherrington, 1931].

The theme of his contribution was the motor unit as the basis of all movement and the expression of the responses of motoneurons. It is illustrated in his comprehensive diagram (Fig. A09) that embodies so much of our thinking on grades of synaptic excitation of motoneurons and their repetitive discharge with the consequent muscle contraction. He embellished this theme with the wisdom achieved in a lifetime of studying reflex coordination in the spinal cord. The book of 183 pages was published in 1932 by the Oxford University Press, being nicely printed in a hard cover. However, in those days the audience for such a book was quite small. The initial printing of 1000 took many years to sell and there was a reprinting in 1938.

Our book provides an excellent account of the Oxford School as created by Sherrington, because by 1932 it had been completed. Actually, the name should be the

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114 Ferrier, David (13.01.1843 – 19.03.1928) UK Scottish neurologist/psychologist. "Cortical mapping".

115 Hughlings Jackson, John (04.04.1835 – 07.10.1911) UK neurologist. Researched epilepsy and aphasia.

Sherrington School. I shall use this name, because it was his creation and the performance at the Oxford Laboratory became very diverse after he left and was not specially related to his influence. In particular, except for the brief episode mentioned with Pritchard, I was to leave the central nervous system for the rest of my Oxford career in order to study the heartbeat and the synapses in sympathetic ganglion and smooth muscle as will be described below. It was of course related to the synapse, with impulse generation and its control.

Q. Oxford 1932

This year of Oxford was the pinnacle of the Neuroscience that Sherrington had created and that we had enjoyed and lived with. In retrospect one can sense that it was a year of dramatic climax. Firstly, there was the conjoint effort of the book, which incorporated the scientific discoveries of the last decade. Secondly, there was the Nobel Prize to Sherrington, shared felicitously with Adrian of Cambridge. At the age of 75 and with severe crippling coming on with rheumatoid arthritis Sherrie could experiment no more beyond 1932, though he still had great contributions to make in biography and philosophy.

His first tentative approach to the mind-brain problem was the Rede Lecture at Cambridge in 1933 ["Brain and its mechanism"]. That called to my mind the spiritual voyage that I set out on so many years before coming to Sherrington in Oxford. Then came after some years Sherrington's Gifford Lectures "Man on his Nature". I myself seemed to be dallying on my great project, but I believed that I had still far to go before attempting to transform our understanding of the brain so that it could be recognised as being associated with transcendental properties, the self-conscious mind that each of us recognises in the experience of self. It was to take decades of my scientific life before I could seriously challenge the entrenched materialism of the neuroscientists and philosophers. I seemed to subscribe to the dictum "Better to journey than to arrive"! But I did arrive in the end as I tell much later.

In 1932 I was awarded the Rolleston Prize that was given to Oxford or Cambridge scientists for outstanding research in the whole field of biological and medical science. The Prize of £115 came in very nicely for having the house redecorated and central heating installed in part. While this was being done in July 1933, we and our 3 children drove to the village Coverack in Cornwall near the Lizard to stay at a waterfront informal house that I rented fully equipped from the wife of a Cornish doctor for the ridiculously cheap rate of £4–4–0 a week for all July. We soon discovered a secluded sandy cove to which we drove each day.[A] I used this period to escape from science into culture with the collection of books I had brought. We spent there the July's of 1933, 1934 and 1935.

R. Sherrington's Nobel Prize

During the second visit of Ragnar Granit, a Swede, from Finland, we often talked about the strong claims that Sherrington had for a Nobel Prize. Then in November 1931

I had a letter from Professor T. Graham Brown[116] asking me to help him in his nomination for the Nobel Prize, that he had been invited to make by the Nobel Committee. As an old associate he was nominating Sherrington, but wanted to include discoveries and concepts from Sherrington's Oxford period. I asked for advice of John Fulton and Pat Liddell and sent to Graham Brown (Dec. 22nd 1931) a comprehensive draft of Sherrington's claims with special emphasis on his recent work. Already late in 1931 I had had a letter from John Fulton telling of a strong nomination from America, and asking me to give them an account of Sherrington's recent work and publications, which I immediately sent to them.

Then, we waited for the day of the announcement in October 1932. I can still remember the hammering on my door with Ragnar Granit shouting "He's got it. He's got it!" Daisy's mother who stayed with them had heard it on the radio. We telephoned Sherrie, but he was out at a dining club to which he belonged. They had been told of the award on the telephone that afternoon by the Swedish Ambassador. So, we warned Lady Sherrie that the department plus wives would come to await Sherrie's return from a Dining Club at Merton College, where he had not mentioned his award, so as not to disturb their relaxed evening! All of us came and we had an enjoyable and uproarious party. It was a glorious climax for his life as a brain scientist and for us, his associates. Ragnar specially remembers Sherrie saying "The Swedes are great people". We drank a toast to Sir Charles and Lady Sherrie in sherry and we departed in an hour or so. Sherrie at age 75 was happy to be linked in the Nobel Award to his dear friend Adrian, who was much younger (43).[A]

It is sad to realise that this great celebration was the ending. of an era of happiness that we had enjoyed so much in their beautiful Oxford home. A few days later Lady Sherrie became seriously ill. She had an ovarian cancer from which she died in 1933. So, Sir Charles was accompanied to Stockholm by his daughter-in-law, Margaret Sherrington.

Sherrie stayed on in the house which was run by Ethel Davis, Lady Sherrie's niece. He wanted to resign forthwith, but we persuaded him to stay on. Fortunately, he agreed because he realised that his presence in the laboratory was most helpful in this post-Nobel period, even though he could no longer carry out experiments. He could be a wise adviser with his immense knowledge and he gave the laboratory an international status, attracting many distinguished visitors.

Sherrington's Nobel address was given on Dec. l2th 1932. With the title "Inhibition as a coordinative factor". It was an inspired summing-up of the essence of his life's work on the nervous system. It was particularly important for me in the next decades. He concluded: "In the working of the central nervous machinery, inhibition seems as ubiquitous and as frequent as is excitation itself. The whole quantitative grading of the operations of the spinal cord and brain appears to rest upon mutual interaction between the two central processes 'excitation' and 'inhibition', the one no less important than

116 Brown, Thomas Graham (27.03.1882 – 28. 10.1965) UK Scottish physiologist. "Central pattern generators".

the other". In 1963 my Nobel Lecture was also on inhibition. "The ionic mechanism of postsynaptic inhibition"!

Unfortunately, Sherrie was during 1933-34 stricken by a painful and crippling rheumatoid arthritis. He had to spend many months at Droitwich Spa, where I visited him. His indomitable spirit triumphed over adversity, and to meet him was still a joyous experience. He recovered very well as can be seen in the photographs; (Fig. A10) taken in 1934 at a luncheon given at Exeter College by two of my research students, Odoriz[117] from Argentina and Obrador[118] from Spain, also (Fig. A11).

Finally, Sherrie in 1935 announced his impending retirement and his house was sold and his books distributed. He prophesized to me that future investigations would have undreamed-of success because of the great advances in technology that had already begun with amplifiers and cathode ray oscilloscopes.[B]

It was a very moving experience at the close of his great scientific career for me personally to witness this humility and this generosity with no taint of jealousy for those of us such as myself who were to spend our lives building upon what he had built so well.[C] I continued contacts with letters and visits of Sir Charles to Oxford and of me to Ipswich [see Fig. A11 and also Fig. F5 in Section **FB**].

S. Cultural Memories

My life as a neuroscientist was enlightened by most enjoyable interludes, some of which stand out in my memories.

The years 1925 to 1932 were the great days of the Repertory Theatre in the great brick "barn" at the split between Banbury and Woodstock Roads. In the eight-weeks terms, Michaelmas and Hilary, there was a different play for the six nights of every week. Besides Shakespeare plays there were plays by the "moderns"; Shaw[119], Barrie[120] and Drinkwater[121]. I still have books of their collected plays. The demands were too much for some of the actors and we were used to frequent prompting but that did not dampen our enjoyment.

The great attraction was the beautiful and accomplished actress, Thea Holme[122], wife of the producer Stanford Holme[123]. She always knew her parts perfectly. I remember Pat Liddell telling me how thrilled he was when Thea acted the part of Yasmin in Flecker's[124] "Hasan", attired only in a black bikini - before the days of

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117 Odoriz, Jose. Bernado. (1908 – 1971) AR Neurophysiologist/electro-encephalographist.

118 Obrador, Sixto (16.11.1911 – 27.04.1978) SP Neurosurgeon. Also studied pathology of epileptic seizures.

119 Shaw, George Bernard (26.07.1856 – 02.11.1950) IR Prolific Irish playwright, critic and activist. (NP 1925).

120 Barrie, James Matthew (09.05.1860 – 19.06.1937) UK Scottish novelist and playwright "Peter Pan".

121 Drinkwater, John (01.06.1882 – 25.03.1937) UK English poet & dramatist, play: "Abraham Lincoln".

122 Holme, Theodosia Mabel "Thea" (27.12.1904–04.12.1980) UK actress and writer.

123 Holme, Stanford (07.02.1904–28.19.1985) UK Actor/producer at the Oxford playhouse.

124 Flecker, James Elroy (05.11.1884 – 03.01.1915) UK English novelist/playwright. Verse drama "Hassan".

bikinis - and of course I was there the next night! I remember also her seductive role as Cleopatra in Shakespeare's play. Unfortunately, she was soon lost to the West End theatres of London.

There were also good plays in the New Theatre being tried out for London, and a two-week session in the summer term of Gilbert and Sullivan operas. I was taken there many times by Lady Sherrie. In the summer we had Oxford University Dramatic Society plays (OUDS) where professional actresses joined the men student actors in classical drama. My memory draws me to the wonderful production of "A Midsummer Night's Dream" in the South Park, Headington. There was the famous Viennese producer who emphasized the role of the fairies and the dancing was by the Danish Ballet in white diaphanous very revealing gowns, led by the famous Nina Theilade[125], as "Titania". It was a magical evening. Other memories I have are of Marlowe's[126] "Tamburlaine the Great" in Worcester College Gardens, where the large garden pools became magnified to great lakes in the night lighting. Also, in that Garden there was "Alice in Wonderland" with real pigs. My final memory of Oxford plays is in mid-June 1937 the night before leaving Oxford for Sydney, when Nevill Coghill produced the play, "Everyman", beautifully staged in the Fellow's Garden at Exeter College.[A] Next morning to Sydney!

T. Rhythmic responses

The analysis of reflex responses led to some understanding of the excitatory and inhibitory responses of motoneurons as revealed by the action potentials and contractions of motor units. However, I recognised that these were artificial conditions because physiological responses such as in posture and movement were composed of repetitive motoneuronal discharges as in Sherrington's diagram (Fig. A09). A key problem was presented by the generation of these discharges, which were known to have no relation to any rhythmic stimulation. Already Denny-Brown had shown that an antidromic impulse resulted in a resetting of the rhythm, so it must have penetrated to the synaptic mechanism that generated the rhythmic discharge. As can be seen in the small rhythmic action potentials of Fig. A12 an antidromic impulse inserted randomly into the regular rhythm not only reset the rhythm, but also, when it was early in the rhythmic cycle, there was a longer pause before the cycle restarted. Evidently the antidromic impulse was disturbing the generation of the rhythmic impulse; and the disturbance was greater, the earlier the antidromic impulse acted on rhythmic generator. The greatest lengthening was to about 1.5 times the cycle. Under special conditions with no antidromic impulse the motoneuron spontaneously generated a double discharge, and there was a longer subsequent cycle, exactly as for an antidromic impulse.

I was led on to an intensive study of neuronal rhythmic discharge, over 10,000 rhythmic discharges being measured and calculated. Furthermore, I was attracted to try

125 Theilade, Nini Arlette (15.06.1915 – 13.02.2018) DK dancer, choreographer and teacher.

126 Marlowe, Christopher "Kit" (26.02.1564 – 30.05.1593) UK dramatist, playwright, poet and translator.

to develop a mathematical theory which was given in the paper, when I presented it to the Royal Society on Feb. 25th 1932. This mathematical theory gave an excellent prediction of all the experimental findings, but only by assuming that the generation of an impulse caused the destruction of half of the c.e.s. of the motoneuron! This half-or-nothing hypothesis was criticised by my good friend William Rushton[127], who proposed a complex alternative mathematics! I recognised that we were missing the role of the negative and positive after-potentials that were just coming into significance in relation to impulse generation. The fast, negative nerve impulse is followed by slow potentials, negative and then positive, with respectively an increased and then a decreased tendency to fire an impulse. Fig. A13 diagrammatically illustrates the manner in which c.e.s. and the positive after-potential cooperate in setting the rhythmic discharge and in the response to an applied antidromic impulse. To get to this understanding required several years of research as will be described later.[A]

However, I will anticipate briefly in order to consider the nature of a nerve impulse and how it travels along a nerve fibre. In Fig. A14A a nerve fibre is shown in1omgitudinal section with to the left the electrical charge across the membrane, negatively inwards. This is ahead of the impulse travelling as indicated by the arrow. At the impulse the inward movement of sodium ions, Na^+ reverses the membrane charge. Later the efflux of potassium restores the charge. The time course of an impulse (Fig. A14B) with its brief negativity is about 1 msec. Fig. A14C shows diagrammatically the flow of electric currents across the membrane as the impulse propagates along the nerve fibre. It is the depolarization ahead of the impulse that causes the inward flow of sodium ions (Fig. A14A) that generates the impulse. This account of the nerve impulse was not known in the 1930's, but is useful in my attempt to talk of synaptic mechanisms.

U. Giant Nerve Fibres

As an aside to the main developments in 1932, H. B. Stough[128] visited Oxford with a problem on the three, giant nerve fibres of the earthworm. He had stimulated the earthworm with a gentle touch and had found that the large medial fibre conducted antero-posteriorly and the two smaller lateral postero-anteriorly. He did this by selective injury of the fibres. He had also shown that all three fibres have transverse septa at each segment, and thought that these septa could be responsible for polarizing the conduction. J.Z. Young dissected out the ventral nerve cord of earthworms and I set up recording in a moist chamber by a Matthews oscillograph.[A] The two lateral fibres conducted as one fibre, presumably due to minute transverse connecting fibres, that unified the impulse in our threshold testing. By the collision technique it was shown that each fibre conducted in both directions. The polarization found by Stough was due to the head or tail location of receptors activating the fibres, and not to the transverse septa exerting a polarizing action. This small study (Eccles, Granit & Young (1932)

127 Rushton, William Albert Hugh (08.12.1901 – 21.06.1980) UK physiologist. “Colour vision”, “univariance”.

128 Stough, Howard Brown (1887 – 1976) US Univ. of Idaho biologist. “Structure of earthworm giant axons”.

[1A-020]) was the first ever on giant nerve fibres. Rushton and Bullock[129] later made more comprehensive studies confirming all of the original findings. The much more important giant fibres of squid and sepia were not recognised until several years later by J. Z. Young. Unfortunately, pressure of the ganglion work prevented a full publication with figures.

Editorial note: Section **V.** was not included in this autobiography. The reason for this is unknown. It might have been reserved for a special subject, then forgotten, or dropped, or perhaps merely omitted through an oversight by the author during typing.

W. Technical developments in 1932-35

As one was imagining into the future of neuroscience, I realised early in my Oxford life that, good as were, our frictionless optical myographs with their accurate recording sensitive to contractions of single motor units, the future belonged to electrical recording. Gasser, Erlanger and Bishop[130] led the way with the first cathode ray oscilloscopes [CROs], at St. Louis, but it was an heroic procedure only fit for recording propagated nerve impulses with its necessity for superposition of many faint traces to give images. Meanwhile Matthews[131] at Cambridge had designed a mechanical oscilloscope [oscillograph] with mirror recording that Adrian and he were using to great advantage. So, in early 1931 Sherrie bought me one with the appropriate amplifier to replace my string galvanometer that I had used from 1929 to record muscle action potentials. It gave me the opportunity to record electrical responses of nerve fibres and neurons.

However, it proved to be a very temperamental instrument with a proclivity to go into oscillations, particularly if the input resistance was high. I recognised that I needed advice from Adrian and Matthews at Cambridge. When I told Adrian of my troubles at the Cambridge meeting of the Physiological Society in the summer of 1932, he immediately invited me to Cambridge to learn about their techniques. I was to come by train from Oxford, have dinner with him at Trinity College, stay at his home, spend the next day with him and Matthews in the laboratory, and return home that night, a beautiful arrangement. It shows the very happy relationship of neuroscientists. Adrian of course knew me well as Sherrington's pupil, but I was still not 30. He had examined me for the Final at Oxford and also for my D.Phil.! I was more than surprised when he was waiting with his car at Cambridge station. Then we went to his home to meet Hester Adrian before departing to dine with him at High Table at Trinity where I was seated between two great physicists, Rutherford and Eddington[132], but I knew some of their works.

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129 Bullock, Theodore Holmes "Ted" (16.05.1915–20.12.2005) US neurobiologist/neuro-ethologist.

130 Bishop, George Holman (27.06.1889 – 11.10.1973) US neurobiologist (also gifted Inventor/engineer).

131 Matthews, Bryan Harold Cabot (14.06.1906 – 23.07.1986) UK physiology professor. "Aviation physiol.".

132 Eddington, Arthur Stanley (28.12.1882 – 22.11.1944) UK astronomer/mathematician general relativity.

At the laboratory I learned quite a lot, and realised that my troubles lay in the too cramped electronic assembly in the Matthews oscilloscope. On returning to Oxford I worked with G. L. Brown[133] who was on leave from his Leeds position for the last months of 1932. Our first task was to rebuild the Matthews amplifier by assembling it on a "bread-board", the name in those days for a large piece of plywood used for electronic assembly. We were very happy when this simple resistance-capacity coupled amplifier worked perfectly in its new assembly. I used it for many years.

It also worked well when in 1935 I changed over to a cathode ray oscilloscope of the new Cossor design that was being made in London.[A] The days when one could procure a CRO assemblage ready for recording were many years off. In 1935 one just bought the CRO tube plus socket and did the rest yourself! The other big improvement was also in early 1935 when I had constructed a completely shielded room to provide complete electrical silence. It was modelled on the only shielded room in Britain, at the Post Office Research Institute, Dollis Hill [London]. I visited them and they were most helpful. I learned that for electromagnetic shielding iron was five times better than copper, which is still not recognised in shielded rooms design. I also had an elaborate design for the door, to complete the shielding. Inside, everything was run by batteries, even the 800V on the CRO! Brown and Dale[134] had a similar shielded room constructed for the Medical Research Council laboratories in London.

There were still not good designs for an accurate and linear time base for the CRO. I had O'Neill rebuild the moving plate camera for faster movement by making it a rising plate directly coupled to a heavy dash-pot control. The maximum plate speed was up to 2m/sec and was very steady. So, for my last years at Oxford I had excellent facilities with recording rooms, one for the CRO, the other for the Matthews oscilloscope. Right through my scientific life I have struggled for excellence in the experimental arrangements. In the early decades it had to be largely built in the laboratory, usually by me and associates. The great instrument companies did not come until the 1950's.[B]

X. The Heart Rhythm; 1931-1932

After our experiments with rhythmically firing neurones I was attracted in 1931 to begin a study of the most perfect physiological rhythmic mechanism, the pacemaker of the mammalian heart. It was easy to locate the pacemaker in the sino-auricular node of the exposed cat heart which was completely denervated.[A] An electrode was fixed over the pacemaker for stimulating on recording with other electrodes on the auricles. However, as reported by other investigators, we were unable to detect any evidence of pacemaker depolarization that we expected to precede the impulse generation, as would be observed with neuronal generation (Adrian & Matthews, 1934), neither a potential change nor an increased excitability. So, the generation process remained an enigma. We then carried out a most ambitious study of the effect of beats generated by pacemaker stimulation on the subsequent rhythmic beats. We were lured on by the

133 Brown, George Lindor "Lin" (09.02.1903 – 22.02.1971) UK physiologist; Waynflete professor1960-1967.

134 Dale, Henry Hallett (09.06.1875 – 23.07.1968) UK pharmacologist/physiologist "acetylcholine". (NP 1936).

amazing accuracy of the beat generation by the denervated pacemaker, a variation of less than 1 in 200 in beat to beat.

We studied the lengthening of the cycle after one or two premature beats, but it was possible to develop only a minimal hypothesis that in the pacemaker a condition called "excitement" increased during the cycle to the threshold for impulse generation, which caused depression of the excitement that then was rebuilt for the next impulse. It was assumed that the "excitement" was the integrated state of the tangled fibres of the sino-auricular node. The only surprising finding was that a premature beat, set up very early in the rhythmic cycle, was followed not by the usual partly compensatory pause, but by a much earlier response, and this in turn by a lengthened cycle. It was proposed that the rhythmic centre had been fractionated, which indicates that it has normally an integrative character and that, early in its recovery from refractoriness, a part only generates an impulse and has its excitement depressed, leaving the other part unscathed and able to generate the abnormal response. However, this most strenuous investigation did not cast any light on the rhythmic responses of neurons.

This was a frustrating period of my life, and during 1932-1933 I felt myself to be verging on a "nervous breakdown" from overwork. I made a strenuous effort in 1932-1933 to write up the three heart rhythm papers. All that time I was sustained by playing golf with Eric Barber, the classical don at Exeter and tennis with Wolfenden, the chemistry don, but I had a heavy load of tutorial teaching, some students being very dull. I had to do it for the finance of 15 shillings per hour! The good students were a pleasure, it was the dull students!

I was not happy with the three papers on heart rhythm (Eccles and Hoff, [1934]) that Sherrie submitted to the Royal Society in August 1933. Nevertheless, I was greatly disturbed when they were returned for revision. For months I could not bear to look at them, much less to work on them. So, they remained untouched for many months. I was saved by my good friend Rob Aitken and by his dear wife Madge. Rob suggested that they could come up for Easter 1934 to help. Heart rhythm was in his field as he was a Professor of Medicine in London. So, we spent a happy and profitable Easter with his wise advice and changed nomenclature. The papers were resubmitted in April 1934 and accepted essentially as I had already written them, but with the cosmetic touches so effectively provided by Rob, to give them a clarity for easier reading. It gives me joy as I remember this wonderful friendship of Rob and Madge over 50 years ago.

Y. Vagal inhibition of the heart

The experimental success in recording from the sino-auricular node led us in 1932 to study the effect of vagal inhibition in its slowing of the heart-beat. Hoff was leaving and by a very nice arrangement, already mentioned, G. L. Brown (Lin) came down from Leeds to work through the summer and autumn of 1932. Those were the days when research grants were hard to get, so Lin Brown came on his teaching salary with his Professor (B. A. McSwiney) doing all his work in Leeds until the end of the year. It was surprising that there had been no definitive study of such a well-known action as that of the vagus on the heart. Brown and I accomplished this study in 1932 - with most interesting results, with preliminary notes in 1932/1933, but not submitted finally for publication until June 1934. I had, as I told above, been too intensely occupied on the rhythmic mechanism of the heart!

We immediately discovered that a single volley in either the right or left vagus always caused a prolonged slowing of the heart (Fig. A15). Up to that time it had been believed by some that repetitive vagal stimulation was necessary, the so-called iterative action. Two observations were of particular interest. Firstly, the vagal stimulus had to be applied 120 to 160 msec. before an anticipated beat in order to delay its generation. This long latent period was only to a small extent accountable to the conduction time of the vagal impulses and their relay time in the ganglion in the heart. The full explanation will be given later when considering the two kinds of chemical transmission.

Secondly, the vagal slowing persisted for many seconds, as illustrated in Fig. A15. Loewi[135] had demonstrated that the action of the vagus on the heart was due to the liberation of a chemical substance which had been accepted to be Acetylcholine (ACh). So, the long time-course of the slowing could very nicely be attributed to the long persistence of the liberated ACh. As would be expected, the slowing was enhanced by eserine, because of its inhibition of the enzyme (ACh esterase) that destroys ACh (Fig. A16A). Furthermore, atropine had the well-known effect of diminishing the action of ACh in slowing the heart (Fig. A16B) and two vagal volleys summed their action by addition of ACh.

So, our experiments were nicely in accord with the ACh hypothesis of vagal slowing, with the exception of two findings; the long latent period and the frequently observed double action of a single vagal volley as illustrated in the lower curves of Fig. A16A and Fig. A16B. This fast initial and later slow wave were often much more prominent, and still have not been satisfactorily explained.

It has been believed since the time of Langley[136] and Dale that the pharmacological-agents, nicotine and acetylcholine, acted at receptor sites on muscle and glands. Acetylcholine receptors were eventually recognised to be of two kinds, muscarinic and nicotinic, the former blocked by atropine, the latter by curare and bungarotoxin. Furthermore, it is now known that these are two quite distinct actions of acetylcholine on specialised receptor sites as illustrated in a recent diagram (Fig. A17). This detour is important because it accounts for the electrical versus chemical controversy that resulted from inadequate understanding. In the 1930's I had regarded the action of acetylcholine as always having a relatively long latency but not necessarily as long as the action of the vagus on the heart (Fig. A16). This muscarinic action is now known as metabotropic because, as in Fig. A17B, it acts with long latency through a second messenger system. By contrast the nicotinic action of acetylcholine is ionotropic, as in

135 Loewi, Otto (03.06.1873 – 25.12.1961) AT(J) Pharmacologist. Studied role of acetylcholine. (NP 1936).

136 Langley, John Newport (02.11.1852 – 05.11.1925) UK Cambridge prof. “Chemical receptors & transmitters”.

Fig. A17A, and it works extremely fast by opening ionic channels. However, in the days of the controversy of chemical versus electrical this sharp distinction of ionotropic and metabotropic actions had not yet been recognised. So, our previous study of the time of action of the vagus on the heart (Fig. A15, Fig. A16) made me believe that chemical transmission must be too slow for the initial stage of 10^{-3} sec. synaptic transmission; hence the controversy!

There was one good development that came from the vagal-heart story. Dale was much impressed when he saw the eserine-atropine story. Brown was attracted from Leeds to Dale's Institute in London where he participated in the great work that led to Dale's Nobel Prize in 1936, and to a further distinguished career, but that is a later story.[A]

Z. Synaptic transmission in the sympathetic ganglion (SCG).

At this time there was a belief that the mode of operation of neuroscientific processes had to be unravelled by methods like those of physics with precision techniques. But one needed precise theories to test, and these were difficult or impossible to discover at that time - so one was left with vague concepts, like "excitement", in order to account for what was observed. So, we had precise investigations, but obscure hypotheses. They are still obscure. It was better at the next stage, the SCG [superior cervical ganglion] that was concerned with membrane potentials, and so to intracellular recording 15 years later.

As the complex investigations on the rhythm of the heart beat and the vagal action on the heart beat were coming to an end, I wanted to return to a further study of synapses between nerve cells that had been the theme of my last studies with Sherrington. However, I recognised the neuronal complexity even of the spinal cord with complex interneuronal systems, so I decided to mount an attack on what seemed to be a simpler synaptic system, namely, a sympathetic ganglion.

So, I started my long 'affaire' with sympathetic ganglia from 1933 to 1945. 1 always experimented alone though of course in that long period I was with my colleagues on other research problems. From the outset I had chosen the superior cervical ganglion (SCG) because of the accessibility of both the presynaptic and postsynaptic components. It was soon established that all the pathways through the SCG were monosynaptic. The disadvantage of the SCG was that it was composed of 4 different pathways in parallel, as had been shown in 1932 by Bishop and Heinbecker.[A] However, all studies were restricted to **s_1** and **s_2** components. **s_1** components were the fastest with the lowest preganglionic threshold and exclusively projecting postganglionically to structures in or related to the eye, including the nictitating membrane, and they were preferred for more subtle problems. The slower and larger pathway, **s_2**, was widely distributed to blood vessels and to piloerector muscles of the skin.

The experiments on the SCG delivered some degree of understanding of the synapse. It was of great significance that at the synapse there was a complete break in the transmission line in accord with the neuron doctrine of Ramón y Cajal. The presynaptic impulses gave only a minimal electrical signal when the recording was postsynaptic as in Figs. A18A and A18B between electrodes C and A and Fig. A18B electrodes E and G. In traversing this synaptic cleft there was a brief delay measured in milliseconds between the presynaptic impulse and the postsynaptic impulse. Furthermore, synaptic transmission was never one fibre to one neuron. Convergence of impulses in many presynaptic fibres on a neuron is necessary for transmission. There must be summation of the excitatory synaptic potentials set up on a neuron by many converging impulses.

It was at that time that several investigators in Dale's laboratory demonstrated that acetylcholine was involved in the synaptic transmission. This was the beginning of the chemical versus electrical controversy as will be described later. I was studying the same preparation as they were, the superior cervical ganglion, but by quite different procedures. As shown in Fig. A19A the preganglionic nerve was mounted on stimulating electrodes and the recording was with one electrode on the ganglion and one on the end of the severed postganglionic trunk. So, in the simplest situation a volley of impulses would propagate up to the ganglion and the recording would be of the electrical responses so generated in the ganglion cells relative to their axons (Fig. A19B).

My choice of the SCG for a simple synaptic system was signally unfortunate. Through the 1930's it gradually became evident that there was a fast and a slow synaptic transmission. I always recognised that the slow transmission was mediated by acetylcholine. Dale, Feldberg[137], Gaddum[138] [and G. L.] Brown had established the important role of ACh as a transmitter, but we differed on the identification of the fast transmitter mechanism. From my study on the vagal action on the heart as an example of ACh action, I believed that the fast, ganglionic transmission with synaptic delays of about *3* msec. could not be chemical, so I proposed instead an electrical transmission. At that time the modes of action of both electrical and chemical transmissions were very poorly defined. The essential background information was lacking, for example the actual synaptic structure. The two distinctive ACh actions had not yet been recognised, and the postulated electrical transmission across the synapse was not precisely related to flow of electric currents. Another complication through the 1930's was the possibility of synaptic inhibition as well as excitation. Other complications were the large after-potentials that were generated by the ganglion cells both when synaptically and antidromically excited. These slow potentials acted as excitants or depressants of the ganglion cells.

At about the same time as my ganglionic studies of 1933 to 1935 Gasser and Graham[139] (1933-34) were showing that in isolated peripheral nerve the brief negative potentials, the spikes, set up by propagated impulses were followed by negative, N, and positive, P, after-potentials similar to those seen in the ganglion investigations (Fig.

137 Feldberg, Wilhelm Siegmund (19.11.1900 – 23.10.1993) DE(J) physiologist. “Histamine & acetylcholine”.

138 Gaddum, John Henry (31.03.1900 – 30.06.1965) UK pharmacologist. Neuropeptides. “Substance P”.

139 Graham, Helen Tredway (21.07.1890 – 04.04.1971) US pharmacologist. “Histamine measurement”.

A20). However, the ganglionic N and P waves were much larger. It was shown that N waves were set up even when no impulses were generated, that is c.e.s. Hence the possibility was considered that some of the P wave was c.i.s., though it was doubted if some preganglionic fibres had a direct inhibitory action matching the excitatory fibres and c.e.s. Large P waves were generated by antidromic impulses that presumably would have no synaptic action. Some years later the stellate sympathetic ganglia gave more favourable conditions for studying the generation of the N and *P* waves, so further discussion can be postponed until this section.

I have to confess that for many years of my synaptic studies I was under the influence of a strange hypothesis that I developed in relation to the experiments that Lorente de Nó[140] published in 1935 on the synaptic mechanisms of the very fast eye muscles. Interaction experiments showed that the synaptic excitatory process at a synapse was no longer than 1 msec., which was much shorter than our evaluation for c.e.s. So, I gave the name 'detonator' process to the very brief excitatory action that seemed specially designed for generating impulse discharges. Its nearest analogy in the peripheral nervous system was the local excitatory state that Keith Lucas demonstrated in electric excitation of nerve. However, some years later with the greatly improved recording conditions in the stellate ganglion it was shown that the synaptic excitatory action in generating a depolarization was much faster than had been recognised for the c.e.s., so the detonator response was no more than the fast-rising c.e.s. A final story on this strange hypothesis was found 15 years later by intracellular recording of synaptic excitatory potentials (EPSP), as described in a later section. There is a transition of local responses on the rising phase of the EPSP that leads on to the generation of the all-or-nothing impulse discharges. These transitional local responses have some resemblance to the postulated detonator response. Meanwhile in 1937-1938 the electric excitation of peripheral nerve had revealed to Rushton and Hodgkin[141] that in impulse generation there were transitional "new-born" action potentials that may grow up to fully propagating impulses, or may abort (Katz, l939), Electric excitation of nerve). These "new-born" action potentials correspond to the local responses of Keith Lucas and so to the detonator responses. Neuroscience is so rich scientifically that it in this way seems open to apparently discarded hypotheses. This will be seen later in the electrical synaptic transmission at specially designed excitatory and inhibitory synapses.

In summary it can be stated that my "affaire" with the superior cervical ganglia did not transform our understanding of the synapse, as I had hoped. However, it led on to the experiments on the stellate ganglion some years later. These were most significant for synaptic understanding. Meanwhile, the centre of interest in this period was the nature of synaptic transmission. Was it chemical or electrical?

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140 Lorente de Nó, Rafael (1902 – 1990) ES/US neuroscientist. Studied brain cerebral cortex.

141 Hodgkin, Alan Lloyd (05.02.1914 – 20.12.1998) GB physiologist. "Intracellular potentials". (NP 1963).

In those busy times of' working on the superior cervical ganglion I had accumulated an enormous mass of data; photographic records, plotted curves and tables. It seemed that I would never get it organised into manuscripts for publication. One had to do all the typing in those primitive days, where there was not even one typewriter in the department. Then by a strange circumstance I was severely afflicted by scarlet fever at the beginning of the summer term of 1935. One was confined to bed for 3 weeks. So, I had to arrange for my teaching to be let out, and I had a bed table with good lighting and pillows to type for many hours a day. So, the three large ganglion papers were completed and sent for publication on June and July, altogether 95 pages. The large antidromic paper was sent in on May 1936. My life was certainly busy, because by May 1936 I was fully occupied in the enormous review for the *Ergebnisse der Physiologie*.

AA. Chemical versus electrical Synaptic Transmission

When envisaging how transmission occurs across a synapse, the best picture of the 1930's was that of the single synapse in Fig. A06. Without defining the situation in detail, it was generally thought that in some way the electrical currents of the presynaptic impulse would excite the postsynaptic membrane. One such impulse would have a negligible action, but the convergence of many as shown by the clustered boutons of Fig. A06 could be an effective electric excitant.

Then in 1933 came a revolutionary new concept by Dale and his associates (Feldberg, Gaddum, M. Vogt[142], Brown) that, when the presynaptic impulse invades the bouton, there is secretion of a minute amount of a specific chemical substance, acetylcholine (ACh) that diffuses across the synapse and excites the postsynaptic membrane.[**A**] This hypothesis was supported by convincing experiments. For example, the ACh was secreted from the presynaptic fibres as predicted, and it powerfully excited the postsynaptic membrane to discharge impulses as tested by contractions of the nictitating membrane.

There was one deficiency in all the array of pharmacological experiments, and that was the time course of the release and of the action of the acetylcholine. As we have seen with vagal ACh action on the heart (Fig. A15, Fig. A16) there was a delay of over 100 msec. whereas the synaptic delay for the s_1 synapses in the ganglia was as short as 3 msec. So, in my comments on the chemical transmitter hypothesis, I accepted that ACh was a transmitter, but only for a delayed action. My experiments indicated that there was an initial fast transmission across the synapse that I proposed could be electrical, and then many milliseconds later came the chemical transmission by ACh. This started the so-called chemical-electrical controversy,[**B**] that spread to the proposed neuromuscular transmission by ACh (Brown, Dale and Feldberg, l936), where the ACh evidence was even better than for the ganglion. However, in the central nervous system it was never satisfactorily shown that ACh was a synaptic transmitter in the synapses of the spinal cord and no alternative substances were discovered in the 1930's.

142 Vogt, Marthe Louise (08.09.1903 – 09.09.2003) DE Pharmacologist. Neurotransmitters. “Epinephrin”.

In assessing the transmitter controversy retrospectively it can be recognised that until electron microscopy transformed the histology in the mid-1950's (Fig. A06) there was an inadequate appreciation of the exquisite design for fast chemical transmission with a synaptic cleft of only 200 Å across and of the chemical transmitter being held in synaptic vesicles that were arranged in a specially designed structure, the presynaptic vesicular grid for emission directly into the synaptic cleft, as revealed by Akert et al. three decades later.[C] That design provided a much more effective and rapid transmission than could have been imagined in the time of Dale.

As has been described already (Fig. A17), it was much later recognised that the transmitter (ACh) acts through two quite distinct mechanisms. In the so-called ionotropic action, ACh attaches to a specific postsynaptic receptor site and opens an ionic channel that depolarizes and excites in a millisecond or so. In the other mechanism ACh also acts on a specific postsynaptic receptor site, but there it triggers a complex sequence of metabolic reactions to give a slow postsynaptic action measured in 10's of milliseconds. ACh acts in both mechanisms that are sharply discriminated by the blocking drugs.

The initial experiments on the chemical transmission hypothesis were rather imprecise pharmacological studies, concentrating on the role of ACh as the transmitter. I was at that time recording electrically from the SCG and showing a very fast transmission, 2-3 msec. synaptic delay, and a facilitation phenomenon with successive stimulations that was not lengthened when the enzymatic destruction of ACh was blocked by the anticholinesterases, eserine and prostigmine. It seemed therefore that Acetylcholine was not involved in these fast-synaptic actions. Meanwhile the pharmacological experiments of Dale and his associates (Feldberg, Gaddum) had made it certain that ACh transmission did occur, so I developed the dual hypothesis of transmission: that there was an initial action too fast for ACh mediation and the later ACh action.

The Physiological Society meeting in May 18th, 1935, stands out in my memory as the most severe confrontation between me and the Dale school. I was demonstrating precise recordings of the nictitating membrane contractions in response to maximal preganglionic and postganglionic stimulations. I had a very sensitive frictionless mirror myograph. These contractions differed by no more than 1%. When the enzyme acetylcholinesterase (AChE) that destroys ACh was blocked by eserine, there was still identity of the two contractions, but after one second there was slowed decline of the nictitating membrane contraction evoked synaptically, exactly as would be expected if the synaptically liberated ACh were generating a prolonged after-discharge from the sympathetic ganglion cells. A similar prolonged response was evoked by intra-arterial injection of ACh. Hence the hypothesis of the initial fast electrical transmission received good experimental support.[D]

These Society meetings where the controversy was generated aroused great interest with crowded audiences. No one had dared to criticize Dale and his hypotheses and here was I as a quite junior member of the Society daring to do so! I was warned by friends not to indulge in criticism of Dale and his associates. However, I was headstrong and I enjoyed the controversy because it was carried out in the proper academic tradition: criticism in the effort to attain closer to scientific truth, but with absolutely no personal animosity. I am happy to say that Dale and his associates remained good personal friends. Brown and I would sit next to each other before and after the tough exchanges, laughing together! Some people thought that our confrontation was a kind of "shadow boxing"! But it was serious science carried out in the best manner. What surprised many was that Sir Henry Dale appreciated the confrontation, stating repeatedly that it aroused more interest in his research than ever before and that it had the great value of inciting them to do better and better experiments in order to answer my criticisms! He much appreciated the very long review that I published in 1936 with a full account of the controversy in which Brown helped me in tricky places and also with figures for publication.

The final story is that towards the end of the controversy Dale in 1935 had seconded Sherrington 's nomination of me for the Royal Society, to which I was elected in 1941, and that that there was great acclaim by us all when Dale was awarded a Nobel Prize in 1936. I have a wonderful collection of his letters in later years when in 1951 I finally became his disciple. Excerpts from some of the letters have been published. That is a later story. Also still later is the transformation wrought by electron microscopy of the synapse with the revelation in the 1950's of a structure beautifully designed for fast chemical transmission with the transmitter substance packaged in vesicles fronting the synapse cleft.

However, many years before that (1951) I had carried out intracellular recording from neurons that finally convinced me that synaptic transmission, both excitatory and inhibitory, was mediated chemically.

AB. My Oxford Career, 1933-1935

I had realised for some years that the Final Honour class had no adequate teaching in the most important new developments in neuroscience and the related biophysics. In my time Sherrington had lectured well on his reflex studies in the first-year lecture course, but he lost his ability to interest his class in later years. He could not even be heard in that bad lecture room, so the students stayed away after their first trial. We never spoke to Sherrie about his class rapidly dwindling to zero. It was too delicate a matter.

So, I asked Pat Liddell how I could become a lecturer to the First Honour Year. He said in his characteristic terse way: "Very simple: no approval is required, just mention it to Sherrie, find a suitable time to fit in with the existing Physiology and Biochemistry Lectures and put up a Notice". So, from 1933 onwards I lectured for one hour a week in the eight-week Hilary term.[A] Of course, I received no extra emolument beyond the £300 a year I was receiving as a Demonstrator for seven hours a week.

These lectures were most important to me as a training in lecturing skill. I took them very seriously with fully prepared illustrations. The criterion of success or failure would be unambiguous. Would the students come to my lectures and keep on coming? I am happy to remember my success! I still have my lecture notes with their emendations from year to year. The course began with simple biophysics with membranes and ions and mathematical equations long before there was the understanding of Fig. A14A. The simplest biological units were long plant cells, *Nitella*, before single nerve fibres could be studied.**B** The course then moved to peripheral nerve stimulation and conduction with the properties much as in Fig. A14C, and so to synapses, reflexes, c.e.s., c.i.s., chemical versus electrical synaptic transmission, much as I have been describing in this autobiography. And this is how I learned to lecture.

In the summer of 1934, I was elected to a Tutorial Fellowship of Magdalen College at an initial salary of £600, rising by £100 every 5 years to £l000. It was a permanent position; however, on grant of £300 a year, so I was then less well-off for 5 years. All I had in addition was £300 a year as a University Demonstrator. However, I had just been appointed as an Examiner in the Final Honour School that added about £70 a year for 3 years that I was an Examiner. At Magdalen I assumed control of the tutorial system, without any permission, in order to gain relief from the burdensome hours-long tutorials of junior students that numbered 6 to 8. I instituted tutorial classes, two a week for those students, which were informal lectures with discussions. They still did their weekly essays, which I corrected and returned with comments. There was no complaint from the students, who realised that it was better for them. I still did the hour tutorials for the senior students, who were much better than those at Exeter.**C** They scored far more First-Class Honours than any other College, in fact about one third of the total number.

It will surprise present Oxford students to learn that once a year the students invited my wife and myself to a black-tie dinner and theatre party. They were often invited to Sunday afternoon teas with memories of the Sherringtonian hospitality. Each year this spontaneous arrangement was their giving of thanks.

In 1935 there came up the problem of election of a successor to Sir Charles Sherrington. Sherrie never spoke to me about it, and I of course knew that the retiring professor was not allowed any influence in the election of his successor. The Election Committee was appointed by a Statute. Strangely, it eliminated all physiologists except the Cambridge Professor, who was the respiratory physiologist, J. Barcroft[143], at that time. It was also composed of the Oxford Regius Professor of Medicine [Sir Edward Farquhar Buzzard[144]], the Professor of Biochemistry at Oxford, The President of Magdalen, an appointee of Magdalen College and the Dean of the Medical School. The Waynflete Professor of Physiology was a Professorial Fellow of Magdalen, hence the Magdalen representation. I heard through Liddell that I had been considered, but at age 32 was regarded as too young, though I had published over 20 major papers with many preliminary notes and was conjoint author of the book of 1932. John Mellanby[145] from St. Thomas' Hospital, London, was appointed at the age of 58, seven years from

143 Barcroft, Joseph (26.07.1872 – 21.03.1947) UK physiologist. Used manometry to study blood oxygenation.

144 Buzzard, Edward Farquhar (20 12 1871 – 17 12 1945) UK physician.

145 Mellanby, John (12.06.1878 – 15.07.1939) UK physiologist. Waynflete professor 1936-1939.

retirement. I was told "on the grapevine" that an “oldish” man was appointed so that in a few years (?) the chair would be waiting for me. In a way I was sorry for Mellanby because he did not transplant well from the London medical world into the intellectual milieu of Oxford. It was recognised that the Department of Physiology was losing the international reputation it had acquired under Sherrington.

I have two "asides" on this appointment. I heard that, when Sherrie was told that the electors thought I was too young at 32, he said "Didn't they know that Shakespeare was little more than 32 when he wrote Hamlet"! The other was many decades later from Lord Florey[146], who, as Chancellor of the Australian National University, was making in Canberra a farewell speech on my departure in 1966. In 1935 he had just been elected Professor of Pathology at Oxford, and in his farewell speech told in detail how Sherrie had illegally asked him to influence the electors in favour of my appointment! Sherrie and I never talked on the events of 1935.[D]

In 1935 I already had several Ph.D. students, the first being the two Hoff brothers from U.S.A.; one, [H. E. Hoff[147]] the physiologist who worked with me on the rhythm of motoneurons and of the heart, the other [E. C. Hoff[148]] on synaptic degeneration, Fig. A06 being one of his pictures. Others were Magladery[149] and Lloyd, who moved on to most distinguished careers in U.S.A. Whitteridge[150] and Pritchard did research for BSc's. Whitteridge was most meticulous in his study of ciliary ganglion transmission and had a most distinguished career, eventually becoming the Waynflete Professor of Physiology at Oxford. Pritchard, an excellent student with first class honours proved to be the most incompetent experimenter I have ever had. After our brief association he correctly became a Professor of Anatomy! Other research associates were Obrador and Odoriz who appear in the picture (Fig. A10) after a stylish lunch that they gave at Exeter College for those associated with their work at Oxford. They returned to distinguished careers in Madrid and Buenos Aires.

The last of my D.Phil. students was Bill Gibson[151] from Canada, studying the histology of the sympathetic system. His appointment makes a story. Wilder Penfield[152], the great neurologist, was visiting Oxford, and I asked Sherrie to help me in getting a replacement for a vacant histology position that I had with E. C. Hoff and Heusner[153] in Carleton[154]'s Histology department. So, we had afternoon tea with

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146 Florey, Howard Walter (24.10.1898 – 21.02.1968) AU pharmacologist/pathologist. “Penicillin” (NP 1945).

147 Hoff, Hebbel Edward (02.12.1907 – 01.05.1987) US neurophysiologist, teacher and writer.

148 Hoff, Ebbe Curtis (12.08.1906 –17.02.1985) US neurophysiologist. Contributed to aviation medicine.

149 Magladery, John William (11.10.1911 – 27.11.1977) CA Rhodes scholar; later Professor of neurology.

150 Whitteridge, David (22.06.1912 – 15.06.1994) UK neurophysiologist/physician. Waynflete prof. 1968-1979.

151 Gibson, William Carleton (04.09.1913 –04.07.2009) CA neuropathologist. Autobiog “No time to slow down”.

152 Penfield, Wilder Graves (26.01.1891 – 05.05.1976) CA pioneering physiologist & neurosurgeon.

153 Heusner, Albert Price (09.09.1910 –23.09.1963) US anatomist and neurosurgeon.

154 Carleton, Harry Montgomerie (13.02.1896 –05 .12.1956) UK Author of “Carleton’s Histological Technique”.

Penfield and he said "there is a young Canadian of 21 years who has just done his first degree with me in excellent style". So, Sherrie insisted that we send Bill Gibson a cable offering him an appointment in Histology to do research with me for 3 years for his D.Phil. The surprising outcome was that Gibson arrived at Oxford in 2 weeks. He got the cable, way out on a summer vacation on a Canadian Lake. He immediately rushed to Montreal to catch the first ship to Liverpool, usually a 10 day's journey. We had had no reply, so our astonishment was great when he appeared in Oxford at such a short time. His subsequent career after the D.Phil. was to go into Neuropathology and then also into the History of Medicine with several books. He has now (1991) just retired from being Chancellor of Victoria University on Vancouver Island in British Columbia. We wrote a book together on Sherrington, published by Springer in 1979.

I here interrupt my main story to tell of a strange concatenation of events relating to adrenergic transmission and that occurred the year before I wrote the review. I was at that time deeply disturbed, so it should be briefly reported in my autobiography.

The great physiologist, W. B. Cannon[155] of Harvard, had developed the hypothesis that the sympathetic nervous transmission was due to an adrenaline-like transmitter, and had carried out good experimental testing. Then, about 1932, an extraordinary Mexican, Arturo Rosenblueth[156] joined him at Harvard. There was developed the hypothesis that the transmitter "Ad.-substance" became effective only when it combined reversibly with a substance provided by the target organ, for example by the smooth muscle of the nictitating membrane, to form Sympathin E. Sympathin E then caused the excitation of the smooth muscle.**[E]** The postulate of Sympathin E depended entirely on the experiments of Rosenblueth and associates on the effect of various frequencies of stimulation and doses of the transmitter. A rectangular hyperbola was obtained when the responses were plotted against frequency or dose. This curve would be expected on the Sympathin E hypothesis. My mathematical propensity was aroused by the over-interpretation of unsure and imprecise observations that could just as well have fitted other mathematical relationships. Rosenblueth had similarly investigated the action of the vagus on the heart. Brown and I (Section **Y**) concluded that there was no acceptable demonstration of the postulated hyperbolic relationship.**[F]**

Rosenblueth was very disturbed by this brusque rejection [Rosenblueth, (1937)], and in a series of letter exchanges I gave him my detailed criticisms. Some months later, Alex Forbes, the distinguished Harvard neuroscientist wrote me a six-page long severe criticism of my scientific position. I realised that Rosenblueth had written this letter and my good friend Alex had signed it. Furthermore, carbon copies were sent to Dale and Adrian, and they were asked to subdue Eccles so that I would not disturb Anglo-American concord! I was much disturbed by this action of dragging my good friends Adrian and Dale into the controversy. What could be the outcome for me, a still junior scientist? Eventually Dale, Adrian and I met at the Royal Society to consider this

155 Cannon, Walter Bradford (19.10.1871 – 01.10.1945) US Harvard University professor of physiology.

156 Stearns, Arturo Rosenblueth (02.10.1900 – 20.09.1970) MX physician /physiologist. "Cybernetics."

almost unbelievable situation. After a few moments we laughed heartily together - the absurdity was too much for us! They then wrote mild replies to Forbes and that was the end.

Only gradually did one realise what an extraordinary person Rosenblueth was. The immediate group around him were completely under his extreme persuasive influence. This was particularly true for Cannon, but also for Forbes. In 1981 the distinguished physiologist Horace Davenport[157] (The Physiologist, vol. 24) told of this Rosenblueth era at Harvard, and referred to Rosenblueth as the "dark angel" on Cannon's life.[G] Bacq[158] and others had also similarly criticized the Sympathin hypothesis and it is now forgotten. However, at the time of 1934 I was disturbed by Rosenblueth's influence on Cannon because it could cause him to lose the Nobel Prize that he so well deserved. Unfortunately, this did happen; the chemical transmitter prize of 1936 went to Loewi and Dale only. The official Nobel report by Professor Liljestrand[159] states laconically (p. 317) that "Cannon's contribution was also declared to deserve an award, but it did not seem appropriate to take it up at the same time as the others". Horace Davenport recognised the lethal influence of Rosenblueth on Cannon's status. In his article he states that ... "in corridor conversation Liljestrand had said that Cannon did not get the Prize because of his association with Rosenblueth and the bad impression made by the Sympathin E and [Sympathin] I hypotheses". Actually, my critical position was shared by most neuroscientists at that time, as can be seen for example in Bacq's excellent review of 1935.

I never had the pleasure of meeting Cannon nor have I any correspondence. He died rather early in 1945 just before my first visit to USA. A few years later, in October 1951, I was very pleasantly surprised to receive a letter from Cornelia James Cannon, Cannon's widow, telling me that she was in New Zealand on a world tour and saying "You are the physiologist of the Antipodes I am most anxious to see because of my late husband's interest in and admiration for you". So, I met in Dunedin this eccentric and charming lady. She had no luggage except for necessities that she carried in a large string bag, but out of that bag she extracted a copy of Cannon's autobiography "The Way of an Investigator", with a dedication "To Dr. J. C. Eccles in the name of Walter Bradford Cannon by Cornelia James Cannon". I treasure this wonderful book filled with Cannon’s unique wisdom and. humour. It is before me now with the letter as I remember Mrs Cannon’s visit. The message is that Cannon must have appreciated my criticisms, just as Dale had done. But he could not escape from the embracing Rosenblueth as has been well told in Horace Davenport's article. Apparently, he did escape after his retirement and Rosenblueth’s departure for Mexico. Rosenblueth failed to secure tenure in Harvard and Cannon missed a Nobel.

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157 Davenport, Horace Willard (20.10.1912 – 29.08.2005) US physiologist, text-book writer and historian.

158 Bacq, Zénon Marcel (13.12.1903 – 12.07.1983) BE radiobiologist, inventor, physiologist. “Nerve impulses”.

159 Liljestrand, Göran (16.04.1886 – 16.01.1968) SE Pharmacology/physiology. “Euler-Liljestrand mechanism”.

Many years later I met Rosenblueth at the Woods Hole Marine Biological station and we had an enjoyable time with the past forgotten. The Sympathin story had completely disappeared. He had then developed with Norbert Wiener[160] a mathematical theory of control systems. Still later, Rosenblueth asked me to accept his brilliant student Riccardo Miledi[161] with a Rockefeller Fellowship in my laboratory in Canberra, - this interlude finished with "All's well that ends well".

AC. My first International Adventure

In early January 1936 Professor Leon Asher[162] of Bern asked Liddell for a contribution from the "Oxford School" to the most distinguished reviewing journal, the *Ergebnisse der Physiologie*. Liddell suggested me, and Asher invited me to write the review much on the lines of the review published by Professor Z. M. Bacq on "Chemical transmission in the autonomic nervous system", 1935. On Jan. 8th 1936 I wrote to Professor Asher giving him a most ambitious proposal under the title "Synaptic and Neuromuscular transmission". Professor Asher enthusiastically accepted my proposal on January 14th. We had a good exchange of letters, which I have preserved. All of Asher's letters were handwritten in English. I was encouraged by the letter from Asher that I should emphasize the role of Action currents in synaptic transmission.

I had set myself a most heroic task. I had to do all the typing and figure preparation as well as the extensive list of references but it was received by Professor Asher on the due date 18th September, there being about 200 pages of manuscript and 24 figures. I was completely exhausted and on the day of posting drove off to a quiet hotel on the Dorset coast for 2 weeks of recuperation before the start of term in October.

In November I received the proofs and found that all the figures had been redrawn and re-lettered in excellent style. Finally, the [review was] published late in December in a total time of just 3 months. It is a far better performance than one gets now. In those days, publication was done by dedicated experts and craftsmen long before the deterioration of the computer age. I have found only one typographical error in this publication of 104 pages! It is not appropriate to review here the immense scientific studies of synaptic transmission in these diverse sites. This has been done in the sections dealing with the experimental studies and also it is the theme of many sections. related to the chemical – electrical hypothesis. For example, in the review I was attempting to do full justice to the evidence for ACh as the transmitter in sympathetic ganglia and in neuromuscular transmission. But at that time the synaptic histology was quite primitive (Fig. A06). The exquisite design for extremely fast chemical transmission was eventually revealed some two decades later by electron microscopy (Fig. A07), and in still later studies by Akert and others.[A]

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160 Wiener, Norbert (26.11.1894 –18.03.1964) US mathematics professor and pioneer in the field of cybernetics.

161 Miledi, Ricardo (15.09.1927 – 18.12.2017) MX California University neurophysiologist. "Neuromodulation".

162 Asher, Leon (13.04.1865 – 08.08.1943) DE(J) physiologist. Medicine Professor Bern Univ. "Leopoldina".

Unfortunately, I wrote this comprehensive review at a time when I was taken over by the detonator hypothesis that I critically evaluated in **Section Z**. This hypothesis was specially related to the hypothesis of electrical synaptic transmission with its analogy to the local excitatory action set up by electrical stimuli. In my review I gave a full illustrated account of Lorente de Nó's experiments that I referred to in **Section Z**. Lorente de Nó was an ardent advocate of the electrical hypothesis of synaptic transmission and remained so. I agreed with him in 1936 for the initial fast component in synaptic transmission, but in the years l943 to 1951 more refined experiments gradually caused me to accept an exclusively chemical transmission.

This gradual recognition that my cherished electrical hypothesis was in error caused me great travail which was not resolved until I learnt of Karl Popper's philosophy of science in 1944, as I shall describe in my Dunedin section.

In the section: The Action potentials of the spinal cord I assembled and discussed all the evidence with particular reference to the slow N and P waves studied by Gasser and associates. However, there is immense complexity in these action potentials due to the responses of the internuncial neurons. There was the general conclusion that negativity of the cell body of a neuron relative to its axon (N wave) caused a tendency to fire impulses, while with positivity (P wave) there was depression. What was needed was a method for utilizing the electrotonic transmission along a nerve axon to record selectively from its neuron, as was being done by Barron[163] and Matthews at that time, and which I was also beginning to do with Pritchard in 1936.

It was then that Gasser stayed as my guest at Magdalen College Oxford for several days and we had long discussions on this problem of how to utilize electrotonic transmission for selective neuronal recording. But for Gasser I think the most enjoyable part of his stay was the game of bowls that the Fellows played after dinner in the cloister quadrangle during the long summer evenings. I have never seen him relax as he did then. He was an austere bachelor with an unfortunate disability. At the end of his stay at Oxford he received the invitation to be the Director of the Rockefeller Institute. Some years later (1944) he shared the Nobel Prize with Erlanger for the nerve impulse.

At Oxford, Gasser and I were discussing the hypothesis that he and associates had developed in 1934 and 1936 in explanation of inhibition in the spinal cord by the P wave depression in neuronal circuits. It was a clever idea for flexor reflexes, but could not account for the very fast inhibition of extensor muscle responses in the knee jerk. As will be seen below, it was finally eliminated by the intracellular recording that I developed in 1951.

This long section of the review helped to define the problems and to coordinate the various experimental findings. It can be thought of as merely a prelude of what was to come in my Dunedin investigations, up to the climax in 1951.

The section on neuromuscular transmission was an important part of the review because it gave an account of the beautiful work of the Dale school on ACh transmission. It was quite unexpected that the very fast neuromuscular transmission

163 Barron, Donald Henry (09.04.1905 – 1993) US reproductive biologist. “Slow potential wave in spinal cord”.

with a synaptic delay of only 1 msec. could be chemically mediated. I can well remember my incredulity when I heard of the idea! However, it was demonstrated that ACh was liberated from the motor nerve endings, but it was technically impossible to show that this liberation was in time for the neural excitation of the muscle fibres. The most important evidence was given by the very effective excitation of ACh administered by intra-arterial injection, and the demonstration that this was blocked by curare, exactly as occurs for neuromuscular transmission. Other key experiments by Brown and associates demonstrated that the anti-cholinesterase, eserine, caused a single nerve impulse to generate a repetitive discharge of muscle impulses, exactly as would be expected from its action in prolonging the ACh action. The principal difficulty of the ACh hypothesis was to account for the extremely rapid action for nerve impulse to ACh action across the motor endplate. The final explanation was delivered by the EM studies of 1955 onwards. The action current hypothesis was never fully tested and was finally abandoned in 1943, as will be stated below. The ACh hypothesis was a great triumph for the Dale School, but I was reluctant to assert it fully for several years. It seemed too fast before we had the EM studies.

The final long section of the review dealt with transmission from sympathetic nerve fibres to smooth muscle excitation. As referred to above (Section **AA**) excellent mechanical studies were being made with the nictitating membrane, so I proposed this as a subject for a D. Phil. thesis to Magladery who had just arrived from US as a Rhodes scholar with a medical degree. He set it up for contraction and electrical recording. I thought that it would give a simple electrical response like a slow version of a skeletal muscle responses. As soon as I saw the complexities of the first experiment, I recognised that I had to join him! The first published records form the last of my major sections in the review.

The principal finding was that the neural excitation set up all-or-nothing propagated impulses at 50 to 80 cm/sec in the smooth muscle fibres. These impulses resulted in the muscle contraction, just as with striated muscle, but much slower. There is, however, an important difference in that the impulses in several nerve fibres have a collusive action on to each smooth muscle fibre. The transmission is by an Ad-substance resembling adrenaline, as shown by intravenous injection. The response evoked by a nerve volley is firstly an N wave, just as with a sympathetic ganglion, then a complex of impulses that propagate along the smooth muscle fibres causing the contraction, and then, if sufficient adrenaline has been liberated, there is a later rhythmic discharge at 3 to 1 per second together with associated contractions. The initial action potential of smooth muscle is double, the A, B composition. It now seems likely that the A wave is due to ionotropic action by Ad-substance (Fig. A17A), [while] the later B wave is metabotropic (Fig. A17B). This accords with the finding that the Ad-substance blocker (933 F) has no-effect on the A wave, but depresses the B wave.

The situation is much more complicated than with striated muscle because of the convergent action of several nerve fibres on each smooth muscle fibre. This convergence effect is due to diffusion of the liberated Ad-substance. The synaptic delay can be as short as 10-20 msec. It would seem that neuromuscular transmission to smooth muscle is unambiguously chemical. There have been comparable investigations at about the same time and later to other smooth muscles.

At the end of the long review, I considered the important concept that Dale derived from the experiments of Langley and Anderson on regeneration of peripheral nerve. They showed that the criterion of regeneration gave three classes:

A: efferent fibres from the spinal cord, both motor and preganglionic sympathetic

B: sympathetic postganglionic fibres

C: afferent nerve fibres

Dale pointed out that all of class A were cholinergic fibres and that any such fibre could replace any other. However, further consideration shows that a crucial factor is in the re-growing along the degenerating stump rather than to the chemical specificity to the target when it is reached, and it is not simply a cholinergic action.

At the end of this long review there is a proposal by Dale that there has been an evolutionary development utilizing a primitive chemical transmission with the release and action concentrated at the site of action. This is precisely what was observed much later by electron microscopy.

By special arrangement with Herbert Gasser, I submitted for Physiological Reviews a much shorter and simpler review that was published in 1937 with the same title.

AD. The Physiological Society

In those years when I was at Oxford the Physiological Society was our life line to the outside world. Each year there were about four meetings in London including the annual general meeting in University College, a 2-day affair. Each year there was also a Cambridge and an Oxford meeting. The meetings were great occasions not only for presenting scientific papers and demonstrations, but also for meeting at lunch, afternoon tea and dinner, all very inexpensive. The presentation of papers was limited strictly to 10 minutes, and discussion could be for 5 minutes more. The discussions could be very critical, but had to be asserted in a sporty-way! I published 21 communications in my Oxford period.

I remember well an Egyptian student who was instructed beforehand on the strict rules, but nevertheless continued on despite the red light and the alarm. Without saying a word A.V. Hill stood up and moved out silently, along with all the audience, leaving only the chairman and one member in deep sleep. We waited outside until the end, then silently returned!

I have one other memory I like to present: Sir Thomas Lewis[164], the famous cardiac physiologist, gave a paper in 1936 on reflex vascular responses in the human skin that he attributed to a special "nocifensor" system of nerves. R. J. S. McDowell[165] asked a silly question and was strongly rebuffed by Lewis, as was his custom. Nevertheless, I then asked a question concerning the location of the nerve cells belonging to that postulated nocifensor system and how it could be experimentally studied. In reply

164 Lewis, Thomas (26.12.1881 – 17.04.1945) UK cardiologist. Pioneered use of string galvanometer.

165 McDowell, Robert John Stewart (1892 – 1990) UK Physiologist. King's College. Bk: "Whiskies of Scotland".

Lewis admitted that it was still not known. As he walked up the aisle after his lecture, he beckoned to me to follow him. The audience believed that I was being taken out for a severe scolding as also did I! Lewis said nothing as I followed him into the adjacent laboratory where he turned on a hot tap. Briefly touching the tap with the back of his finger, he told me to do likewise. I was amazed that I experiencedtwo pains, a sharp initial and, after l second or so, slow burning pain. He had just made this discovery, and it was published next year, with Pochin[166]. He said: "This is how I return my thanks for your good question. You are the first to experience it".[A] We then agreed that the two pains he had discovered belonged to two fibre systems – **A** for the fast and **C** for the slow. So, we returned elated by our conjoint experience to a lecture room filled with the inquisitives! Lewis and I had always been friends but now we were better friends than ever. Like Cannon, Lewis was unfortunate to miss a Nobel Prize in 1924 for his cardiac investigations as told by Liljestrand on pages 263-265 of the Nobel book.[B]

The great virtue of the Physiological Society was that there were no class distinctions. On the social breaks the most junior could talk to the most senior without any introduction. It was completely democratic without a President, but only the working officials; - Secretaries, Treasurers and the Committee. All official decisions were made by open voting of the members at a special meeting. I have always regarded that as an ideal society. I have been a member for 63 years, and an Honorary Member since 1982. The Physiological Society also makes a great contribution to Physiology by its great Journal of Physiology.

There is an amusing story about John Fulton who visited the Physiological Society meeting at Oxford in 1936. I remember well the dinner in the magnificent hall of New College. The Roughtons[167] and we sat at one of the long dining tables opposite to John Fulton and the Liddells. The usual drink was "champagne cider" that was distributed in large jugs along the centre of the table. I was surprised to see John mysteriously give a roll of banknotes to our waiter, but had no explanation. However, we had a good dinner, even remarking what excellent cider New College had! The two jugs opposite were soon emptied and refilled with another roll of notes to the waiter and again much enjoyed. After dinner we walked in the garden in the beautiful summer evening. I can remember that we were noisily happy. Then some weeks later malicious rumours began filtering across the Atlantic that Oxford and Cambridge dons could not distinguish the best French Champagne from cider! The rich John Fulton had preferred for gastric reasons to have Champagne instead of cider so he had secretly the jugs opposite us filled up with champagne so not to be conspicuous in his choice of champagne. The payments to the waiter were explained!

AE. Last years at Oxford, at Magdalen College 1934-1937

When I missed the Professorship at Oxford in 1935, I put out the suggestion that there could be created a Readership for me, but that came many years later.

166 Pochin, Edward Eric "Bill" (22.09.1909 – 29.01.1990) UK physician, specialist on ionizing radiation.

167 Roughton, Francis John Worsley (06.06.1899 – 29.04.1972) UK biochemist. "carboanhydrase".

I was at that time a member of the Medical Faculty of the University, the administrative body presided over by the Regius Professor of Medicine and his Deputy the Dean. So, I had some influence, but apparently not enough. There was at that time the establishment of a series of Nuffield Professorships in the Medical School. The good finance was provided by Lord Nuffield[168] and the new departments were in fields that allegedly Nuffield was interested in supporting for example Neurosurgery (Cairns[169]), Social Medicine (Ryle[170]), Obstetrics, Orthopaedic Surgery (Seddon[171]) and several other clinical departments, but no Finance came to existing departments such as Physiology and Biochemistry. It was all a secret operation between Nuffield and (we assumed) the Regius Professor and Cairns. This neglect contributed to my unhappiness in this period at Oxford.

I was also at that time (1934-1937) one of the three Fellows on the Estates Bursary of Magdalen College to advise the Estates Bursar on the financial affairs of the College. It was one of the richest colleges, with Estates valued at three to four million pounds. It was an unrewarding waste of time! At the most I had some influence on the appointment of Fellows. I can remember that I opposed the most distinguished Professor of Chemistry, Sir Robert Robinson[172], a Nobel Laureate, on the appointment of an official Fellowship in Chemistry. I supported the proposal of N.V. Sidgwick[173] that a Physical Chemist, Dr. Leslie Sutton[174] be appointed as being better for the undergraduate teaching, and Sutton was appointed, soon an FRS, and a valuable College Fellow for life.

From 1932 onwards to 1935 I was becoming recognised as a promising physiologist and received three invitations to apply for university professorships at· Leeds, Aberdeen and Sheffield, where Howard Florey was Professor of Pathology and keen for me to join him in Physiology. However, conditions in those Universities were much less attractive than Oxford where I had developed quite good research facilities and where I had a rather good house within walking distance of the Laboratory.

In the department John Mellanby was kind to me, but rather aloof. By a strange coincidence in 1936-7 Mellanby and his associate were studying the smooth muscle of the nictitating membrane, but we never communicated on our closely related problems. I never even knew of what they were doing. There was a kind of inferiority complex. The department had lost its open style that was so characteristic of the Sherrington era.

My contacts with British Universities were mostly through the Physiological Society to which I gave 21 communications during my Oxford period and to the 5

168 Nuffield, William Richard Morris (10.10.1877 – 22.08.1963) UK Morris car manufacturer & philanthropist.

169 Cairns, Hugh William Bell (26.06.1896 – 18.07.1952) AU neurosurgeon. “Head injuries/motorcycle helmets”.

170 Ryle, John Alfred (12.12.1889 – 27.02.1950) UK physician/epidemiologist. “Nasogastric intubation”

171 Seddon, Herbert John (13.07.1903 – 21.12.1977) UK orthopaedic surgeon. Classified nerve injuries.

172 Robinson, Robert (13.09.1886 – 06.02.1975) UK chemist. Waynflete Professor of Chemistry from 1930.

173 Sidgwick, Nevil Vincent (08.05.1873 – 15.03.1952) UK chemist. “Valency bonding of atoms”, “H_2 bond”.

174 Sutton, Leslie Ernest (22.06.1906 – 30.10.1992) UK chemist. Chemical bonding/electron diffraction/dipoles.

occasions in London when I presented papers to the Royal Society, being introduced by Sherrington and taken to dinner by him at the Athenaeum afterwards. Towards the end of my Oxford life there was in 1937 a symposium on neuroscience organised by the Royal Society and that was specially related to synaptic transmission. Unfortunately, I was at that time still attached to the detonator response, and had just published experimental evidence and analysis in the Journal of Physiology. So, in retrospect I recognise that I did not take full advantage of this, my last opportunity for presenting a fully acceptable story on synaptic transmission to the participants, Adrian, Dale, Sherrington, Bryan Matthews, Rushton, Brown, Feldberg, Hodgkin. I left England two months later, not to return for almost 15 years, when in 1952 I had the triumph of presenting my intracellular story with EPSP and IPSP, as I will describe later.

It has to be recognised that those days before air travel and the negligible supports for travel were in complete contrast to the present over-supply of travels! Up to 1952 I had not visited one physiology department on the continent of Europe. I was unable to afford the IUPS meetings in Roma (1932) and in Leningrad (1955). However, I do remember with joy the visit of Ali[175] and Andrée[176] Monnier with Herbert Jasper[177] to Oxford in 1935. They had been working on synaptic transmission to smooth muscle, and the findings of Bacq and Monnier were quoted with approval in my review. Monnier had written a good doctoral thesis that I still have, and I used an extract from that in the examination where French and German texts were set as optional questions. He had managed to extricate himself from the domination that Lapicque had exercised for many years over French neurophysiologists, as also had done Fessard[178]. Lapicque was a fanatical electrical transmission devotee.[A] I can remember that my wife and I took the Monniers and Jasper for a picnic lunch on a beautiful day to the secluded meadows along the Thames River above the Trout Inn. It was a favourite place of ours for swimming and sun bathing all the years that we were at Oxford. Later there was much merriment at a photograph of Herbert apparently wearing an open shirt and nothing else! We did have some good neurophysiological discussion as well as enjoyment.

Jasper was later responsible for securing Canadian money to start up the International Brain Research Organization (IBRO) which has become most important for the world-wide advancement of Neuroscience. I was closely associated with IBRO for many of its early years that no-one now remembers.

At about the same time there was a nice visit by Fessard and his first wife with similar entertainment. All these friendships were for a lifetime. Another remembered

175 Monnier, Alexandre Marcel "Ali" (25.08.1904 – 21.08.1986) FR Sorbonne Neuro-histology/neurophysiology.

176 Monnier-Dumont, Andrée Louise (1901 – ?) FR neuroanatomist. Also, French-English translator.

177 Jasper, Herbert Henri (27.07.1906 – 11.03.1999) US/CA psychologist/neurophysiologist, EEG, 10-20-system.

178 Fessard, Alfred (28.04.1900 – 20.02.1982) FR electrophysiologist. Torpedo fish, oscilloscope developments.

visit was from Ralph Gerard[179] of Chicago, who stayed at Magdalen like Gasser did. He was a good physicist, physical chemist and was the beginner of the enormously important neurochemistry. After the war I often visited him in Chicago and then later at Irvine in California, and he once came to visit me in New Zealand.

Of course, John Fulton was an annual visitor to Oxford bringing us news of US developments. But there was only one opportunity to have funds for visiting US and that was to the important Cold Spring Harbor Symposia on Long Island, but sadly I was never invited.

Further in the Oxford period I have happy memories of Jack and Alice Roughton. He was examining with me for two years in the summers of 1935 and l936. He was the distinguished physiologist with the most advanced studies on haemoglobin and its combination with gases - O_2, CO etc. We proved to be a good examining team. The written papers on the four 3-hour periods of the 60 or so students were a big task that we subdivided with the third examiner, an Oxford biochemist. But it was necessary for Jack to come to Oxford for the week-long practical and oral examinations. So, Jack and Alice came to stay with us for a most enjoyable working week. Actually, Jack had a bad problem of allergy, so he could not come with Alice on the visits to the river for needful refreshment. So, we developed a good friendship and stayed often with them in their grandiose Cambridge house. We did enjoy the work together and only had one disagreement. There were only two candidates from Magdalen which I graded one as a good first class, the other as a good second class. But my two colleagues defeated me by giving both first classes, which was a quite unprecedented happening and particularly suspicious for students of an examiner!

The Aitkens have already been mentioned and there were other good occasions together. The McSwineys of Leeds, then of London, were particularly dear friends. Brian and I had a walking trip for a weekend in the Yorkshire Swale Dale. It was very hot so we visited each Inn on the way for a pint of shandy. We amusingly told later that we did 3 miles per pint! It was he who did Brown's work at Leeds so that we could work on the vagal heart· problem. Later he came to visit me in Dunedin, but tragically died of a pulmonary embolism soon after returning to London. I must also mention the Rushtons, William and Marjorie, who were contemporary neuroscientists at Cambridge. I have given (in **Section T**) his justified criticism of my half-or-nothing hypothesis! We were the dearest friends and it was a joy to stay with them in their informal Cambridge home and to appreciate their musical knowledge. It was Rushton who studied electrical stimulation of nerve with his superb mathematical understanding, and so gave an insight into an analogy to the postulated detonator response. Later he made an amazing change to do superb work of Nobel quality on human colour vision, actually with his own eyes! I have of course preserved a considerable correspondence from all these friends. It is sad for me to write because almost all are gone. We loved them all.

179 Gerard, Ralph Waldo (07.10.1900 – 17.02.1974) US neurophysiologist/behavioural scientist "schizophrenia".

Life at Magdalen with the numerous Fellows was more complex than at Exeter, and less enjoyable. The Magdalen Common Room was rather dominated by Harry Weldon[180], a very clever hedonist, atheist, philosopher. Unfortunately, he attracted some fellows to alcoholism. He was always friendly to me as he appreciated science, but he ridiculed C.S. Lewis[181] for his religious beliefs. I wonder if Weldon ever knew of the secret life of Lewis when he escaped from College to live for intervals in Headington as is told by A. N. Wilson[182] in a recent biography [Wilson, (1990)]. I certainly knew nothing of it although my first house was in Headington. Antipathy to Weldon probably helped Lewis to decide to go to Cambridge in 1954.

At my last College meeting I had Dr. Hugh Sinclair[183] elected as my successor to provide another biochemistry tutor as desired by Professor Peters. Also, we elected to a research fellowship Peter Medawar[184] with his great career beginning. There were many fellows who thought that my good friend Brian Maegraith[185] should have been my successor. I was unhappy not to advise his appointment, but I believed that Hugh Sinclair would be much better able to teach students for the Final Honour Course. Brian had had no experience with this Course and was doing Pathology with Howard Florey. I knew him well as a Rhodes Scholar from Adelaide, and was even at his wedding to his lovely wife Lorna Langley[186] at St. Cross Church. Many years later I confessed to Lorna my feelings at deciding against Brian. She surprised me by saying: "Jack, I have always been grateful to you because if Brian had gone to Magdalen, he would have been taken over by Harry Weldon and his alcoholism". So, Brian survived to become a world figure in Tropical Medicine.

AF. Oxford to Sydney; the decision

During late 1936 I was becoming exceedingly worried about the successive aggressions of Hitler[187] and the failure of England, France and US to realise the menace. It seemed that England was in no state of preparedness and Chamberlain[188] knew this, hence his appeasements. There would be mass air attacks and then invasion. What Britain could do, except for the Navy, would be too little and too late. The subsequent events showed how justified I was in my terrible fears. One could not imagine the success of radar which came only just in time, in 1940. I was unhappy in

180 Weldon, Thomas Dewar "Harry" (05.12.1896 – 13.05.1958) UK philosopher. With "Bomber Harris" WW2.

181 Lewis, Clive Staples (29.11.1898 – 22.11.1963) IE theologian/writer (Oxford "Inklings") "Mere Christianity".

182 Wilson, Andrew Norman (27.10.1950 –) UK writer of critical biographies and popular history.

183 Sinclair, Hugh Macdonald (04.02.1910 – 22.06.1990) UK physiologist. Nutrition. "Fatty acids".

184 Medawar, Peter Brian (28.02.1915 – 02.10.1987) BR/UK zoologist. Tissue grafting etc. (NP 1960).

185 Maegraith, Brian Gilmore (26.08.1907 – 02.04.1989) AU pathologist & tropical medicine. "Malaria".

186 Maegraith, Lorna Elsie nèe Langley (16.08.1907 – 02.12.2006) AU teacher.

187 Hitler, Adolf (20.04.1889 – 30.04.1945) AT/DE dictator 1939-45. Began WW2 1939 by invasion of Poland.

188 Chamberlain, Arthur Neville (18.03.1869 – 09.11.1940) UK. Prime Minister 1937-1940 "Munich agreement".

missing the chair of Physiology at Oxford and the decline of the department. So, I decided to return to Australia with the young family.

The chair of Physiology at Melbourne University was about to become vacant, so I consulted my good friend Charles Kellaway[189], Director of the Medical Research Institute linked to Melbourne Hospital and to the University. I heard that the Vice-Chancellor of Melbourne University, [Priestley[190]] the famous scholar and Antarctic explorer was coming to England, so I invited him and his wife to stay with us at Oxford for a weekend. They were very charming and it was arranged that I would be invited at an increased salary to be Professor of Physiology when they returned to Melbourne. Unfortunately, the Council of Melbourne University was hoping for another local candidate, whose name was not yet disclosed. The recommendation of me by the Vice-Chancellor was not accepted, but I could apply when the position was advertised. The situation was most serious for the Vice-Chancellor who also had other problems with his reactionary Council. He resigned, causing some scandal, and I was advised by Kellaway not to apply for Melbourne, where I would challenge their as yet unknown candidate, but to apply for an alternative position in Australia, the Directorship of the Kanematsu Memorial Institute of Pathology at Sydney Hospital.

Kellaway hoped that there I would be able to build up an Institute matching his Institute in Melbourne. I knew Kellaway well from my earlier years in Melbourne and I trusted his judgement, unwisely as it turned out. So, in early 1937 I accepted the Sydney position with some misgivings. Meanwhile the Hitler menace drove me into a state of near panic. So, I resigned from my Magdalen fellowship from August 1937 and also from my University Demonstratorship.

In retrospect I think I would have dared to stay on in Oxford if I had been appointed to the Oxford Professorship; but I felt very unhappy at the declining state of the department and Mellanby would be there until 1943. The fact is that I was really frightened out of my presently unhappy Oxford life by Hitler. However, I did not know that my decision would turn out to be final for life. I was never to return to live in my beloved Oxford, where I was created as a scholar and as a scientist, and nowhere was I to have so many friends. I was leaving on what I later called "My Scientific Odyssey". Of necessity I became a wanderer. But, almost unbelievably, I have never experimented anywhere except in my own Department or Institute. I have never carried out even a single experiment as a visitor to some other Institute.

Early in 1937 I began the unhappy task arranging for the move. Mellanby very kindly allowed me to take all the equipment of my two rooms with me to Sydney. It had largely been bought by grants that I had received and by my work. So, the last experiments were done in June 1937 and expert packers took over. I was allowed costs for travel as second class on a P&O Boat, the Maloja,[A] for my family and a Danish servant, with much furniture, household goods, books etc. and equipment.

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189 Kellaway, Charles Halliley (16.01.1889 – 13.12.1952) AU anatomist/physiologist. "Snake venom research".

190 Priestley, Raymond Edward (20.07.1886 – 24.06.1974) UK geologist. Antarctic 1907-1913, glacier research.

Unfortunately, the Oxford house could not be sold before we left, but at £2000 it was an amazing bargain even for those days of the depression. It was later sold for £1900.

As a farewell we arranged for a large afternoon party for a hundred or more of our friends in Magdalen College, Cloisters and garden. It was tragically ruined by a disastrous thunderstorm with everything flooded, as if Oxford was lamenting our departure! That evening there was the play "Everyman" in Exeter Fellows Garden, also much disturbed by rain. The next morning, we all set off for London where I was leaving the very nice Austin car we had sold. To safeguard our journey our good friend, the histologist Humphrey Leach[191], drove behind us with an empty car! And so, to London where we left by train from Liverpool Station for Tilbury Dock. There were at Liverpool Station the Aitkens and McSwineys to farewell us and also Lin Brown, who came with us in the train to the ship at Tilbury Dock. To our happy surprise Alice Roughton had driven her car from Cambridge to Tilbury and was awaiting to see our cabins on the ship for the 6-weeks journey and to bid us with Lin Brown a fond farewell. They and we realised it was for an unknown future, almost like a final departure from this life! Actually, it was for almost 15 years and after the indescribable horrors of World War 2.

191 Leach, Ernest Humphrey (1890? –?) UK histologist, collaborated with HM Carleton in histology text books.

STAGE 2: – Figs. A01-A20

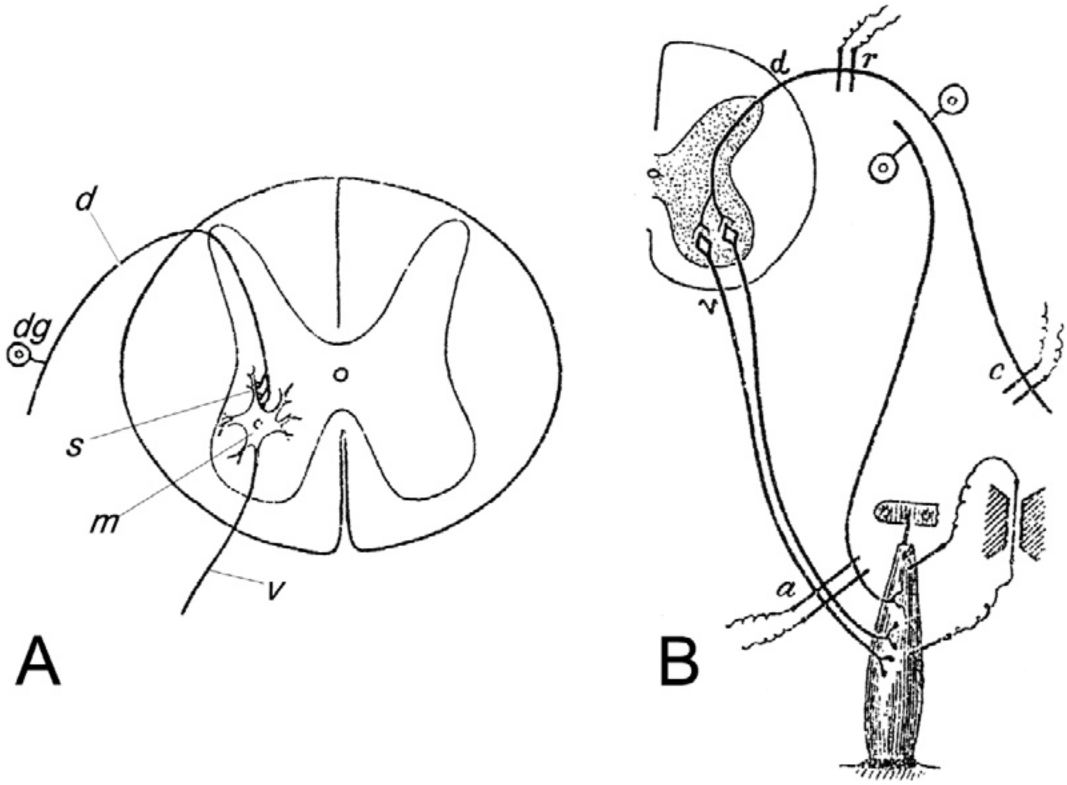

Fig. A01. Illustrations of reflex pathways and recording electrodes. [J, K]

A. Diagram of a simple reflex arc in the spinal cord. ***d***, dorsal nerve-root; ***v***, ventral nerve-root; ***dg***, ganglion of dorsal root; ***m***, motor-nerve cell in ventral horn; ***s***, region of synapse. From Creed et al. (1932) [1B-a01], p. 2, fig. 1.

B. Schema of reflex pathway and recording systems; ***v***, ventral root; ***d***, dorsal root; ***a***, electrodes on uncut nerve to muscle; ***c***, electrodes on afferent nerve. From Creed et al. (1932) [1B-a01], p. 39, fig. 16.

[Figures and legends updated from Eccles & Sherrington (1931) [1A-011], p. 552, fig. 6 and Eccles & Sherrington (1931) [1A-010], p. 513, fig. 1.]

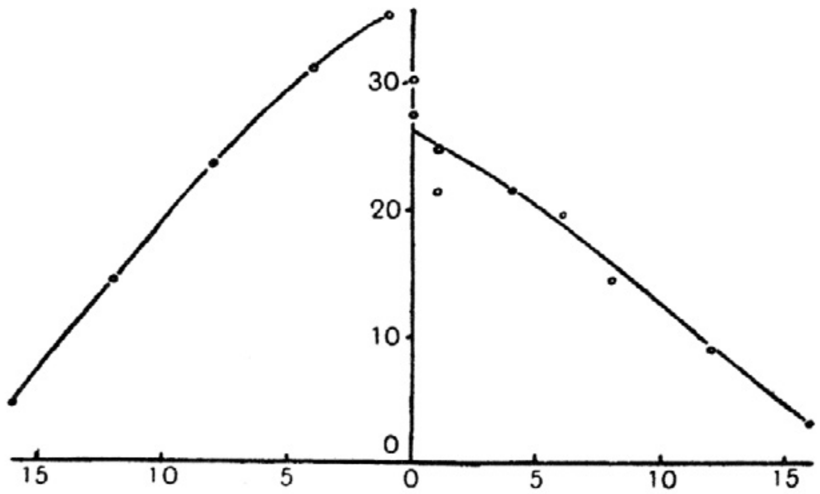

Fig. A02. Reflex responses. [K, O]

Responses of *tibialis anticus* to two stimuli (each one of which alone is just threshold) to *med. gastroc.* n. and *lat. gastroc*. n. at various intervals. Abscissae; stimulus interval in stigmata (msec.). Ordinates; tension in grams. To right of zero, *lat. gastroc*. n. is stimulated first, to left of zero, *med. gastroc*. n. first. Curve shows relation of resulting tension to stimulus interval. From Creed et al. (1932) [1B-a01], p. 32, fig. 13.

[Legend updated from that in Eccles & Sherrington (1930) [1A-006], p. 5, fig. 1)]

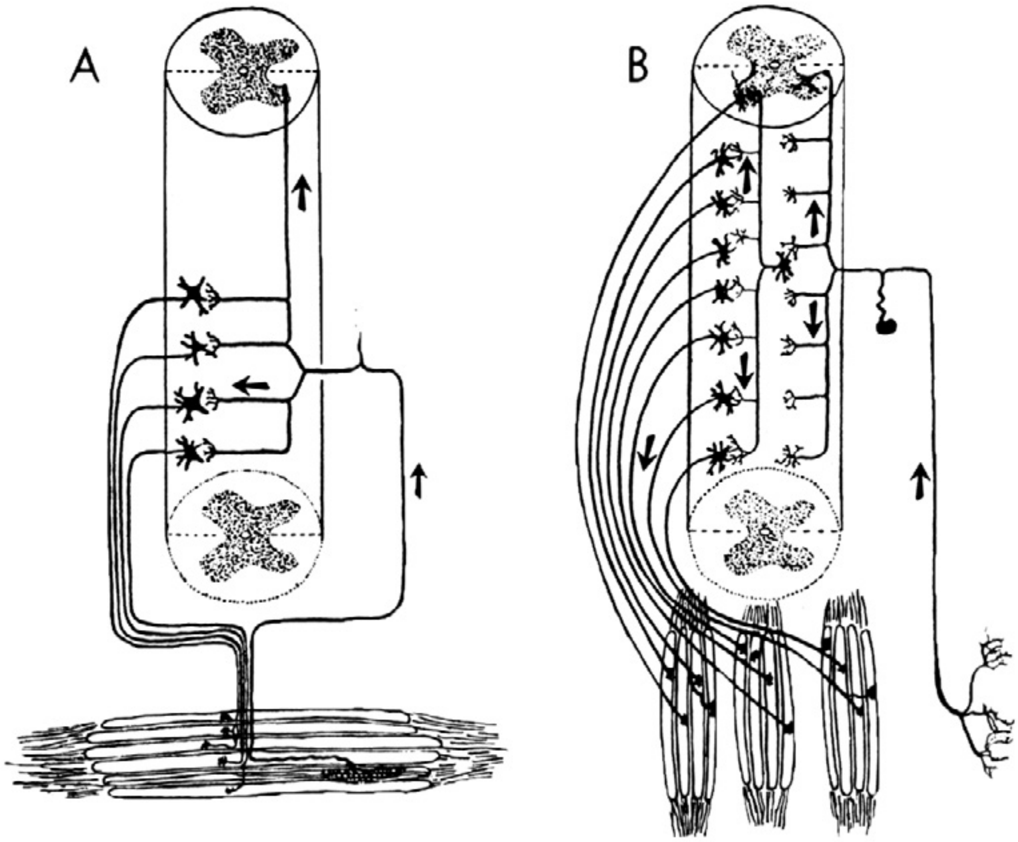

Fig. A03. Reflex pathways. [K, O]

A. For monosynaptic reflex arc, with afferent fibre from annulospiral ending:

B. For polysynaptic flexor reflex, with cutaneous afferent fibre: The three muscles in **B** represent flexors of hip, knee and ankle. (Modified from Ramón y Cajal, 1909).
From McGeer et. al., (1978) [1B-a16], p. 36, fig. 2.1.

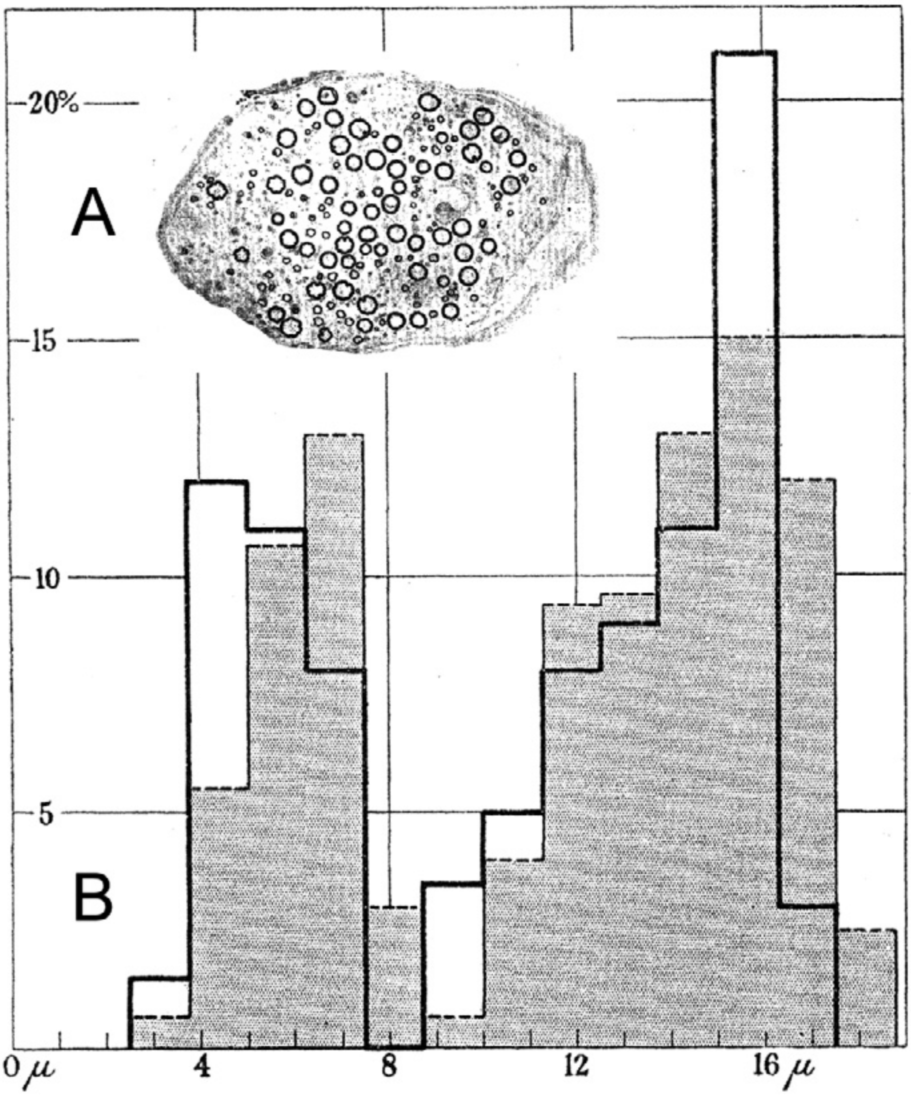

Fig. A04. Individual motor unit of muscle. [L]

A. Nerve-trunk of *biceps femoris* (x 320) showing myelinate efferent fibres (all afferent fibres removed).

B. Deafferented nerve of *biceps femoris* (solid line) and deafferented nerve of *semitendinosus* (dotted line).

From Eccles & Sherrington (1930), [1A-007], A: p. 356, plate 28, fig. 2 (rotated 180°); B: p. 339, chart 2.

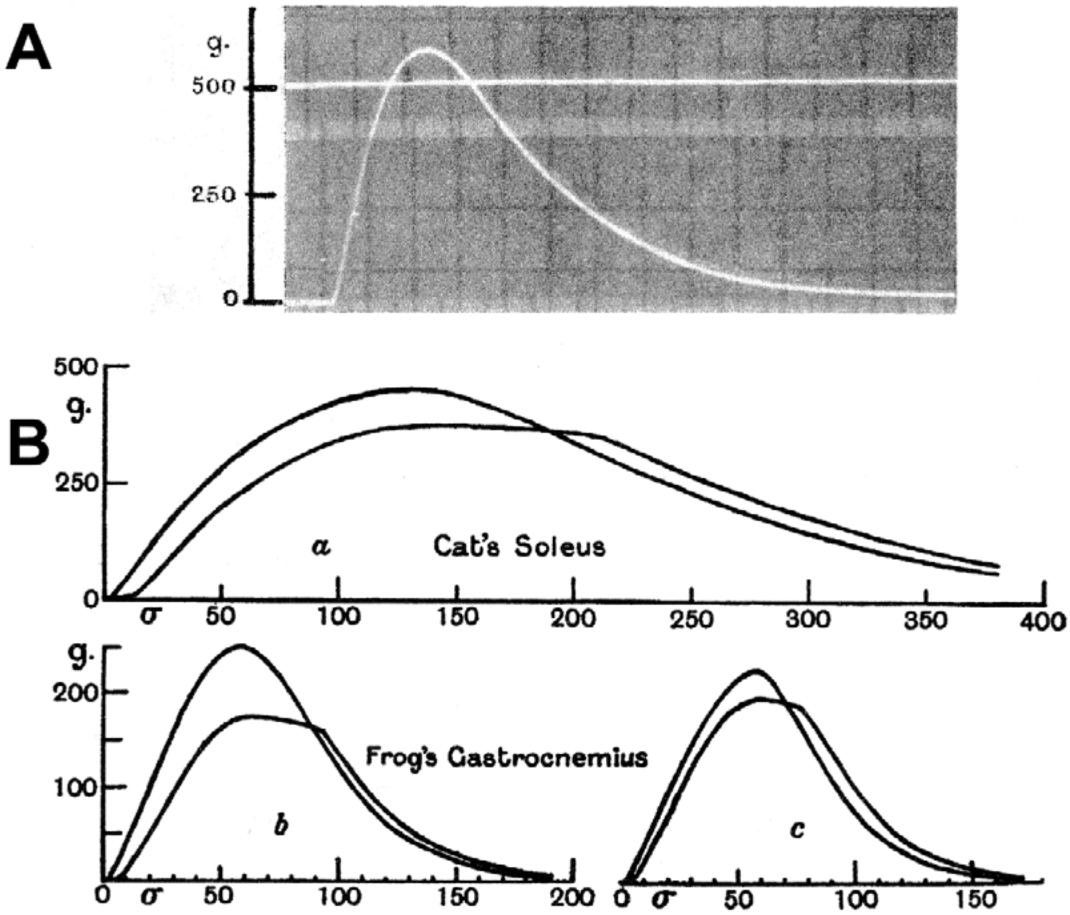

Fig. A05. Frictionless myographs and the "angle". [M]

A. Isometric motor twitch of *extensor digitorum longus* in the cat, recorded by a "frictionless" myograph.

B. Superimposed mechanical records by the two types of myographs (with and without friction). Each pair was obtained from the same muscle in quick succession and is reduced to the same tension-time coordinates.

From Cooper & Eccles (1929), [1A-005], A: p. iv, fig. 1; B: p. iv, figs. 2a, 2b & 2c.

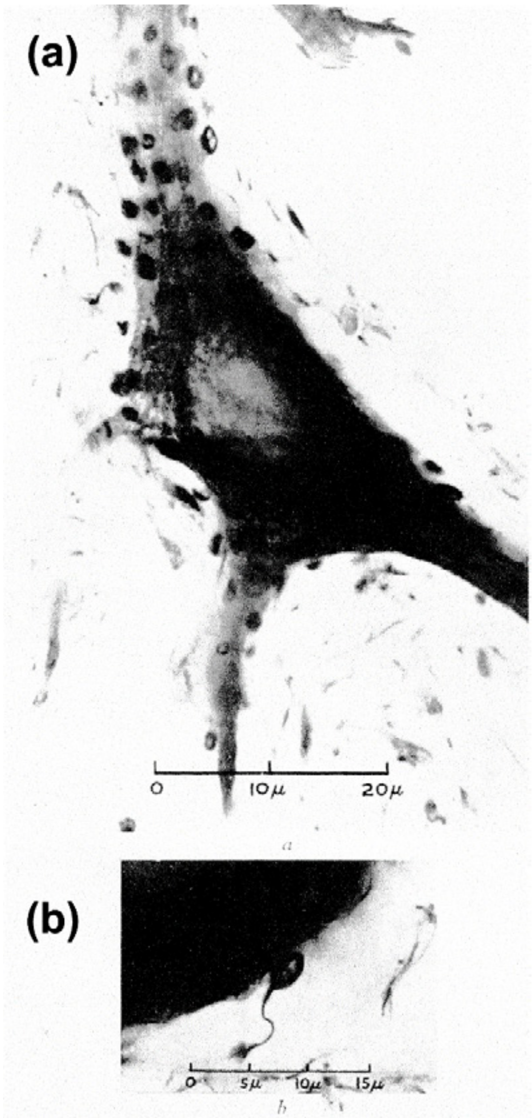

Fig. A06. E.C. Hoff's light microscopic demonstration of Cajal's *boutons terminaux*. [AA, AC]

(a): Section of cell in dorsal region of grey matter in spinal cord of adult cat, showing '*boutons terminaux*' in contact with the cell surface. (About 100 '*boutons*' were counted on the surface of this cell, although, of course, that number is not visible at one focus). Compare this figure with the model of a nerve cell shown in Fulton, (1926), p. 534, fig. 204.

(b): Same magnification of one '*bouton*' in contact with the surface of a nerve cell of adult cat. In both these figures, the '*boutons*' are somewhat degenerated: (a) 43 hours; (b) 24 hours. From Creed et al (1932) [1B-a01], p. 5, fig. 5.

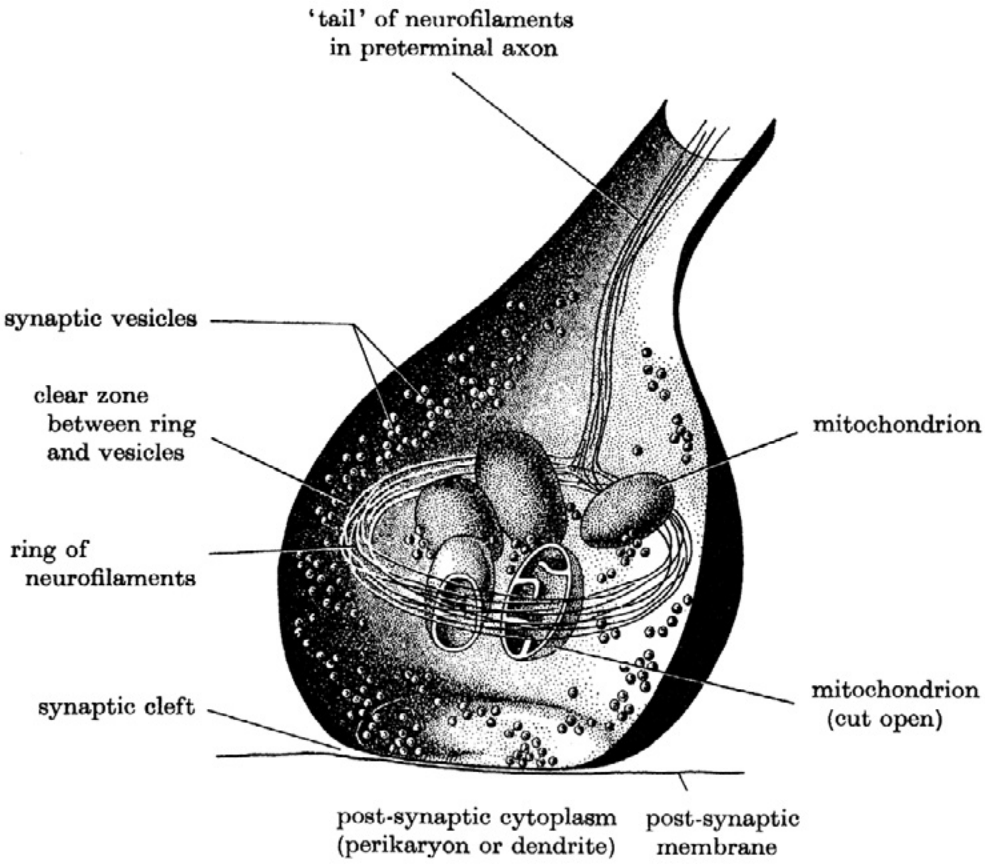

Fig. A07. Three-dimensional diagram of presynaptic *bouton* with ring of neurofilaments. [BM]

These *boutons* reach 5µ in diameter. Each contains synaptic vesicles (~ 500 Å in diameter) and a bundle of neuro-filaments (each filament ~100 Å in diameter) usually oriented in the form of a ring. A "tail" of neurofilaments is sometimes observed extending up the axon from the ring. Numerous mitochondria are also present, most of which lie within the ring. The synaptic cleft is about 200 Å across. Synaptic vesicles form aggregates near the presynaptic membrane bounding the cleft. The membrane thickenings that are present at these regions have been omitted since their three-dimensional appearance is not known. Also, details of the post-synaptic component and the cell processes surrounding the *bouton* have been omitted. The figure is not drawn strictly to scale.

From Boycott, Gray & Guillery (1961), p. 152, fig. 1.

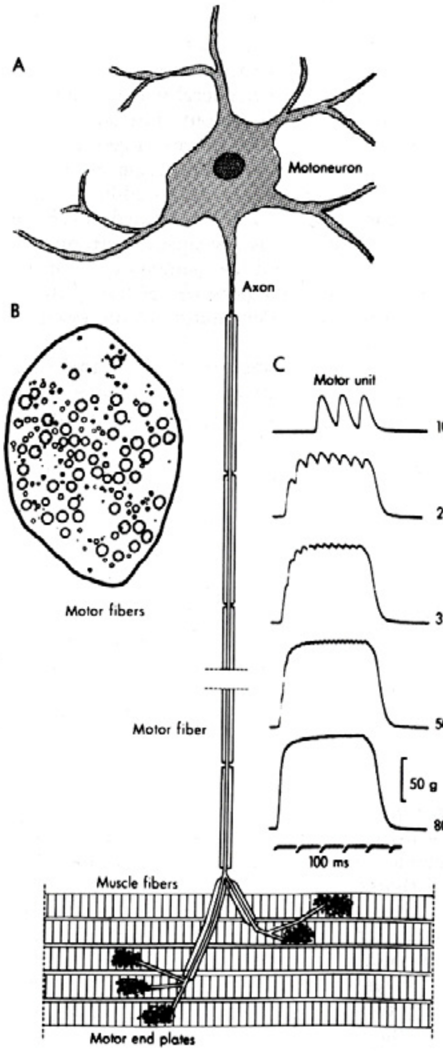

Fig. A08. The motor unit. [BK]

A. Motoneuron, with its axon passing as a myelinated nerve fibre to innervate muscle fibres.
B. Transverse section of motor fibres supplying a cat muscle, all afferent fibres having degenerated (Eccles and Sherrington 1930 [1A-007] p. 356, Plate 28, fig. 2.)
C. Isometric mechanical responses of a single motor unit of the cat *medial gastrocnemius* (MG). The responses were evoked by repetitive stimulation of the motoneuron (cf. **A**) by pulses of current applied through an intracellular electrode at the indicated frequency in cycles per second. [See Devanandan et al. (1965), p. 361, fig. 1, Record *D* for further information.]
From McGeer et al., (1978) [1B-a16], p. 72, fig. 3.1.

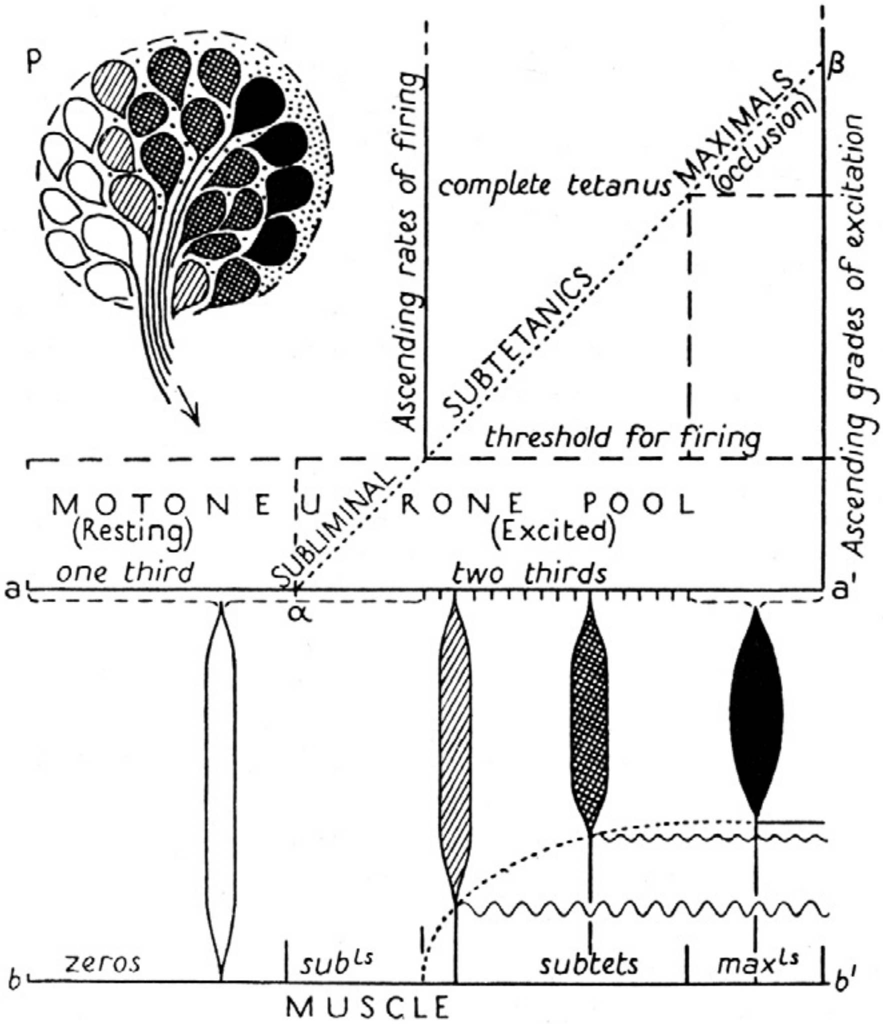

Fig. A09. Excitement distribution for a muscle's reflexly active motoneuron pool. [BM, P, T]
Grades of excitement plotted against numbers of motoneurons (abscissa a --á) and of motor units (abscissa b --b′). α---β denotes excitements in active fraction of pool.
From Creed et al. (1932) [1B-a01], p. 122, fig. 61.

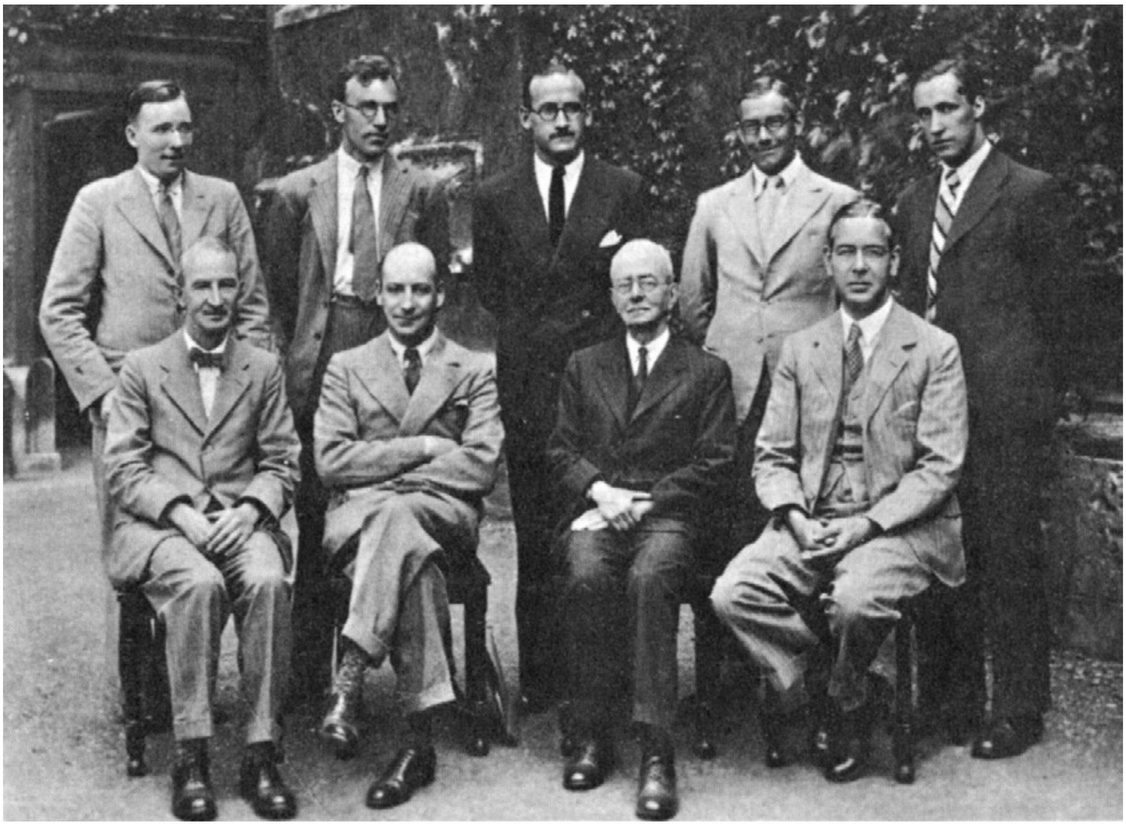

Fig. A10. Group photograph with Sherrington in 1934. [R, AB]
Back row: J. H. Wolfenden, J. C. Eccles, J. B. Odoriz, J. P. V. D. Balsdon, S. Obrador.
Front row: C. Wilkinson, H. M. Carleton, C. S. Sherrington, E. G. T. Liddell.
Photograph taken outside the Hall of Exeter College Oxford after a lunch given by two research students in the Physiology Department: J. B. Odoriz and S. Obrador.
From Eccles & Gibson (1979) [1B-a18], p. 73, fig. 5.

Fig. A11. Sir Charles S. Sherrington in his seventies. [R]
Photographed in the Old Physiology Laboratory by Mr. A. H. Bodle.
From Granit, (1966), p. 36, Plate. 1.
(See also Fig. F5 in Family Reminiscences section [**FB]** for C. S. Sherrington with John Eccles)

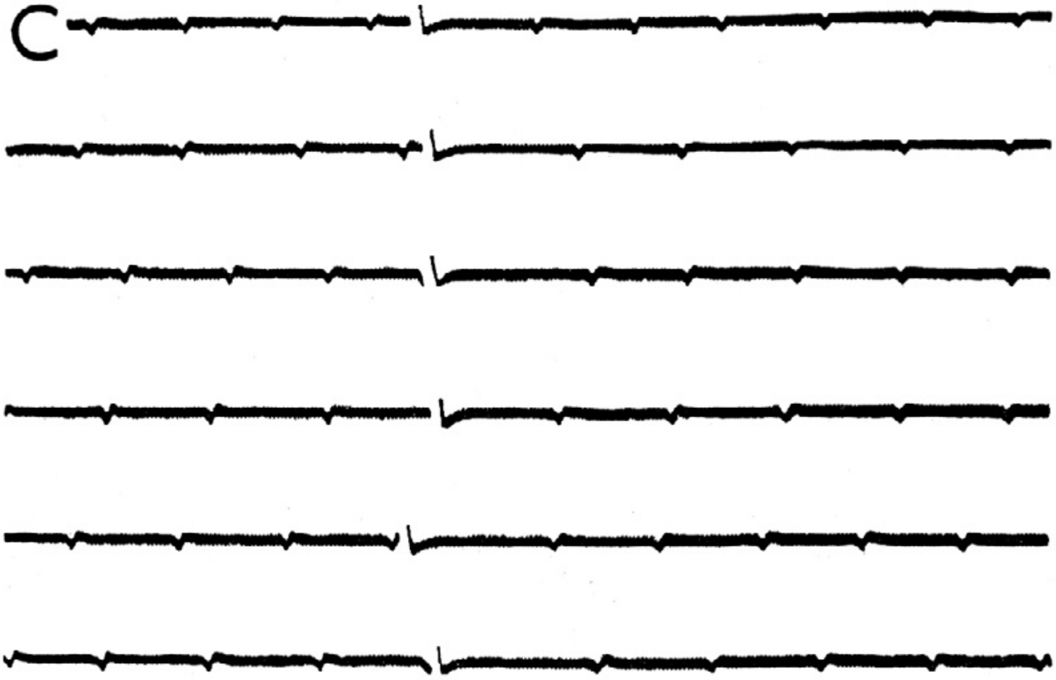

Fig. A12 The Effect of a Single Antidromic Impulse. [T, BM]

Rhythmic responses of a single motor unit of *soleus* muscle, interrupted by a single stimulus (antidromic stimulus) applied to the intact motor nerve, as shown by the large motor action current. Note the varying length of the subsequent compensatory pause.
From Eccles (1953) [1B-a02], p. 175, fig. 59C.

[See also Eccles & Hoff (1932) [1A-018], p. 504, Plate 24, fig. 5 to view the original traces recorded during this experiment.]

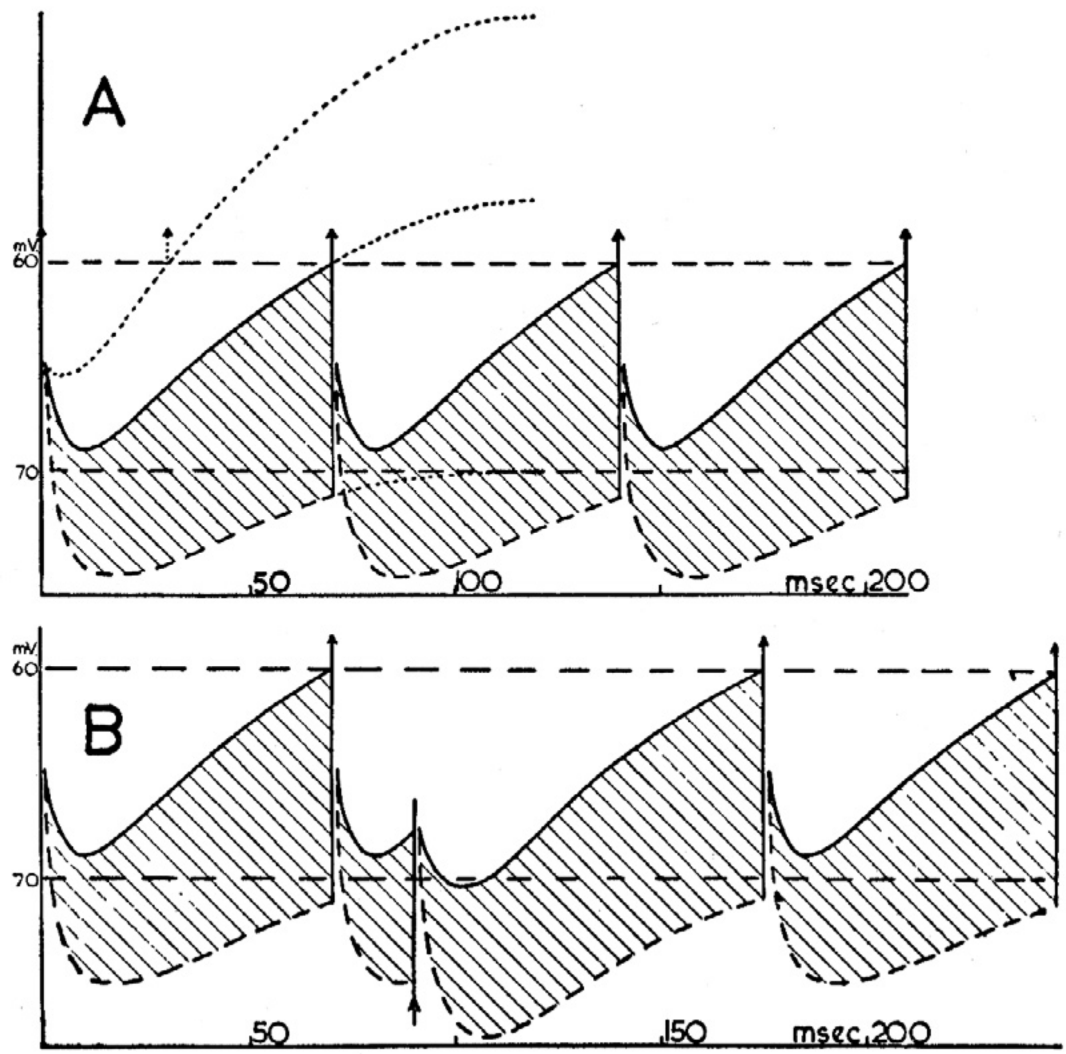

Fig. A13. Suggested explanations for rhythmic discharges and interruptions. [T]

A. Diagram illustrating suggested mechanism for generating rhythmic discharges of motoneurons.

B. Diagram illustrating manner in which an antidromic impulse interrupts a rhythmic cycle and is followed by a partially compensatory pause (cf. Fig. A12).

From Eccles (1953) [1B-a02], p. 176, figs. 60A & 60B.

[See pgs. 174-178 in article referenced for a full description.]

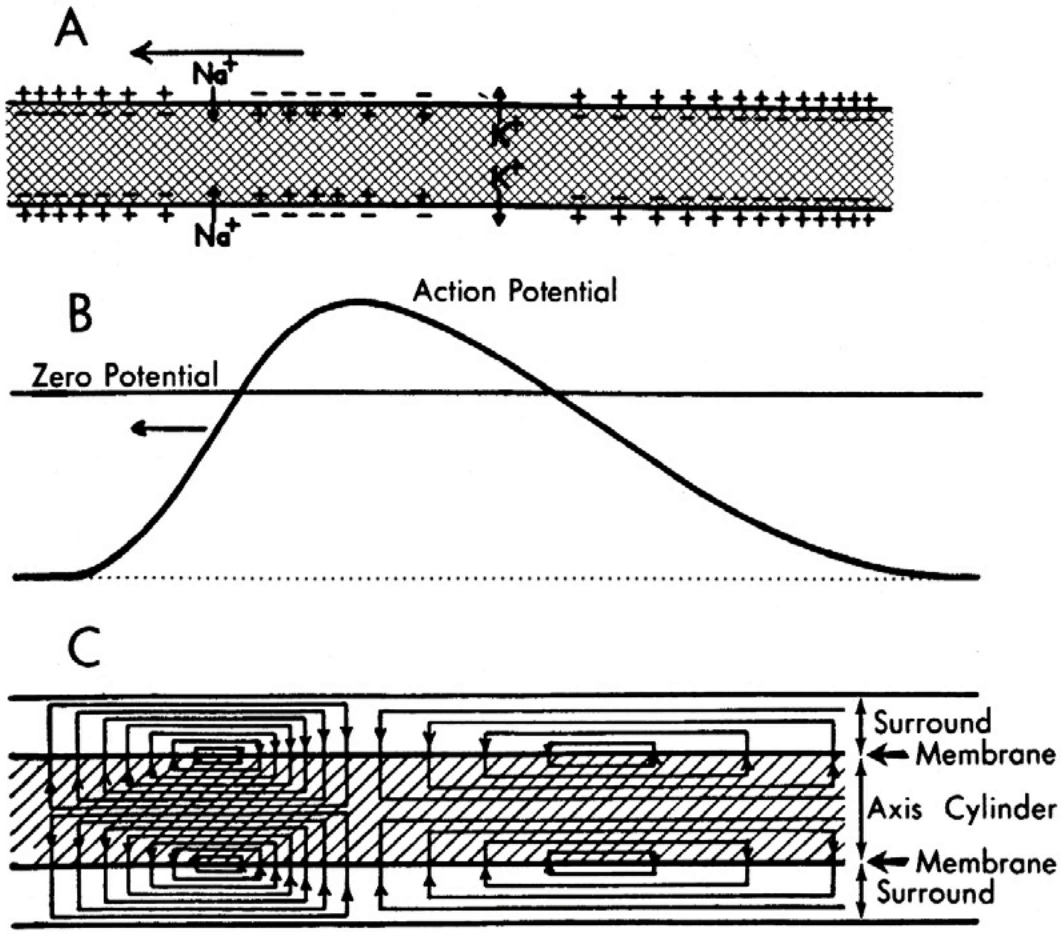

Fig. A14. Propagation of a nerve impulse: Ionic flux & current flow. [T, AJ, BG, BP]

The impulse propagation is here shown frozen at an instant of time.

In **A** are the ionic fluxes.

In **B** are the membrane potential values.

In **C** are the lines of current flow between the axis cylinder and the surround, illustrating the cable properties of the nerve fibre.

The direction taken by the "frozen" nerve impulse is from right to left.

From Eccles (1953) [1B-a02], p. 6, figs. 2A & 2B. (modified)

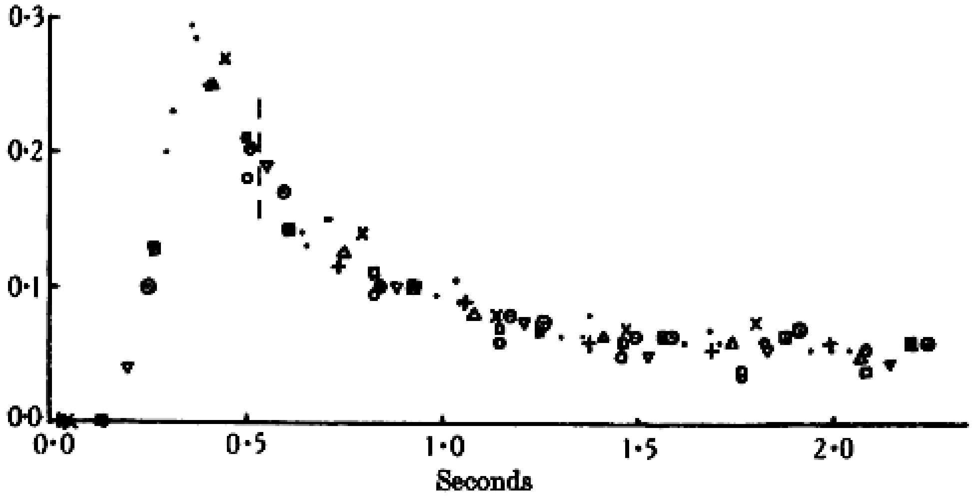

Fig. A15. The inhibitory curve produced by applying a single stimulus to the left vagus. [Y]

The lengthening of each cycle, i.e., the amount by which it exceeds a normal cycle, is expressed as a fraction of a normal cycle. In this way, a series of points is obtained for each observation. Figure 15 comprises series of points from thirteen observations, nine series being marked in a characteristic way. With all points to the left of the perpendicular broken line (at approx. 0.55 sec.) the previous cycle was not inhibited; with points to the right, it was [inhibited].

From Brown & Eccles (1934) [1A-028], p. 213, Text-fig. 1.

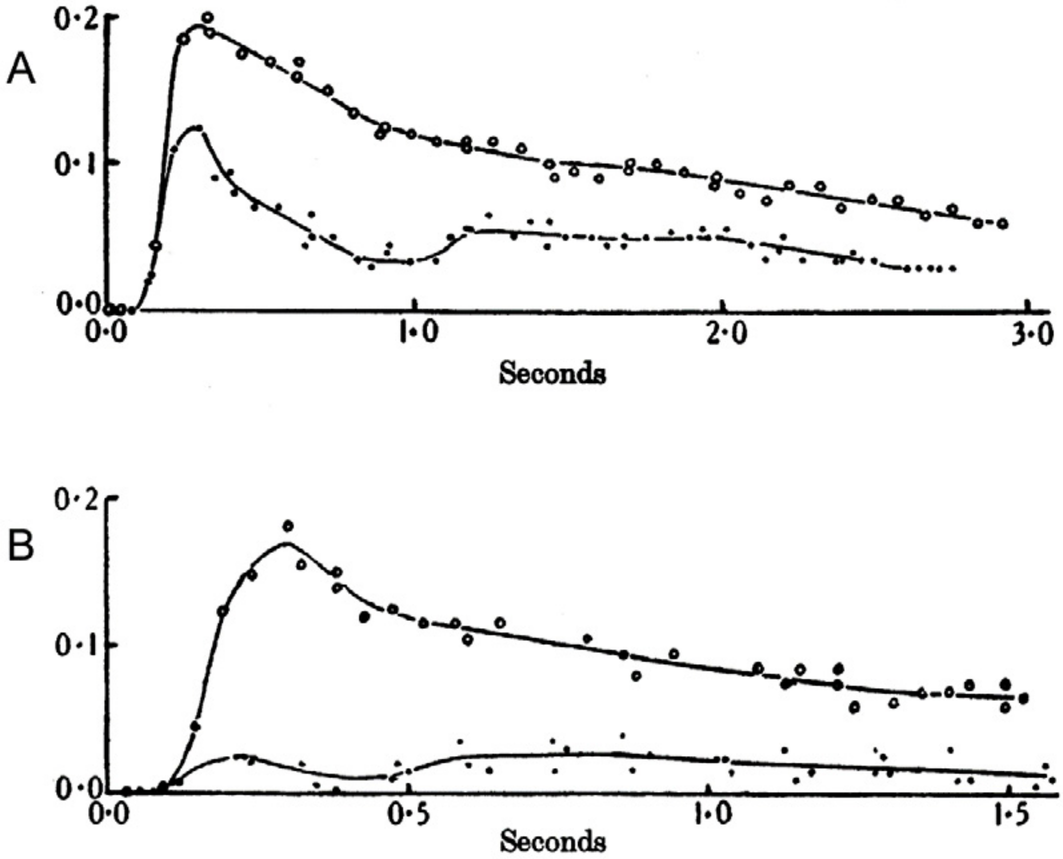

Fig. A16. The effects of eserine and atropine on vagal heart slowing. [Y]

A. As in Fig. A15, but in another experiment. The upper curve was obtained 2½ -7½ min. after injection of 50γ eserine. Weight of cat, 2.75 kg.
From Brown & Eccles (1934) [1A-028], p. 226, Text-fig. 15.

B. As in Fig. A15 but in another experiment where the right vagus was stimulated. The curve through the dots was obtained after injection of 25γ atropine. Weight of cat, 2.75 kg. [Gamma, symbol: γ, is a deprecated non-SI unit of mass, equal to one microgram.]
From Brown & Eccles (1934) [1A-028], p. 227, Text-fig. 17.

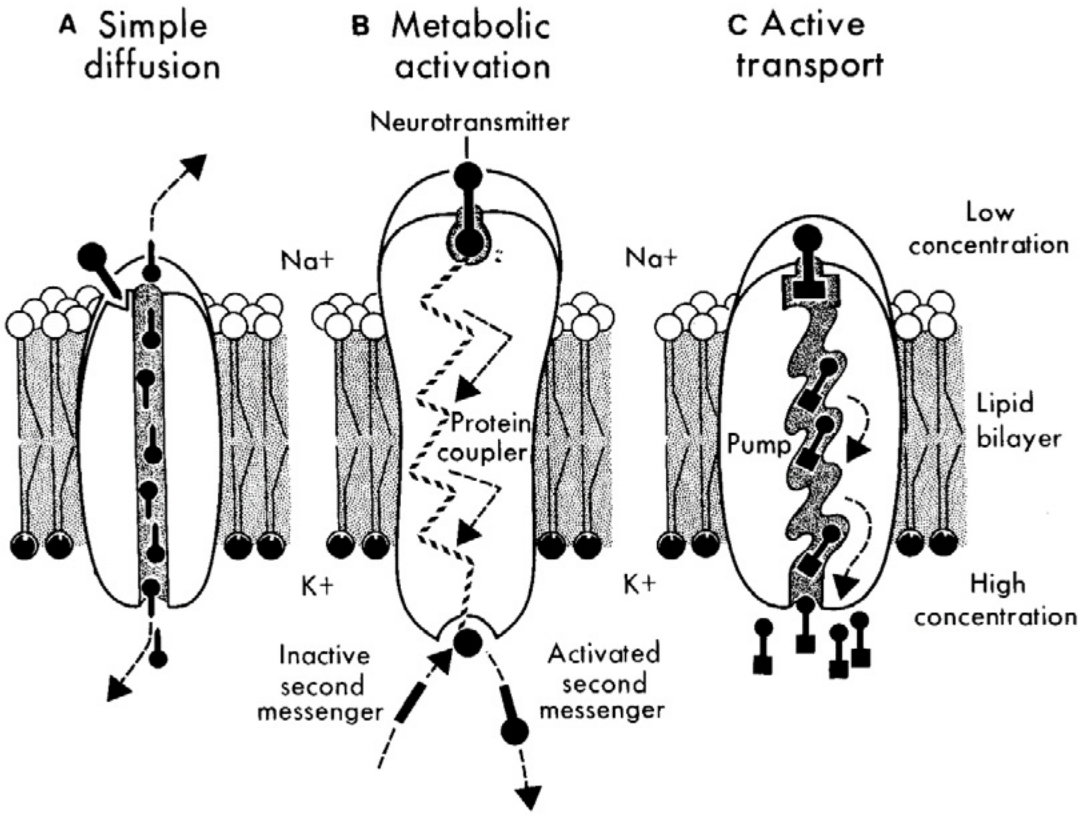

Fig. A17. Organization of the outer cell membrane. [Y, AA, AL]

The basic structure is a bimolecular leaflet of phospholipid molecules with their hydrophilic parts at the surface. Structural proteins (not shown) are attached to both outside (top) and inside (bottom) surfaces to provide stability. This figure shows diagrammatic depictions of three types of receptors:

A. An ionotropic receptor which opens ion channels on activation by a neurotransmitter.

B. A metabotropic receptor, which, on activation by a neurotransmitter, triggers a transmembrane activation of a second messenger.

C. A high-affinity neurotransmitter uptake system, which "pumps" extracellular neurotransmitter at a low concentration into a nerve ending at a high concentration.

From Eccles (1990) [1A-586], p. 3771, fig. 2.

[Updated from McGeer et al., 1987 [1B-a16], p. 29, fig. 1.16.]

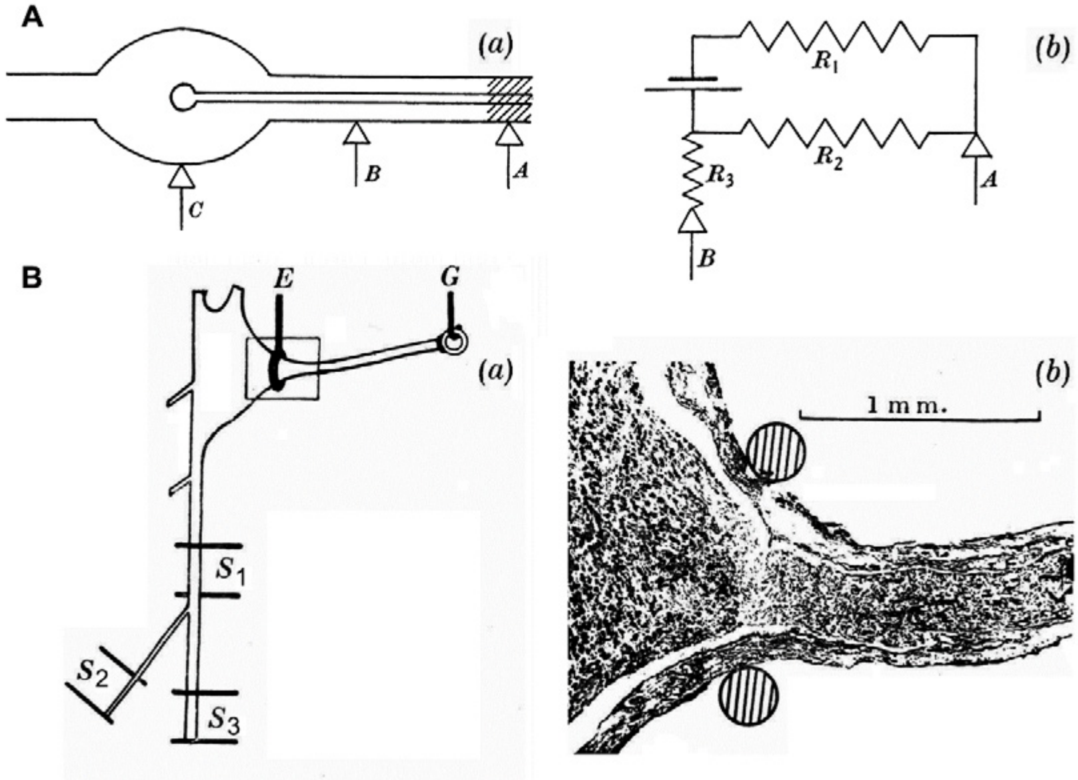

Fig. A18. Recording synaptic potentials & transmission in cat's stellate ganglion. [Z, AQ, BE]

A. Upper diagrams. **(a):** Diagram of ganglionic and postganglionic trunk, showing relation of leads to a schematic ganglion and its axon. **(b):** Diagram showing electrical conditions obtaining for leads ***B*->** and ***A*->**.

From Eccles (1935) [1A-033], p. 185, Text-figs. 3 & 4.

B. Lower diagrams. **(a)**: Sketch of stellate ganglion showing position of recording (***E***, earth and ***G***, grid) and stimulating electrodes (S_1, S_2, S_3). **(b):** Photomicrograph of ganglion section included in the rectangle ***E*** of (a). The two circles show the position and approximate size of the silver ring, which is seen to lie slightly beyond the sharp boundary between the ganglion cells and the cardiac nerve. A connective tissue sheath surrounds both the ganglion and the nerve.

From Eccles (1943) [1A-068], p. 466, fig. 1.

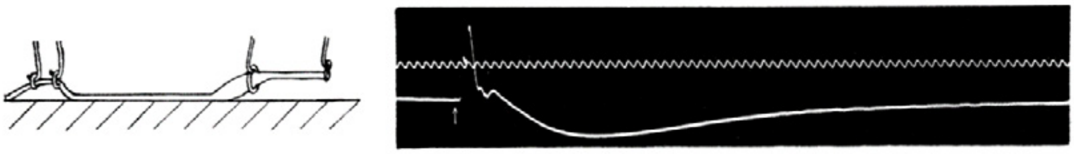

Fig. A19. Stimulation and recording of synaptic transmission. [Z]

Left. A single induction shock is applied through electrodes on the preganglionic trunk (to the left of the diagram), and the action potential so set up in the ganglion is recorded with the earthed electrodes on the ganglion and the grid on the isolated postganglionic trunk. Both stimulation and recording leads being raised from the cat (shown in the diagram by the shaded area).

Right. An upward deflection in this and all subsequent records indicated a negativity of the earthed lead relative to the grid lead. The arrow indicates the stimulus artefact (which can barely be detected) about 6 msec. before the action potential. 1 d.v. = 10 msec.
From Eccles (1935) [1A-033], p. 183, Text-fig 1.

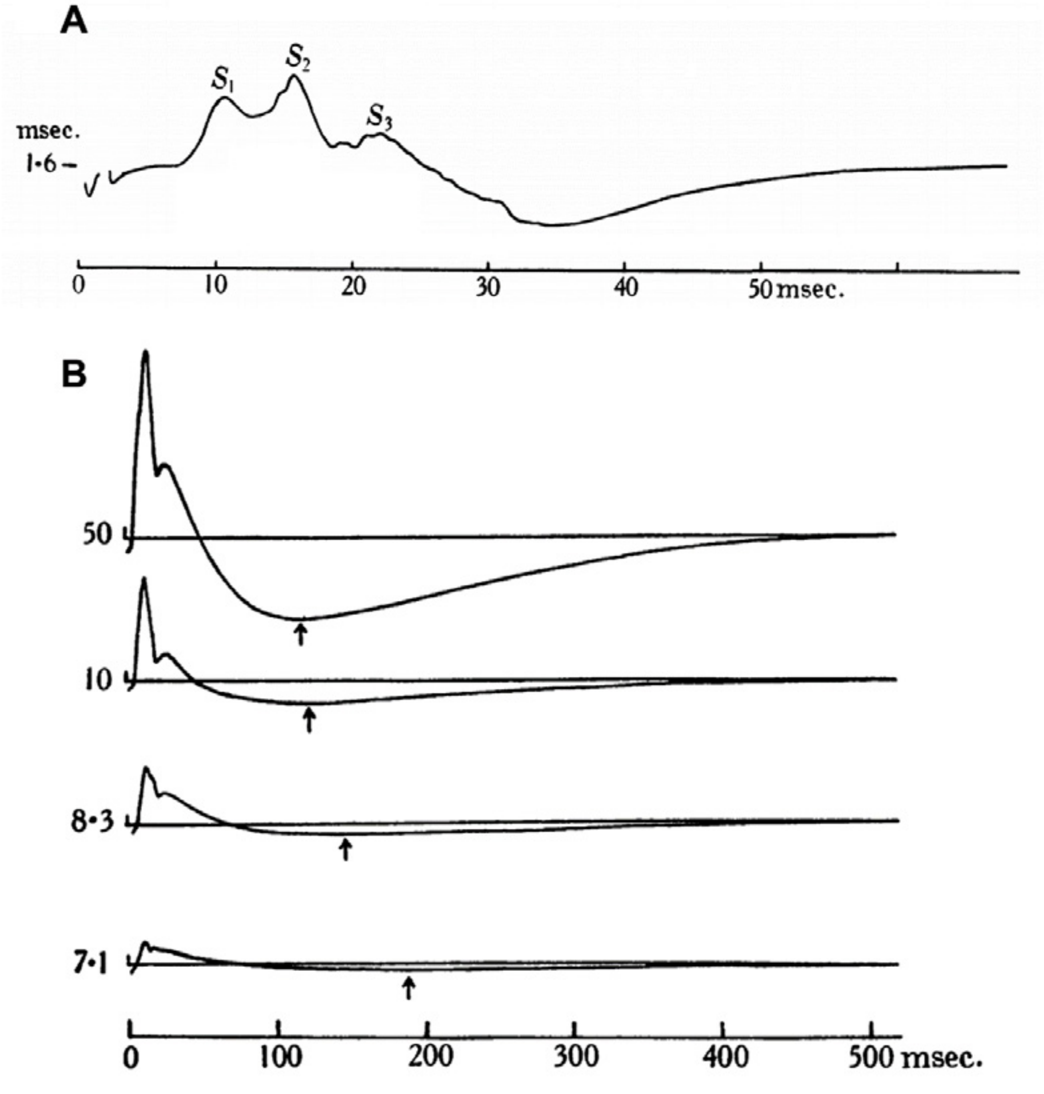

Fig. A20. Postganglionic action potentials set up by two maximal preganglionic volleys. [Z]

A. At maximal stimulation three spikes (S_1, S_2, S_3) are recognizable. The first stimulus occurs at zero of the time-scale, the second at the beginning of the break of the curve.
From Eccles (1935) [1A-033], p. 196, Text-fig. 8, (uppermost curve only selected).

B. Ganglionic action potentials set up by stimuli whose strengths in arbitrary units are shown to the left of the initial base lines. The arrows mark the points of maximum positivity.
From Eccles (1935) [1A-035], p. 475, Text-fig. 7.

STAGE 3: Research in Sydney: 1937-1943.
(Sections AH to AS)

AH. Starting up at the Kanematsu Institute and our Accommodation

In applying for the Directorship of the Kanematsu Institute I had to stress the importance of my broadly based program for research into the nervous system and on neuromuscular transmission, with associated pharmacological studies. It was an unknown academic and medical world that I was venturing into, entirely on the advice of Kellaway. I sent in quite a strong document with an excellent testimonial by Sherrington, also I sent in the bound copies of my publications up to and concluding with the *Ergebnisse* Review. In due course I received notice of my appointment as Director of the Kanematsu Memorial Institute of Pathology at Sydney Hospital. I had only to exercise general supervision of the clinical sections of the Institute that were fully housed in the three lower levels of the fine new Kanematsu Building (Fig. A21) that had been built as a Memorial to Fusajiro Kanematsu[192], a Pioneer Japanese Merchant in Australia, however, the finance for operation came from Sydney Hospital, the State Government and the Council for National Health and Medical Research.[A] It was enough for a modest beginning. My task was to be fully engaged in Medical Research in cooperation with part-time or full-time associates. It was certainly a challenge and I knew nobody in Sydney, but I had a nice welcoming letter from Professor Keith Inglis[193] of the Pathology Department Sydney University and previously also part-time Director of the Kanematsu Institute. I was gifted with great energy and enthusiasm as well as a wide range of research experience for my challenging new position.

I thought much of my future during the six weeks on the ship. We passed south of Spain and could see in the mountains, signs of the Spanish civil war that was still on. As we passed through the Suez Canal, I felt relieved to have left behind Europe with the ever-growing Hitler menace. At Melbourne in late July. there was a great welcoming by my parents and my sister. There we left the four children plus the Danish maid while we continued on the ship to Sydney for a most stressful two weeks. Prof. Keith Inglis welcomed us, and we had temporary hotel accommodation.

The visit to the Kanematsu Institute was immediate and very intense. Dr. Harold Ritchie[194] was the Senior Physician of Sydney Hospital and became my dear friend and adviser through all the troubling years that later afflicted me. But at first all was well and the wise John Travers[195], the President of Sydney Hospital, told me that he trusted

192 Kanematsu, Fusajiro (21.05.1845 – 06.02.1913) JP businessman/merchant. "Customers are always right".

193 Inglis, William Keith (11.02.1888 – 26.01.1960) AU Sydney pathology prof. Kanematsu director 1933-36.

194 Ritchie, Harold John (19.06. 1884 – 08.09.1953) AU Sydney Hospital clinical medicine lecturer 1926-1946.

195 Travers, John (01.01.1866 – 16.04.1943) IE shipwright/company director. President Sydney Hosp. 1927-1938

me completely. He was a business man and was of the Kanematsu Advisory Committee.

In a few days I had decided to advise on a drastic remodelling of the upper floor of the Institute in order to provide for research rooms. There was in fact only the Director's office with a wonderful view of the Harbour (Fig. A21) and two minor rooms at the back. All else on that floor was a large pathology museum (two windows to left of Fig. A21) and a Library Lecture Room (the next two windows). It was necessary to move the Pathology Museum to the floor below in more restricted, but still adequate space, and to use all that vacant space for two research laboratories with two shielded recording rooms. A room behind could be set up for aseptic operations, and another room behind for a workshop with lathe and other machinery. Fortunately, the Advisory Committee agreed at once, and appointed an architect to prepare plans for that floor under my direction and also a small animal room on the partly developed floor above. Meanwhile the crates with the Oxford equipment and our belongings were stored in the Institute. An advertisement led me to an excellent furnished house in Mosman which I accepted for immediate occupation. Mosman, across the Harbour from Sydney with an excellent ferry service, was the chosen site also for permanent living and I was fortunate to buy a wonderful large house for £3,300 with beautiful views over the harbour and a lawn tennis court. The house needed renovation, the addition of a double garage and some internal remodelling. The same architect took over the task and had plans drawn for letting the contract. Finally, I bought a new Ford V8 1937 model for £220! It was still depression prices. Within the two weeks we drove back to Melbourne for the family. I marvel still at how much was accomplished but these were still times of the depression with low prices and dedicated work.

On returning to the nice furnished house, I was expected to play on the tennis court belonging to the owners next door! I immediately started up at the Institute and visited the University. Also, on week-ends there was plenty of work to do in the garden of the house we had bought. The temporary tenants soon left, for the renovations costing about £1000 and that would take several months. Meanwhile all our possessions were stored there in the packing cases. Also, the plans for the research rooms had been drawn. I approved and work started forthwith.

AI. Sydney University

I now visited the University. It was about 3 km away by a tram from the centre of the city. Sydney Hospital with the Kanematsu Institute was very well situated just above the city and fronting the Domain with nearby the exquisite Botanic Gardens going right down to the Harbour. The University had very large grounds – several km^2 - and enormous buildings, but was in a poor surround. As I expected, most of the University was dismal scientifically, particularly the Medical School, which was just a teaching institution. Unbelievably, the whole building was completely sealed with padlocks outside by janitors at 5 PM! All staff had to scurry out to avoid imprisonment for the night! The Library was also sealed at 5 PM and also for one to two hours at lunch time. Some professors had the important library journals locked in their offices.

For example, Physiological Reviews was taken by the Professor of Biochemistry. There was no other copy in Sydney! I met the Physiology staff – "Pete" Davies[196], the professor, had done good respiration in his younger days, but now lived and drank in the University Club. Personally, he was a charming man from a distinguished musical family in Adelaide. All my arrangements as regards the lectures I proposed to give were done with Dr. Cotton[197] who was at least doing research on the effects of centrifugal force on volunteers using a human centrifuge. It was important for air pilots in combat.

The best department in biological sciences, Botany, was with Eric Ashby[198], professor, and Bob Robertson[199], associate professor. We became very good friends and they have had most successful careers. We also became good friends of Prof. V. A. Bailey[200] (Physics) who lived in Mosman with his nice family and was active in research, and also in tennis. Les Wirsu[201] from his department gave valuable help to us technically. I soon heard of the best scientist in Sydney; Dr. Rudolph Lemberg[202], who was Director of Research at the Royal North Shore Hospital, and a world authority on porphyrin chemistry and biochemistry. He was never given any position in the University and never even invited there, which was a scandal. He was my best friend in Sydney. Since being of Jewish origin, he lost his good position in Heidelberg University and as a refugee was appointed to this modest position in Sydney. He and his wife Hannah were Quakers and wonderful scholars. She did creative work in weaving, which was in much demand in Sydney. They were a joy to meet, which we often did, particularly on bush walks, where Rudi became an authority on Australian wild flowers. These flowers, of unbelievable beauty, flourished in the nature reserves that fringed the Sydney suburbs. Like Rudi, I was never offered even a modest honorary position by Sydney University.

AJ. Kanematsu Institute 1937-1938

At the Institute the construction of the research rooms went off well. There were two good shielded rooms with forced ventilation and with good doors like those I had in Oxford, and associated dissection rooms. Chapman who was my technician at Oxford had arrived in Sydney soon after me, and he was with me for 28 years, a most faithful man. He soon had everything in order with glassware, chemicals, instruments etc and we had a good aseptic operation room with sterilizers and an excellent overhead operating light and facilities for microdissection. It was to impress the clinicians! I hired a technician for the workshop and we bought the necessary technical equipment.

196 Davies, Harold Whitridge "Pete" (27.06.1894 – 07.06.1946) AU physiology prof. "Respiration in disease".

197 Cotton, Frank Stanley (30.04.1890 – 23.08.1955) AU physiology professor. Physical strain. "Ergometer".

198 Ashby, Eric (24.08.1904 – 22.10.1992) UK botany professor at Sydney University, 1938-1946. Baron Ashby.

199 Robertson, Rutherford Ness "Bob" (29.09.1913 – 06.03.2001) AU Sydney Univ. botany lecturer, 1939-52.

200 Bailey, Victor Albert (18.12.1895 – 07.12.1964) UK Sydney University physics professor, 1924 to 1960.

201 Wirsu, O. L. "Les" (?–?) AU? Electro- & Radio-physicist. CSIRO and Australian National Airways.

202 Lemberg, Max Rudolf (19.19.1896 — 10.04.1975) DE(J) Kolling Institute, biochemist. "Porphyrin structure".

Before that, the Institute did not even own a screwdriver. All was done by the Hospital engineers. I was aiming at self-sufficiency and I succeeded. I also attempted self-sufficiency for the Library because of the inadequacies of the Medical School Library and its remoteness with limited hours of access. The Library was in the large room just off my office and faced the Harbour. It also served as an occasional lecture room with micro-projection. When I added my chosen list, there were paid subscriptions to 52 journals and also 10 donated journals. Of course, the library, though housed in the Institute, was for the Hospital staff as well. This may seem to be too ambitious, but I was building for an expanding future, which was in the minds of the Advisory Committee in those days of pre-war optimism with Kellaway hoping that I would build up an equivalent of the Hall Institute in Melbourne.

Here is an interlude: I was greatly pleased and disappointed to receive an invitation to contribute to an international Symposium, my first. It was to the most distinguished occasion by the University of Bologna and the City of Bologna to celebrate the Second Centenary of birth of Luigi Galvani[203], the most distinguished Bolognese Scientist and the father of electrophysiology. My disappointment was that I could not accept their offer of travel from Oxford and accommodation in Bologna, because I was already in Sydney! The letter of invitation was greatly delayed and all I could do was to send a polite refusal. My association with Galvani is shown pictorially in the cover picture of a recent book (Fig. A22). In 1978 I was visiting Bologna and had been looking at the Galvani statue with the frogs outside San Petronius. A very polite cultured man told me about Galvani, not realizing that I knew much more than he!

Immediately confronting me in Sydney was the difficulty in securing good research staff. The intellectual poverty of the Medical School resulted in the very few medical graduates that were interested in a research career. I only found one in Sydney, Dr. A. K. McIntyre, who was doing research in the Department of Surgery. I tried unsuccessfully at that time to attract him.

When the changes in the Institute were completed late in 1937, the Hospital Board and the Kanematsu Advisory Committee invited the Japanese Ambassador and staff to visit the newly fitted Kanematsu Institute. I did my best to impress the Japanese visitors, who were extremely polite, so all went well until they crowded into the elevator at the top floor, far in excess of the maximum. The result was that the elevator almost crashed onto the basement and it took a major performance to get them out. It was still of course some years to Pearl Harbour!

In late 1937 I had time to appreciate the members of the Kanematsu Institute, who were responsible for all of the clinical testing carried out by teams of graduate students in the Institute. For me the most attractive member was Dr. A. D. Gillies[204], the Senior Pathologist. He was a highly skilled and most dedicated young doctor with a lovely family, Jean and two very young sons. I was hoping to attract him to move his research

203 Galvani, Luigi (09.09.1737 – 04.12.1798) IT Physician. Discoverer of bioelectricity.

204 Gillies, Alan Douglas (23.03.1907 – 19.05.1941) AU Sydney Hospital senior pathologist.

interests into neurohistology. I can still feel the terrible shock when Harold Ritchie burst into my room in late 1940 with the tragic news that Alan Gillies had fulminating hypertension and would be dead within four weeks.**[A]** Jean was a most dedicated mother to the two young sons who grew up, like their father, to become distinguished doctors and medical scientists. Another valuable member of the part-time staff was Dr. Marjory Little[205], the Bacteriologist and Haematologist.

In 1938 I was fortunate to attract Dr. W. J. O'Connor[206] for the year of 1938 when he was holding a research fellowship of the National Health and Medical Research Council. He had had a most distinguished career at Adelaide and planned to go to England in 1939. Meanwhile we worked together very successfully through 1938. We published five communications to the Physiological Society and 2 papers in the Journal of Physiology, one of almost 50 pages being published in 1939. I am most grateful to John for that excellent year.

I had decided to concentrate on neuromuscular transmission because it could be given clinical significance. The general problem under investigation may be stated as follows... Muscle contraction is brought about by nerve impulses discharged from the nervous system (brain and spinal cord). These impulses are brief electrical waves, about 1/2000 of a second in duration (Fig. A14) which travel at about 80 metres a second along the fine motor nerve fibres that innervate the muscles. Each of the nerve fibres supplying a muscle later branches into a hundred or more fine nerve fibres so that each of the 100,000 or more muscle fibres in a muscle is supplied by a fine nerve fibre. At this region of contact the nerve fibre ends in a specialized part of the muscle fibre called the motor endplate.**[B]** Fig. A23 is an example of the best histology of the mammalian nerve-muscle junction that we had at that time. At this point a muscle impulse is produced about 1/1000 of a second after the arrival of the nerve impulse, and this muscle impulse travels along the muscle fibre, causing it to contract. The aim of our research was the investigation of the way in which the nerve impulse sets up the muscle impulse - an essential link in the chain of events whereby every muscular contraction is brought about. Moreover, this particular link is important because it is especially susceptible to modification by drugs such as curare and eserine.

The widely distributed innervation in a cat muscle presented too much complexity for electrophysiological study of a unitary kind. So, in 1938 we attempted under microscopic dissection to cut down the innervation to one small nerve innervating a superficial strip of the muscle. This technique resulted in a most valuable preparation, a narrow. innervated strip of muscle innervated in the mass of inactivated muscle which for electrophysiological purposes was equivalent to an isolated strip of innervated muscle immersed in a conducting medium. The best preparations were in *soleus* muscle where a small branch from the motor nerve innervated by a cluster of endplates a superficial strip of *soleus*, which is shown at rest in Fig. A24A and contracted in Fig.

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205 Little, Elaine Marjory (02.06.1884 – 02.05.1974) AU pathologist. Consulting haematologist.

206 O'Connor, Walter John (28.09.1911 – 1995) AU Sydney Hospital renal physiologist, later at Leeds Univ.

A24B. The hind limb with much exposure for recording was in a moist warm chamber constructed in the workshop.

In Fig. A24C there is recording from such a strip under two levels of paralysis by curare. Curare was originally used as an arrow poison by South American Indians to paralyse their enemies! In Fig. A25 trace 3a the recording electrode was on the endplate focus with recording of the muscle spike potential and in Fig. A25 trace 3b it was on the innervated strip far from the endplate focus, where the muscle spike was much later. Fig. A25 traces 2a and 2b are similar, but with much higher amplification during the almost complete curarization, and in Fig. A25 trace 1 there is a simple endplate potential (EPP) with complete paralysis and an amplification of 50 times that in trace 3. This is one of the first endplate potentials ever to be recorded (1938). In Fig. A25 trace 2a there is a small muscle spike potential superimposed on the EPP, but in trace 2b it does not propagate away from the endplate, as it does in Fig. A25 trace 3b. This abortive spike was often found at transitional stages of paralysis and resembles the new-born impulses that have already been referred to in studies of the nerve impulse by Rushton and Hodgkin.

When two stimuli are applied to the motor nerve at an interval just longer than the absolutely refractory period the second volley produces in the uncurarized preparation only an endplate potential, which is superimposed on the initial spike response. With lengthening of the stimulus interval from 1.6 to 1.9 msec. the second stimulus may evoke an EPP on which is superimposed an abortive muscle spike that does not propagate. At still longer intervals the second EPP sets up a fully propagating muscle spike. Thus, under these critical conditions there is an abortive spike just as in the critical curare paralysis of Fig. A25 trace 2a.

As a result of precise analytical studies, it was gradually becoming clear that there was no need to postulate that on intermediate excitatory response, the detonator response, acts as a mediator between nerve impulse and EPP. The recorded endplate potential was found to be so early and fast that it was an adequate mediator. The strip potential allowed accurate measurement of the rate of propagation of the muscle impulse from the endplate. It was 3 to 4 m/sec for *soleus* and 5-6 m/sec for the fast muscles, *peroneus tertius* and *tibialis anticus*. This 1938 investigation can be regarded as preliminary to the 1939 to 1942 studies with my new associates, Stephan Kuffler and Bernard Katz.

AK. How to succeed in an Academic Wilderness

I was fortunate to have John O'Connor working with me during 1938. The only possible associate I could discover in Sydney was Dr. A.K. McIntyre that I have already referred to. He had had a distinguished career in Sydney Medical School and was now engaged in research in the Department of Surgery. He still preferred to stay where he was doing well. Actually, we later became very closely associated for many years. So, I was feeling the isolation pretty intensely. The Medical School was so poor that even the best students had no idea of research. I knew that situation very well in Melbourne 15 years earlier.

Then, just as O'Connor was leaving, I had a telephone call from an old Jesuit priest (Father Richard Murphy[207]) that I had got to know because of his intellectual interests. He told me of a young Austrian doctor who was desperately searching for a university position. He had had a Pathology position in the University department of Vienna. Dr. Kuffler's family were associates of Dollfuss[208] and he [Kuffler] was the leading anti-Nazi in the Medical School. He managed to avoid arrest by escaping through to Hungary the night the Nazis entered Vienna. Through his uncle in London, he got permission to come to Australia with a boat ticket and some financial support. So, he arrived in Sydney unknown and tried to get a university position in Pathology. All he got was permission to work in the department, but at no salary! So, after some months he was in desperate financial trouble, and that brought him to Father Richard Murphy because Dr. Stephan Kuffler had been a pupil at the great Jesuit College in Vienna. I learnt all this on the telephone from Father Richard Murphy, and also that Steve Kuffler had been twice Junior tennis Champion in Austria. I was of course most happy to have a good Austrian doctor join me at the Kanematsu, who was also a good tennis player.

In order to make our meeting as informal as possible I told Father Murphy to bring Steve to my house at 14 Clanalpine St. Mosman, where we could play tennis and then talk about the future. The lawn tennis court was now in good shape. It was a most attractive meeting and we both enjoyed it greatly. His tennis was excellent and so was Steve as a person. I would immediately arrange for him to be appointed as an associate at £500 a year, and he should get a more acceptable apartment in Mosman. So, in December 1938 there was now the promise of a good blossoming in the Academic wilderness. And what a blossoming it was! Steve Kuffler became one of the greatest neuroscientists of the world.

At the Institute we settled down to plan for the future. Steve quickly understood the technical procedures employed in the study of the nerve-muscle problem. However, he and I recognised that in Vienna he had had no biophysical training and no modern neuroscience. The scientific teaching had been most deficient in that great clinical centre, the University of Vienna.

I can remember giving Steve for a weekend study a just-published paper by Alan Hodgkin "The sub-threshold potentials in a crustacean nerve fibre". Steve arrived in on Monday deeply depressed, as he could not understand it. He wanted to give up neuroscience. I got the message and set about giving him a personal teaching course. It was in dissection that he displayed great skill.

I can still remember my flash of imagination that, if Steve could make by his superb skill in dissection an isolated nerve fibre-muscle fibre preparation, it would give him an enormous help into his future. He was enthusiastic to accept the challenge. We chose the very thin *sterno-cutaneous* muscle of the frog for the dissection. It was a tremendous task. He had a good binocular microscope and the finest surgical

207 Murphy, Richard James Francis (24.04.1875 – 13.11.1957) IE medical ethics lecturer at Sydney University.

208 Dollfuss, Engelbert (04.10.1892 – 25.07.1934) AT Austrian Chancellor, 1932-1934. Assassinated by Nazis.

instruments used for eye operations, but Steve made minute knives from cut-down safety razor blades mounted in glass tubes by sealing wax. He was completely dedicated to the challenge. However, we also worked together at least 2 days a week continuing on from the 1938 program. Then came the great success for Steve. Never before had anybody done such a dissection, as was shown in the microphotograph (Fig. A26A); furthermore, it could be mounted at an oil-saline interface for recording by special electrodes he had designed.

By dedicated and heroic work, he thus was able to create a preparation of a single nerve fibre innervating a single muscle fibre. He was successful in every one or two weeks, but one preparation gave new levels of understanding. A preliminary account was published in Nature in 1941, and then came several papers in the Journal of Neurophysiology - all by Steve alone.[A] It enabled Steve to carry out the most precise physiological and pharmacological work in the world on the neuromuscular junction. It was eventually superseded when Fatt[209] and Katz introduced intracellular microelectrode recording of the neuromuscular junction in 1950-1951, but that was almost a decade later. Fig. A26 shows the EPP almost as large as the later spike potential and the effect of progressive curarization with the all-or-nothing muscle spike eventually eliminated to reveal the full time-course of the EPP.

During 1939 Steve and I carried on from the studies of 1938 with John O'Connor. We had now perfected the technique of recording from the isolated *soleus* strip. Over 100 strips were prepared. Also, there were a few *peroneus tertius* strips with similar results. Of particular interest were the *soleus* strips in which a clear endplate potential preceded the muscle spike (Fig. A26). This strip preparation was exceptional, presumably because the nerve terminals to the strip were closely bunched. Steve and I studied the strip preparations in the attempt to understand the relation of the EPP to the muscle spike potential during all levels of curarization to complete neuromuscular blockage. We also had started to study the EPP at all stages of the muscle spike potential that could be set up by stimulation of the muscle strip remote from the innervated focus. Then came the arrival of Bernard Katz!

I had seen Katz at Physiological society meetings in 1936 and 1937, when he was a guest in A.V. Hill's Laboratory. In early 1937 I had asked Feldberg who would be the best of the refugees for me to try to get to Sydney. He said Katz was the best. To my surprise A.V. Hill approved of me inviting Katz, particularly because Katz had to get his parents out of Germany. Katz had not only a M.D. of Leipzig, but also a Ph.D. for his work on nerve stimulation in Gildemeister's department [University of Leipzig]. Then Gildemeister[210] advised Katz to go to A.V. Hill in 1935. There was a hope to get a Carnegie Fellowship [Carnegie Corporation of New York] for Katz to go to Australia for 2 years if I could guarantee a supplement to his Fellowship for the 2 years and a full support for a third year. I was able to negotiate with the Kanematsu Institute Committee

209 Fatt, Paul (13 01 1924 – 28 09 2014) UK(J) neurobiologist "quantal hypothesis" for neurotransmitters.

210 Gildemeister, Georg Eduard Martin (21.02.1876 – 18.110.1943) DE physiology professor/apparatus designer.

for £200 a year addition to give £750 a year and the full £800 for the third year. In those days that would be adequate for Katz with his mother and father. All these negotiations with Sydney and with the Carnegie Trust took much time and it was not till 1939 that Katz was appointed. Only then could there be the complicated arrangements, whereby his parents were allowed to leave Germany, book and pay for their travel to Australia and arrange to transport all their belongings by a cargo ship. It was really a most complicated operation. I have 20 letters and 3 cables from Katz before his departure from London with his parents.

Due to the extremely crowded schedule of the Society for Protection of Science and Learning in London in the application for a Carnegie Fellowship for Katz, there was a muddle. I was not told that I, at the Kanematsu Institute, had to make the application for the Fellowship. This was immediately done on Feb. 3rd 1939, my good friends Gasser, Gerard and Fulton acting as referees and on March 27th came the news of his appointment by cable. Only then could I proceed with the permissions for Katz and his parents to land in Australia. With the enormous number of applications Harold Ritchie of the Kanematsu and I had to act personally at Canberra. But there came a Cabinet crisis that caused a delay of several precious weeks. Only with these permissions could the advance bookings for ship travel be secured. Finally, all was cleared on June 5th and Katz and his mother and father left on Aug. 4th 1939 by a ship Belveran to Colombo, with transfer by the Cathay, getting to Sydney on Sept. 14th. All their furniture and possessions were sent from Hamburg on Aug.4th to arrive in Sydney on Sept. 24th. So, all arrangements seemed OK. However, war started when the Belveran arrived at Colombo and their transfer to the Cathay was cancelled when it was commandeered by the British navy! So, there was much more trouble for some weeks at Colombo, and more Canberra help from my old Magdalen College friend, John Hood[211], before they left Colombo on the Orient liner Oronsay [SS Oronsay; launched in 1924, sunk on 1942] on Sept. 24th and arrived in Sydney on Oct. 14th, when I was at Woolloomooloo Dock to welcome them.

After all this terrible stress we all needed some good luck! They had meanwhile correctly given up ever seeing all their possessions on the German ship Leuna [launched in 1928, sunk in 1942], so we looked at one of the furnished apartments I had discovered at Mosman; 3 Mosman Street, close to the Ferry wharf and also to where Stephen and I lived. It was the whole top floor of a nice old house in a garden. The two old owners lived below and insisted on quiet tenants, which was immediately evident with the Katz's, so all was fixed at the very low rental, I think of £3-10-0 a week. So, Bernard with his mother and father were excellently fixed up for the many years they were in Sydney – in fact until his parents left for London. So, the second flower to come to my original Academic wilderness involved enormous stress, but in the end, there was a wonderful flowering.

The Kuffler flower was a gift; in contrast the Katz flower was secured only with immense difficulty. The permanent research staff of the Kanematsu Institute was listed

211 Hood, John Douglas Lloyd (31.05.1904 – 03.10.1991) AU diplomat. Studied in Oxford under C. S. Lewis.

as Eccles, Katz and Kuffler for several years and Fig. A27a shows us three walking together in front of the GPO in 1940 on the way to lecture at the Physiology Department of the University. It was a uniquely successful staff, and we three were devoted friends for life.[B] Two of the three eventually received Nobel Prizes in part for the work done at the Kanematsu. Kuffler could have been selected with Hubel[212] and Wiesel[213] in 1981, had he not died inadvertently in 1980, but that is a later story.

AL. Focal endplates, frog *sartorius* & cat *soleus* (with Kuffler & Katz)

We had now excellent electrophysiological equipment in our conjoint efforts to do precise studies of the nerve-muscle junction. This was the synapse most accessible for the focal studies that I had already developed with John O'Connor, the strip *soleus* preparation (Fig. A24) and that showed the EPP in the curarized preparation (Fig. A25).

We could now show (Fig. A28A) EPP's of the cat *soleus* strip with a beautiful time course of fast rise to the summit in about 0.8 msec. and a subsequent exponential decay with a time constant of about 4.5 msec. With an uncurarized preparation it was sometimes possible to see the EPP preceding the generation of the muscle spike potential (Fig. A28B). Evidently there was a sharp focus of motor endplates immediately below the recording electrode. Often an initial EPP could be recognised, but not so well as in Fig. A28B. However, the preliminary EPP was well revealed in many preparations with transmission delayed by a weak curarization. Fig. A29 shows superimposed tracings of such a progressive curarization in the preparation of Fig. A28B, there being full curarization in the lowest trace with a pure EPP. Arrows mark the onset of the spike in the other traces. It is clearly shown that curare effects neuromuscular blockage by causing a large diminution of the EPP, which was about fourfold for blockage at all endplates. So, the safety factor for transmission would be 4. Curare acts solely by diminution of the EPP. It does not alter its time course, nor does it affect the excitability of the muscle fibres at the motor endplate.

The isolated frog *sartorius* was a valuable preparation because the nerve endings were often close together at about 10 mm from the pelvic end (Fig. A30 inset). In Fig. A30 the EPP's of the curarized frog *sartorius* were recorded at various distances from the pelvic end, there being a sharp focus at 11 mm, and electrotonic decline and slowing at successive millimetre shifts of the recording electrode in either direction. There was a spatial decrement to half in 0.9 mm from the endplate focus.[A]

In every respect the EPP behaves as a local potential set up by an electrical stimulus. It is generated at the endplate by a fast-depolarizing action that is largely over in about 0.8 msec. for the cat *soleus* and 2.3 msec. for the frog *sartorius* at 20°C. The EPP interacts with a muscle spike potential exactly as does a catelectrotonic potential.[B]

With the frog *sartorius* a second nerve volley sets up an EPP 80% to 100% larger at short intervals and declining to control in 0.1 sec. With the cat *soleus* the second EPP

212 Hubel, David Hunter (27.02.1926 – 22.09.2013) CA neurophysiologist. Studied visual cortex. (NP 1981).

213 Wiesel, Torsten Nils (03.06.1924-) SE neurophysiologist. Visual system information processing. (NP 1981).

was reduced to 80% and takes several seconds for recovery. These values give an indication of the time of replenishment of the transmitter.

The analysis of the action of a nerve impulse at a neuromuscular synapse has revealed that it exerts a single brief depolarizing action of about 1 msec. (cat) and 2.3 msec. (frog). The catelectrotonus so produced, the EPP, can be as large as 50% of a muscle spike potential, and in every respect, it is similar to the catelectrotonus produced by the action of a brief depolarizing current pulse. The action of curare in depressing neuromuscular transmission is in accord with its action in depressing the depolarizing action of acetylcholine. We therefore studied the effect of eserine on neuromuscular transmission because of its known action in inhibiting the action of cholinesterase, which inactivates ACh by hydrolysis of acetylcholine to acetic acid plus choline.[C]

The most direct test of the action of the anticholinesterase, eserine, is to apply it to a neuromuscular preparation that is deeply curarized. The superimposed tracing of Fig. A31A show that 1 in 100,000 eserine acts very early on the EPP, which continues its rising phase to a much-increased summit from which there is a delayed decline. This reveals precisely the anticipated action of cholinesterase (ChE) which acts almost immediately that the ACh is being liberated. Fig. A31B is for the cat *soleus* and is similar to Fig. A31A except that the curarization had to be deepened from ***i*** to ***ii*** in order to avoid the superposition of a muscle excitation when eserine was given. The figure with trace ***ii*** compared to trace ***i*** clearly shows that eserine resulted in the prolongation of the rising phase to a higher summit and the much slower decline of the EPP, all of which are in accord with acetylcholine as the transmitter. In the absence of curare, the muscle spike potential complicates the interpretation of the curare action, but it is displayed by a prolonged negative potential that supervenes after the spike potential for 100 msec. or more.

In summary of this focal endplate study, it can be stated that when a motor nerve impulse reaches the nerve terminal on a motor endplate (Fig. A23) there is liberated within 1 msec. a brief jet of ACh that depolarizes the motor endplate producing an EPP with a fast rise to a summit in 1 msec. and a slower exponential decay. Normally the EPP generates the discharge of an impulse travelling in both directions from the endplate and causing a muscle twitch contraction. Curare blocks the neuromuscular junction by reducing the effectiveness of ACh to depolarize the motor endplate. Eserine counteracts this blocking action of curare by reducing the very fast rate at which acetylcholinesterase hydrolyses the ACh. It thus increases the effective size of the liberated ACh jet. Finally, the liberated ACh, because of the eserine blockage of AChE, can linger to cause a delayed endplate depolarization that may last for seconds. As a new idea I would suggest that as with other transmitter sites this very slow effect is due to a metabotropic action (cf. Fig. A17B) on the motor endplate.

I attempted by lectures and reports to give some information about the research work of our group in the Kanematsu Institute. Nevertheless, as I learnt from Harold Ritchie and other favourable clinicians there was a group of clinicians with very limited understanding of medicine who thought our research was too esoteric and unlikely to have clinical value.[D] Their complete refutation is provided by modern anaesthesiology.

Its techniques for muscular relaxation during surgery are based on the physiology and pharmacology of neuromuscular transmission that we contributed to in those few years of the Kanematsu flowering in which we led the world.

AM. Election to a Fellowship of the Royal Society of London.

Sherrington told me in 1935 that he had submitted a Certificate nominating me for the Royal Society; with Dale as seconder, other supporting signatures being Adrian, A.V. Hill and Thomas Lewis. Year after year I was disappointed. I had left England for Australia in 1937 and I feared that I had been forgotten particularly in those terrible war years. Then came in March 194l the wonderful surprise of a Beam Wireless message "Heartiest congratulations Royal Society Election, Adrian". Immediately it was announced to the Sydney Press by Harold Ritchie. He had hoped, mistakenly as it turned out, that this would help me in my troubles with Sir Norman Paul[214]. For my friends it was a great occasion. The Lembergs, Katz, Kuffler, Baileys and many others gathered at our home, 14 Clanalpine St., Mosman. Katz has a good memory of this evening 50 years ago and that they all sang together "For he's a jolly good fellow". There was one minor embarrassment. Two other Australians had also been elected that same year, but did not hear till some days later because of the disordered communication in 1941. One was Sir David Rivett who was so kind and appreciative of me in my Chemistry exam in 1920. Actually this 1941 Royal Society election could be regarded as a Battle for Britain list. The list contained 17 names, including Winston Churchill, the two Rolls Royce engineers who were responsible for the Spitfire aeroplane engine, Watson-Watt[215] for Radar, Florey for Penicillin, Rivett for the Australian CSIRO, a British Admiral etc.

Now, 50 years later, my wife and I are being entertained in a celebration dinner at the Royal Society on Dec. l2th by Sir Michael Atiyah[216], the President of the Royal Society and the Officers of Royal Society. Also invited will be the wives of the Officers and a group of our friends including Sir Bernard Katz and Lady Katz.

I had been in 1938 elected as a Foundation Fellow of the Royal Australasian College of Physicians soon after my arrival in Sydney and often went to meetings in its most attractive Headquarters in Macquarie Street. So, I had some clinical recognition.

AN. Life in Sydney

In those years Sydney had the joy of an excellent orchestra that performed often in the Town Hall with George Szell[217] as conductor. Also, there were frequent recitals and chamber music concerts in the Conservatorium of Music in the Domain quite close to the Kanematsu Institute. In the Independent Theatre, North Sydney, there was a very

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214 Paul, Charles Norman (26.03.1883 – 25.05.1959) AU dermatologist. Sunlight effects. Cutaneous Neoplasms.

215 Watson-Watt, Robert Alexander (13.04.1892 – 05.12.1973) UK Scottish radar & direction-finding pioneer.

216 Atiyah, Michael Francis (22.04.1929 – 11.01.2019) UK/Lebanese mathematician (geometry).

217 Szell, Georg (07.06.1897 – 30.07.1970) HU(J), American orchestral conductor and composer.

good Repertory Theatre group as a frequent attraction. We often saw and knew personally an Austrian group of bare-foot dancers in the style of Isadora Duncan[218]. Associated with that group was Austrian sculptor Artur Fleischmann[219], introduced to us by Steve Kuffler. Later our son John at about 5 years old posed as a nude model for Fleischmann in his statue of child beauty in a memorial fountain that he created for the garden of Government House, Canberra. I hope it is still there.

A very interesting friend was the Rev. Alan Tory[220] of St. Stephens Presbyterian Church in 197 Macquarie Street. Alan had been a film producer in Los Angeles and later a theologian. He was dedicated to ecumenical Christianity, much to the embarrassment of many of the Church Elders, who acted as Pharisees. Alan was ahead of his time, and so was a most attractive friend. I once preached a sermon in St. Stephens, on science and religion and also helped him on discussion evenings. Eventually the recalcitrant Elders forced him to leave. I greatly appreciated Alan's caricatures of these Elders! I had given lectures to a Catholic religious group that were reported in a Catholic journal. They were of course rather advanced in their scientific character of presenting an evolutionary account of human origins, much as in my recent book[**A**] with its creation of the self as a divine mystery. The consequence was that I had to visit Cardinal Gilroy[221] for a reprimand. It was no use arguing. His early training was as a radio operator on a ship in the First [World] War. On his conversion he became renowned for his holiness with a rapid advance in Rome to be a Cardinal despite his inadequate education and intelligence![**B**]

My wife and I were intimately associated with a Dutch Catholic group, “The Grail” .[**C**] They believed in making religion a source of joy to the young. Though nuns, they wore attractive street clothes and fostered music, dancing and drama. We often visited their weekend religious festivals, and we taught for them Cecil Sharp[222] English Folk Dances that we had learned at Oxford. Steve Kuffler often came along and there he met Phyllis Shewcroft[223], a medical student, who he later in Spring 1943 married in St. Mary's Cathedral with me as the Best Man!

We had good holidays with the children at beautifully unspoiled beaches about 150 miles south of Sydney where we had rented apartments on the beach at Killalea, and there I was as free for cultural reading as I had been at Cornwall in the 1930's.[**D**]

Of course, the principal recreation was on our tennis court where Steve and I played every weekend. There we taught Bernard enough tennis so that he would be able to join a tennis club. It gave him a social life that he was so happy to have, and it was so

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218 Duncan, Angela Isadora (26.05.1877 – 14.09.1927) US dancer, focusing on natural movements.

219 Fleischmann, Arthur John (1896 – 02.03.1990) SK sculptor, lived in Australia from1939 to 1948.

220 Tory, Alan Percival (1904 – 1984) US evangelist/writer. Minister at St. Stephens Sept. 1939 to Mar. 1951.

221 Gilroy, Norman Thomas (22.01.1896 – 21.10.1977) AU the first Australian-born Catholic Church Cardinal.

222 Sharp, Cecil James (22.11.1859 – 23.06.1924) UK Started folk-song and country dance revival in England.

223 Shewcroft Kuffler, Phyllis May (1914 – 2003) AU, later educational psychologist/painter Woods Hole, US.

successful that he there met Rita Penly[224] to whom he became engaged. Later, on 27th October 1945 they married. I was told that it was in St. Mark's, Darling Point where there were many fashionable weddings and that Bernard and Rita were given a guard of honour by the RAAF. Bernard was an Officer.

I was fortunate to discover in Sydney my old Oxford friend John Flynn[225], in the same vintage (1925) of Rhodes Scholars. He was now a rich lawyer, and he and his wife often entertained us in their magnificent home that they had built together with a tennis court. Then I got to know his elder brother James Flynn[226] who was our ophthalmologist, and who, as a Surgeon Lieutenant Commander, consulted me about the sunburns of the retina that he detected in the gun crews of his ship (Australia) after the Dakar battle. So, we cooperated as described below.

But I should return to the Sydney life. The conditions were extremely attractive. Firstly, there were the ferry journeys each morning and evening. When we worked late, we had dinner at an Italian restaurant, the Florentine, that we knew well. Then there was the last rush down the Sydney streets to catch the last ferry at midnight. We never missed! Lunch was always very nice in this sunny warm climate. We brought sandwiches and fruit and had our favourite venue in the beautiful Botanic Gardens sitting in the grass with enjoyable talk. We three were the best of friends, though of course we argued scientifically. It was amazing how Steve had learned the theory of neuroscience. When Bernard arrived in 1939 and Steve had already succeeded with his unitary preparation, Bernard once remarked to me. "Though you and I, Jack, know so much more than Steve, yet he is doing the best science". I was happy to hear this well-deserved recognition. So, our intimate association of "The Three Musketeers", as we were called, continued on for three years until Hitler invaded Russia and Katz became "a friendly alien". He immediately enlisted and was accepted to study to be a Radar expert.

My religious interests brought me into contact with Charles Birch[227] of Wesley College and of the Department of Biological Sciences, University of Sydney. Like me he was dedicated to a reconciliation of Science and Religion. We had much in common, but Charles was more dedicated to Whitehead[228] and Charles Hartshorne[229]. I was at that time an orthodox Catholic dedicated to an openness in religion and in philosophy. In particular I could not accept the Panpsychism that Charles Birch seemed to espouse in his philosophy in which he was similar to Rensch[230].**E** However, in later years Birch became more sophisticated in his religious philosophy and was this year very worthily

224 Penly Katz, Marguerite "Rita" (1921 – 1999).AU Aust. Broadcasting Corp. Children's program overseer.

225 Flynn, Victor John (01.1904 – 1962) AU Sydney solicitor, also in Australian Institute of Political Science.

226 Flynn, James Aloysius Foedus (30.05.1899 – 15.07.1969) AU ophthalmic surgeon. "Photo retinitis".

227 Birch, Louis Charles (08.02.1918 – 19.12.2009) AU Theologian/Geneticist. "Population ecology".

228 Whitehead, Alfred North (15.02.1861 – 30.12.1947) UK mathematician/philosopher. "Process & reality".

229 Hartshorne, Charles (05.06.1897 – 09.09.2000) US philosopher. Religion & metaphysics. "Process theology".

230 Rensch, Bernhard (21.01.1900 – 04.04.1990) DE evolution biologist/ornithologist. Ethology, "Superspecies".

honoured by the award of the Templeton Prize. I regret that we have not been more closely associated since the Sydney period.

During the war years at Sydney, I became more closely associated with Eric Ashby, who was dedicated to bring science into the many problems that were completely misunderstood by the military officials. He had many good stories of the way they were fighting this war with the mentality of the last war. I was much helped as I shall describe in a later section on photo-retinitis by Dr. Briggs[231] of the Physics Department of the University. Also V.A. Bailey of Physics was a good friend. His associate, Les Wirsu helped us very much in electronic design. At that time the newly appointed Professor of Physics. Harry Messel[232], became a dedicated propagandist for physics, often to an extreme degree in his effort to get industrialists to give money. However, his science was inadequate. For example, later he was never elected a Fellow of the Academy. The best joke about his excessive publicity was a slogan "Empty Messels make the most sound".[F]

AO. Additional research with clinical applications

I was mindful that my responsibility in a hospital position was to devote some of my efforts to do science that was clearly related to clinical problems.

1. Muscle atrophy from disuse!

Patients immobilized in bed for long periods suffer muscle atrophy as a troublesome complication. I attempted to discover how much stimulation should a physiotherapist give in order to prevent the atrophy, which one assumed was due to disuse. It should be possible to cause complete inactivity in the hind limb of a cat by section of the spinal cord in the upper lumbar region and of all the dorsal roots below the section. This was accomplished aseptically under anaesthesia in the special operating room that had been constructed. With careful nursing by my technician Chapman from Oxford the animals remained in good condition for many weeks, but the muscle atrophied to less than 60% and still more in their contraction strengths. An attempt was made to counteract the atrophy by daily tetanic stimulation of the muscle nerve. A wide range of stimulus durations was chosen. It was unexpected to find that 10 seconds was as effective as 2 hours a day. The stimulation was applied intermittently, 10 seconds on, 10 seconds off, with the muscle kept in a normal position. With flexor leg muscles, *tibialis anticus* and *extensor digitorum longus* the atrophy was almost prevented, but with the extensor muscles, *gastrocnemius* and *soleus*, there was much less maintenance of the muscle weight. Unfortunately, with all muscles the stimulation procedure did little to improve the contraction. It was later found that the best results were obtained when the stimulated muscle was free to contract, but even then, the contraction power could only be maintained at about 80%. Nevertheless, these results can serve to guide physiotherapists and were fully published in the Journal of Physiology

2. Muscle atrophy and weakness due to Tenotomy.

231 Briggs, George Henry (23.03.1893 – 24.07.1987) AU physics prof. Radioactivity & measurement precision.

232 Messel, Harry (03.03.1922 – 08.07.2015) CA Physics professor 1952-1987. “International Science School”.

A related problem was the atrophy of a tenotomised muscle. As might have been anticipated the atrophy is largely controlled when the muscle is prevented from shortening. The other explanations that have been proposed, underactivity or overactivity of the nerve supply are rejected on experimental testing. So surgical treatment of tendon repair to prevent muscle shortening is indicated.[A]

3. Muscle degeneration after nerve section.

Kuffler carried out exquisite studies on the acetylcholine sensitivity of muscle fibres and the endplates during the degeneration caused by nerve section. Kuffler also investigated tetany in relation to the ionized calcium in the blood stream after parathyroidectomy. Kuffler was later joined by an American neurologist, Major A. M. Harvey[233], who had studied under Sir Henry Dale and who was now in the American war hospital in Sydney. They carried out investigations on muscle and nerve war-time injuries using the excellent electrophysiological and pharmacological testing procedures at the Kanematsu Institute. After the war Mac Harvey became Director of Neurology of the Johns Hopkins Medical School, and that led to a future of Kuffler in US.

As a contribution to medical education, I arranged with Dr. Cotton of the Physiology Department to give each year a short course of lectures to the Medical School. In 1938 I gave six lectures to the third-year medical students on the general physiology of nerve and muscle and two lectures to the fourth-year students on the pathology of neuromuscular transmission. There were two medical students doing a BSc in Physiology and they spent several weeks at the Kanematsu Institute learning about research. In 1939 I repeated the six lectures course to the third-year medical students. In 1940 Dr. Katz and I each gave 4 lectures to the third-year medical students. A street photographer took our picture outside the GPO on the way to the tram to the University. (Fig. A27a). Steve picked up the ticket, but characteristically did not tell us that he collected the photograph. More than 30 years later my wife detected this photograph on the top of his bookshelf in his Harvard office and he admitted his guilt! This photograph has been often reproduced and in 1972 we three were photographed again during the Meeting at Oxford, displaying the effect of time (Fig. A27b).

Unfortunately, on that day in 1940 a group of students interrupted my lecture by loudly proclaiming continuously "We want notes". It was the custom of the lecturing staff to give typed notes for each lecture. Student attendance at the lecture was compulsory and they did not have to concentrate by taking notes, but at each lecture got copies for mugging up for the exams. My lectures were not in the exams course, and I have never given out notes. Students have to concentrate with notes and drawings as was done at Oxford. Anyway, for these honorary lectures I had refused the task of writing lectures and having them typed and reproduced. I was amazed that Prof. Cotton sitting in the front row timidly made no attempt to keep order, so Katz and I just walked off and we never returned to the Physiology Department to lecture. However, as a gesture to the interested students each year up to 1943 I gave four lectures in the

233 Harvey, Abner McGehee (30.07.1911 – 08.05.1998) US physician. At Hopkins 18th General Hosp. in WWII.

Kanematsu Institute and following each lecture Drs. Katz and Kuffler gave demonstrations and discussions in the research rooms. About 50 students came to each occasion and behaved very well. This number was as many as we could accommodate.

AP. War-time work in the Kanematsu Institute

1. Blood Serum Preparation was carried out (1941 onwards) in four rooms of the Kanematsu Institute under Red Cross direction. As the Pacific war intensified there were in an adjacent Hospital ward up to 1400 bleedings a week, each of one litre. In the Institute I was responsible for the preparation of blood serum from the blood plasma delivered in 18 litre glass containers. It was a tricky task that I had learned, to get the fibrin wound around the central glass tube. Later we designed and had made a machine to do this. Bob Walsh[234] was a military doctor working for the Red Cross. Bob was excellent and he, Prof. Hugh Ward[235] of Bacteriology and I in the evenings did the aseptic operation of transferring the serum into 1 litre bottles for storage and then, as needed, for dispatch to hospitals in the war zones. So, we spent two nights a week bottling up to 700 litres a night.[A] The serum we processed amounted to 80% of the total requirements for the whole Pacific war, including the US forces. Bob Walsh became a world authority on blood groups in all the diverse peoples of the South Pacific. It was a most friendly arrangement in the Kanematsu with Dr. Helen Tooth[236] of the Hospital resident staff providing a luscious supper in her gracious style. She eventually became Mrs Walsh!

2. Katz and Radar. When the Nazi invasion caused Russia to extend the war, Dr. Bernard Katz managed to secure the status of a friendly alien. His father was a Czarist Russian. So, he enlisted in the R. A. A. F. at the beginning of 1942 and was on active service continuously until the end of the war. He was trained in the secrets of Radar. It was an extensive course with testing examinations for the class of physicists, radio engineers and electronics engineers. Bernard told us of his embarrassment every time the exam marks were posted. He, as an M.D. and Ph.D. in Biophysics, was always in the 80's, but none of the physicists and engineers ever got above the 60's! So, they developed a song at each posting: "Katz up in the belfry".[B]

Then with an associate army officer he commanded a group of 75 Australians on Goodenough Island, North of New Guinea and behind the Japanese lines. He wisely took with him a duplicate of all the Radar equipment; so, in that tropical moisture he was never "off the air" in the 10 months he was there. So, he was relieved of his duties at a fixed station to be a travelling service expert to keep in working condition all the Radar stations in the north. So, Katz on leave of absence from the Kanematsu Institute performed well for Australia, becoming an officer of the RAAF.

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234 Walsh, Robert John (03.01.1917 – 20.07.1983) US Prof. Human Genetics. "Blood Transfusion Service".

235 Ward, Hugh Kingsley (17.09.1887 – 22.11.1972) AU. Prof. Bacteriology at Sydney Hospital 1935-1952.

236 Tooth, Kathleen Helen (27.08.1916 –19??) GB Medical Superintendent at the Sydney Hospital 1940-1943.

3. From 1941 onwards, I was a member of the Armoured Fighting Vehicle Committee and the Flying Personnel Research Committee and Chairman of the Vision-Lighting and the Noise-Hearing Intercommunication, Air-Sickness Subcommittees. Most of my time has been spent on work that has been published in secret documents. Archie McIntyre carried out the main duties as he was now a Military officer. He acted as an excellent associate in working on a multitude of problems arising in vision, hearing, noise and communication in tanks and aeroplanes in maximum activity. It was a most valuable cooperation

4. In 1942 there was constructed with a grant of £2,500 from the National Health and Medical Research Council a special Acoustic Testing Laboratory on the roof of the Kanematsu Institute under the direction of N.E. Murray[237], an expert telephone engineer and a most dedicated performer. All communication equipment for tanks and planes in the Australian Army was tested there, with medical students as unpaid volunteers. Their task was to recognise communications in combat conditions with the noise level up to 120 db. Protective coverings for the ears gave them maximum acoustic advantage.

5. Sunburns of the Retina (with Surgeon Lieutenant Commander James Flynn) When looking into the sun, anti-aircraft spotters may suffer from scotoma due to burning of the retina by the sun's image. By means of animal experiments the heat intensity of the image just required to burn has been determined. It has further been shown that the whole effect can be explained as a thermal lesion, and the pathology of this condition has been studied in serial sections through the burnt areas. From these experiments the degree of dark-glass protection required for spotters has been determined. All tests were carried out on anaesthetized rabbits on the roof of the Kanematsu Institute in 1942 and with the scientific advice of Dr. G.H. Briggs of the National Standard Laboratory, Sydney University. There was immediate use of the results by Dr. Flynn in the redesign of Australian protective goggles. I was surprised to hear from Dr. H.F. Blum[238] of Berkeley when I met him in February 1946 that our secret report was the basis for the redesign of American protective goggles in the latter part of the war. After a considerable interval, Dr Flynn and I published our results in the Medical Journal of Australia on April 15th 1944.[C] At the end of this section, I would like to pay tribute to all who participated in this war-time work. I have never had the pleasure to work with such dedicated people, and with skills to match their dedication.

AQ. Synaptic transmission in a stellate ganglion

I have already mentioned that towards the end of my Oxford period I recognised that the stellate ganglion as investigated by Bronk[239] and associates,[A] was a simpler sympathetic ganglion to investigate, but more inconvenient for access.[B] It did not have

237 Murray, N. E. (?-1972) AU? University of Sydney engineer. Head of National Acoustic Laboratories,

238 Blum, Harold Francis (12.02.1899 – 29.09.1980) US physiologist. "Time's Arrow and Evolution".

239 Bronk, Detlev Wulf (13.08.1897 – 17.11.1975) US Biophysicist. President Johns Hopkins University.

the complexity of the diverse inputs to the cervical ganglion. So, in the periods of freedom from war activity I was able to return to the sympathetic ganglion studies on the stellate, while Katz and Kuffler were working on other projects. Fig. A18 shows the manner of mounting the stellate for optimal recording of the responses to preganglionic inputs, as in Fig. A32A, where in (***i***) there is the initial diphasic spike with a large prolonged positive after-potential and in (***ii***) the block of all discharge by curarization left only the slow synaptic potential with a fast, rising phase and a very-slow, approximately exponential decline.

Fig. A32B and Fig. A32C illustrate the responses to two maximal stimuli at varying intervals. There is very good summation of synaptic potentials resembling that for the neuromuscular junction, and in Fig. A32C at a less curarization the summation gives a small spike potential. In these respects, the stellate ganglion is rather similar to the curarized neuromuscular synapses of frog or cat (Fig. A25). However, the stellate synaptic potentials are very different from the EPP's in the reaction to the anticholinesterase, eserine. Often doses as high as 6 mg/kg of eserine had no significant effect on the synaptic potential evoked by a single presynaptic volley (Fig. A33A). This finding corresponds to the usual finding on the superior cervical ganglion. Fig. A33B illustrates the largest effect, which is in contrast with Fig. A31A and Fig. A31B. So, there is confirmation of the original study of the SCG that led to my rejection of ACh as the transmitter for the fast component (Section **AA**).

In Fig. A33B, analysis of the synaptic potentials on the basis of the observed exponential decay of the curarized synaptic potential (Hill's focal potential theory) suggests that it is produced by a fast, depolarizing action of about 10 msec. duration followed by a small slow action that is increased with full eserinization, the dotted line. Correspondingly the synaptic potential shows a delayed summit and later slowed decline.

With repetitive preganglionic stimulation there is very effective summation of the slow phase of the synaptic potential, which may persist for as long as 300 msec. and be associated with after-discharges.

When eserine inactivates the AChE that hydrolyses ACh, there are the expected great increases in the slow responses generated by repetitive stimulation and which can be assumed to be due to ACh. In the uncurarized ganglion after a preganglionic tetanus of 20 to 50 impulses the after-discharge may persist for as long as 10 seconds. There are correspondingly long durations of the synaptic potential of the curarized ganglion.

All of the findings on the long duration of synaptic actions are in good accord with the acetylcholine hypothesis. The theoretical uncertainty arises solely on account of the fast component of the synaptic transmission (Fig. A33). How can this very brief duration of the transmitter be accounted for if it is due to ACh, and that still remains brief even when AChE is inactivated by eserine (Fig. A33A). The simplest hypothesis is that the fast component is due to electrical stimulation by the preganglionic action potentials, the slow being due to ACh. Alternatively, in a unitary hypothesis it could be postulated that ACh is also responsible for the fast synaptic transmission, and that the ACh is liberated focally and in such an intimate relation to the receptor sites that rapid removal is by diffusion. Diffusion carries it to the more remote ACh receptors in relationship to the AChE sites where eserine exerts its action.

Evidently, most refined electron microscopy is called for in investigating such an attempt to reconcile ACh transmission with an initial fast phase virtually uninfluenced by eserine. With neuromuscular transmission there is no such problem since eserine very effectively increased and prolonged the fast phase (Fig. A31A, Fig. A31B). Hence electrical transmission was discarded in the 1942 Eccles, Katz and Kuffler paper.

I am happy with these two stellate ganglion papers that brought my Kanematsu scientific life to a close. There were magnificent studies of the slow transmitter action of ACh, but there still remained the enigmatic fast transmitter action. So electrical synaptic transmission remained as a tenable hypothesis for the fast component of a dual action. Such a dual action was particularly attractive for synapses in a simple part of the central nervous system, the spinal cord, which will now dominate my story for the many years after I had left the Kanematsu for Dunedin.[C] The stellate ganglion study was a good return for neuromuscular transmission to synaptic transmission in the central nervous system.

AR. Devastation by Sir Norman Paul.

(President of the Sydney Hospital & Chairman of the Kanematsu Advisory Committee)

Conditions had become difficult when Paul had succeeded Mr. John Travers at the end of 1938. Paul was an Honorary Dermatologist when I arrived, and was wealthy with political ambitions. He secured a knighthood, presumably with the wealth of the Paul family. His father was the owner of a big chain butchery - Paul's Butchery - being advertised everywhere in Sydney. Unfortunately, as it turned out, Sir Norman Paul's political ambitions were linked with ignorance and stupidity. He repeatedly declared in public and private that Medical Practice did not need more research. Enough Medical Science was known. Public Hospitals should concentrate on providing medical treatment for the sick poor and abandon research! It was a most discouraging atmosphere, but I hoped that I could bear with it, and that we would achieve recognition because of the great scientific successes of the Kanematsu Institute with its international reputation and my FRS. I was confident that our war effort would be recognised by most of the hospital staff. Each year I produced a report of the scientific research and other clinical activities that were being done, as well as the lists of publications. I assumed that these reports were sent by the Hospital to all the Honorary Staff. This report gave also a brief account of all the war-oriented Activities as I have described above as extracts from the reports.

However, Paul was opposed to war-oriented activity in the Kanematsu even when Australia was desperately involved in the war. He was opposed to the blood serum production being done in the Kanematsu Institute, though it did not interfere in any way with the clinical activity of the Kanematsu Institute. Necessarily my research did suffer by all the war-related activities I have described, but that was of no concern to Paul. He particularly disliked the Acoustic Testing Laboratory and managed eventually to get it shifted to the University. I told Kellaway of my trouble and in his witty way (letter of July 20th, 1943) said I needed a motto "*Nihil bastardi carborundum*", which he translated as "Don't let the bastards wear you down"![A]

The crisis came unexpectedly a few days later when I heard from my technicians that Paul with Hospital Board Officials came into the Institute while I had been away one day on war work. They were accompanied by architects who had plans and took measurements. I had been told nothing, but immediately there was a Hospital Board meeting that agreed to a plan to build on top of my Institute (Fig. 2l) two further levels for housing the Hospital residents. I had enquired on arrival in 1937 about the possibility of adding to the building and found out that it had been built with all provisions for adding two more floors. It was a most valuable facility for expansion when I needed it. This last indignity by Paul was confirmed by the Secretary of the Hospital. It was more than I could stand.

Apparently, Paul knew of my future plans eventually to extend the research facilities of the Kanematsu. Not only would he block that by his move, but would deteriorate the Kanematsu from its academic peace by having 20 or so residents using the elevator and staircase all hours of day and night. I was never told anything! He planned this take-over without informing me. It was his way of deteriorating[B] me and the medical research staff of the Kanematsu.

I could have stayed on at the Kanematsu and challenged Paul. But he was rich and powerful and most of the Honorary staff of the Hospital also did not care about Medical Research. That reflected the failure of the Medical School at that time. I would have had to fight the Sydney Hospital Board politically. Instead, I chose to leave as soon as I could secure a good opportunity for my future. I have done this repeatedly in my life as I now dispassionately survey it. There were several occasions where I left without a fight, as told in this autobiography. Countless precious hours of my life were saved by my departure to build a scientific life elsewhere. I have always chosen science, truth and values in my life-long struggle against political fighting, skulduggery and evil. I am not by nature aggressive. On the contrary, my life has been dedicated to love and not to hatred. I have struggled all my life in the quest for truth. The subsequent story of Paul and the Kanematsu showed how wise I was to leave without a fight.

When I left, Alan Canny[240] was appointed as Director of the Kanematsu Institute, but he suffered from Paul just as I had done. Finally, in April 1946 Paul closed down all research in the Kanematsu Institute firing all the research staff. Drs Alan Canny and Vickers[241], Director and Assistant director of the Kanematsu, resigned forthwith, even though they had no job to go to. I already had a position to go to when I resigned! There was full publicity in the Medical Journal of Australia[C] and Sydney Newspapers, to which I also wrote. An appropriate heading for the newspapers would be "Paul's Butchery"!

240 Canny, Alan Joseph (1903 – 25.09.1963) AU later pathology Professor, University of Queensland, Brisbane.

241 Vickers, Thomas Henry (?-?) AU also later pathology lecturer, University of Queensland, Brisbane.

AS. The ultimate fate of the Kanematsu Institute.

I was emotionally dedicated to the Kanematsu Institute which I hoped to develop into a world class Institute when the war was over. I was confident that neuroscience would enter into a limitless future, with the new technical advances as with electronics. What I did later in Dunedin and Canberra could optimistically have been accomplished in Sydney. As I am writing this section, I have the advantage of a well-informed history of the Kanematsu Institute by Prof. F.C. Courtice[242], Director 1948-1958, in Historical records of Australian Science (December 1985).

After the tragic closure of the research activities of the Kanematsu Institute on 1st April 1946 that evoked Canny's resignation, there was public concern, and reactions thereto by the Hospital Board and the Hospitals Commission. Eventually after 2 years the *status quo* of the Kanematsu Institute was restored and Dr. F.C. Courtice of Oxford University Physiology Department was elected as Director. However, on arrival in 1948 he was immediately confronted by the same Hospital Board decision that led to my resignation in 1943. There was to be construction of two floors on top of the Institute for an Institute of cancer research! He immediately recognised that his future expansion would be blocked, so three days after arrival he decided to resign and return to Oxford! I learnt from him a new name for Sir Norman Paul - Subnormal Paul! Eventually it was all fixed up and he remained as Director for 10 years, carrying out research on the lymphatic system which appeared to be more clinically oriented than was the case under my Directorship. That was a good period of the Kanematsu Institute, but thereafter there was a slow decline of fundamental research from 1958 onwards.

There were conflicting demands for clinical research as against fundamental research, which was the principle originally proposed by Professor Inglis in 1934 and that eventually lead to my appointment in 1937. Professor Inglis continued to stress that fundamental research should predominate in the work of the Kanematsu Institute. But the forces for "clinical research" were too strong and he collapsed and died in his final efforts during a Hospital Board meeting, in January 1960.

So "clinical research" was in the ascendency with the eventual creation of a number of clinical units with special technical facilities. It was dedicated to technical innovations, not clinical research so I put it in inverted commas! Amazingly, three more floors were now added to the Kanematsu Institute for accommodating teaching facilities for the clinical professors of Sydney University, two in 1964, one in 1970.[A] The Kanematsu Institute had finally become orientated towards facilities for clinical investigation and medical teaching. The principle of fundamental research died with Inglis in 1960. Though I was in Canberra up to 1965 I did not once visit the Kanematsu Institute after the Courtice period. Eventually in 1982, Sydney Hospital was moved to a large teaching hospital associated with a new medical school at the University of New South Wales. A 100-bed emergency hospital remained in the city, but most of the original Sydney Hospital and the Kanematsu Institute (Fig. A21) were demolished in

242 Courtice, Frederick Colin (26.03.1911 – 29.02.1992) AU medical scientist; Kanematsu director 1948-1958.

some architectural extravaganza to restore the area to its pre-1900 state! But all that has been done since 1982 has been demolition. That fine Kanematsu Institute (Fig. A21) remains as a hole in the ground.[B] There remains nothing substantial to commemorate Fusajiro Kanematsu, though two different investigating groups use the name Kanematsu. My good friend Keith Inglis remains just a memory of a lost cause, though there are occasional memorial lectures.

We can ask why was his advocacy of fundamental research a lost cause in Sydney right up to 1960? The answer I will give is that the teaching in the Medical School was so poor in such basic disciplines as Biochemistry and Physiology. Generation after generation of medical graduates had no concept of the insights given by fundamental research into the new advances in clinical medicine. In my time this ignorance was dominant in the honorary staff, particularly in the younger groups. The two senior honoraries, Harold Ritchie and George Bell[243] and also Ken Noad[244] were my good friends and understood what we were trying to do in the Kanematsu Institute, but most of the Hospital staff were indifferent or critical. They did not object to Paul's nefarious operations. This did not happen in Melbourne where the Hall Institute under Kellaway developed into the magnificent research institute it now is, but it had a controlling committee quite separate from the Hospital.[C]

I left Sydney Hospital without even a courtesy farewell from the Hospital Board. However, in 1970 as an extremely belated gesture the Hospital Board appointed Katz and me as honorary neurophysiologists of Sydney Hospital! Inexplicably Kuffler was left out!

My criticisms of course are not of the Sydney medical students. In the post-war years the Medical Schools of Sydney University and of the newly founded University of New South Wales developed into good teaching and research institutions with world recognition. But this was too late for the Inglis principle of fundamental research for the Kanematsu Institute.

As I have already mentioned, Katz, Kuffler and I gave lectures and demonstrations to the medical students for several years, but we had no support from Sydney University. By far the worst tragedy was in Biochemistry, where the best biochemist in Australia, Dr. Rudolph Lemberg, FRS, directed a small hospital laboratory at the North Shore Hospital in Sydney. He was never invited to lecture and was not even given an Honorary position in the University. So, for 20 years medical students of Sydney University lacked modern biochemistry.

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243 Bell, George (10.07.1882 – 22.08.1970) AU visiting surgeon Sydney Hospital 1921-42. "Flying Doctor".

244 Noad, Kenneth Beeson "Bob" (25.03.1900 – 24.05.1987) AU Sydney Hospital physician and neurologist.

STAGE 3: – Figs. A21-A33

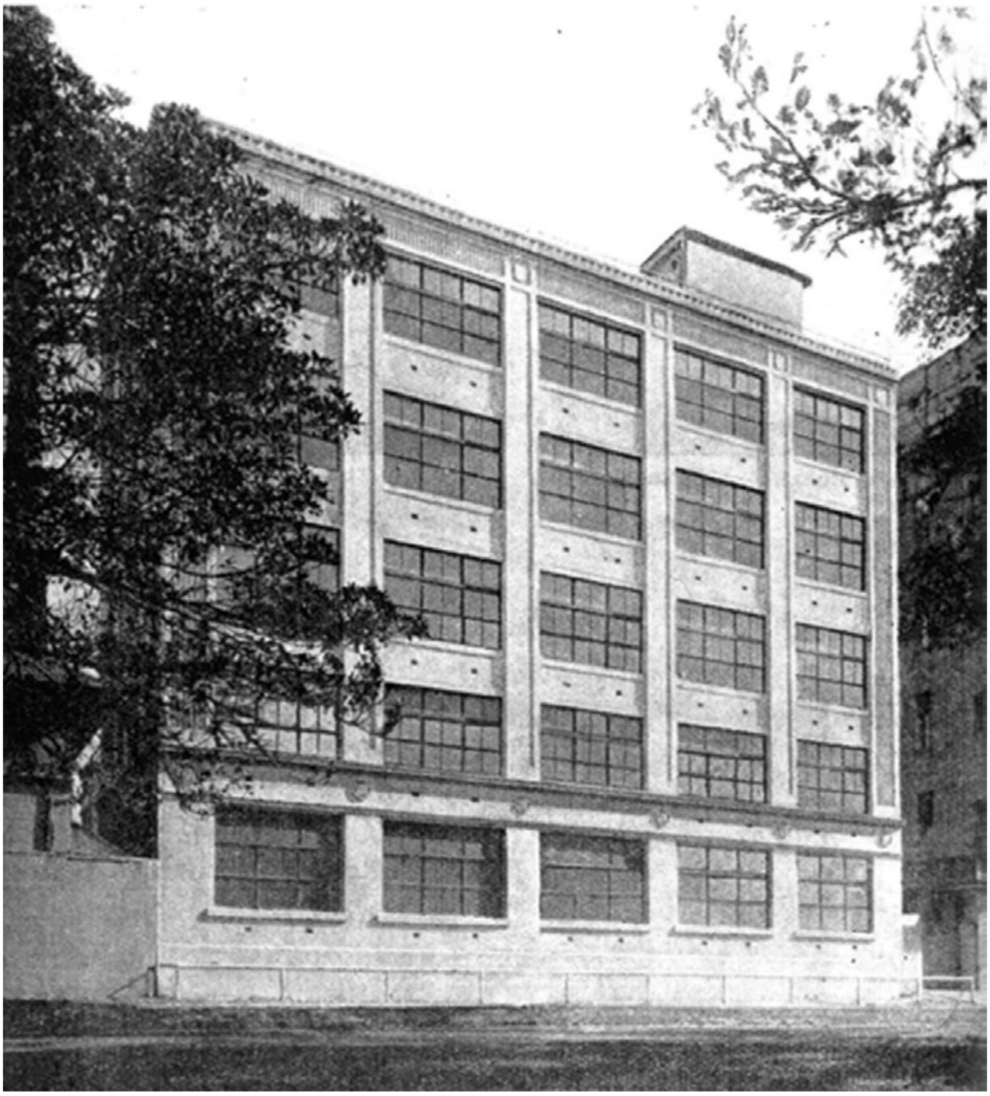

Fig. A21. The Kanematsu building at Sydney University in the 1930s. [AH, AS]

Eccles and his research group at the Kanematsu Institute occupied the complete top floor between 1937 and 1943. On the otherwise undeveloped roof area can be seen Eccles' small-animal room at the right-hand side.
From Winton[245] 1997.

245 Winton, Ronald Richmond (04.04.1913 – 13.02.2004) AU Medical doctor. Editor of Medical J. Australia.

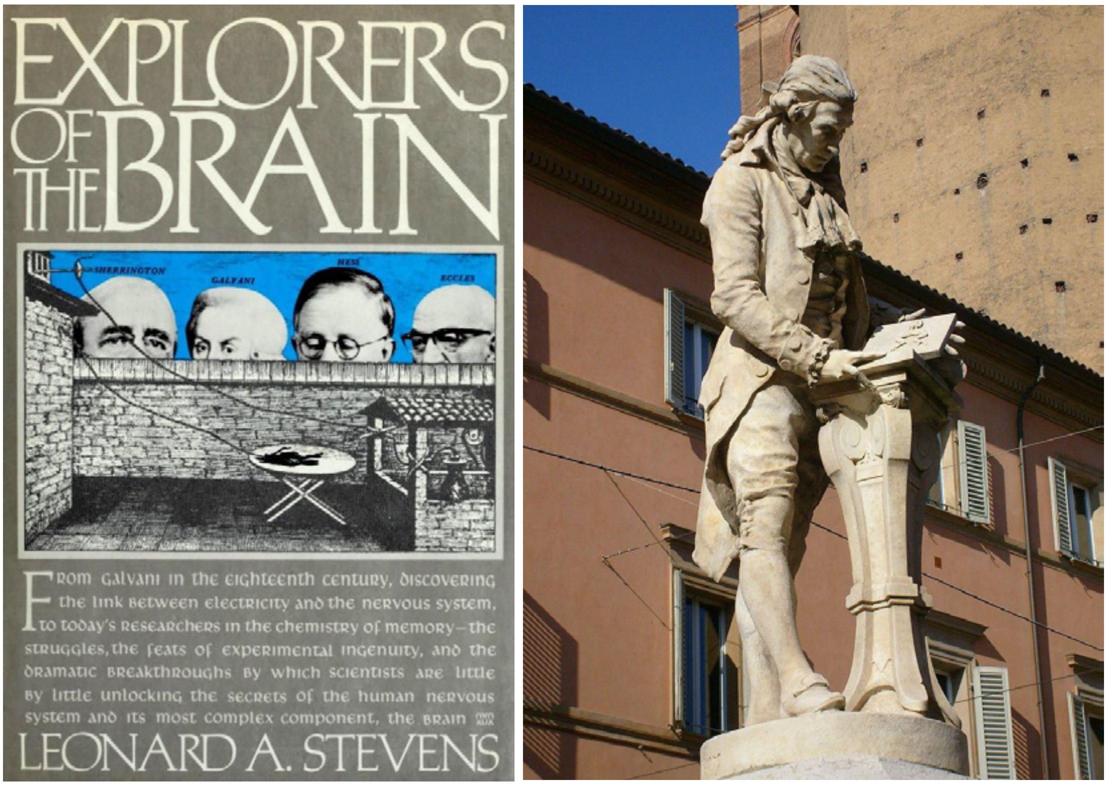

Fig. A22. John Eccles and Luigi Galvani associated together. [AJ]

Left. Book dust jacket showing upper-face images of C.S. Sherrington, L. Galvani, W.R. Hess[246] & J.C. Eccles.
From Stevens, Leonard A (1971) *Explorers of the Brain*.

Right. Luigi Galvani statue in Bologna, Italy
(1879 by Adalberto Confetti (20.06.1847 – 4.11.1907).
From photo by Luca Borghi in:
https://commons.wikimedia.org/wiki/File:Luigi_Galvani%27s_monument_in_Bologna_2.JPG

246 Hess, Walter Rudolf (17.03.1881 – 12.08.1973) CH Zürich Neurophysiologist. (NP 1949).

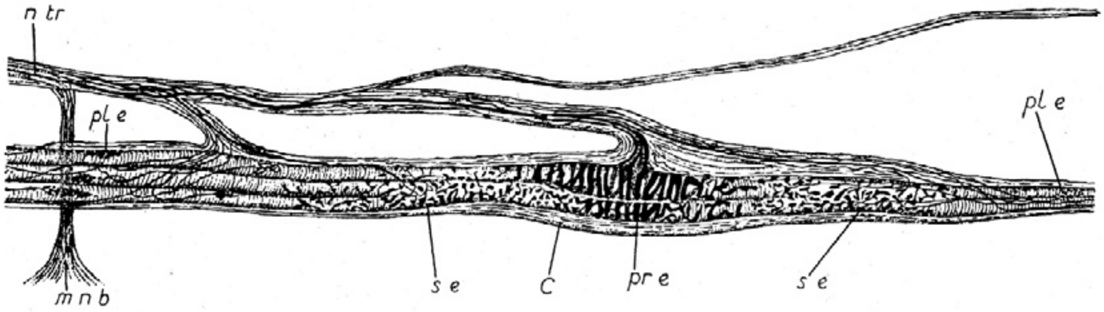

Fig. A23. Light Microscopical knowledge of the muscle-spindle in adult cat. [AJ, AL]

C, capsule, which has come in contact with intrafusal muscle-fibres owing to dehydration of peri-axial lymph-space by glycerine used in teasing preparation; ***n tr***, nerve trunk; ***m n b***, motor-nerve bundle, ending exclusively in motor-endplates ***pl e***, in muscle-fibres; ***pr e***, primary ending of afferent fibre; ***s e***, secondary endings. After the original diagram by Ruffini, (1898). From Creed et al. (1932) [1B-a01], p. 161, fig. 68.

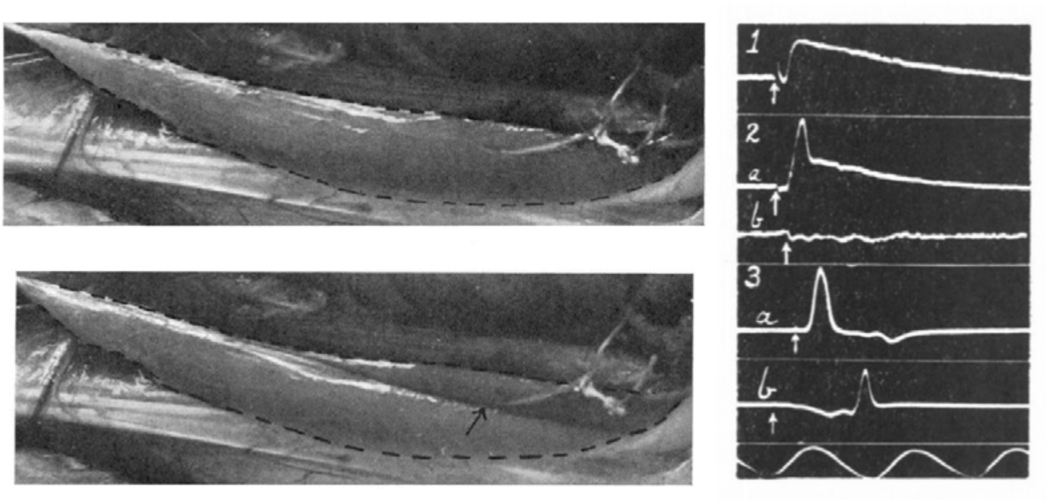

Fig. A24. *Soleus* preparation with innervation restricted to a superficial strip. [AJ, AL]

In the **left-hand lower** image, the *soleus* strip is contracting (cf. resting condition shown in the **left-hand upper** image) in response to maximal tetanic stimulation of the motor nerve through the electrodes seen on its right. The arrow indicates the approximate position of the endplates on the strip. Distortion of the tissues is much less with contractions evoked by single or double stimuli.

From Eccles & O'Connor (1939) [1A-058], p. 48, fig. 2.

In the **right-hand** picture, ***1***, shows the effect of full curarization on the endplate potential, ***2a***. less curarization, ***3a*** & ***3b***, no curarization [see Fig. A25 for more details].

From Eccles & O'Connor (1938) [1A-053], p. 10P, fig. 1, fig 2a&b, fig. 3a&b.

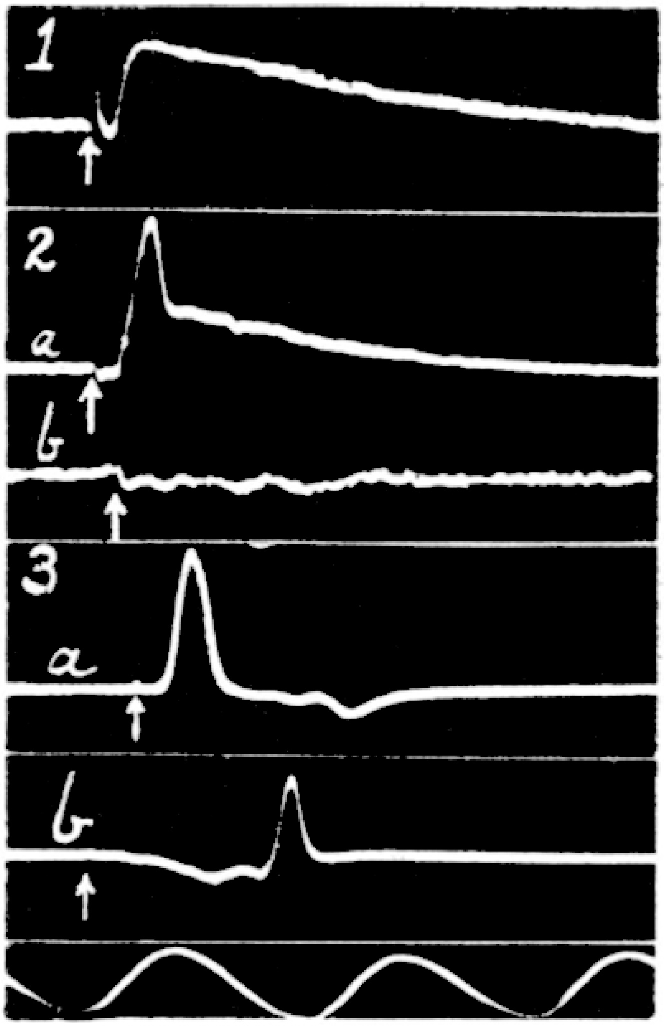

Fig. A25. Effect of curare on the motor endplate response. [AJ, AL, AQ, BE]

Trace ***1***: Full curarization, showing the slow wave alone. Amplification 50 times that of trace ***3a***.

Traces ***2***: Less curarization, showing (**a**) the spike response at the endplates; (***b***) no potential at 2 cm from the endplates. No contraction. Amplification of trace (**a**) 25 times that of trace ***3a***; (**b**) 75 times that of trace **3a**.

Traces (**3a**) and (**3b**): Corresponding records, before curarization.

Bottom trace (sine-wave timer); Time=10 msec.

From Eccles & O'Connor (1938) [1A-053], p. 10P, fig. 1, figs. 2a&b, figs. 3a&b, sine wave.

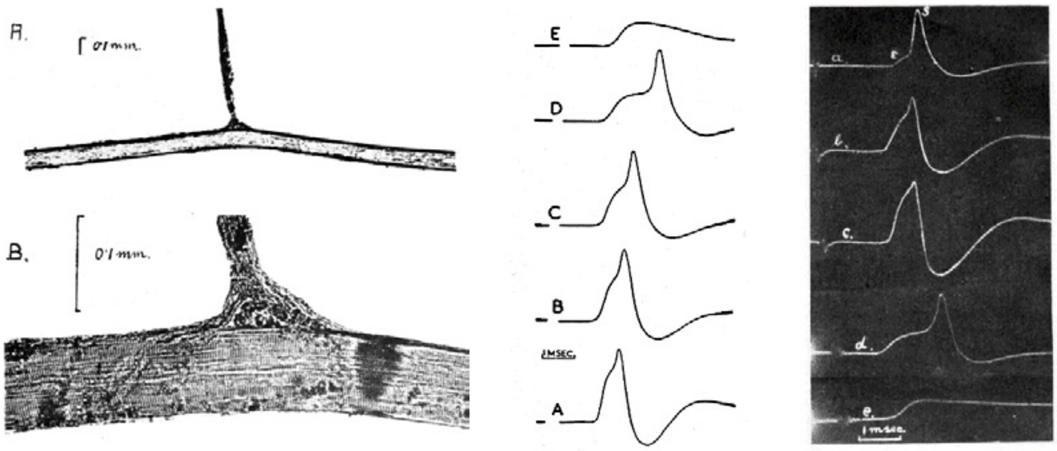

Fig. A26. Steve Kuffler's isolated nerve-fibre/muscle-fibre preparation. [AK]

Left A & B: photomicrographs of his preparation at low and higher magnification. Dark area to the right of the nerve entry is a small air bubble.
From Kuffler (1942), p. 19, fig. 1.

Centre Traces **A-E**: Potentials generated by nerve impulse at the endplate region of a single muscle fibre, recording being by an external electrode applied to the fibre immersed in saline: **A**, normal e.p.p. and spike response; **B** to **E**, progressive curarization causing blockage at **E**.

Right Traces ***a-e***: Recording at different positions on the muscle fibre. **a**, at the nerve muscle junction; ***b***, ***c***, ***d***, at 80μ, 230μ and 500μ distance from the junction. ***e***, after careful placement of the electrode ***on*** the endplate, no spike action potential is observed.
From Kuffler (1942), p. 21, fig. 3.

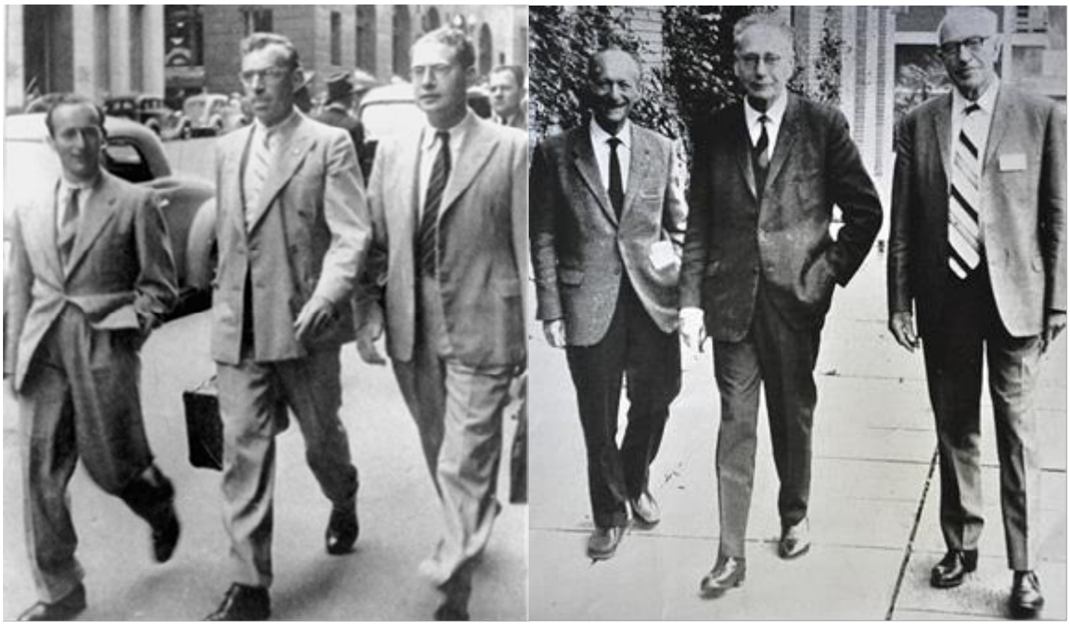

Fig. A27. Two photographs of the Kanematsu neurophysiology research trio. [AK, AO]
Left: Photo from 1940 by a street photographer in Sydney. (Kuffler, Eccles and Katz). From Mennis (2003), p. 20.
Right: "Reminiscence" photo dated 1972, taken in Oxford. (Kuffler, Katz and Eccles).

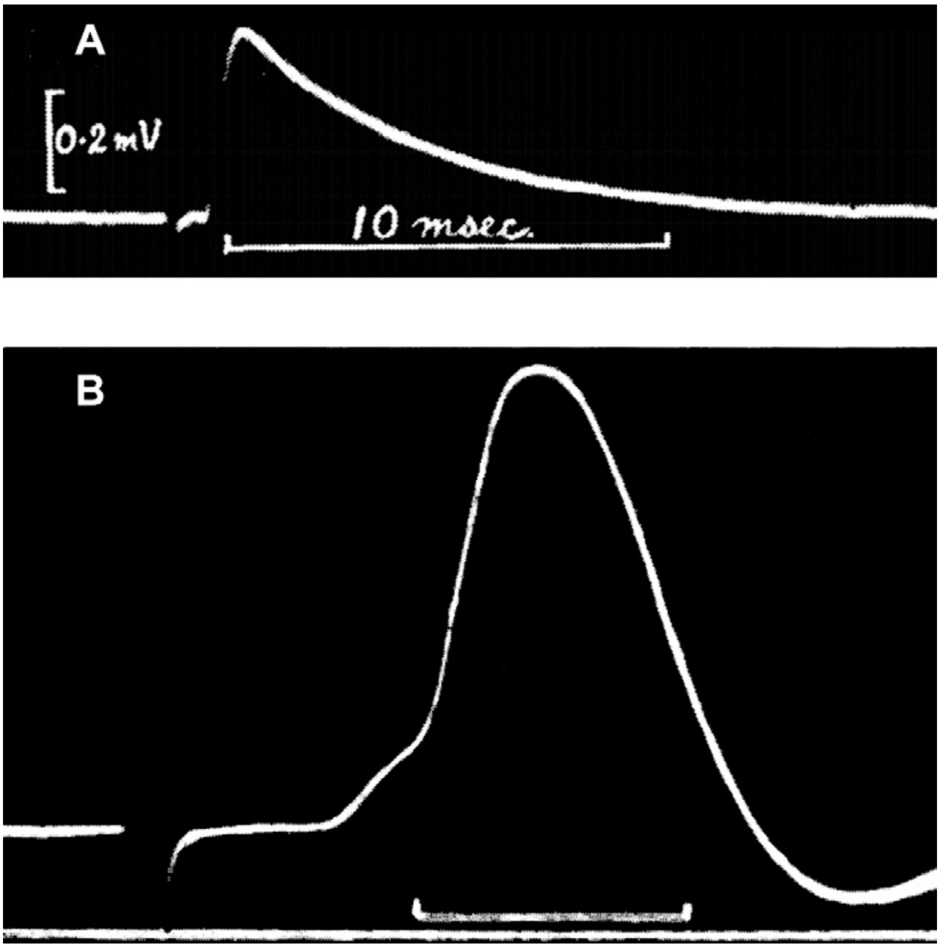

Fig. A28. Endplate potentials "epp's" in curarized muscles. [AL, BE]

A: EPP in cat's *soleus* muscle at 38°C. **Note**: the small wave preceding the epp is due to the action potential of the intramuscular nerves.
From Eccles, Katz & Kuffler (1941b) [1A-063], p. 363, fig. 1B, trace 1.

B: Double step action potential set up at endplate zone of normal cat's *soleus* by a single nerve volley. Time scale = 1 msec.
From Eccles Katz & Kuffler (1941a) [1A-059], p. 357, fig. 5.

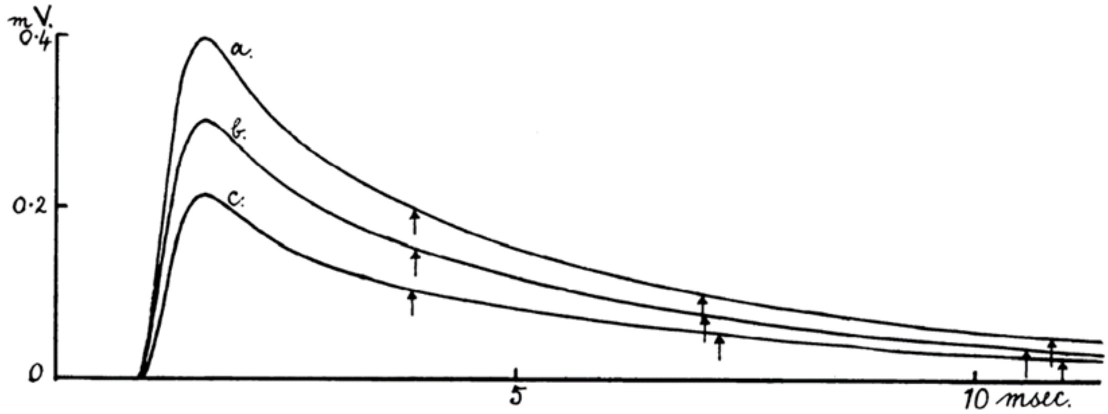

Fig. A29. Cat's *soleus* epp's, showing points for response decay. [AL]

Arrows show points for decay to ½, ¼, and $^1/_8$ of the summit height.

a: single nerve volley;

b: diminished response to second nerve volley at 24 msec. after first;

c: response to single volley diminished to nearly one half by further curarization.

There is no significant difference in the three curves and their successive half times progressively increase, being approximately 2.3 msec, 3.3 msec and 3.7 msec.

From Eccles, Katz & Kuffler (1941b) [1A-063], p. 363, fig. 2.

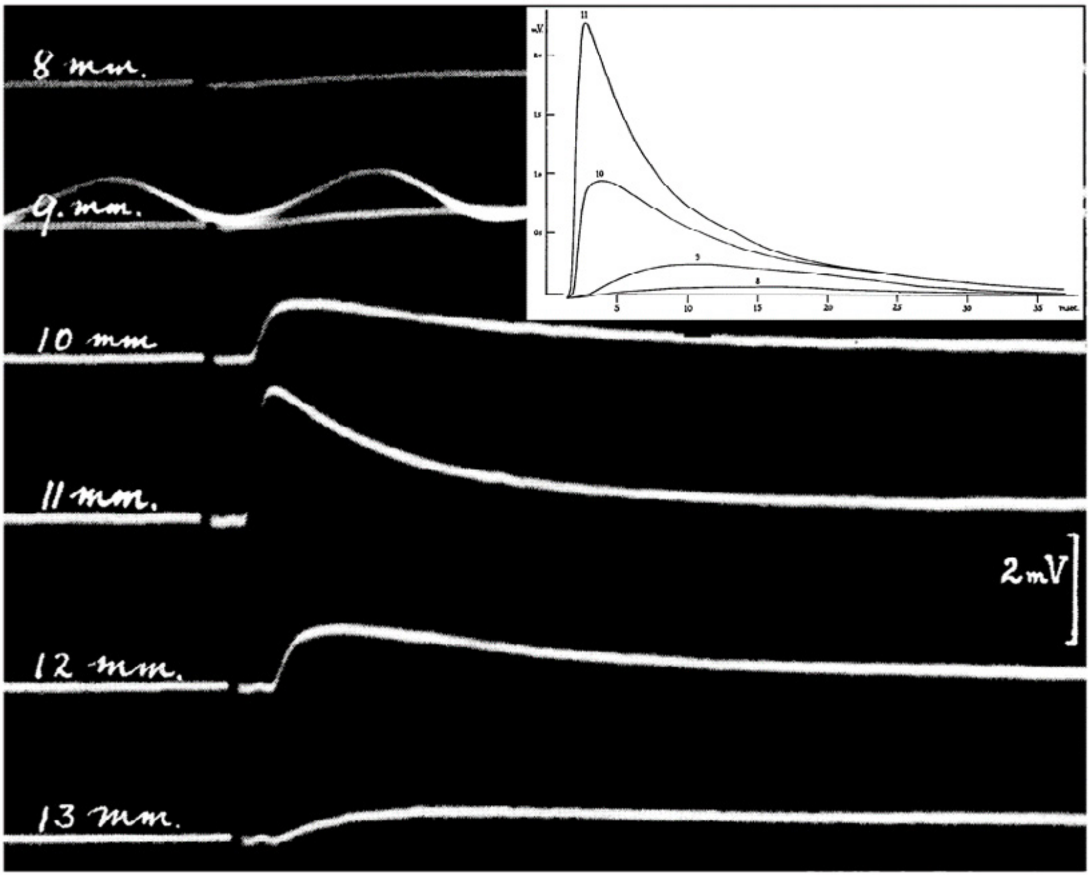

Fig. A30. Spatial spread and decrement of e.p.p. in relation to electrode positioning. [AL]

Main figure: Spatial spread of e.p.p. Records taken with grid lead at pelvic end and earth lead at a distance of ***8-13*** mm., as shown. Time signal: 1 d.v. = 10 msec. Note appearance of small nerve spike preceding the e.p.p. as electrode is moved towards nerve entry.

Inset: Spatial decrement and accompanying change in time course of e.p.p. Records of the main figure plotted and superimposed. Position of earth lead, successively from above; ***11***, ***10***, ***9***, ***8*** mm distance from pelvic end. Abscissae: Time after nerve stimulus. Curarized frog's *sartorius* at 27.5°C.

From Eccles, Katz & Kuffler (1941) [1A-063], p. 365, fig. 4; (inset is from p. 365, fig. 5).

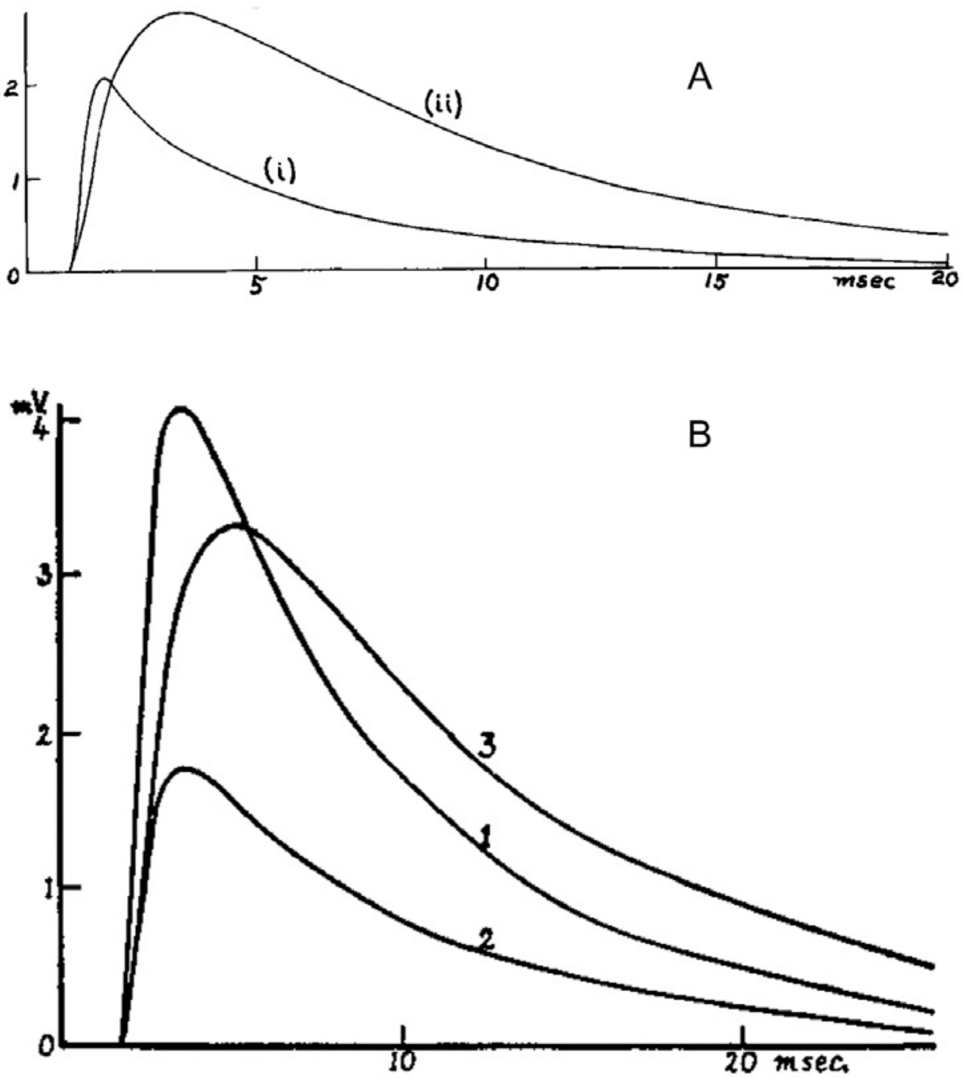

Fig. A31. Endplate potentials in curarized and eserinized muscles. [AL, AQ, BE]

A: Endplate potential produced by single nerve volley in (***i***) curarized muscle, in (***ii***) fully eserinized muscle to show the delayed summit and slowed decay. The rate of rise is slower than in (***i***) on account of the deeper curarization.

B: Endplate potential in curarized muscle. ***1***: after 6 µmol. curarine; ***2***: after 9 µmol. curarine; ***3***: after 9 µmol. curarine + eserine 10^{-5}. Frog's *sartorius*. 23°C.

From Eccles, Katz & Kuffler (1942) [1A-067], p. 218, fig. 7.

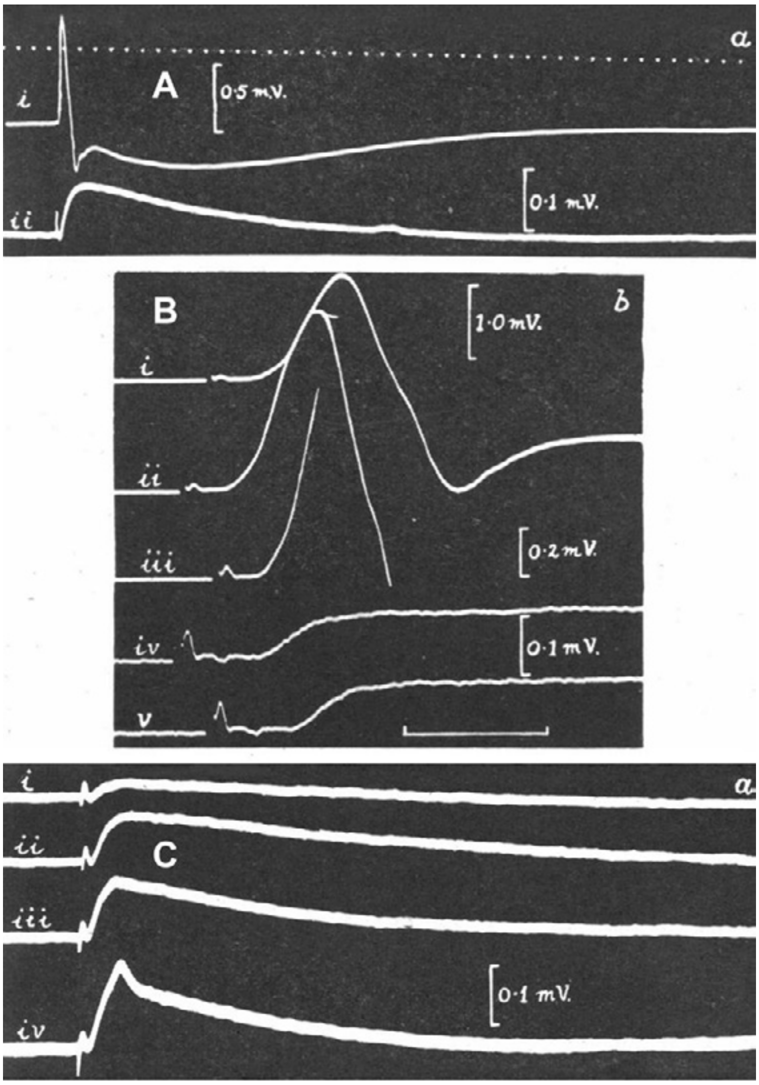

Fig. A32. Action potentials from stellate ganglion (SCG). [AQ]

A. Action potentials (***i***) before and (***ii***) after complete curarization. Time = 10 msec.

B. As in **A**, but at faster speed; (***i***), (***ii***) and (***iii***) before curarization at progressively increasing amplitude to show double-step rise. (***iv***) and (***v***) after complete curarization and at still higher amplification. Note the lengthened latent period. Time line shows 10 msec. Voltage scales shown for (***i***), (***iii***), (***iv***) and (***v***).

C. Action potentials from stellate ganglion showing gradual recovery from the deep curarization of observation (***i***). Spike is first shown in (***iii***) and is large in (***iv***).

From Eccles, (1943) [1A-068], **A**: p. 467, fig. 2a; **B**: p. 467, fig. 2b; **C**: p. 470, fig. 3a.

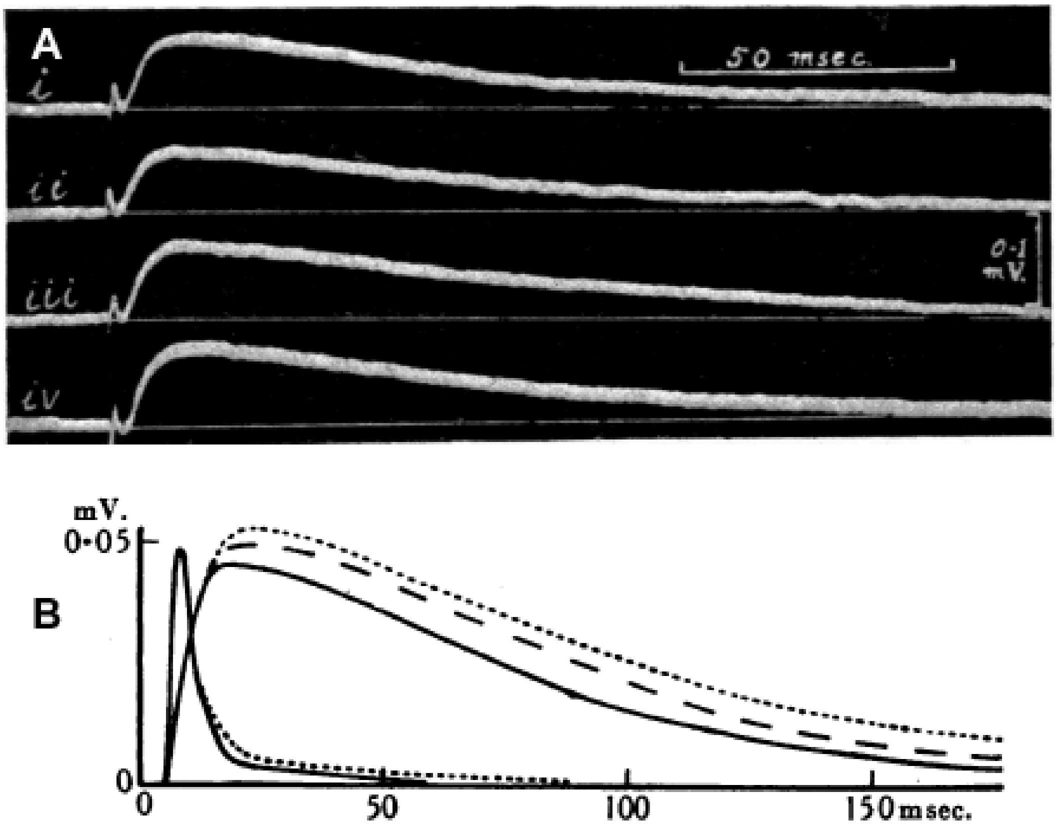

Fig. A33. The action of eserine on the synaptic potential in the stellate ganglion (SCG). [AQ]
Synaptic potentials set up in the curarized stellate ganglion by single preganglionic volleys:
A. (***i***) before eserinization; between (***i***) and (***ii***) 0.5 mg. eserine/kg. injected intravenously; between (***ii***) and (***iii***), and (***iii***) and (***iv***) further doses of 2.0 mg./kg. At the same time small doses of curare were injected in order to maintain the complete synaptic block. The base-line for each record has been drawn in order to facilitate comparison.
B. The slow rounded curves show synaptic potentials set up in another curarized ganglion, the continuous line before eserine, the broken and dotted lines after injection of 0.5 and 6.5 mg./kg. eserine respectively. Potential scale for dotted curve 0.8 times that shown. The continuous and dotted peaked curves have been determined by analysis of the corresponding synaptic potentials.
From Eccles (1944) [1A-070], p. 28, figs. 1 & 2.

STAGE 4: Teaching & Research in Dunedin: 1944-1952
(Sections BA to BU)

BA. Professorship of Physiology, University of Otago, New Zealand

At about the time of the Kanematsu crisis I was informed that the chair of Physiology at Otago University Medical School in Dunedin was becoming vacant with the retirement of the old Professor Malcolm.[247] There were no opportunities for me in Australia, and I did not want to return to Britain in war time (1943). The Otago Medical School was an integral part of the University of Otago founded in 1870, the only Medical School in New Zealand with a 2 million population and it was well regarded with good buildings (Fig. A34) and adequate Government support.[A]

In the advertisement, the Professor of Physiology was also required to teach Biochemistry as had been done in the past. So, I wrote to enquire from an old friend of mine Dr. Charles Focken.[248] At Oxford he was 2 years ahead of me as the Victorian Rhodes Scholar, and I knew him quite well. He was now Senior Lecturer in Physics at Otago. It proved an excellent move because Charles gave me superb advice. There was a very good biochemist who had been briefly the Senior Lecturer in Physiology; Dr. Edson[249] was a medical graduate of the University of Otago with the highest honours. He had a scholarship as first in the year that took him to England to do a Ph.D. with Hans Krebs[250], the biochemist, famous for his research on enzymes within cells, for which he got a Nobel Prize in 1953. Edson returned to Otago as Senior Lecturer in Physiology. Prof. Malcolm, however, would not allow Edson to lecture on the enzymes in cells. All he recognised were enzymes in the digestive juices. Edson resigned and took a small medical research position.[B] I immediately contacted Norm Edson. I proposed that I would recommend that he and I should run a conjoint Physiology - Biochemistry department. He immediately replied enthusiastic acceptance.

In my application for the Professorship of Physiology I gave it as a condition that Dr. Norman Edson be appointed to share with me the Department of Physiology and Biochemistry. We would share the teaching responsibilities and all the facilities and the finance. My application was of course very strong as I had had such a good Oxford record and a wonderful testimonial from Sir Charles Sherrington. I had just turned 40 and had been elected FRS two years before, with 70 papers published or in press. Fortunately, the Dean, Dr. Charles Hercus[251], Professor of Bacteriology, understood my plans for development very well. I had heard from Kellaway how enthusiastic he was.

247 Malcolm, John (31.08.1873 – 17.06.1954) UK 1st Otago physiology professor from 1905-1944. "Vitamins".

248 Focken, Charles Melbourne (23.10.1901 – 15.08.1978) HK Otago physics lecturer. Later museum director.

249 Edson, Norman Lowther (01.03.1904 – 12.05.1970) NZ biochemistry prof. Metabolic pathways, polyols.

250 Krebs, Hans Adolf (25.08.1900 – 22.11.1981) DE(J) physician & biochemist. "Krebs cycle". (NP 1953).

251 Hercus, Charles Ernest (13.06.1888 – 26.03.1971) NZ Professor of public health & Dean at Otago University.

So, I was appointed forthwith and sent a formal notice of resignation to the Hospital Board from the end of the year. I did not meet them or Paul. I knew that Bernard and Steven were planning to leave soon. As the war was coming to an end. Bernard would go to A.V. Hill in London and Steve to Ralph Gerard in Chicago. It was a sad ending to what could have been a good start for Medical Science for Sydney, following on the success of the Hall Institute in Melbourne. What damage an ignorant fanatic can do with his money and his political ambitions!

BB. The way to a new home in remote New Zealand

It was very sad to dispose of the beautiful home in Sydney. It had to be sold for just what I paid for it plus the reconstruction costs because of the government war-time regulation. I once saw it more than a decade later from the outside and was shocked to see that the lovely lawn tennis court was converted into a rose garden! I looked no more, but resolved that one should not return to visit the home where one once had happily lived. So, my scientific Odyssey, as I have called it, was across the ocean to an even more remote home. But the war was still on; and there was an attraction in this remoteness in the age of atomic weapons.

The Japanese war was still on when we left Australia at the end of December 1943, but fortunately, ships were still available, though under conditions of secrecy. Our possessions were crated to go when a cargo ship was available to Dunedin, but only at a few days' notice did we discover that we had to go to Melbourne to embark on the ship to New Zealand. It was good to see my parents and sister again. We drove the car and stayed there for the ship departure, but we still did not know where in New Zealand we would arrive. The Japanese submarines were still around, so the ship kept changing the course. Eventually we arrived in Wellington after about a week. Then we had a great trouble to get on the ship to Christchurch. It was an overnight journey with early morning arrival at Lyttleton to Christchurch by train to Dunedin in eight hours. It was quite a journey with the seven children. I had been in touch with Norm Edson by telephone from Wellington and he was to meet the train and make arrangements for accommodation. I had never been in New Zealand before and had never met Drs. Hercus or Edson. It was in the middle of the summer holidays and Dr. Hercus and his wife were on holiday for 3 weeks, but we were invited to stay at their lovely home to which we were taken by Norm. Of course, we were scrupulous and there were arrangements for the children to sleep outside on the veranda. It was summer weather. The children got the message, so all was in perfect order when the Hercuses returned, rather apprehensively!

Meanwhile we had been extremely fortunate because Professor Bell[252] of Surgery wanted to sell his fine large house with six bedrooms and three bathrooms for a smaller house in a more stylish suburb.

252 Bell, Francis Gordon (13.09.1887 – 28.02.1970) NZ Otago University Professor of Surgery, 1925-1952.

BC. Dunedin, the University of Otago, Medical School and social life.

The story of Dunedin should be briefly told as it played such an important role in my life. It was the first settlement in southern New Zealand, being founded in 1848 by a break-away Presbyterian Free Church from Edinburgh. Their two ships landed at the head of the long Otago Harbour and set up Dunedin, the old Scottish name for Edinburgh. The city of Dunedin still has the street names transplanted from Edinburgh. More Scots came to this predominantly Presbyterian settlement that extended into rich agricultural land with sheep and cattle and fruit in prosperous farming. Then in 1861 came the riches of alluvial gold and Dunedin became the principal city of New Zealand, as the north was held back by the Māori Wars. Education was the principal concern of the city with excellent colleges and in 1869 the University of Otago was founded by the Presbyterian Church that created and paid for the first four professorships; Philosophy, English, History and Physics. The Medical School was set up as early as 1876.[A] Meanwhile the northern cities had recovered and set up the University of New Zealand as a degree giving body, the teaching being by University Colleges, Auckland, Wellington and Christchurch. At that time, Dunedin was the largest city and was the commercial centre because of its gold wealth.

The situation had greatly changed in 1944 when I arrived. Auckland, Wellington (the capital) and Christchurch were much larger. Still, the University of Otago was the most important university, as it still had the only Medical and Dental School and its student population (2500) was well maintained. However, the city population of 85,000 provided inadequate clinical teaching facilities for the large medical school - 120 students a year, so the 6th year was held in the Hospitals of the three northern cities. Eventually, many years after I left, there was established a second medical school in Auckland (1970).

There were many attractive features in Dunedin with its dedication to culture derived from its Scottish foundation. For example, in the main street there were more book shops then dress shops, and a second-hand bookstore with 300,000 volumes! The University buildings were spacious in good grounds and the pre-clinical medical school had large facilities (Fig. A34). The impressive Town Hall in classical style was good for concerts.

There were excellent sandy beaches fronting the Southern Ocean, but for sun-bathing rather than swimming in the cold Antarctic water! Attractive hilly, woodland areas were close to the city and one could live on the suburban edge as we did with a large garden and mountain views only 5 minutes drive down the hill to the Medical School. Moreover, living was very cheap and there was a government allowance of £65 a year for each child up to 21 and completely free hospital and medical services.

Besides the Hercuses and Edsons we had excellent friendships with many University staff - Smirk[253] in Medicine, Focken in Physics, Murray Falconer[254], the neurosurgeon,

253 Smirk, Frederick Horace (12.12.1902 – 18.05.1991) UK Otago Prof. of Medicine 1940-1960. “Hypertension”.

254 Falconer, Murray Alexander (15.05.1910 – 11.08.1977) NZ Otago Neurosurgery Prof. 1943-1947 Aneurysms.

who went on to a distinguished career in London, and particularly Frederick Soper[255] and Eileen Soper[256] in Chemistry. Also, Galway[257] (Music), [Ferguson[258]?] (Psychology) and Findlay[259] [& Raphael[260]] for Philosophy.

For entertainment, we had an asphalt tennis court and developed a large basement with a concrete floor for folk-dancing.**[B]** It was an informal occasion every Friday night, and now our larger children participated. Horace Smirk was an enthusiast as also the Sopers and Eileen's lovely sister who played for us on the piano those dances we did and have records for. I give these glimpses to show that despite the hard work there were occasions for relaxation in those eight strenuous years at Dunedin. Also, our original Ford V8 car was still with us and it could be converted for sleeping and there were wonderful sites on the inland lakes for a few days of recovery.

BD. The Medical School, University of Otago.

I had the enormous responsibility of reorganising the whole teaching program in Physiology, not only for the two medical classes of 120 a year for the 3 terms a year, but also for the dental class of about 70 a year and the Home Science of about 30, each being for 3 terms. There were part-time teachers for these other classes, but I took over the medical classes, particularly the senior medical class for both the lecturing and the practical. Right through this early Dunedin period I was obsessed by my experience of the deplorable state of the preclinical teaching at Sydney, and determined to give a scientific basis for medicine in the way that was done in the Final Honour School at Oxford. Norman Edson was motivated by the same ideals, having done his PhD in the Biochemistry Department at Cambridge and was a student of Hans Krebs for many years. We were embarking on a complex teaching experiment. It has to be recognised that the medical class at Dunedin was highly selected, because the 120 places each year were eagerly sought by the best students from the whole of New Zealand.

I had 2½ months to prepare for the first term. Physiology and Biochemistry had two 3-hour practical classes a week for the 10- week term that we shared. In Physiology there were 30 groups of 4 students each, and we set up 30 experimental arrangements so that with rotation each group would come to a different experiment each week. My immediate problem was to organise the 30 experimental set ups. Laurence Malcolm[261] and Charlie Morris of the workshop were heavily engaged. Amazingly, when term started in early March, all was ready and I had composed the instructions for the 30 experiments, that were duplicated and ready for the opening day! Of course, not all of

255 Soper, Frederick George (1898 – 01.01.1982) UK Otago Chemistry Prof. 1936-53, Vice chancellor 1953-63.

256 Soper, Eileen Louise née Service (14.12.1900 – 24.10.1989) AU married FG Soper 1938. Writer/historian.

257 Galway, Victor Edward (24.05.1894 – 09.07.1960) UK music Prof. 1939-54. Organist, conductor, composer.

258 Ferguson, Henry Hall (1906 – 10.2004) UK experimental psychology lecturer 1930-1947. "Road accidents".

259 Findlay, John Niemeyer (25.11.1903 – 27.09.1987) ZA African philosopher. Rational mysticism, tense logic.

260 Raphael, David Daiches (25.01.1916 – 22.12.2015) UK(J) philosophy Prof. 1946-49 "Adam Smith, Hobbes".

261 Malcolm, John Laurence (1913 – 09.10.2001) NZ physiology senior lecturer 1942-47. later Prof. in Aberdeen.

the experimental set ups were new. Some were a carry-over from the old courses. The animal experiments were rather few, copied from the Oxford Sherringtonian mammalian class. But in over 80% of the experiments the students were the subjects.[A] I was particularly pleased with the three 3-hour experiments on pain - cutaneous, inflammatory, anoxic muscle and joint. Vision, hearing, respiration, urinary secretion, circulation, cutaneous sensing, voluntary contraction and reflexes made up some of the other experiments. The junior medical class remained rather conventional, largely based on frog experiments, and these Laurence Malcolm arranged well.

I gave some of the lectures to the first year, but concentrated on a sophisticated course at the Final Honour level of Oxford with which I had had so much experience. But I had to work very hard in mastering the many advances since my Oxford days. The lecturing conditions were rather primitive with little projections of slides. I had to draw on the blackboard with coloured chalk throughout the lecture, much as had been done at Oxford. However, we introduced discussion groups bringing several of the 4's together with a series of problems to discuss that arose out of the preceding lectures, together with texts of review articles etc. They had 3 hours discussion and I and other staff moved around, to be asked questions. This strategy worked well for the serious students. It gave all a chance to confront the lecturer. It was quite encouraging to experience the enthusiasm of most students to this participatory teaching.[B]

I wrote out and illustrated each of my lectures in a loose-leaf file so that each year additions could be made. In the first 3 years I did the whole of the lecturing for the senior class. We were terribly understaffed. Laurence Malcolm as Senior lecturer did the junior year lectures, which were fewer than the senior year. Other part-time lecturers did the dental and home science lecturing.

In order to get some part-time assistance Norm Edson and I revived a medical science course that had lain dormant. At the end of the senior year, students could elect to do a year of research, being examined at the end on their research and its significance. They delayed their course for one year, but got a degree, BMedSc. and had experience in research that often was published. Also, they could have a modest salary as part-time demonstrators. So, after the first year, 1944, six of the best students elected to do a BMedSc. and that helped in 1945 and so on for successive years.[C] It was for me almost beyond my capacity in the first year when the senior lecture course had to be created, in such diverse fields as renal secretion, endocrinology, respiration, circulation, reproduction and the nervous system; peripheral and central. Edson and I had good agreement on the sharing of fields that involved conjoint physiology and biochemistry. It was easier in those days than it would be today.

My ambitious attempt to restructure the physiology teaching had a cost to me, particularly in the initial year. I calculated that in term time I was "confronting" students for 20 hours a week, and in addition had to spend much time in relearning the subjects for lectures, so that the students would be given authentic insights into the progress in each field. However, we did not demand detailed memories in the examinations, and the passing rate was much higher than in anatomy. I kept telling the students that the course was stories and pictures or imagery, not the memory load still demanded in anatomy.

I hoped all the students would appreciate that, and they did, except for one unfortunate incident where a student wrote several letters to the local newspaper complaining that my teaching was for medical research workers, not medical doctors.[D] His father was an old-fashioned doctor who thought that the knowledge he had would be adequate for his son. I did keep on telling the students that we were educating them for their whole lifetime of medical practice - even up to 40 years after graduation. I was working so hard at that time that I was almost at breaking point, particularly as no students came to my defence. I told the local newspaper that if they published any more such letters, I would leave Dunedin. I had good offers from several other Universities in that immediate post-war period.

There were no more letters, but there was a good sequel about 15 years later. Long after I had left Dunedin for Canberra, I was visiting Auckland for a general medical conference at which I was invited to lecture. In the reception afterwards, I noticed a group of about twenty young doctors who seemed very embarrassed in approaching me. Then they told me that eventually they had come to realise what Edson and I were doing in our teaching course. They were just country medical doctors, but said that thanks to our teaching they could understand all the medical advances described in the Lancet and BMJ. It was quite rewarding to hear their delayed appreciation. I wonder if the letter writer was there![E]

There was of course immediate appreciation from the best students. Most went overseas for postgraduate work, but later many returned to New Zealand. Almost all of the senior staff of the newly established Medical School at Auckland were our students from those years at Otago.[F] Some had had distinguished careers. Graham Liggins[262] as Professor of Obstetrics at Auckland discovered the cause of the onset of parturition, using sheep as subjects.[G] There was in the foetus a complicated sequence of hypothalamus, pituitary gland, cortical adrenalin and finally via prostaglandins to the maternal endometrium. For that he was awarded in FRS in 1980. Others were Bill Liley[263] who was able to counteract foetal death in 85 % of the RH-neg foetuses. That was before the days of immunological treatment. John Hubbard[264] was distinguished for his studies on neuromuscular transmission.[H]. Marianne Fillenz was in the 1944 year, with top place, then a BMedSc. in 1945 and eventually moved to Oxford with a Fellowship at St. Anna's College and a lecturer in Physiology. She has just published a most important monograph "Noradrenergic neurons".[I] This very incomplete list does illustrate that in those Dunedin years many medical students went on to distinction, often in fields far removed from my own expertise.[J] I am optimistic in thinking that many did learn to become scientists in some branch of medicine or at least as medical

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262 Liggins, Graham Collingwood "Mont" (24.06.1926 – 24.08.2010) NZ Medical scientist. Hormone injections.

263 Liley, Albert William (12.03.1929 – 15.06.1983) NZ Auckland University Prof. of Perinatal Physiology.

264 Hubbard, John Ingram (01.12.1930 – 01.10.1995) NZ Otago University Prof. of Neurophysiology.

doctors did appreciate the importance of medical science in a manner that had been very deficient in Sydney.

BE. The first experiments at Dunedin

I was impatient to get started in research as soon as my research room had been completed. I had brought from Sydney the equipment of my research room that I had originally brought from Oxford. Amplifiers, cathode ray oscilloscope, camera, stimulators etc. I left the other room at the Kanematsu for Kuffler. The apparatus of that research room was never recovered by me from the Kanematsu after Kuffler left.[A] However, for the present I had my equipment set up by the very good local technician, Charlie Morris and Arthur Chapman who had come with me from Sydney.[B] I needed a good electronics man to replace Les Wirsu, but had to be patient until the wonderful Jack Coombs[265] arrived from the Physics school where he had taken his degree. Charles Focken helped in this arrangement; he brought Annand[266] as an excellent electronic technician in 1949.

I made only one good experiment in the first year, 1944, but in 1945 all went well. I was not much concerned about this delay that was caused by my concentration on teaching. Almost everywhere the war had impeded research. It took till 1945 or even 1946 for high level neuroscientific research to get started in the world. The exception was Lloyd and Renshaw[267] at the Rockefeller Institute with Gasser as Director and also Lorente de Nó. I realised that I would have to make a big effort to catch up and even surpass them in the next few years - but this I did in Dunedin. I was particularly helped by the great electronic skill of Jack Coombs.[C]

I concentrated on synaptic potentials of the cat spinal cord using selective recording from the ventral roots of the catelectrotonic potentials transmitted from the central synapses on the motoneurons (Fig. A35) exactly as had been done with the stellate ganglion in Sydney (Fig. A18B). Progressive anaesthesia resulted in suppression of the monosynaptic spike potential and also of the after discharges (Fig. A36), leaving only an excitatory synaptic potential at five times larger amplification, as with the stellate ganglion under curarization (Fig. A32A). I had in 1937 reported on a preliminary investigation on the cat spinal cord with Pritchard at Oxford. The synaptic potential in Fig. A36 would be generated monosynaptically on motoneurones by the dorsal root volley as described by Lloyd for the largest afferent fibres (group **Ia**) from the muscle spindle (Fig. A35A). By recording from the ventral root (Fig. A35B) at progressive distances from the spinal cord it was found that the synaptic potential had a spatial decrement of a reasonable value of 6 to 7 mm, so one could derive its actual size and time course at the monosynaptic generating sites on the motoneurons. The synaptic

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265 Coombs, John Saxon (17.01.1917 – 30.07.1993) NZ physicist at Otago & ANU. Designer of the "ESRU".

266 Annand, Arnold Ernest (12.02.1922 – 14.08.2011) NZ electronics technician at Otago University

267 Renshaw, Birdsey (10.10.1911 – 23.11.1948) US Neurophysiologist. "Inhibitory neurons/Renshaw cells".

potentials are homologous with the endplate potentials of striated muscle (Fig. A25, Fig. A28A) and the synaptic potentials of the stellate ganglion (Fig. A32).

The large group **Ia** afferent fibres (Fig. A35A) from the muscle would converge on motoneurons of the muscle of origin and also converging are the group **Ia** fibres from synergic muscles acting similarly at the joint (Lloyd, 1946a). So, when the nerves to synergic muscles were stimulated, there would be expected to be convergence onto the motoneurones of afferent fibres from synergic muscles. For example, in Fig. A37 the afferent volleys from the medial and lateral *gastrocnemius* nerves were stimulated alone (records 3 and 7 from top) or at various intervals. At the shortest intervals (records 4 and 6) summation of the synaptic potentials resulted in a large impulse discharge. With lengthening intervals, the discharge was smaller and it did not occur at the longest interval (10 msec.). The time course of facilitation with a maximum at simultaneity resembles that of the earliest synergic recording in Fig. 2. Lloyd, (1946b) had also observed this time course of decay of facilitated monosynaptic reflex discharges. These investigations establish that the monosynaptic input to motoneurons has a time course of decline to zero in about 10 msec.

The experimental evidence indicated that the anaesthetic[D] acts by diminishing the production of the synaptic potential and also the generation of impulses by the synaptic potential. This experimental investigation of synaptic potentials in the central nervous system by electrotonic techniques revealed that with monosynaptic stimulation the synaptic delay is as brief as 0.7 to 0.8 msec.

Similar experiments were carried out with the isolated frog spinal cord surviving in an oxygenated medium. With both the frog and the cat there was investigation of repetitive stimulation at up to 200/sec in the frog and up to 400/sec in the cat. There was no sign of the delayed decay at the end of the tetanus that was such a feature with the stellate ganglion and that was attributed to the surviving ACh.

The nature of the synaptic transmitter was of particular concern in these first systematic studies of the spinal cord. Although there had been investigations studying the output of ACh from the stimulated central nervous system and of the distribution and action of cholinesterase there was not convincing evidence that acetylcholine was acting effectively in synaptic transmission in the frog spinal cord. In 1947 I published a systematic investigation with such procedures as abolishing cholinesterase activity by 6×10^{-5}M prostigmine (neostigmine) and then soaking the spinal cord in an enormous concentration of ACh - even up to 6×10^{-3}M ACh, which had only a mild depressant effect! Comparable negative results were obtained with the un-anaesthetized frog spinal cord. It was concluded that ACh is not an effective synaptic transmitter in the frog spinal cord. Since that time, it has been shown that ACh has important action at higher levels of the mammalian brain, but this is a metabotropic action (Fig. A17B) and is blocked by atropine. In this 1946 paper the duration of the synaptic transmitter for monosynaptic action was shown by the Hill analyses (cf. **Section AQ**) to be about·2 msec.

BF. My living dialogue with Popper, opening stages May-Nov.l945

It was not until 1945 that I could look beyond. I had heard marvellous stories from my colleague, Norm Edson, about the academic stir that was being made by a philosopher, Karl Popper, in Canterbury University College at Christchurch some 250 miles to the North, but still in the South Island of New Zealand. It was a great and welcome surprise, as I had regarded my New Zealand venture as an academic exile after my many years at Oxford. I heard that Popper was particularly appreciated by the scientists at Canterbury (Packer[268], Parton[269] and Allan[270]) and that he had revolutionary ideas on the philosophy of science.

So, in the early part of 1945 Edson and I began to make arrangements for a course of five lectures by Popper to the University of Otago, the faculty and students of all faculties. It seems incredible today that one could make such an invitation with an offer only of private hospitality (at my home) and a second-class railway fare for an intensive course of 5 lectures! Popper accepted graciously and the course was arranged for the week of May 22nd to 26th. I first met Karl at the Dunedin railway station on May 22nd. He was then a most active, vivacious man at the height of his powers at the age of 43. The train was very late, so the lecture perforce had to start about 30 minutes later to a crowded audience of at least 500 in the largest lecture theatre of the University. It was a unique occasion for the University, so remote and in war time. The crowded attendance held through the whole course.

I was an immediate convert to the Popperian message that in science one had firstly to define a problem. Secondly there was the creative task to develop hypothetical solutions. Finally came the attempts to test these proposed hypotheses by the most searching experiments, that is the attempt at falsification. I fully appreciated the devastating attack by Popper on the inductive method of science, in which up till then I had naively believed. I particularly remember the picturesque metaphor, that, according to Bacon[271] and Mill[272], you collected the grapes (of experimental observations) in a big barrel and then sat on it so squeezing out the pure wine of truth!

The copious lecture notes that Marianne Fillenz and I took were welded into a typed text that was duplicated under the general title "Principles of Scientific Method" with the 5 lectures entitled respectively:

1. The Hypothetical Deductive Method
2. Testing of Theories
3. The Problem of Objectivity in Research
4. Probability

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268 Packer, John (1899 – 1971) AU University of Canterbury Chemistry Professor.

269 Parton, Hugh Noble (28.11.1906 – 1991) NZ University of Canterbury Chemistry lecturer/Otago Professor.

270 Allan, Robin Sutcliffe (07.07.1900 – 05.07.1966) NZ University of Canterbury lecturer/Professor of Geology.

271 Bacon, Francis (22.01.1561 – 09.04.1626) UK philosopher & statesman. Wrote in 1620 “Novum Organum”.

272 Mill, John Stuart (20.05.1806 – 07.05.1873) UK philosopher. Wrote in 1843 “A system of logic, Vol. 1”.

5. Teaching and organisation of science

In addition, there were two seminars entitled:

1. Principle of Indeterminacy
2. Atomic Theory and Biology

About 100 copies of our typed notes (24 large pages) were distributed, and I have one before me as I write.[A]

There were two aftermaths of that intensive week: One was that the scientists and philosophers spent weeks in discussions that I participated in; the other was that between Karl and me there arose an intimate and devoted friendship that has shone on us without cloud ever since.

The post-lecture discussions were often critical because many scientists were loath to give up the inductive theory of science in which they had so implicitly believed. I had all the enthusiasm of a neophyte and expatiated at length on the lectures and had strong discussions with the sceptics.

At that time there was no English text of the Popperian philosophy of science, "hypothetico-deductivism" as it came to be called.[B] A copy of the German text of Popper's book "*Logik der Forschung*" and the English translation: "*The logic of scientific discovery*", [which] was not published until 1959, was briefly available to me. However, the lectures and the discussions had given me all that I needed to know. For me the great inspiration was that I could reorganize my own scientific work in the light of this new deliverance - namely that it was not an occasion for remorse if one's scientific theory was falsified. On the contrary a scientific theory has to be formulated so clearly and unambiguously that it invites falsification. It should not be a theory simply covering and restating the immediate scientific findings. Rather it should be formulated so as to go beyond them with great explanatory power and predictive capacity. The scientific status of a theory is to be judged by its scope and by the challenge that it offers to rigorous experimental testing and possible falsification. I delighted in the prominence given by Karl to creative imagination. Science had now become for me an exciting adventure and not a routine collecting of facts with cautious interpretations by provisional hypotheses, often called "working hypotheses", so that one was protected from the stigma of having uttered a scientific untruth! [C]

All of this was very welcome news for me because in 1945 I was in trouble with the electrical theory of synaptic excitatory action that I had been espousing for a decade as stated above (Section **AA.**). I had postulated in 1934 that transmission across the synapses of the sympathetic ganglion and the neuromuscular junction was effected by an initial fast electrical mechanism and that the chemical transmission by acetylcholine demonstrated by Dale and his associates was a later and slower excitatory mechanism. However, in 1942, as a result of drug investigations on neuromuscular transmission, I had with some misgiving accepted acetylcholine as the sole transmitter at those synapses. With the synapses of the central nervous system there was no good evidence for acetylcholine or other chemical transmission, so I continued to believe in a fast, electrical transmission in the central nervous system and possibly in the sympathetic ganglion. With Popper's encouragement I formulated the hypothesis of electrical synaptic transmission in terms of precise models that were based upon experimental studies. It came about like this.

After that memorable visit of May 1945 there was an enormous correspondence between us. Unfortunately, I do not have copies of my letters to Karl, but from June to December 1945, I have 14 letters from Karl totalling 73 pages. In addition, we met in Christchurch on the occasions when I was passing through on the way to conferences in Wellington. Karl would meet me on arrival at Christchurch station and travel with me to the harbour at Lyttleton whence I would depart by ship with conversation continued as long as possible from ship to shore! I particularly remember one such occasion when we were in deep discussion until the ship departed beyond shouting distance. Two days later, when the ship arrived at 6.30 AM at Lyttleton, I was amazed to find Karl on the wharf for renewal of the discussion that continued on the drive to his lovely home in the Cashmere Hills for breakfast and so to the train departure from Christchurch to Dunedin.

I learned much from these occasions snatched from our busy lives, and in December 1945 I published in Nature a theoretical paper on excitatory synaptic transmission that was built upon models of electrical transmission at synapses. The manuscript was most valuably criticized by Karl in two long letters so that the revised text for publication owed very much to him, as was acknowledged in a footnote. It incorporated a list of six experimental observations that were accounted for by the hypothesis together with an account of predictions that could be experimentally tested. His letters of June 16th, July 4th, July 16th, July 27th show that he had studied the literature on synaptic transmission and had arrived at a most valuable strategy for developing and presenting the rival electrical and chemical theories. These letters reveal that he could very effectively move from the general to the particular, and show in detail how his scientific methodology could be applied to specific scientific problems.

Unfortunately for me Karl left New Zealand in December 1945 to take up his appointment as Reader in Logic and Scientific Methodology at the London School of Economics.[D] Except for letters our living dialogue was interrupted for several years. It was not until January 1952 that I could visit England again after a long absence of 15 years.

BG. Electrical synaptic transmission

Under the influence of Popper, I developed a much more precise statement of the hypothesis of electrical synaptic transmission than had hitherto been attempted. There was the advantage that the electrical responses of nerve were now much better understood and that electrical interaction between nerve fibres had been studied both in the intimate relations occurring naturally and artificially in what are called "ephapses".[A]

Fig. A14C shows diagrammatically the flow of current between the interior and exterior of a nerve fibre as an impulse propagates towards the left. If there is a second giant fibre in close apposition in a conducting medium, this passive fibre will be subjected to action currents as shown in Fig. A38, there being an initial anodal influence (A1) in advance of the impulse and a cathodal influence (c1c2) during the summit of the impulse with finally an anodal (A2) during the impulse propagation away. This is the simplest electrical interaction of an ephapse.

A model more related to a synapse is drawn in Fig. A39, where in an ephapse a presynaptic element is shown ending perpendicularly to the postsynaptic element. When the impulse approaches the ephapse, its action currents have an initial anodal action Al and when it reaches the ephapse there is a cathodal action c2. Fig. A39 thus illustrates the simplest ephapse that could be developed to be the model for an electrical synapse where action currents of the presynaptic nerve impulse by structural and functional specializations could act as synaptic transmitters.

The theoretical paper in Nature (Dec. 8th, 1945) was the direct result of Popper's visit. He wanted me to set up the most challenging hypothesis for falsification. This paper had one serious defect. It should not have been extended to neuromuscular transmission, where the ACh evidence was so conclusive. Of course, the ACh hypothesis was inadequate, even primitive, pharmacologically, biochemically and histologically. This can be recognised now with such techniques as electron microscopy, and concepts of specific sites and of ionic channels of molecular structure, and of controlled exocytosis of synaptic vesicles etc. However, the ACh hypothesis was ready for this transformation by the most sophisticated studies. I should have also left aside sympathetic ganglion transmission for which the ACh evidence was so strong, though still in trouble with the failure of anticholinesterases to delay appreciably the decline of the postsynaptic potentials (Fig. A33). Already in1944 I had demonstrated the improbability that ACh was an effective transmitter in the spinal cord, there being a final publication in 1947 (Section **BE**). Moreover, no possible alternative transmitter substance had been discovered. Katz and Kuffler in personal letters had severally criticized my Nature paper, but the criticism was only for the neuromuscular transmission and I accepted it.

The paper that I presented at the New York Academy of Sciences in February 1946 concentrated on the possible ephaptic relationships in models of synapses; (Fig. A38 and Fig. A39) being reproduced from that paper. It was shown how properties of synapses could be modelled by electrical transmission at ephapses; with such properties as irreversibility of transmission, synaptic delay, and the brief active phase with subsequent electrotonic decay.

In retrospect it can be recognised that the years 1946 to 1951 were occupied in intensive experimenting on the possibility of electrical synaptic transmission in the spinal cord. This was a valuable prelude to the revolution wrought by intracellular recording from 1951 onwards These years from 1946 of precise extracellular recording provided us with the techniques and background knowledge for the intracellular age that was still years away.

BH. My first American visit, February 1946.

(*Written on return in March 1946)*

After almost ten years of isolation from one's colleagues abroad it was very exciting to receive a cabled invitation from the New York Academy of Sciences to partake in an International Congress on Neurophysiology under the control of David Nachmansohn.[273] The difficult problem of travel seemed to be largely solved by the generous offer of all expenses by the Rockefeller Foundation. However, it turned out that there was much besides fares to be solved in post-war Pacific transport, and my arrival in New York on the very eve of the congress provided an episode as exciting for me as it was worrying for the organizers of the Congress. There were no passenger ships, all having been sunk, and of course commercial air travel was years off.

I left Wellington on a comfortable but slow American Navy cargo boat, the Sword Knot of 2,300 tons, that left Wellington on January 17th l946 and that was due to get me to Honolulu about February 3rd some five days before the opening of the Congress. But head winds delayed the arrival till February 5th and only when the winds dropped during the last hours of the journey was it sure that I would catch the San Francisco flight that afternoon on an old China Clipper, a most expensive flight, $300. The China Clipper [Fig. F16] was an enormous flying ship with a fine dining room, bathing facilities and sleeping bunks.[A] I was met at the arrival of the Sword Knot and conveyed to the flying ship departure in the harbour, an hour before. With arrival at San Francisco at 10,30 on the morning of the 6th, I was presented with the tough problem of immediate air transport to New York. However, the names of the Rockefeller Foundation and the New York Academy of Sciences worked wonders and I was on a DC-3 TWA plane at 4 PM on Feb. 6th for a flight having 16 stops and taking 22 hours. So, I arrived in New York at 5 PM on the 7th. A telegraph strike had prevented the delivery of all my telegrams.

Having no information, I went on the airport bus to Grand Central Station. A fellow passenger advised me to try the Commodore Hotel. I told my story at the checking desk and the nice lady said that one month in advance was necessary, but the Vice-President might be able to help a lost New Zealander. The Vice-President in evening dress was so kind. He gave me an excellent room for 4 nights at the unbelievable price of $ 4.50 a night. I quickly bathed, shaved and telephoned to Nachmansohn. He was at the opening dinner at the Haystacks Restaurant, Washington Square to which I immediately went by Taxi. The first intimation that I was nearer than Honolulu was when amidst great excitement I walked into the opening dinner at 7.50 just two courses late! That handicap proved quite within my capacity, stimulated as I was by the convivial company of friends that recalled faraway Oxford days.

The Congress itself provided a programme that literally packed the next two days with interest. Most of us thought it too full and too long, but it was amazing how the interest was sustained. In brief the theme of the Congress was concerned with the role of acetylcholine as a transmitter of the nerve impulse, more particularly along the nerve fibres not across the junctions. Nachmansohn was the chief proponent of this idea, but despite the array of evidence that he presented, the neurophysiologists remained

273 Nachmansohn, David (17.03.1899 – 02.11.1983) UA(J) DE/US biochemist “bioelectricity & acetylcholine”.

sceptical. There was much that could not be explained and the new evidence by Gilman[274] and Gerard that accumulated during the second day proved pretty decisive against it. At the finish of the Congress neurophysiologists felt happy that they could go on believing with a good conscience that the propagation of the nerve impulse is explained by the sudden breakdown of the nerve membrane that occurs when it is depolarized to a critical degree by the "eddy" currents. No doubt a use would have to be found for the acetylcholine, and we would all be happy if it could help us to explain some of the metabolic properties of nerve fibres.

My own contribution concerned the elaboration of an electrical hypothesis of synaptic transmission.[B] It bore on the main Thema of the Congress in that it dealt with the problem of how far synaptic transmission was chemical and how far electrical. I was allotted the whole afternoon of the first day, as the other contributor for that afternoon (Alexander von Muralt[275] of Bern) had not been so fortunate as I with the exigencies of post-war travel. Catastrophic head winds over the Atlantic had delayed the European ships for many participants. As a consequence, I was permitted to exceed my time allowance - the audience thought a journey such as mine should carry some privileges! Suffice it to say that my contribution was as provocative as I could have wished, but that despite the subsequent two hours' discussion no criticisms were forthcoming that had not been already levied at it in Dunedin. However, it is fair to add that the critics I feared most were only just returning from war service and no doubt found their weapons a little rusty for use at such short notice!

But the formal proceedings of the meeting (published as Annals of the New York Academy of Sciences, 47 part 4, 1946, [1A-077]) can be regarded in many ways as only the excuse that we scientists have for getting together before and after the event. And one might add as an aside, also during the event, because I have often been a bad listener to the formal presentations of a subject, and so even during the meetings some of us continued our informal discussions outside. There was so much to talk about after all those years of isolation and so little time to do it in! To an onlooker it would have looked as if we were slacking, but in retrospect these occasions were some of the best and most stimulating features of the Conference.[C]

If I were to give the names of some of the three to four hundred at the meetings there would be many familiar to those generations of students brought up on the new American text-books edited by Bard[276] & Fulton. Though I had met some during their visits to England, and several (Fulton, Hoff, Lloyd and Ruch[277]) had been Rhodes Scholars up at Oxford, I was meeting a great many for the first time. I felt rather like Dante[278] in the Divine Comedy (I hope students won't be impertinent enough to apply

274 Gilman, Alfred Zack (05.02.1908 – 13.01.1984) US pharmacologist/textbook writer. "Chemotherapy".

275 von Muralt, Alexander Ludwig (19.08.1903 – 28.05.1990) CH physicist and Professor of physiology.

276 Bard, Philip (1898 – 05.04.1977) US Professor of physiology at Johns Hopkins University. Text book editor.

277 Ruch, Theodore Cedric (1906 – 1983) US Professor of physiology & biophysics. Textbook writer.

278 Dante Alighieri (1265 – 14.09.1321) IT poet & philosopher. His major work: Poem "Divina Commedia".

the analogy to the first circle of the Inferno!), the first circle of meeting all the great ones of the past.**D** It was rather fun seeing how far the reality corresponds with the mental picture one had formed from their correspondence and their publications, and no doubt they were having reciprocal fun on their side. I found it of particular interest to meet friends from war-devastated countries: Bremer[279] of Belgium; Fessard, Bugnard[280] and Couteaux[281] of France; and Feng[282] of China. They had all been brought by the Rockefeller Foundation to America in order to renew contact with the main stream of scientific thought from which they had been separated so long, and also in order to carry on with their research while they were arranging for the re-equipping of their own laboratories. The story of the denudation of the French laboratories was almost unbelievable. They lacked even hook-up wire. And of course, there was nothing whatever left in China. I was glad to be present at a meeting at Columbia University, where plans were made to transfer to French and Belgian authorities electrical and radio equipment from the American forces there. From the components they hoped to rebuild much of their apparatus.

I would like to pay a tribute to the extremely friendly and helpful attitude of the American scientists to their colleagues from other countries. They even wished to know if they could be of assistance to post-war scientific rehabilitation in Australia and New Zealand. But I felt that, in comparison with the war-devastated countries we were so well off that we should ask for nothing.

During those two weeks in Eastern US, I had much delightful hospitality – week-ending with Prof. Fulton at New Haven and with Prof. Harvey at Baltimore. A notable dinner was given by Gasser, Director of the Rockefeller Institute and a recent Nobel Laureate. It really was a neurophysiologist's party: – Bremer, Lorente de Nó, Lloyd, Renshaw, Fessard, besides Gasser and myself. Such occasions make landmarks in one's life.

One incident, which in journalese would be called felicitous, was the informal dinner of the New York Academy of Sciences in the Dinosaur Hall of the Natural History Museum. There is something singularly poignant in neurophysiologists having Dinosaurs as table decorations. For if the Dinosaurs could have taken the advice of neurophysiologists and gone in for higher conduction velocity in nerve fibres and better cerebral cortices, they might never have descended to mere survival in a museum!

Of course, I also had to "pay my way" by lectures and seminars. Besides lecturing to the medical classes at Columbia, Yale and Cornell, I gave seminars at Yale and Johns Hopkins. I found the seminars particularly interesting and, in the discussions, afterwards there were many pertinent criticisms and suggestions. On these occasions

279 Bremer, Frédéric (28.06.1892 – 07.04.1982) BE pioneer of neurophysiology, “sleep research”

280 Bugnard, Louis (07.07.1917 – 12.06.1978) FR professor of biophysics at Toulouse. “Medical physics”.

281 Couteaux, René Jean (23.06.1909 – 12.12.1999) FR neurocytologist. “Neuromuscular junction ultrastructure”.

282 Feng, De Pei “T. P. Feng” (20.02.1907 – 10.04.1995) CN neuroscientist/physiologist Shanghai Med. College.

one can realise that the great strength of Medical Science in US lies in the large number of enthusiastic junior workers. It bodes well for the future.

The New York Academy of Sciences held a second congress a week after the first. Since it was on "Physico-chemical Mechanisms of Muscular Contraction", it was also of great interest to me. Some of the technical methods showed how advanced American biologists were. Such methods as electron microscopy and electron diffraction patterns were used to investigate the molecular pattern of the muscle proteins myosin and actin, and from such investigations are derived possible models of the molecular mechanisms involved in muscle contraction.

All too soon I had to rush westward for a plane from San Francisco. During a few hours at Chicago, I saw the Physiology Department there, and we had a sort of round table discussion in the Library with Gerard as host, and then, after dinner with my old pupil Stephen Kuffler and his wife, I was once more on a west-bound train.

I got a message on the train at Cheyenne that the delivery of the plane was delayed for almost two weeks. So, I got off the train at Berkeley. I hoped to stay at the home of my old Oxford friend Olmsted, now Professor of Physiology at Berkeley. I telephoned, but unfortunately, he was away on long leave, and living in his home was the biophysicist Dr. B.(H?) F. Blum who knew of me and invited me to stay at the guest room below. It was a most fortunate arrangement as hotel accommodation was almost impossible. In the many days I visited Berkeley Biology and then San Francisco and as far as Stanford, Blum and I became good friends and I much appreciated the good book "Time's Arrow and Evolution" [Princeton University Press, 1951] that he gave me. I was particularly impressed by the friendly academic atmosphere of Stanford, which has a lovely rural campus some 30 miles south of San Francisco.

I would think that life was pleasanter here than at any other University I saw in America, but it was definitely less intense than in the principal eastern Universities. I much enjoyed the stimulating atmosphere of the East for the two weeks I was there, but I doubt if I would stand up to New York life for long periods. Whereas I am sure I could survive at Stanford indefinitely!

Then the plane at last was finished. The day after it left the Douglas works in Southern California on its test flight to San Francisco, we were on our two-day flight to Melbourne! On that long ocean flight, I had much time to ponder on what I had seen of American Medical Science. Its strength lies in high quality both of the staff and of the equipment in the leading Universities and Research Institutes - for example at Yale, Columbia, Johns Hopkins, Chicago, and at the Rockefeller Institute in New York, the Johnson Foundation at Philadelphia and the Massachusetts Institute of Technology at Boston. But to some extent it seemed to me that the scientific performance did not always measure up to this promise. At the scientific meetings there was not always that spirit of adventure in ideas that stimulates one to give of one's best. On the contrary the fear of making a mistake seemed to inhibit the freedom that is so essential for making a paper stimulating both in its presentation and its discussion. Only rarely, therefore, did the meetings work up to the exciting condition when one suddenly gets ideas and new visions (brain waves if you like). Too often, discussion was brought to a close by the characteristic phrase "afraid to stick my neck out", and so we had at times the presentation of much skilful investigation without any clear picture of the ideas which lay behind it. What was needed was the influence of Popper's philosophy of science. Nevertheless, despite this limitation the general impression is one of outstanding achievement in Medical Science. In that field the leadership of America stands unchallenged in the world of today. I hope that we in New Zealand may link our scientific future ever closer to our great and friendly neighbour across the Pacific.

In conclusion I would like to express my gratitude to the Rockefeller Foundation, and particularly to Drs Gregg[283] and Lambert[284] for their great kindness and helpfulness, and also to the New York Academy of Sciences for providing this great occasion for me, and to Dr. David Nachmansohn for his invitation. The Pacific flight had stopovers at Honolulu, Canton Island, Fiji and landed in Melbourne.[E] It was not a passenger flight, but was a DC-4 for the Australia Airlines. It carried 20 passengers by special arrangements, and a steward was recruited in San Francisco, who arranged for the provisioning. The pilot and navigator had not flown that route before. They used a National Geographic map of the Pacific Ocean that they had bought in San Francisco for this first flight by a commercial company across the Pacific. They presented the passengers with the map. In the lottery I was successful and have it before me, with the signatures of the passengers.

My immediate task was to get back to Dunedin, a few days late for the term! It was my first visit to US and my first contact with Euro-American world since May 1937 - almost 9 years.

BI. Investigations on monosynaptic transmission in the spinal cord

Having proposed an electrical transmission theory my task was to investigate it by the most searching experiments. Already there was recording of the potentials electrotonically transmitted from the motoneurone out along the ventral root fibres as described in **Section BE** (Fig. A36, Fig. A37). A most important addition to the recording system was provided by an extracellular electrode placed in proximity to the selected motoneurone. Such experiments had been carried out in several laboratories, but the results were complicated by injury. A great effort was made in 1946 to perfect extracellular recording by fine needle electrodes. Stainless steel or tungsten rods were ground down in a precision lathe so that the terminal 3 mm was a 50 µm diameter needle. It was insulated by baked-on enamel and the tip ground to a sharp chisel point. Problems of fixation, manipulation and insertion were gradually solved, thanks to excellent work by my technician, Charlie Morris. So, when Chandler Brooks[285] arrived from Johns Hopkins University at Baltimore on September 1st 1946, extracellular

283 Gregg, Alan (11.07.1890 – 19.06.1957) US physician, active in public health & medical research funding.

284 Lambert, Sylvester Maxwell (28.12.1882 – 10.01.1947) US public health physician and writer.

285 Brooks, Chandler McCuskey (18.12.1905 – 29.11.1989) US physiologist. “CNS-endocrine relationships”.

microelectrode recording was being used for studying the synaptic potentials set up in the *quadriceps* nucleus by an afferent volley in the *quadriceps* nerve.[A]

Chandler Brooks was associate Professor of Physiology at the distinguished Johns Hopkins Hospital Medical School under Professor Bard. He was advised by my Johns Hopkins friend, Mac·Harvey, who had worked with Kuffler at the Kanematsu to come to me in Dunedin for learning new research on the spinal cord. We had correspondence in 1945 and met in February 1946 in Baltimore. He applied for a Guggenheim Fellowship to pay for one year in Dunedin for his wife Nelle and himself, which I enthusiastically supported. He must have been one of the first Americans to come to New Zealand for research experience. They arrived by ship on September 1st 1946 and left in September 1947. He did not help in the main teaching, but gave occasional lectures and was examiner for the main examinations in November-December 1946.[B]

Our collaboration was most fruitful; with eight major papers largely concerned with investigations on synaptic excitatory and inhibitory action in the spinal cord using needle electrode recording.

Now that there had been developed a precise theory of electrical synaptic excitation, Brooks and I set about testing interaction of monosynaptically generated potentials. We now had adopted permanently the arrangement whereby the exposed spinal cord plus roots was in a warmed pool of medicinal paraffin as had been developed in the Rockefeller model. Usually, the medial and lateral *gastrocnemius* nerves were the synergic afferent inputs, the ventral roots having been cut and the spinal cord severed at L_2 to L_3 level in the decerebrated cat. We repeated the Lloyd experiment with recording of the monosynaptic reflex discharges to the two synergic inputs.

However, in several experiments where there was a very large reflex response to the conditioning input, we observed an extraordinary double response to the testing input (Fig. A40). This can be seen in the three records above the control conditioning spike, and it also appears when there is an analysis of the interacting responses in the upper records. The second wave (***β*** beta) is the usual monosynaptic response with a synaptic delay of 0.85 msec. and a decay of the facilitation with a half time of 2 to 3 msec. (cf. Fig. A37). The first wave (***α*** alpha) has a very brief synaptic delay (0.4 msec.) and is not observed with stimulus intervals longer than 1.0 msec.

Alpha responses are only seen when there is a very strong conditioning reflex. There seems to be only one explanation of this alpha response. As argued by Brooks and Eccles and illustrated in their Fig. 6,[C] it is an example of electrical synaptic transmission. The very strong conditioning depolarization causes an effective action by the cathodal phase of the testing input, C2 in Fig. A39.

This evidence for electrical synaptic excitation raised in our minds the question whether there is an electrical synaptic inhibition.

BJ. My dream of central inhibition, - the Golgi cell hypothesis.

Brooks and I had been concentrating on the mechanism of synaptic transmission in the central nervous system and were experimentally studying both excitatory and inhibitory synaptic transmission in the simplest situations, as exhibited in the spinal cord. Always I was mindful of Popper's advice that one should attempt to define scientific problems with great clarity so that there would be optimal conditions for crucial testing by experiments. For over 20 years several explanatory theories had been developed for the inhibitory action of central synapses, but none of these could be accommodated to the new precise experimental investigations by Lloyd. Thus, inhibitory synaptic action provided a particularly challenging problem for the formulation of an electrical hypothesis that would be complementary to the electrical hypothesis of synaptic excitation. Already it was known from Lloyd's excellent studies of the group **I** afferent volleys that the simplest inhibition of a reflex discharge had a time course of action that was a mirror image of the simplest reflex excitation. Lloyd called it direct inhibition. We were engaged on an electrical study of the synaptic actions of these group **I** afferent volleys hoping for an inspiration that would lead to the defining on Popperian lines of an electrical theory of synaptic inhibition.

The inspiration came on the night of December 18th, 1946 in a dream after an experiment that lasted far into the night. On awakening I fully remembered the dream, and before sleeping again I critically examined it in detail so as to impress it on my memory. The next morning, I remembered it fully and wrote it out with diagrams before going to the department where I excitedly discussed it with colleagues, particularly with Chandler Brooks. To my delight it accounted well for all the experimental findings on inhibition and it could be illustrated in a simple model that could be shown to exhibit all the properties that had been experimentally demonstrated for synaptic inhibition of the simplest pathways in the spinal cord. As soon as it was provisionally written up, I sent a copy to Karl Popper for his critical comments.[A] He was enthusiastic, not because of its evident success at the present level of knowledge, but rather because of its generality and of its challenge to new types of investigation. So, it was written up in a form matching the earlier theoretical paper on synaptic excitation and similarly was duly published in Nature on June 7th, 1947. This is the only scientific dream that I have ever experienced.

Fig. A41 illustrates the simplest situation in which the postulated electrical inhibition could occur. The excitatory input, E, to a motoneuron, M, is inhibited by an input I, with the same time course of action as the excitatory input, E. As partly illustrated in Fig. A37, the facilitation responses to the E synaptic action decline from an early maximum to zero at about 15 msec. interval. In the electrical inhibitory hypothesis, the distributed currents generated by the subliminal excitation of the G neuron (the Golgi cell) by the I input would have the same time course as the E input to the M neuron. It is proposed that the I-inputs to G neurons produce too weak a depolarization to evoke impulse discharges. For the whole duration of the subliminal excitation of the G neuron, currents will flow that set up anelectrotonic foci on the M cell, as at X. These foci of hyperpolarization would act to prevent the excitatory action of the E input to M from setting up impulses. Thus, an inhibition would be produced by the flow of the electric currents generated by the subliminal activation of the G cell. It would have a time course similar to that of the excitatory synaptic input, and thus be in accord with the time course originally described by Lloyd in 1946. For several years the "dream" hypothesis survived testing by the extracellular recording techniques on the simplest inhibitory actions in the spinal cord, as shall now be described.

BK. Experimental testing of the Golgi cell hypothesis of inhibition

Focal recording by needle electrodes of the potentials generated by a *quadriceps* group **I** afferent volley and by a group **I** volley in the antagonist *hamstring* nerve gave good testing conditions. In order to have the most extensive extracellular study the recording needle electrode was inserted along a series of tracts through or close to the concentration of motoneurons activating the *quadriceps* muscle as is illustrated for the 4 tracks in Fig. A42. The extent of the *quadriceps* nucleus is outlined by the dots in the inset, and the broken line shows the boundary between the grey and white matter of the spinal cord.

The negative focal synaptic potential for the excitatory Q (*quadriceps*) volley is seen in Fig. A43a after an initial brief positivity. In Fig. A43c the inhibitory hamstring volley sets up a long low positivity. Superposition of the two volleys in Fig. A43b shows that the I volley had a very small depression of the E response in Fig. A43a. A volley on a cutaneous nerve has a complex polysynaptic inhibition. In Fig. A43d, e, f it produced a much larger positive focal potential which was also prolonged as in Fig. A43f. These positive focal potentials are in accord with the Golgi cell hypothesis. However, it was realised that extracellular recording could not be crucial, even when done by the finest needle recording of field potentials.

Another testing procedure for the Golgi neuron hypothesis utilised the neuronal responses generated by antidromic invasion as simply diagrammed in Fig. 3B. In Fig. A42 the focal potentials generated by an antidromic volley into *quadriceps* motoneurons have been recorded at sites along 4 needle electrode tracks. As shown in the inset track B just grazed the *quadriceps* nucleus on the lateral side. At depths of 1.5 and 1.8 mm in particular there was the predicted initial positivity as the antidromic impulses propagated up to the motoneurons and a large negative potential, beginning about 0.3 msec. later with the neuronal invasion. Tests showed that only some of the motoneurons were antidromically invaded, there being with the others impulse blockage at the axon-soma junction.

This blockage occurred because of the large increase in the neuronal membrane that had to be invaded by the antidromic impulse at the axon-soma junction (Fig. A08). There was developed the concepts of non-labile and labile for the antidromic responses. The non-labile were generated by impulses on the motor axons and were about 0.5 msec. in duration, and the labile by the soma and dendrites with a spike duration of about 1 msec. Lability was demonstrated both by the increased invasion when there was depolarization by synaptic activation of the soma and dendrites and by the decreased invasion when there was neuronal depression by a preceding antidromic invasion.

It was of particular interest that inhibition of *quadriceps* motoneurons decreased the antidromic invasion, but these were small differences when compared with the inhibitory depression of synaptic excitatory responses. These differences could be explained on the Golgi neuron hypothesis. In particular the inhibitory action by the assembly of anelectrotonic foci on the motoneurons gave a satisfactory account of the observed inhibitions, whereas other inhibitory theories were ineffective, particularly for the direct inhibition first observed by Lloyd with a time course of decay similar to that given by monosynaptic excitation.

However, it was recognised that even our refined recording of extracellular responses did not deliver sufficiently discriminative results for crucially testing synaptic theories. Nevertheless, extracellular recording gave field potentials which suggested that antidromic propagation into a motoneuron did not extend to the finest dendritic terminals. This concept was of importance, and is still valuable in the attempt to understand the neuron. The large positive potentials in Fig. A42 tracks were recognised as being due to injury of the *quadriceps* motoneurons by the penetrating needle electrode. Track B avoided this serious complication and as we have seen gave field potentials in accord with prediction. On occasion the antidromic potential was dominated by a brief positivity of up to 0.5 mV that was interpreted as the all-or-nothing response of a single injured motoneuron. We were on the way to consider the possibility of intracellular recording from motoneurons. Many years before, Graham[286] and Gerard had recorded from single muscle fibres by a fine glass micropipette.[**A**] However, the resistance of several megohms [MΩ] was far too high for the amplifiers at that time. All they could record were the membrane potentials at rest in various ionic media. As often happens in science, a crisis in investigation leads to the discovery of the way on. However, before going on to that exciting stage of my scientific life, there are some earlier ideas and discoveries in the Dunedin period that were also important in my scientific life, so I shall briefly describe them to clear the air for the great investigation.

The experimental set up in Dunedin enabled a series of precise extracellular studies not only on synaptic transmission as just described, but also on electrical properties of neurones continuing on from the spike potentials. As described in Sections **Z** & **AC** above, Gasser and associates had studied the after-potentials, N and P, that followed the spike potential of a nerve, and such potentials had been recognised in sympathetic ganglia. The excellent conditions for recording the after-potentials of motoneurons were exploited in the years 1946-7 (Brooks) and 1948 (Downman[287]) in addition to the studies already described in testing the Golgi neuron hypothesis of inhibition.

As already described with antidromic invasion of motoneurons there is an initial non-labile axonal spike potential that immediately leads into the large labile spike potential due to invasion of the soma plus dendrites. The subsequent positive after-potential was similar to that of the nerve, but much larger. It was associated with depressed excitability of the soma both to orthodromic testing and to electrical stimulation. No new properties were introduced in accounting for these responses.

286 Graham, Judith Ethel (01.06.1919 – 13.07.1975) US(J) Blood physiologist. “Haemophilia - factor VIII”.

287 Downman, Charles Beaumont Benoy (22.08.1916 – 04.01.1982) UK physiol. Prof. Royal Free Med. School.

These investigations, both the techniques and the interpretation were most valuable when we essayed intracellular recording, from 1951 onwards, but in 1948 that was an unknown future.

In the subsequent paper orthodromic input was substituted for antidromic. Again, there was a large positive after-potential attributed to the impulse discharges of the soma-dendrite complex. The one difference was that after the duration of the antidromic depressed excitability (about l00 msec.), there was a much longer depression of response as revealed by a later testing orthodromic input. At that time no satisfactory explanation was provided, but now it can be recognised as being due to a depletion of the transmitter substance, as will be described later. We have now reached the end of the experimental testing of the electrical excitatory and inhibitory hypotheses, that was published in eight major papers. These hypotheses had not been falsified for the synapses on motoneurons, and were ready for crucial testing with intracellular recording in 1951.

BL. My Colleagues in the Physiology Department

I have been so obsessed with the problems of developing the Physiology Department (Section **BD**) that I have overlooked the story of the subsequent years. Laurence Malcolm continued as the Senior Lecturer, but I had great difficulty in recruiting additional staff. Even New Zealanders thought Dunedin too remote, so few medical graduates were available for part-time teaching. Later I did have the BMedSc students to help in the practical and discussion classes. So those early years (1944-1947) were a heavy burden. I sensed that Laurence Malcolm wanted some temporary overseas arrangement, and I was able through the kind help of my good friend Brian McSwiney to arrange an exchange of Senior Lecturers. Charles Downman came to me in 1948 and Malcolm did his work at St. Thomas's Hospital Medical School in London, each carrying his position and salary. Charles Downman and his young wife Thais Barakan[288] were most attractive colleagues in Dunedin, and we published many papers related to excitatory and inhibitory synaptic action in the spinal cord particularly on antidromic invasion. of motoneurons, as has been described in Section **BK**. They returned to London at the end of 1948, where I visited them often.

However, Malcolm did not carry out his obligation to return. He tried to stay in England as long as possible with salary from his Dunedin position and was applying for jobs in England, even asking me to write testimonials for him! He never returned, and managed eventually to become Professor of Physiology at Aberdeen.

I had during 1948 a highly gifted New Zealand scientist as Senior Lecturer, Vic Macfarlane[289], a top graduate in both Chemistry and Medicine.[A] We published in 1948 a great paper describing biophysical studies on seven anticholinesterases acting on the curarized frog *sartorius*. This investigation answered all the criticisms that had been levied against the ACh transmission hypotheses by me and others. Vic also gave a

288 Barakan, Thaïs Helèna (1917 –2005) Physiologist (and wife of Charles Downman).

289 Macfarlane, Walter Victor (27.09.1913 – 26.02.1982) NZ Physiologist, later Professor in Australia.

comprehensive set of lectures for the Senior Class. Unfortunately for me at the end of 1948 he left with his dear wife Pamela, an artist, to become Professor of Physiology in the University of Queensland, where I often visited them. So, I was at the lowest point of my staffing, being the only Academic member of the Department to continue from 1948 to 1949. Relief came just in time when Archie McIntyre came on March 8th 1949 as Senior Lecturer and he was my most able right-hand man through the remainder of my Dunedin period, and appropriately replaced me as Professor in 1952.**B** Also, I had in 1949 my earliest pupil Marianne Fillenz as a Lecturer for one year before she left for her career at Oxford.

Now I must introduce you to Ainsley Iggo[290] who became the most distinguished of my Dunedin associates.**C** As he often recalls, it all started with spending a penny! It was for the telephone call from Dunedin Railway Station as he was passing through to Invercargill. He would like to see me on the return journey a few days later in order to discuss coming for a year's study of Physiology. He had the 1st place in the M.Agr.Sc. examination for New Zealand with a scholarship for 2 years at the Rowett Institute in Scotland, but felt the need for more Physiology. I was of course enthusiastic and told him of a B.Sc. course I was instituting in Physiology. So, he did the course. My daughter, Rosamond[291], was also a student for this first year at the end of her science course. By that time, Wilfrid Rall[292], distinguished in Physics and Biophysics, had arrived from US and he helped with Biophysics, being appointed Lecturer in Biophysics. The course was Biophysics plus the Senior Medical Year. Ainsley did well and stayed on for another year to do research and further study in Physiology. He and Betty McCurdy, a Lecturer in Biochemistry, became good friends. Then in 1951 he left for Scotland to carry out a most ambitious research program on the small non-medullated fibres, the C fibres, that innervate the sheep's rumen. He struggled on heroically at the Rowett Institute where the facilities were inadequate. Eventually I got David Whitteridge to give him a position in the much better equipped Department of Physiology at Edinburgh University. From then on it was a wonderful success story for Ainsley. He was the first to record from and study the C fibres, and for this became soon Professor of Physiology in the Department of the Veterinary Medicine, Edinburgh University and in 1978 FRS. In 1950 I had managed to get Betty a position at Oxford, in Hugh Sinclair's Nutritional Institute, where she continued with the Biochemical research from Dunedin. She and Ainsley were married in 1952. We have often visited them in their Edinburgh home, particularly when I was giving the Gifford Lectures at Edinburgh University in 1978 and 1979.**D**

In 1948 I had an enquiry from Dr. Wilfrid Rall, a Physicist and Biophysicist, if I had a position for him to do research and teaching in Biophysics. He wanted to come from US in order to avoid further secret work on nuclear weapons. So, in early 1949 he came

290 Iggo, Ainsley (02.08.1924 – 25.03.2012) NZ neurophysiology Professor in Edinburgh. “C-fibres”.

291 Mason, Rosamond M. “Rose” (15.06.1929 – 03.11.2024) UK neurophysiologist. J. C. Eccles’ eldest daughter.

292 Rall, Wilfrid (29.08.1922 – 01.04.2018) US neuroscientist at NIH. Developed concept of “cable theory”.

to Dunedin with his attractive wife Ava Lou. He developed and taught a course in Biophysics and we published several papers. They stayed for many years before returning to the Neuroscience department of the Institute for National Health and Medical Research at Bethesda.**E**

In 1945 I recruited a good electronics technician, Peter Suckling[293], who had an M.Sc., and he helped in electronics. Chandler Brooks persuaded him to accompany him to Johns Hopkins when he left in Sept 1947. Suckling stayed on there, becoming a qualified neurophysiologist and accompanied Chandler when he went to be Professor in the Brooklyn Medical School. So, for a while I had no expert electronics engineer. This deficiency was dramatically changed when, through the good offices of Charles Focken, Jack Coombs came from the Physics school. He was one of those shy geniuses, and played a key role firstly in Dunedin and then for my 14 years at the Australian National University at Canberra, my next port of call. He understood exactly the optimum electronic design to give all the facilities for stimulating and recording that we could want, even offering new facilities beyond what we could have imagined. He brought with him as his assistant a most skilled electronics technician [Arnold Annand]. By 1951 they had constructed the perfect instrument - far better than anything in the world in those days before the big instrument companies took over with transistors. We called his first instrument the ESRU - the Electrical and Stimulating Recording Unit, but that is a later story. Besides this greatly sophisticated equipment Jack Coombs was excellent in every aspect of electronic design. In 1951 as a Junior Lecturer, I had a medical graduate, Lawrence Brock[294], initially a mathematician. He became very interested in micro-electrode recording techniques and concentrated on drawing the fine micropipettes that were essential for intracellular recording. Associated with the Physiology department was the thyroid investigation unit of Sir Charles Hercus, with Purves[295], Griesbach[296] and Kennedy[297]. Griesbach gave special lectures for Physiologists on the thyrotrophic hormone. He was an excellent histologist and identified the functions of the constituent cells of the anterior pituitary based on physiological reactions.**F** He and his wife were most charming and cultural, and he was an accomplished pianist on his fine grand piano. Myra Hess[298], a world-famous pianist, stayed with them and gave most enjoyable recitals. Kennedy was also a dedicated

293 Suckling, Eustace Edgar "Pete" (04.08.1915 – 12.07.2005) NZ physiology prof. "ultrasonic microscopy".

294 Brock, Lawrence Gordon (24.10.1923 – 10.09.1996) CN/UK neurophysiologist, surgeon & neuroradiologist.

295 Purves, Herbert Dudley (25.09.1908 – 15.04.1993) NZ chemist, mathematician, Thyroid research.

296 Griesbach, Walter Edwin (17.10.1888 – 10.08.1968) DE(J) Professor, physiologist "Congo Red Method".

297 Kennedy, Thomas Henry "Tom" (19.11.1916 – 15.06.1989) NZ chemist in Purves' Thyroid research group.

298 Hess, Julia Myra (25.02.1890 – 25.11.1965) UK(J) London concert pianist. "WW2 lunchtime concerts".

music lover, and had a great record collection of Bach[299] and Chopin.[300] I tell of these happenings in Dunedin to illustrate our cultural life.

BM. Repetitive Synaptic Stimulation and Synaptic Plasticity

I had recognised for many years that in my concentration on elemental synaptic transmission in the central nervous system I had largely neglected the normal manner of synaptic operation in the brain, which is to repetitive stimulations. All receptor organs fire repetitive impulse discharges into the brain and spinal cord and all neurones almost invariably act by generating repetitive impulse discharges to other neurones or out to muscles (Fig. A09, Fig. A12). Reference should be made to Fig. A01 for the simplest neuronal circuitries. The improved techniques gave an excellent opportunity for Rall and me to study in 1950 the repetitive activation of synapses: the presynaptic impulses, the synaptic potentials and the impulse generation. In Fig. A37 there has been illustrated the synaptic potentials generated by two afferent volleys at various intervals.

Even up to 200/sec there was a good correlation of the presynaptic volleys with the synaptic responses observed either with electrotonic propagation to the ventral root (Fig. A44) or with focal recording. The successive synaptic potentials summed to give a higher depolarization for the second response at frequencies of about 100/sec. However, there was antagonism by the underlying after-hyperpolarization, so that there was a plateau that declined after the tetanus to the prolonged hyperpolarization. The responses resembled those given by peripheral nerve. Impulse generation rapidly declined during the tetanus after a brief initial phase of potentiation (Fig. A45). Inhibition as well as the after-hyperpolarization contributed to this depression of impulse generation.

Following intense repetitive synaptic stimulation Lloyd discovered a large and prolonged increase in monosynaptic reflex discharges. This post-tetanic potentiation was of great interest as a display of what we may call plastic responses of synapses. This plasticity offered the attractive possibility for being a synaptic basis of memory. Lloyd's observations were fully confirmed by Rall and me with post-tetanic potentiations persisting for minutes after severe tetani. It was tentatively suggested that the potentiation was due to an increase in presynaptic effectiveness, perhaps due to swelling of the bouton illustrated in Fig. A07. However, the duration of the potentiation was no more than minutes after severe tetani, as can be seen in Fig. A46A, series N, where the potentiation was almost over by 1 min. 45 sec. Hence post-tetanic potentiation does not provide an attractive base for a theory of memory.

Here was a challenge that McIntyre and I accepted, namely, to search for indefinitely prolonged plastic changes. We got the idea that we should look for plastic changes that occurred in synapses subjected to a prolonged silence of all excitatory inputs. This was accomplished by extra-ganglionic section of several dorsal roots, usually the 6th, 7th and 8th post-thoracic roots on one side. That delicate operation left intact the ganglia with

299 Bach, Johann Sebastian (31.03.1685 – 28.07.1750) DE late Baroque period musician, organist & composer.

300 Chopin, Fryderyk Franciszek (01.03.1810 – 17.10.1849) PL Romantic period composer & virtuoso pianist.

the dorsal root fibres, but prevented all monosynaptic input to the motoneurons of such muscles as *quadriceps*, *hamstring* and *gastrocnemius*, and this silence was maintained for 21 to 40 days. Then these inactive synapses were tested for effectiveness relative to the control side. In Fig. A45A the control (C) monosynaptic responses of the operated synapses (0) were elicited by maximum dorsal root volleys. They were characteristically much smaller than with the control synapses c, of the normal synapses, series N.

As shown in Fig. A45A and Fig. A45B, after a standard conditioning tetanus, the post-tetanic potentiation of the reflex evoked from the disused roots ran an abnormally slow time-course, reaching a later summit and decaying much more slowly. Usually, the time scale has been two to three times longer than normal. Furthermore, after a conditioning tetanus the reflex evoked from the disused roots was abnormal in that it did not return to the initial size, but exhibited a residual potentiation which continued for hours (cf. Fig. A46B).

In Fig. A46B the post-tetanic potentiation of the N synapses plotted as crosses was almost over in 1 min 45 sec, whereas with the N synapses the post-tetanic potentiation, plotted as open circles, continued for much longer, being still almost double in size at 7 min 45 sec. Eventually at almost 500 seconds the responses stabilized far above the initial level, as shown by the two lower broken lines. The potentiation had been maintained for 2 hours. It was further potentiated by a second tetanus shown by the filled circles, the post-tetanic potentiation declining to a still higher maintained potentiation, as shown by the uppermost broken line.

An approximate value for these maintained potentiations was a decay to half in rather more than 3 hours, which would make it about 160 times slower than the decay of the PTP of normal synapses after a similar conditioning tetanus. This was a great advance in the duration of the plasticity. It could be argued that disused synapses were a poor model on which to build a theory of memory. But that misses the point. The significance lies in the demonstration that following activity of disused synapses there was a very prolonged plastic change of many hours' duration, almost 200 times longer than for a normal PTP, which is a great advance on the way to a neural explanation of memory.

There was a preliminary report in Nature in March 1951, and the completed paper with many collateral studies was submitted in mid-1951 to the Royal Society for publication in the Proceedings. Inexplicably it was rejected after a long delay. We were so deeply disturbed, but that is the trouble that one sometimes has with stupid referees! We immediately submitted the paper to the Journal of Physiology, where it was received on February 3rd, 1953. It was very quickly accepted and published in 1953.[A]

Now comes the dramatic climax. Lord Adrian was President of the Royal Society, and in his Anniversary Address on Nov. 30th 1953, he made a most eulogistic reference to our paper, quoting it as one of the landmarks of the year because it gave hope that plasticity of the brain could be the basis of memory. Archie and I hoped that the Royal Society referee, that rejected our paper, got the message from the President! I never told Adrian this story and of our gratitude for his appreciation.

It should be mentioned that 20 years later synaptic plasticity was for the first time investigated at a high level of the CNS, on the hippocampus, firstly by Lømo[301] (1970), then in 1973 in the classic paper by Bliss[302] and Lømo. In our paper we did suggest that the hypothesis of plasticity as a model for memory should be tested at higher levels of the CNS, but that the techniques were not yet adequate. It was Lømo who made it! It seems that this paper on disuse and plasticity has never been duplicated. Technically it is most difficult to sever the dorsal root and yet leave the dorsal root ganglion undamaged, in order to maintain the dorsal roots to the spinal cord. Altogether we had over 10 successful experiments and no failures. This study was of significance because it demonstrated the plastic changes produced by disuse and the compensatory effect of activity on disused synapses. It led on to later trophic studies on synapses.

BN. The Australian National University (ANU)

During the late 1940's I was hearing in Dunedin of the ambitious project of establishing a Research University at Canberra. It eventually came to be known as the Australian National University.[A] It was particularly associated with Mark Oliphant[303], Australia's great physicist, a Professor at Birmingham, England, and Howard Florey, Professor of Pathology at Oxford and becoming famous for his great success with penicillin. Successive Prime Ministers, Chifley[304], then Curtin[305] and finally Menzies[306] all gave generous support. Still, it remained rather nebulous. Canberra was just a provincial town of 20,000 in the early post-war years, though it had a provisional Parliament House and Government House and the Prime Minister's Lodge. I was never consulted about the setting up of the Australian National University. However, I was invited to a kind of pioneer conference that Prof. R.D. Wright[307] of Melbourne University organized to give some Academic start to the ANU, as it came to be called. The principal participant was Professor R.W. Gerard who came from Chicago for the conference. He had long ago stayed with me in Oxford and then I later met him in Chicago in 1946.

The program was evolved by Wright. In a letter he wrote to me on August 7th 1947 the symposium on the nervous system was organized around introductory presentations by Gerard Shaw, a pharmacologist, and me, on some general topics: Neuronal Metabolism, Excitation, Inhibition, Synaptic Transmission, Integration in the Nervous System. Chandler Brooks stayed on in Australia on the way back to US. At the Symposium there were several younger neuroscientists of Australia notably Morell

301 Lømo, Terje (03.01.1935-) NO neurophysiologist. Synaptic plasticity. “Long Term Potentiation, LTP”.

302 Bliss, Timothy Vivian Pelham (27.07.1940-) UK neurophysiologist. Worked with Lømo on LTP.

303 Oliphant, Marcus Laurence Elwin “Mark” (08.10.1901 – 14.07.2000) AU physicist & humanitarian.

304 Chifley, Joseph Benedict “Ben” (22.09.1885 – 13.06.1951) AU Labour politician. Prime Minister 1945-49.

305 Curtin, John (08.01.1885 – 05.07.1945) AU Labour politician. Prime Minister 1941-45.

306 Menzies, Robert Gordon (20.12.1894 –15.05.1978) AU “UAP politician”. Prime minister 1939-41, 1949-66.

307 Wright, Roy Douglas “Pansy” (07.08.1907 – 28.02.1990) AU physiologist. Melbourne University Chancellor.

Draper[308] of Adelaide and Barry Wyke[309] of Sydney. About 20 participants in all. We met in the lecture room of the Institute of Anatomy at Canberra and stayed at the Hotel Canberra from 8th to 12th September 1947. The physical arrangements were quite good with a special gadget for converting all the conference onto a magnetic wire recording. It was just before the days of magnetic tapes. Morell Draper took charge of the recording and there was to be a typescript of the entire conference for eventual publication. I was dubious about this as most of the conference did not measure up to international publication standard. However, all was resolved when I heard that Morrel Draper did not understand the read-out arrangements and had cancelled the whole recording! So, the whole conference is no more than a dim memory! One good outcome was that Gerard visited Australia and then came to see me in Dunedin for several good days!

After the ANU Symposium I was a rather distant observer of the further developments of the ANU. In my autobiography it is appropriate that I give an account restricted to my experiences, which were negligible. In my later years at Dunedin, I realised that with the heavy load of teaching and examining I would not be able to compete effectively in the international competition. I heard that the ANU had an important component, the John Curtin School of Medical Research in the planning, and that there were to be four Professors, Biochemistry, Physiology, Microbiology and Medical Chemistry. Eventually three were appointed and the Professors worked as guest professors in England or Australia. Then Florey visited me in Dunedin and I showed him our Dunedin performance. But he thought of another kind of Physiology than what I was doing. I did hear that he reported at Canberra that I was doing so well in Dunedin that he hesitated to disturb me by an ANU offer.

However, in January 1950, thanks, I believe, to my good friend Wright, I was invited to come to Canberra to discuss the Physiology appointment at a meeting of the Vice-Chancellor Sir Douglas Copland[310] and the Council of the ANU. I remember that in outlining my research program I spoke about studies in neural plasticity and memory with trophic factors revealed by chromatolysis and also studies on synaptic mechanisms and transmitters. I did not even suggest intracellular recording that came so soon afterwards to dominate my Canberra years. I was too unsure if I could manage it. I accepted their Physiology invitation.

My concern at that time was how soon could temporary laboratories be arranged, and I hoped even for space in the basement of the well-constructed Institute of Anatomy. Meanwhile I was to continue in Dunedin until the end of 1951 and then have an extensive "study leave" in US and Britain. So, for the teaching years 1950, 1951 I was more relaxed, particularly as Archie McIntyre was doing so well. I felt relieved that the intense teaching was soon to end. I should have been more concerned about the

308 Draper, Morrell Henry (10.07.1921 – 01.10.2005) AU physiologist/toxicologist. "Meta demography".

309 Wyke, Barry D. (?-?) AU Professor of neurology/neurosurgery and Laryngeal physiology Uni of Sydney.

310 Copland, Douglas Berry (24.02.1894 – 27.09.1971) NZ/AU economist. Founder of think-tank CEDA.

construction of temporary laboratories in the open grassy slopes dotted with trees. It all took longer than I had anticipated because the Canberra construction capacity was in terrible demand in those years devoted to building a capital but that is for a later Section.

BO. The Human Person

In **Sections C, F & Q** I kept referring to the great spiritual mystery, the human self, that is unique for each of us and that is distinguished from the brain in the dualist philosophy that I hoped to formulate at the end of my life-long quest. That faith was leading me on like a beacon light through all my Dunedin life and was specially guiding me in some of my Dunedin activities, concentrating though I was on basic neuroscience.

Right from my first year at Dunedin I introduced at the end of the Senior year six lectures on the human person. There was time for this, and the students were told that it was a cultural addition without examination. The course dealt with self-consciousness, free will and moral responsibility, the uniqueness of the self, values, feelings, compassion, dedication, love, hope and the meaning of life, stressed the human family as a living entity in which the highest values come to be expressed. The students attended well. Then in 1948 there was a change in the Medical Course Structure that the Senior year was reduced from 3 to 2 terms. So, I told the class that there would not be time for my optional lectures on the Human Person. It was a pleasurable surprise when the representatives of the students asked me to give the lecture course at all costs! So, I gave the lectures after-hours at the end of their strenuous day and there was a full attendance of enthusiastic students year after year until I left Dunedin. I have since heard of other such courses for medical students. If there were not such an input of spiritual values in the medical course it would be no different from a Veterinary Course, just learning to treat sick animals!

In 1948 I gave the Graduation Address on the occasion of the graduation in all Faculties of the University. For many years I had been reading and discussing "The Idea of a University" to give the title of Cardinal Newman's[311] great book that I knew well.[A] I here assemble five short excerpts from my lecture as illustration of what I said.

1. *We adventure forward in time, and life should be a great spiritual adventure. We find ourselves here on this great adventure cast up together on a planet for the brief span of our lives.*
2. *Has the University trained you for such a life of adventure and leadership?*
3. *When a student is admitted to a university, he becomes a member of a community which exists to serve the development of culture and the advancement of knowledge. He has his own part to play in its life and work.*
4. *You will no doubt in retrospect see values in your university life which you did not suspect while you were there. I hope that this address will serve to illuminate that retrospect.*

311 Newman, John Henry (21.02.1801 – 11.08.1890) UK Catholic Cardinal. “The Idea of a University”, 1852.

5. So now the University, having given you this seal of graduation says "Go forth into the world trained for this great adventure of life, not replete with all you need to know, but trained to understand, to think critically and imaginatively, to judge impartially, to live up to ideals, and above all to adventure, so that you may continue to learn in all humility throughout your life".

John Passmore[312] came at Popper's suggestion to be Professor of Philosophy at Dunedin after Findlay and Raphael, who had not stayed long. I got to know him well, but recognised that he was a devotee of Gilbert Ryle[313] with Ryle's book "The Concept of Mind" as his bible![B] His language-based philosophy was a subtle materialism, and I found it empty, as also did Popper. Ryle and Passmore took no interest in the central role of the brain in philosophy. In early 1951 I was asked by Passmore to give a lecture in his senior philosophy course. I realised that it was a tough assignment and worked hard on it with Popper's ideas to help me. Following the lecture, I had at least one hour of critical discussion, but it seemed that the philosophy students exulted in their ignorance of the brain, which, unfortunately is usually still the case. I believed that, despite the criticisms, I had made some progress in a dualist solution of the mind-brain problem, so I wrote up my story and it was published in Nature on July 15th 1951.[C]

I had at least broken my silence on the spiritual nature of the Self. In all those years since my **Sections C & F** I had read widely on the Philosophy of the human person. However, I was reticent to publish in that pervasive materialist atmosphere that was dominant in the 1950's and 1960's. In Australia and New Zealand, it was particularly bad with the inheritance of John Anderson's[314] dominating materialism. In retrospect I think I was wise not to exhaust myself in combating materialism in all its guises, behaviourism, conditioning, logical positivism, Skinnerism[315] etc. Eventually Popper and I published in 1977 "The Self and its Brain" that has become a bastion of dualism![D]

As a sequel to my Passmore lecture in 1951 I was an invited speaker at the great occasion of the Second Centenary of the Académie Royale de Belgique in 1973, of which I am an Associé.[E] Passmore had been invited as a participant and at the end of my lecture told of my lecture 22 years earlier in Dunedin! He made the absurd statement that he had the "most varied philosophy department that has ever existed", but for once they were united in rejecting the dualism of my lecture. At least I had the consolation that Passmore linked me with Popper! Furthermore, the lecture that Passmore was so extravagant about, can be seen in Nature 1951, as stated above.[F] It was merely a beginning, and much progress has been made in the next 40 years on the physiology of the cerebral cortex so that the mind-brain problem becomes enormously developed and illuminated, as will be recognised in later Sections.

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312 Passmore, John (09.09.1914 – 25.07.2004) AU philosopher. Book: "Man's responsibility for nature".

313 Ryle, Gilbert (19.08.1900 – 06.10.1976) UK philosopher/critic of Cartesian dualism; "The Concept of Mind".

314 Anderson, John (01.11.1893 – 06.07.1962) AU Sydney Univ. philosopher. Founder of "Australian realism".

315 Skinner, Burrhus Frederic (20.03.1904 – 18.08.1990) US psychologist/behaviourist. "Radical behaviourism"

BP. The ionic mechanisms of the synapse

In 1947 I wrote by invitation an article "Conduction and Synaptic transmission in the nervous system" for the Annual Review of Physiology volume 10, 1948. It was supposed to present a critical appraisal of the publications in this extensive field during the preceding year or so. As stated on the first page of the enormous 2-volume monograph by Lorente de Nó did not make the dead-line - for which I was truly grateful - as I mentioned in my letters at that time, with ironical comments by Katz!

The most revealing feature of the review was in the attempt to account for the ionic mechanisms participating in the nerve impulse. Hodgkin and Huxley[316] (1946) had shown that in impulse transmission in the crab axon there was a leakage of potassium ions that was sufficient electrically for the nerve impulse. It stated on p. 101 that "the escape of potassium during activity must be associated either with a transient membrane permeability to sodium (so that ingoing Na^+ ions exchange with outgoing K^+ ions) or with a diminution of the intracellular indiffusible organic anions". And later I asked "how far is the action potential attributable to a transient period of exchange between external Na^+ ions and internal K^+ ions"? I got close to the ionic mechanism, but still did not grasp it fully. That was already being done by Hodgkin and Katz, and I heard about it in a letter Katz wrote to me on Aug. 25th 1947, that I replied on Sept. 23rd 1947.

The review gives an account of the electrical properties and local responses reported by Hodgkin, Rushton and Katz for non-medullated nerve fibres that is of great importance in our understanding of the responses of the central nervous system, where neurons, dendrites and often axons are non-medullated. Thus, before intracellular recording was accomplished, extracellular studies had been most productive. This has already been recognised in **Sections BE, BI, BK & BM**.

I was much indebted to Bernard Katz for his many letters of 1947-1950 that kept me well informed on the wonderful ionic studies on the squid giant axons that Hodgkin, Huxley and Katz were carrying out at the Marine Biological Laboratory at Plymouth. This work was to form the basis of my synaptic studies on intracellularly recorded motoneurons in 1951.

Fig. A14 illustrates very simply the concept of the ionic mechanisms of impulse propagation that was developed by Hodgkin, Katz and Huxley from 1948 to 1952. The experiments were carried out on the surface membranes of giant axons subjected to various concentrations of sodium and potassium ions externally, and later internally. Hodgkin and Huxley developed a mathematical model that illuminated and provided the basis of the ionic hypothesis of impulse transmission. In Fig. A14C the impulse progresses to the left because the surface membrane is depolarized by electric currents flowing into the active membrane with its reversed polarization. As shown in Fig. A14A at a critical stage of depolarization the membrane becomes very permeable to Na^+ ions that flow down the steep gradient even to reversing the membrane potential

316 Huxley, Andrew Fielding (22.11.1917 – 30.05.2012) UK biophysicist. "Action potential" (NP 1963).

at the summit of the spikes. Already there is the opening of the K^+ ion channels to restore the membrane potential.

In 1950 there came the revolution in electrical recording that resulted from the cathode follower amplifier, thought up, I was told, by Andrew Huxley (see Katz, 1966, p. l6). The resistance of a micropipette that penetrated the surface membrane was up to 10 MΩ when filled with 3 M KCl. The tip diameter was 0,5 µm, in order to minimize damage of the membrane. However, with conventional amplifiers there was catastrophic distortion of any recorded potential transients. Inputs from the micropipette of even 10 MΩ resistance were distorted very little when fed into a cathode follower amplifier.**[A]** The initial studies were done by (Nastuk[317] & Hodgkin, 1950) on microelectrodes inserted into isolated muscle fibres, but immediately after, Fatt & Katz (1950a,b, 1951) used the microelectrodes inserted into the region of the motor endplate to carry out systematic studies of those synapses that went far beyond the pioneer work of Kuffler (1942) almost 10 years earlier on the unitary nerve-muscle fibres preparation (Fig. A26 **Section AL**).

I immediately appreciated the power of intracellular recording to produce definitive results on synaptic transmission in the spinal cord. It was certainly a challenge. Already in **Section BK** it was mentioned that with our crude needle electrodes there was sometimes a stable unitary response that undoubtedly was due to a single badly injured motoneuron. So, we had the basic mechanical techniques for intracellular recording from motoneurons. Two more techniques were required and my two associates, Jack Coombs and Lawrence Brock soon provided them. Jack Coombs built the cathode follower amplifier and all the ancillary equipment and Lawrence Brock meticulously solved the production of micropipettes with a tip diameter of 0.5µm. When filled with 3M KCl the resistance was 5 to 10 MΩ, as was to be expected. The microelectrode track for insertion has been illustrated in Fig. A42, and Fig. A51A which give some picture of the problem of inserting the microelectrode into a motoneuron without seriously damaging it. An important guide for the insertion was to have antidromic stimulation every second of these motoneurons that were the targets, sometimes the antidromic stimulation was switched sequentially from one motor nerve to another, e.g., from *quadriceps* to *hamstring* to *gastrocnemius* nerves. So, in the experiments the completely blind insertion was guided by the antidromic responses extracellularly recorded as in Fig. A42 track B. Penetration was signalled by the appearance of a negativity of about 70 mV in the continuously running DC record, and by the reversal of the antidromic spike potential. However, the situation was usually quite complex with partial insertion and surface membrane damage. It was like fishing - one had to play with the neuron with the cleverest micro-movements, guided by the DC potential and the antidromic responses. Sometimes the microelectrode would just graze a neuron without penetration. In imagination one conceived of neurons as coyly swaying to

317 Nastuk, William L. (1917 – 06.11.1986) US physiologist. "iontophoresis" & microelectrode techniques.

avoid penetration by the approaching microelectrode! An American, Marmont[318], wrote of his microelectrode penetrations of giant nerve fibres as being micro-rapes! There was great satisfaction when one eventually achieved a stable penetration, as shown by a steady membrane potential of about -70 mV, and steady synaptic potentials and spike potentials.

It has to be appreciated that in those far-away days in Dunedin we had to make everything in the laboratory with our technicians and ourselves. The only bought equipment was the film camera in Archie's laboratory. Now that Jack Coombs had taken over the electronics design and manufacture with Annand, mechanical problems were our chief concern - the fixation of the spinal cord of the cat, despite the respiratory and circulatory movements, and the control of the microelectrode insertion. But we did succeed far better than anybody else in the world, as I recognised in my world tour.

BQ. Intracellular recording from motoneurons

In **Sections BG., BI., BJ. & BK.** there have been described experiments related to the controversy, electrical versus chemical, for the simplest synapses in the spinal cord. Our extracellular recordings of focal potentials and ventral root potentials generated synaptically and antidromically with various interactions were unable to produce definitive tests. It was suggested that this could be done with intracellular recording. Moreover, intracellular recording could settle the controversy with Lloyd concerning the location of the site for synaptic facilitation. Lloyd located the site in the prolonged presynaptic depolarization that he found to be restricted to activated terminals of the presynaptic fibres. On the contrary I attributed the synaptic facilitation to residual depolarization of the postsynaptic membrane, analogously to the endplate potential, and already this was displayed in Fig. A37.

It was essential to have the flexibility of recording given by a film camera. Archie McIntyre had the only one in the department and he very kindly invited us to do all the intracellular recordings in his research room.[**A**] Despite all our preliminary arrangements we did not achieve immediate success. The manipulators were crude and the fixation of the spinal cord had to be much improved, particularly with the movements due to respiration and circulation, before we could impale a motoneuron for a sufficient time to run an experimental series. Also, the microelectrode track was often missing the target motoneurons. This was an acute problem not encountered when isolated muscle fibres were impaled under direct vision. Impaling successfully the unseen minute targets - about 50 µm in diameter – presented difficulties of a different order of magnitude. The first successful recordings were done on June 18th 1951. As we struggled with all the technical problems, there appeared to emerge the rule that success only came after midnight!

The first publication on intracellular recording was presented to the Proceedings of the University of Otago Medical School in Dunedin on July 31st 1951. Fig. A47 shows

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318 Marmont, George H. (1914 – 1983) US Chicago University Prof. biophysics. Isolation of nerve cell areas.

the first ever published illustration of intracellular recording from neurons in the central nervous system.[B]

By a strange irony of fate, it wasn't my turn to present a paper at the Meeting. As a consequence, our paper was merely read by title and not one slide was presented. I was rather piqued by this, remarking in an off-hand manner that this work could eventually win a Nobel Prize!

This preliminary figure displayed an excitatory postsynaptic potential, called EPSP, as a depolarization of rapid onset and slow decay over many milliseconds, as would be expected from the potentials electrotonically transmitted to the ventral roots (Fig. A36, Fig. A37). With stronger stimulation to the afferent muscle nerve (ventral roots cut) the larger EPSP sets up a spike potential that is earlier, the larger the EPSP. In frame 2 the antidromic spike potential superimposes on the orthodromic spike. However, the synaptic excitatory action producing the EPSPs of Fig. A47 could be electrical or chemical! The intracellular recording was not definitive.

Fig. A50A from a later experiment shows that with repetitive stimulation, EPSPs sum to generate an impulse discharge in the first trace, at 300/sec. However, summation is ineffective in building up a high level on EPSP because with repetitive stimulation there is depressing in size of the successive EPSPs, and also there is an increasing background of after-hyperpolarization. The intracellular responses of Fig. A50A are similar to the responses electrotonically transmitted to the ventral roots (Fig. A44) as would be expected.

It should be realized that I had already rejected electrical synaptic transmission at the neuro-muscular junction as can be seen in my contribution to the Monnier-Fessard Symposium in Paris in 1949, and which was referred to in **Section BG**. Also, I had there reacted against electrical synaptic transmission in ganglia. So, the intracellular recording from motoneurons was testing for the electrical versus chemical hypotheses in the spinal cord. It is sometimes alleged mistakenly that I believed in electrical transmission at all synapses until I was converted by the intracellular recording from motoneurons. It is important to recognise that electrical synaptic transmission was generally accepted by many leading neuroscientists at that time for example by Gasser, Erlanger, Lorente de Nó, Arvanitaki[319], Lloyd, Monnier, Fessard.[C]

The occasion of our first attempt to record inhibitory synaptic action was especially memorable. We were using a *quadriceps* afferent volley of group **Ia** strength (Fig. A35A, Fig. A53) projecting to a *biceps-semitendinosus* motoneuron. It was already late at night with all telephones off and I was worried that the baby that Dora Coombs was expecting might come some days early! So, Jack and Dr. Brock set off by car to the Coombs house about 4 km away, while I stayed with the cat. But the baby had already come as they got to the house to find Dora holding the baby in her hands. So, Dr. Brock rendered the necessary obstetrical assistance and then came the doctor and midwife that Dora had already telephoned some time before. Meanwhile I looked after the cat, not knowing what happened at least for two hours.

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319 Arvanitaki, Angélique (11.07.1901 – 06.10.1983) FR neurophysiologist. Studied molluscan giant nerves.

On their return all was well with me and the cat and we celebrated the happy event before we began the experiment. I had predicted from Fig. A41 that with electrical synaptic inhibition the intracellular recording would be positive relative to the ground electrode, whereas with chemical synaptic inhibition there would be an increased postsynaptic polarization that would give a negative potential, which would be a mirror image of the EPSP.

So, the excitement. was quite intense when we had the conditions ready on the fateful night and fired the *quadriceps* afferent volley to the antagonist *biceps-semitendinosus* motoneuron which it would inhibit: trace up would be electrical; trace down chemical! It went down - to my amazement and initial chagrin. It was repeated and showed the expected mirror image relationship to the EPSP. The original first records of the experiment 20/8/1951 are reproduced in Fig. A48 with to the left IPSPs evoked by progressively larger *quadriceps* nerve stimulations. These IPSPs were virtually mirror images of the EPSPs. This was a great Popperian occasion, where the rival hypotheses were put to a crucial test. I had in the end to rejoice in the falsification of the Golgi cell theory of electrical inhibition, my dream child that I had cherished for many years!

At that early hour of the morning various comments were made that we recorded on a tape, but unfortunately, they proved to be virtually undecipherable the next morning. The photographic records were beyond all doubt, they still are extant (Fig. A48), but the tape had disappeared! I had immediately realised that chemical transmission must obtain for the inhibitory synapses, and therefore most probably also for the excitatory synapses since they resembled so closely the inhibitory in all respects except sign. So, I became a convert to chemical synaptic transmission in the central nervous system.[D]

That was the most dramatic event of my scientific life.[E] It came as a termination of more than 50 years of scientific disputation. Sherrington had introduced the concept of inhibition as playing a key role in nervous coordination as early as 1900 and in his great 1906 book, synaptic inhibition had a role as important as excitation, as was illustrated in Figure 37, his classic diagram of reciprocal innervation. Reflex inhibition was a major feature of our 1932 Oxford book. Finally, the title of Sherrington's Nobel Lecture was "Inhibition as a Coordinative Factor". There had been many theoretical attempts to explain central inhibition, but no theory had been developed to account for the most basic example, the direct inhibition of Lloyd, whereby afferent impulses in group **I** fibres of a muscle (Fig. A35A) inhibit motoneurons of antagonistic motoneurons with the same latency and time course as monosynaptic excitation.

Fig. A48 precisely accounts for this timing with the mirror image relationship of EPSPs and IPSPs. The traces of Fig. A49 were similarly obtained in a very early experiment with superimposed traces to give precision to the respective time courses of EPSPs and IPSPs that were widely ranging in size, but had a similar time course.

I was concerned that this IPSP story may inadvertently spread long before our results were published. Dexter Easton[320] from Seattle was in our research group and was most

320 Easton, Dexter Morgan (13.09.1921 – 12.03.2010) US Professor of biological sciences at Florida State Univ.

interested to send our intracellular findings to Professor Patton[321], who was also attempting intracellular recording in the cat spinal cord with a preliminary publication in 1952 at the same time as our major paper. I did not mind him sending the records of the excitatory story of Fig. A47 to Seattle. It was a conventional excitatory depolarization. But I was concerned about our unique discovery of the IPSP being sent prematurely to Seattle before we could publish it. I said nothing, but had Chapman print our IPSPs upside down for display, where the IPSPs would look like EPSPs! However, in retrospect I think that I need not have worried. The concepts and techniques of Patton were not equal to the task of duplication and for some years that was true of any other possible rivals.**[F]** This was most fortunate because I was to have no laboratory for more than a year when I left Dunedin in November 1951 and the construction of my temporary laboratories in Canberra took longer than I anticipated to March 1953.

We have regarded it as mandatory to subject motoneurons to afferent volleys generated by carefully controlled stimulation of muscle nerves, the ventral roots having been cut. Stimulation of dorsal roots, as is commonly done, leads to the unanalysable complexity of inputs delayed by traversing polysynaptic pathways. It was discovered that graded stimulation to the hip muscle nerves often exhibited a double composition in the group **I** response recorded by a contact electrode on a dorsal root (Fig. A53C response). Analysis by interaction with a preceding graded stimulus gives a beautiful display of the double composition (Fig. A53) which can be identified as Group **Ia** and Group **Ib**. For our investigations of intracellular responses, it would be desirable to have a virtually pure Group **Ia** input (Fig. A35A) which uniquely evokes the monosynaptic EPSPs and the matching IPSPs. This can usually be accomplished with careful adjustment of the stimuli to nerves of hip muscles, but nerves to leg muscles rarely show the discrimination of Fig. A53.

In that early series of intracellular recordings with the arrangement of Fig. A51A, we had interesting responses to antidromic stimulation of the motoneuron that related to the labile and non-labile of the extracellular recordings. (Section **BK**). Fig. A52 illustrates the antidromic responses to two stimuli over a wide range of intervals. Even at the longest test interval (8.8 msec.) the second antidromic response showed a double composition of the full spike. Then at 4.2 msec. there was blockage of the large spike, and at 1.5 msec. there was blockage of the small spike. It was recognised from the beginning that the small spike was generated in the initial non-medullated segment of the axon and the immediately adjacent soma (Fig. A51B), while the large spike was due to invasion of the soma plus dendrites. So, they were eventually labelled the IS and SD components of the antidromic spikes. This identification aroused much antagonism for many years, but the accumulating evidence has won acceptance for IS and SD. In Fig. A51, IS-SD blockage was a little indeterminate as in the lower record of the middle column. At the two shortest testing intervals of Fig. A52 the blockage of the IS left a very small response which is attributable to the medullated axon (M) from which the IS arises. The IS-SD concept achieves great importance later when the synaptic

321 Patton, Harry D. (1918 – 26.05.2002) US neurophysiologist. Intracellular studies of spinal neurons.

generation of impulses is being considered. With intracellular recording there was very good discrimination between the after hyperpolarization (AHP) following IS and SD spikes. Following the IS the AHP was small as for impulses in peripheral nerve fibres.

It was about 10 times larger with the SD spikes, an hypothesis has been developed on the basis of our whole series of recordings that the observed EPSPs and IPSPs are due to summations of elemental potentials having similar time courses in the absence of stimulation. At high amplification there are often, occurring at random, small potentials like miniature EPSPs. Possibly these are generated by single presynaptic impulses, so they were labelled synaptic noise. They do not form a serious complication. It can be proposed that these elemental EPSPs and IPSPs are compounded in producing all the observed responses with the various delays contingent on the delays of impulse propagation and interneuronal transmission (cf. Fig. A36). Fig. A50B illustrates EPSPs compounded in this way for the stronger stimulations. So, there is a general theory of central synaptic action to all manner of neurons that challenges an immense variety of experimental testing.

It was only possible to carry out eighteen experiments with 60 neurons studied intracellularly before leaving Dunedin for my world tour. It was a strenuous time to write up and submit the principal findings, but I had films of all significant data, so that my lectures and publications could continue to develop as I went to one centre to another.

BR. Review of my eight years in Dunedin, from age 41 to 48

These years were the most strenuous of my life, but I was able to rise to the challenge, and even to introduce what could be regarded as my most important scientific contribution – intracellular recording from neurons of the central nervous system. I had the advantage of very good colleagues.[A] My association with Karl Popper gave me the inestimable advantage of understanding the philosophy of science. Consequently, I was much more flexible and creative ideologically. So, with Popper's encouragement I set up neural models for synaptic excitation and inhibition as illustrated in Sections **BG & BJ**, and these formed the basis of experimental tests in Sections **BI, BK & BQ**. However, the testing procedures even by sophisticated extracellular recording were not discriminative enough. The final solution that it was chemical transmission came with intracellular recording towards the end of my Dunedin life (Section **BQ**). Nevertheless, all those earlier investigations gave valuable insights into the simpler neuronal mechanisms in the spinal cord.

I had concentrated through all the Dunedin period on the simplest level of the central nervous system, the spinal cord of the anaesthetized cat. This preparation had two great advantages. I could use group **Ia** inputs (Fig. A35A, Fig. A53) from muscles that monosynaptically excited homologous motoneurons, i.e., the motoneurons of the muscle of origin and of its synergists (Sections **BI, BD**); and these same group **Ia** afferents produced the simplest inhibitory action, so-called direct, on antagonist motoneurons (Sections **BK, BQ**). As illustrated in Fig. A53 it was possible to excite a large **Ia** response without contamination by group **Ib** impulses that have a quite different synaptic action.

I had studied the response induced by firing an impulse from the motor axon into the motoneuron as described in several **Sections; Q, T, BE, BK**. However, the final understanding came with intracellular recording in **Section BQ** as shown in Fig. A47, Fig. A51B, Fig. A52 with the recognition of the IS and SD components of the neuronal spike potentials.

The study of disused synapses with their extremely prolonged post-tetanic potentiation (Fig. A46A, Fig. A46B) has always appealed to me. It was a demonstration of synaptic disuse and trophic potentiation and a significant discovery in the Dunedin period.

My life in Dunedin had other features besides the scientific achievements.[B] I was devoted to giving an understanding of physiology, and my lecture notes bound in a great folder were a model of what I tried to give in lectures, together with the emendations from year to year. Unfortunately, it has been lost somewhere in my several moves after Dunedin! I was born a teacher. Both my father and mother were trained teachers and they handed their dedication on to me! Actually, in my Oxford and Dunedin periods I spent eighteen years of my life as a teacher. In the fourteen years of my Canberra life there was regular seminar teaching every week. My students have been my devoted friends, though I have lost trace of most of them.

The extracts from my Graduation Address in **Section BO** reveal how I felt about the University of Otago in those eight years of my participation.

Another feature of my Dunedin life was the return to a philosophical attitude to the brain so that I became clearly opposed to the dominating materialism of science, particularly of science as it related to the human person and the brain. This developing dualism appeared first in my Passmore lecture, and then later in the final chapter of my Waynflete Lectures.[C] My good friend, Ragnar Granit, greatly admired my Waynflete lectures except for what he called my naïve philosophy at the end. I began to feel that I needed more philosophical skill before going on with my dualist philosophy. However, as it turned out, Karl Popper appreciated my dualism. It agreed very well with his belief. Nevertheless, I did not publish much on the mind-brain problem during my intense neuroscientific involvement in Canberra and Buffalo.

BS. From Dunedin onwards

As soon as I accepted the position of Professor of Physiology in the Australian National University in January 1950, I enquired about a place to live in Canberra. One had to select a suitable block of land and then have a house built on it. I had officials of the ANU helping me and eventually on October 9th I selected a very large block of land in a very good site adjacent to the Embassy area. The Government owned all the land and one had to make a nominal deposit and then pay a rental of £18 a year which I did on 9th Oct. 1950 for a 99-year lease. Immediately I had to design a house that fitted suitably on the block. I had had experience in house design, so with a little help from a Melbourne architect I drew the plan and then got a modest Canberra architect, Tom Haseler[322], to sponsor the plan and to try to get a builder. It was an uncertain prospect as I came to realise during 1951 on several visits to Canberra. But in the end the house was to be built for £16,000 and was to be ready when I returned from overseas in July 1952. At the same time Lindsay Pryor[323], whom I had got to know as a Botanist and who was Director of gardening at Canberra, was planting free of charge a forest of trees and shrubs and a surrounding hedge.

The house was a good success after some troubles and within 2 weeks of moving from Dunedin in September 1952 we were in our new home, confronted with an immense gardening job in an enormous block of 2½ acres. There was plenty of room: fruit trees and a large vegetable garden as well as a shrub and flower garden, a gravel tennis court and a small swimming pool.[A] Nothing could be done in the laboratories, but I had a room for a secretary and myself, which was used to prepare several papers that were carried over from Dunedin. The temporary laboratories were not available until February 1953. Meanwhile I tell of the enormous success of my world travel.

The central feature of this great occasion was the Waynflete Lectureship that I was invited to hold at Magdalen College Oxford during 1952. The invitation was in a letter of 15th June 1950 from the President of Magdalen, Tom Boase.[324] It was named after the founder of the College in 1458, William of Waynflete, Bishop of Winchester. The first lecture series was in 1945. Adrian was the lecturer in 1946.

It was a quite generous invitation with accommodation in a College set of rooms and College dinner for the whole year of the Lectureship. I had to give a course of lectures preferably in Hilary Term and have them published. There was an honorarium of £300. The invitation could not have come at a more propitious time, as I was due to travel overseas as an ANU Professor just at that time, so all my travel expenses were looked after by the ANU, who were also paying my salary. I was given a ceremonial dinner by the Vice Chancellor, Bob Aitken, on my departure from Dunedin, with a picture of the University that I still have. It was a great contrast to my Kanematsu departure. My great task was to organize the trip carrying all the literature, pictures and slides for many lectures, particularly for the Waynflete Lectures. I left on November 24th 1951 by air to Canberra where I spent several days on the living and working quarters in Canberra that were in course of construction. My flight onwards was to San Francisco on the deluxe BCPA plane with comfortable sleeping for the nights aloft. My travel through US and Canada was fully arranged in mid-October in a series of letters I wrote from Dunedin. I arrived at San Francisco early on December 2nd and then by a direct flight to Chicago arriving at 4.30 PM. I was met at the airport by Ralph Gerard and stayed for two nights at the Quadrangle Club. I gave a lecture and a seminar on

322 Haseler, Thomas Joseph (19.03.1904 – 30.08.1963) AU Canberra architect of houses, churches and schools.

323 Pryor, Lindsay Dixon (26.10.1915 – 17.08.1998) AU botanist. Planned Australian National Botanic Gardens.

324 Boase, Thomas Sherrer Ross (31.08.1898 – 14.04.1974) UK Art historian. President of Magdalen 1947-1968.

intracellular recording from motoneurons. I went to see McCulloch[325], Pitts[326] and Lettvin[327] who were reputed to be recording intracellularly. There was an initial Poker game! I asked to see their records; they asked to see mine first. So, eventually I showed mine and then I said "Please, show me yours". They were embarrassed and said "Not after yours"! From Chicago I flew to Montreal and stayed with Hank MacIntosh[328] and met Jasper and gave a lecture. It was very good to see Hank, Burgen[329] and their group. The US- Canada visit was a triumph, with excellent friends all along the route. From Montreal I went by train to Hannover to spend the weekend with the Wolfendens, my dear friends from Exeter College. From there an early morning train got me to Boston, where I was met by Denny Brown and stayed for 2 days at their beautiful home. It was a lovely occasion and I met Alex Forbes and Mary Brazier[330] with two young disciples who later turned out to be Kandel[331] and Spencer.[332] Then to New York to see Gasser, Lloyd and Lorente de Nó. Then on December 14th-17th a weekend at the palatial home of John and Lucia Fulton, where I had stayed in 1946. From them on December 17th-19th I went by train to Durham to see Rhine[333] and to investigate his Parapsychology work. I was not impressed, but I thought that telepathy might exist. I returned to Baltimore for December 20-29th with the Kufflers and Magladerys and also Mac Harvey, with Christmas at the Kufflers. I returned to New York again on December 29th with Chandler and Nelle Brooks, and finally left New York on January 3rd, a night flight for London, and so I arrived at Magdalen College on January 4th.

This summary does not convey the glorious days of meeting so many good friends and exchanging our scientific ideas. Also, I gave so many lectures and seminars. The Dunedin period had given me advanced scientific thinking on the synapse and on the neuron in a wide variety of scientific studies.

BT. The Waynflete Lectures

The Waynflete Lectures were a great challenge; more than I had ever before experienced. I followed Tom Boase's advice to base my lectures on my Dunedin discoveries and to lecture in a way acceptable for a general cultural audience. I had in mind for the end of the series something rather like the Passmore Lecture that I published in Nature (Section **BO**). So, I chose a double title: "The Neurophysiological

325 McCulloch, Warren Sturgis (16.11.1898 – 24.09.1969) US neurophysiologist. "Neural network" modelling.

326 Pitts, Walter Harry Jr. (23.04.1923 – 14,05.1969) US neuroscience logician. "McCulloch-Pitts neuron".

327 Lettvin, Jerome Ysroael "Jerry" (23.02.1920 – 23.04.2011) US(J) cognitive scientist. "What the frog's eye".

328 MacIntosh, Frank Campbell "Hank" (24.12.1909 – 11.09.1992) CA physiologist. "Cholinergic biology".

329 Burgen, Arnold Stanley Vincent (22.03.1922 –) UK McGill Univ. Canada Physiology Prof. 1949-62.

330 Brazier, Mary "Mollie" Agnes Burnston Brown (18.05.1904 – 14.05.1995) UK M.I.T 1940-61 EEG analysis.

331 Kandel, Erich Richard (07.11.1929) AT(J) neurologist. "Physiological basis of memory" (NP 2000).

332 Spencer, W. Alden (1931 – 01.11.1977) US electro-neurophysiologist at NIH. "Neural pathway plasticity".

333 Rhine, Joseph Banks (29.09.1895 – 20.02.1980) US botanist. Founder of parapsychology. "Telepathy".

Basis of Mind: The Principles of Neurophysiology". I sent the titles of the eight lectures to Tom Boase in a letter of November 7th. The eight lectures would be given in the Hilary Term 1952 at 5 PM on the successive Fridays beginning on January 25th. So, on my arrival at Magdalen on January 4th I had just three weeks to prepare. There were several problems. Slide projection was an essential feature, and I had brought from Dunedin a large collection of films that could be inserted in hinged double slides. I had brought several. So, the projectionist had to insert the films in the hinged slides, one after another, for projection. It was a demanding task of Richard Poyntz-Wright[334] a scholar of Magdalen who eventually got First Class Honours in 1953. There had been much publicity of my lectures. There is no need for me to summarize the lectures since their essential contents have already been described and illustrated in the sections above.

The best help I had was from Katz, Hodgkin and Huxley who sent me their figures in course of publication, and I had them converted to films for projection by Masland, the excellent physiology technician and photographer. I had also the great help of their papers in course of publication. The result was that my lectures in early 1952 gave a full report of their publications appearing in late 1952. There were four such papers referred to in my book 1952a, 1952b, 1952c and 1952d.[A] So those three weeks were all too short. I kept on delaying my visit to see Sherrie at Eastbourne, because I was too pressed for time. I was writing up my lectures in advance and having them typed in an Oxford typing service.

The first Waynflete Lecture was in Magdalen College Hall by tradition. But the preparations for slide projection and even for a blackboard were quite inadequate. Even more inadequate was the seating accommodation for about 100 when at least three times that number came in a great crowd, making chaos outside. That lecture was on the basic membrane ionic story. So subsequent lectures were arranged in the largest science lecture room in Physical Chemistry that would seat up to 300. It was so crowded for Lecture·(2) that I could barely make my way up the stairs and to the lecture bench. Even there I was standing in a dense crowd of bodies on the floor behind the long lecture bench! I remember one amusing incident. I inadvertently dropped the pointer and immediately it was caught and presented to me by several hands, so the audience realised my predicament. There was discussion about the future lecture site. It was hoped that the numbers would dwindle, but they did not, so the last three lectures were given in the cavernous science museum theatre that would seat almost 1000.[B]

These last three lectures were on topics that could interest a wider academic audience.

(6) plasticity, memory, conditioned reflexes;

(7) the cerebral cortex, structure and responses, the electroencephalogram;

(8) the mind-brain problem with hypotheses relating to will and consciousness.

My good friend and scientific enemy, Gilbert Ryle, came to the last two with many philosophers. Fig. A55 was taken at the end of the last lecture where I was illustrating

334 Poyntz-Wright, Richard Curteis (1931 – 11.08.2021) UK Family doctor.

the neuronal network theory. I was of course presenting a dualist philosophy with self and brain. As I left the lecture room with the lights turned on, suddenly they were turned off and the crowd roared with laughter. I turned around and joined in at Fig. A55 that had been constructed by my good old Magdalen friend, Hugh Sinclair. It should be self-explanatory.

That night we celebrated the end of this most successful lecture series by a splendid dinner in Hugh Sinclair's rooms in Magdalen. Amongst those invited were Gilbert Ryle, Tom Boase, Pat Liddell (Waynflete Professor of Physiology). The menu was on prints of Fig. A54. I can remember the luscious lychees that had come by air from China with wines to match. I was happy to have completed this most successful lecture series of my life in such good company. I stayed on for several weeks at Magdalen as I had to send in to the Publisher, Oxford University Press (OUP), the full manuscript with illustrations for the book. The Neurophysiological Basis of Mind: The Principles of Neurophysiology. I was concerned at the unfavourable reaction there would be in those days dominated by Gilbert Ryle to "Mind", and asked the OUP to leave out the first part of the title leaving "Principles of Neurophysiology". However, the OUP would not agree. They thought that "Mind" would secure a larger audience!

BU. Sherrington

After he left Oxford in 1935 Sherrie wrote me many letters. My collection numbers 40, including several cards. The letters were most loving messages from that wonderful man that my wife and I loved so dearly. Some spoke of his later writings on Fernel[335] and Goethe[336] and right through he still had interest in neuroscience and the many neuroscientists that he knew from the past, especially Adrian and Granit. I particularly cherish his last letter of Jan 4th 1951, which closes with: "May God bless you all, Ch. S. Sherrington". On arrival in England after almost 15 years absence I had a visit to Sherrie as a high priority. But I was so concerned with my lectures that I kept on putting off the visit. My daughter Rose was then doing research on intracellular recording from sympathetic ganglia in Hodgkin's laboratory. She had visited Sir Charles at his Eastbourne Nursing Home that was run by Catholic nuns. So, we went together to see Sherrie on Sunday, February 3rd. We arrived before the appointed time and had a winter walk along the chalk cliffs fronting the sea, eating our sandwich lunch before going to see Sherrie. I was rather apprehensive to see him so deteriorated as I had heard. However, once we started to talk all was well. Rose then left us alone for some time before the hour-long visit was over. We talked much about the second shortened edition of his great book "Man on his Nature", 413 reduced to 300 pages. He initially remarked "I must have been a garrulous old man when I wrote it in 1939"! All too soon the time of our visit was up and I promised to come again soon.

I came alone on Sunday February 24th. We had a good open talking as Sherrie was annoyed at some of the reviews of his book, the second edition. The materialist

335 Fernel, Jean (1506? – 26.04.1558) FR physician. Introduced term "Physiology". Described the spinal canal.

336 Goethe, Johann Wolfgang von (26.08.1749 – 22.03.1832) DE poet, playwright, natural philosopher etc.

establishment rejected the sections dealing with the mind and the mental world as the delusions of an old man who had once been a good scientist. Sherrie was particularly unhappy at a review by Prof. J. Z. Young, saying to me "when will this YOUNG ever grow up"? I took several photos that he reluctantly agreed to, and we discussed the great problem of the design and functioning of the brain that gave it the transcendent property of being in liaison with mind and the mental world. He was of course as strong a dualist as I had been right from the start. So, I had to leave with the frustration that I should have come with a tape recorder. There were entrancing discussions that should not have been lost. But I would come with one next time, but there was to be no next time! Nine days later on March 4th in the early morning I heard the Magdalen death toll, and suspected at once that their greatest Fellow had died, which I soon confirmed and saw the Magdalen flag at half-mast out of my window across St. Swithun's quadrangle.

I went to the Ceremony in the College chapel and some days later to the memorial service in St. Margaret's Church Westminster. There I met Margaret Sherrington, the wife of Sherrie's only son, Carl.[337] She was very attracted by my last photograph (Fig. A56) and asked me to send her 50 for distribution. Now Margaret and Carl are gone and their only child, Unity[338], is an unmarried elderly librarian, so the Sherrington genes have gone, but his great creative and imaginative work is immortal, as also I believe, his Soul. At our last meeting he told me: "For me, Jack, the only reality now is the human soul".

End of J. C. Eccles' Autobiography – as given in its present unfinished state to his daughter, Mrs. Mary Mennis, in 1991.

Sir John died on 2nd May, 1997 at his home in Contra, Locarno, Switzerland.
No later version of this, his last work, is presently known to exist.

STAGE 4: – Figs. A34-A56

337 Sherrington, Charles "Carr" Ely Rose (21.021.1897 – 1973) UK Railway Research Service, London.

338 Sherrington, Unity (?– 11.09.2016) UK librarian and historian of musicians and musical instruments.

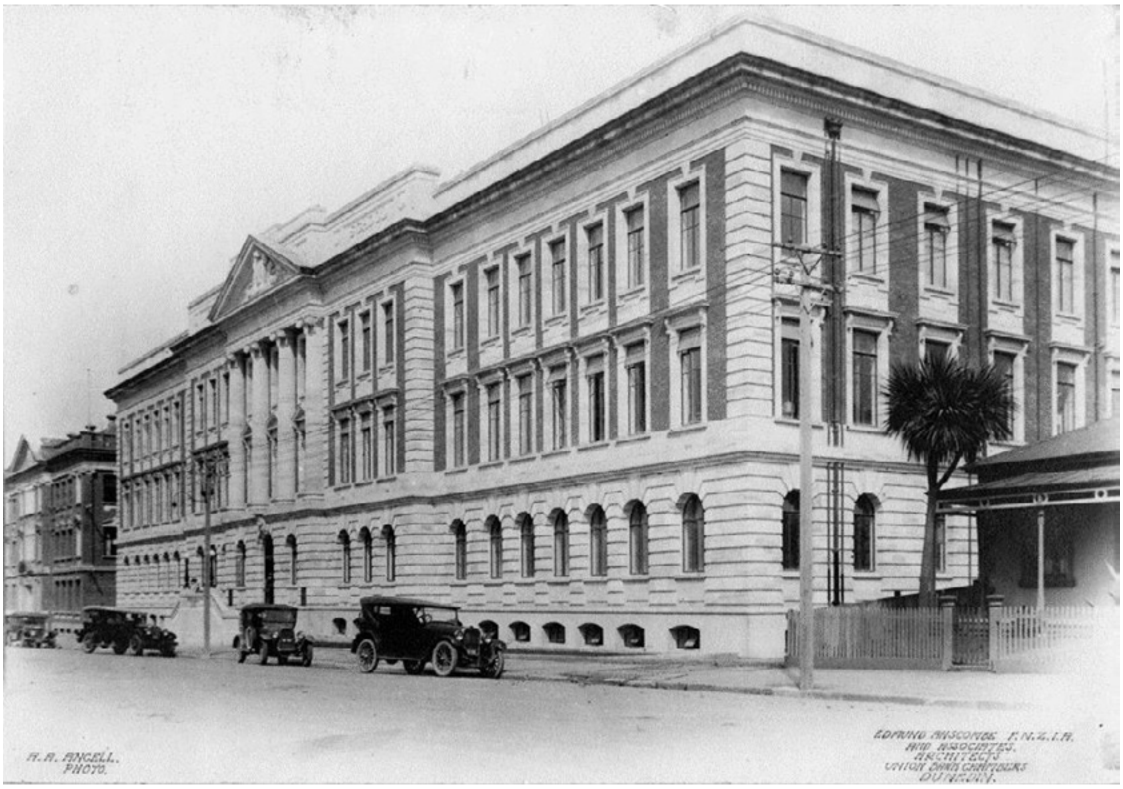


Fig. A34. The Lindo Ferguson Building, at the University of Otago Medical School. [BA, BC]

Named after a pioneering New Zealand ophthalmologist and Dean of the Otago Medical School from 1914 to 1937, this impressive building in King Street, Dunedin (Architect: Edmund Anscombe) was the home of the Department of Physiology since its construction in 1927 until completion of the new Eccles Physiology Building in 2021.
From photo ca. 1926 by Arthur A. Ancell.

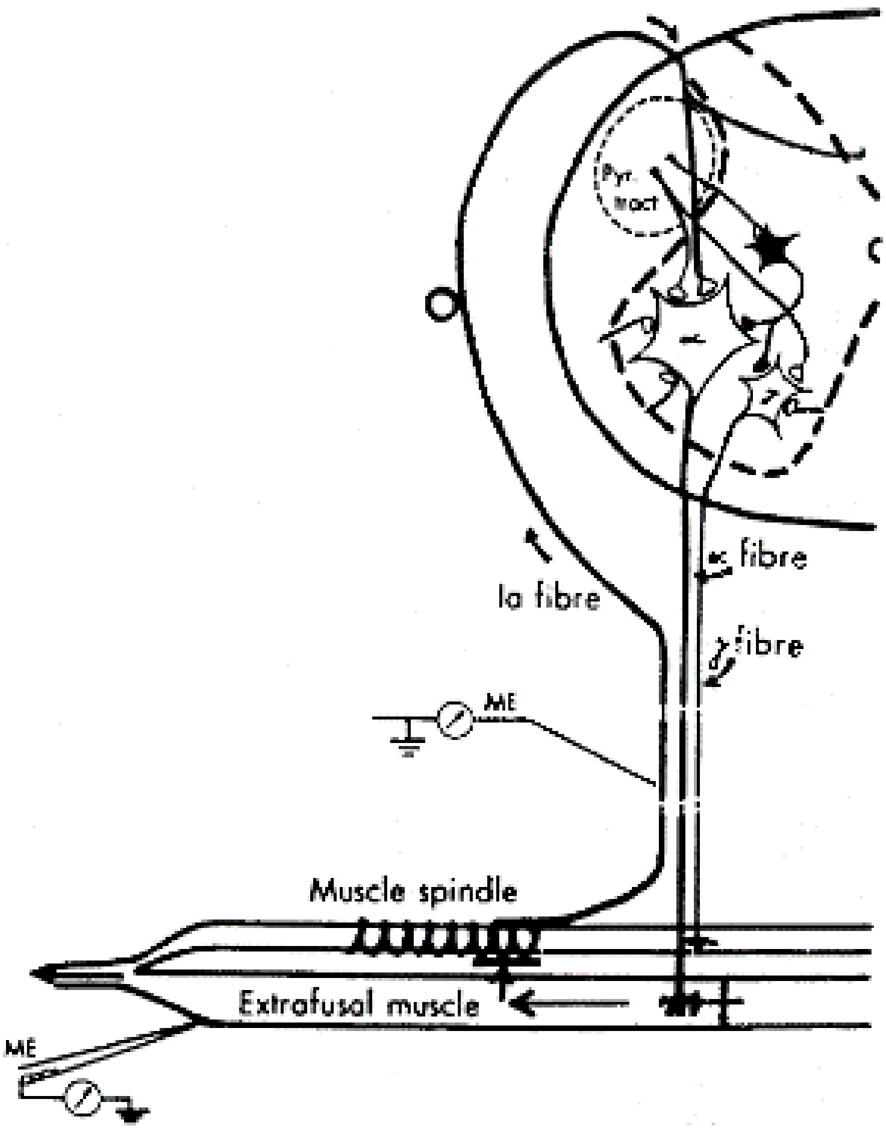


Fig. A35. Spinal cord nerve pathways to and from motoneurons. [BE, BQ, BR]

α-innervation and **γ**-innervation in a diagrammatic representation of nerve pathways to and from the spinal cord showing the essential features of **α**- and **γ**-motoneuron action and interaction. (**Pyr**. = Pyramidal; **ME** = measuring electrodes).
From Eccles (1989) [1B-a25], p. 62, fig. 3.15.
[See also McGeer et. al., (1978) [1B-a16], p. 425, fig.13.8; - derived from Eccles (1953) [1B-a02], p. 184, fig. 62.]

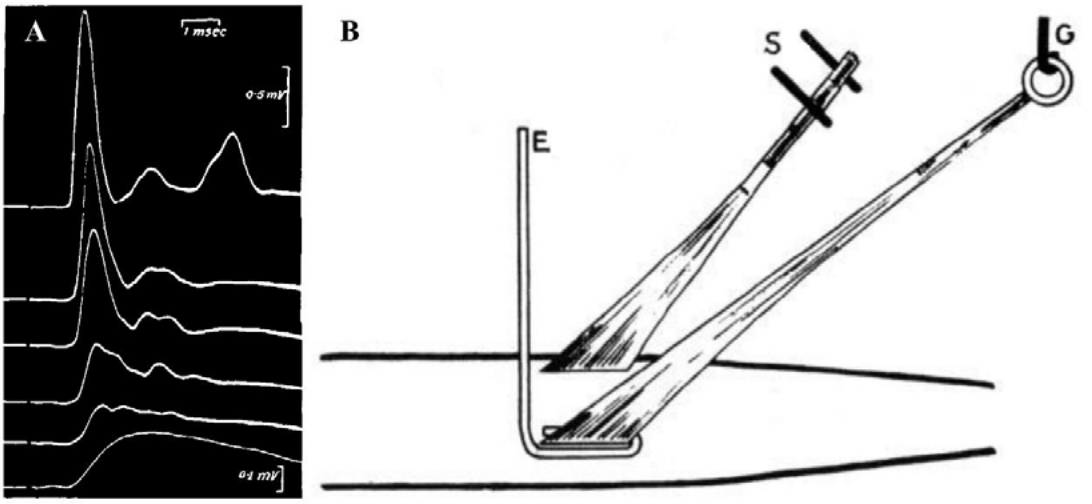


Fig. A36. Synaptic potentials of motoneurons, with blocking by Nembutal. [BE, BQ, BR]

A. Initial record (with leads as shown in B). Then 40 mg. Nembutal per kg. injected intravenously and next four records taken in the following 2½ minutes. Last record shows pure synaptic potential recorded at higher amplification after a further injection of 35 mg. Nembutal per kg. Note the small initial wave due to entering dorsal root volley.
From Eccles (1946) [1A-075], p. 100, fig. 10.

B. Sketch of cat spinal cord showing dorsal and ventral roots as set up for experiment: **S**, stimulating electrodes on dorsal root; **E**, earth lead, an elongated loop of platinum surrounding fan-like expansion of ventral root at its origin; **G**, grid lead, a platinum loop hook which leads from cut end of ventral root by means of a moist thread loop.
From Eccles (1946) [1A-075], p. 89, fig. 1.

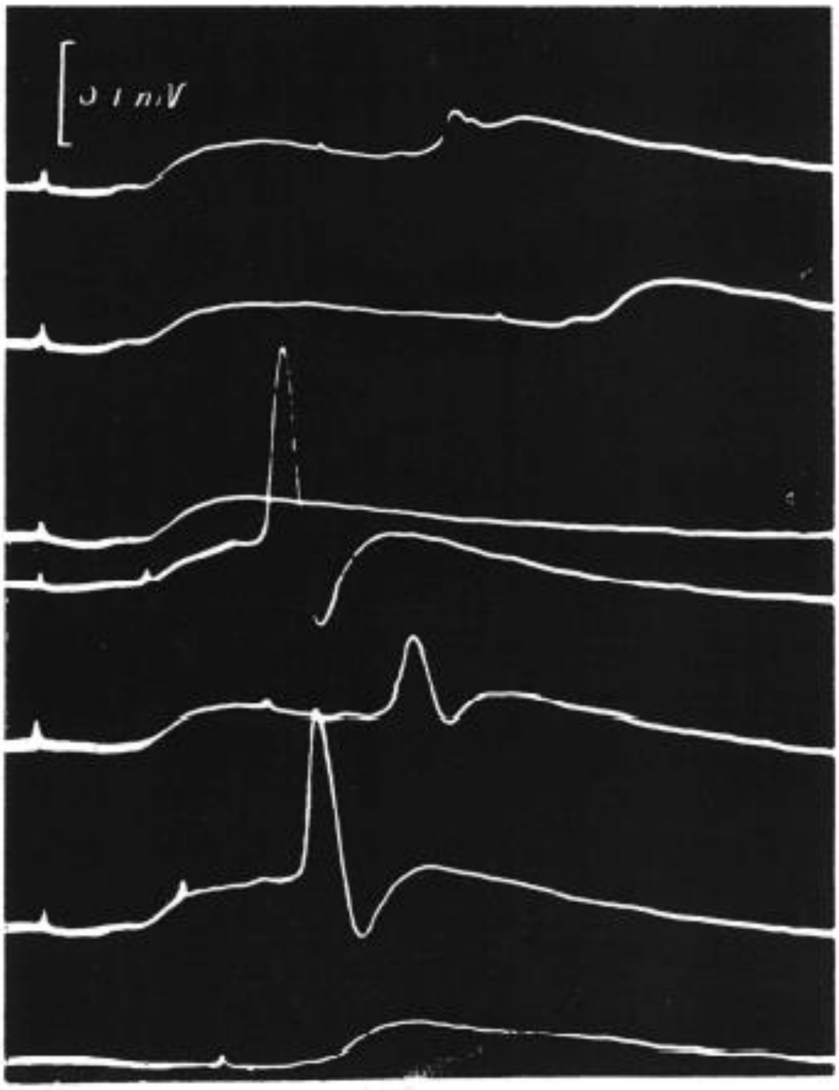


Fig. A37. Anaesthesia effect on action potentials recorded from 8th ventral root. [BE, BI, BQ]

Records from cat 8th ventral root to two *gastrocnemius* volleys at various intervals:

(i) stimulus artefact, **(ii**) 0.3 msec. later onset of small spike potential of the entering dorsal root volley, **(iii)** 0.7 msec. later onset of the above initial slowly-rising potential (seen best by looking along record and in the more amplified record, Fig. 9d), and **(iv)** 0.2 msec. later sharp rise of the spike potential. The sum of these last two intervals gives the synaptic delay for the monosynaptic pathway, provided that it is subjected to a small deduction for the conduction times of the afferent and efferent volleys through the spinal cord-say about 0.05 to 0.1 msec. for a total path of about 5 to 7 mm. The anaesthesia is such that first or second volley alone sets up only synaptic potential, records 3 and 7 respectively. A spike discharge, due to facilitation, is shown for all stimulus intervals up to 7.8 msec. (1st record). Note small initial wave due to entering dorsal root volley.

From Eccles (1946) [1A-075], p. 103, fig. 12.

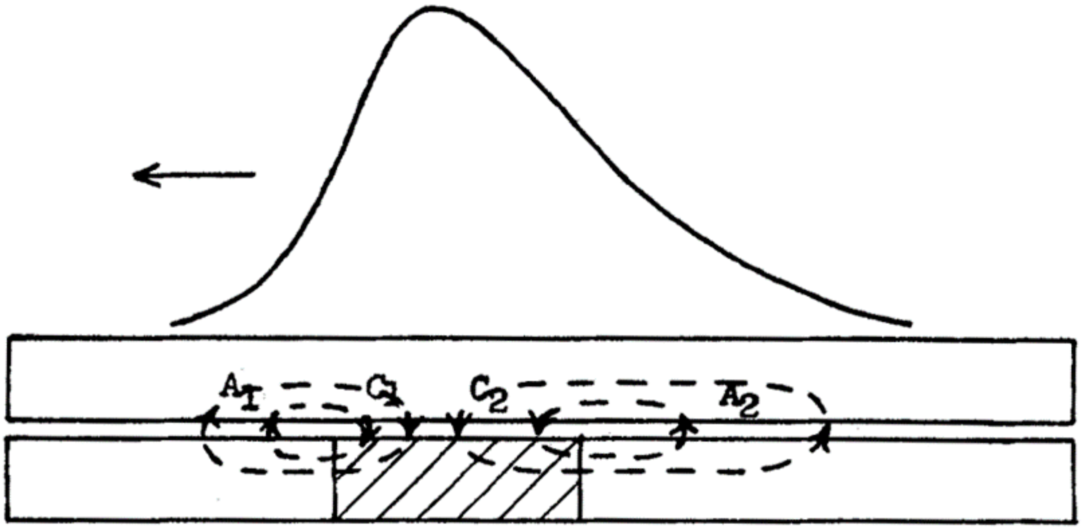
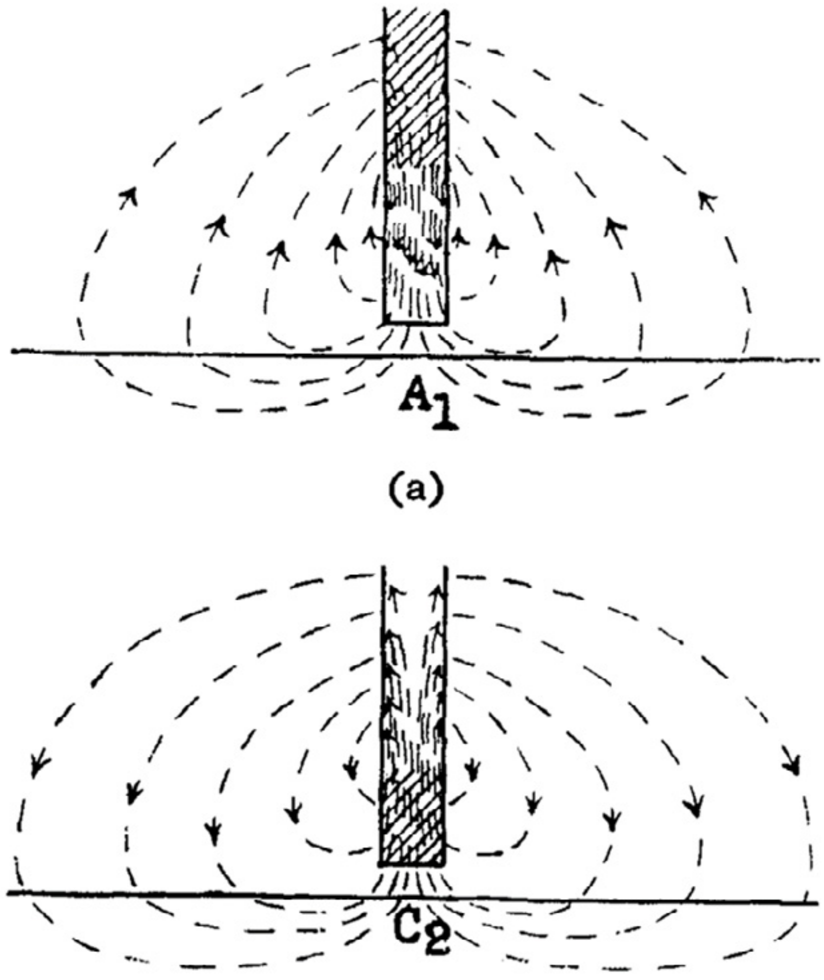


Fig. A38. Reactions of Ephapses (Artificial Synapses). [BG]

Diagram of two contiguous fibres, showing the current flow generated by impulse in active lower fibre and its penetration of the resting fibre (cf. Katz & Schmitt[339], 1940, p. 474, fig. 24). As the impulse (shown above) propagates along the active fibre, any point on the resting fibre is subjected, in turn, to effects **A_1C_1**, **C_2A_2**. Active part of impulse shown by hatched area in this and subsequent figures.
From Eccles (1946) [1A-077], p. 433, fig. 2.

339 Schmitt, Otto Herbert Arnold (06.04.1913-06.01.1998) US biomedical engineering pioneer. "Schmitt trigger".



(a)

(b)

Fig. A39. Diagrams of current flow at a schematic synapse. [BG, BI]

(a). with presynaptic impulse approaching synapse. **(b)**. with presynaptic impulse at the synapse. Note reversal of current flow; the focal anodal $\mathbf{A_1}$ effect being followed by the focal cathodal $\mathbf{C_2}$ effect at the synaptic region of the post-synaptic membrane.
From Eccles (1982), p. 331, fig. 1, [1A-507].

[See also Eccles (1945) [1A-074], p. 681, fig. 2; and Eccles (1946) [1A-077], p. 436, fig. 5.]

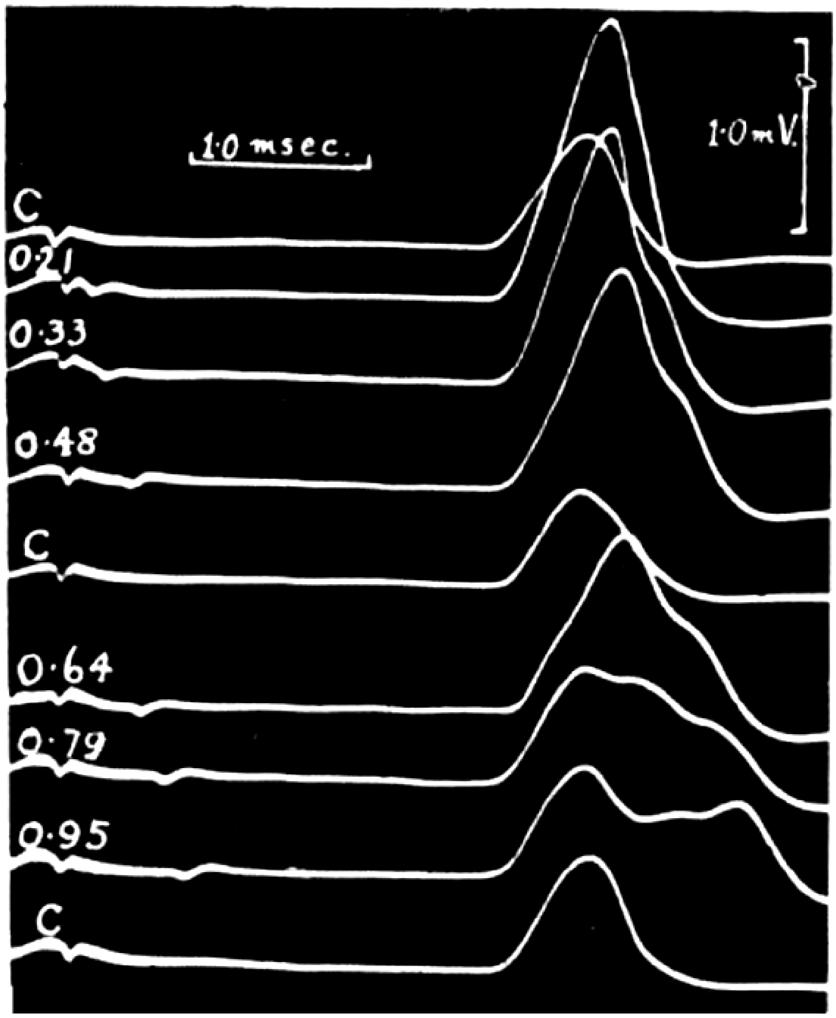


Fig. A40. Spikes recorded from S_1VR in response to volleys in *gastrocnemius* nerves. [BI]

Reflex spikes were recorded from the first sacral ventral root (S_1VR). The three control records (**C**) show the spike set up by two volleys in the medial *gastrocnemius* nerve at 4 msec. interval, only the second stimulus artifact being visible at the extreme left of the records. In the other records a lateral *gastrocnemius* volley (alone below reflex threshold) is set up in addition at the indicated intervals in milliseconds after the second medial *gastrocnemius* volley. Note that with all intervals, except the shortest, the spike response evoked by facilitation is clearly double.

From Brooks & Eccles (1948) [1A-084], p. 368, fig. 2.

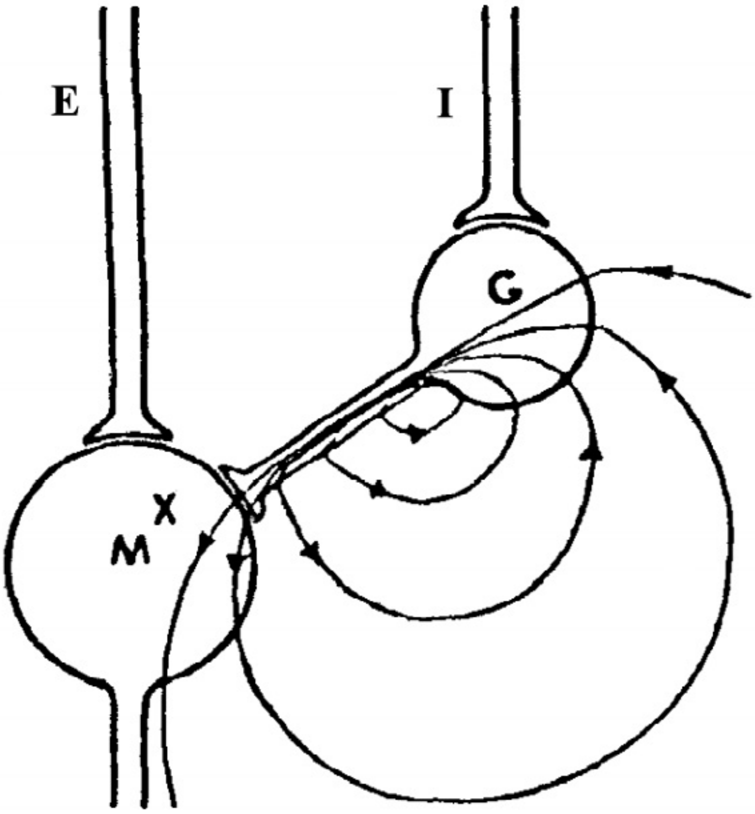


Fig. A41. Eccles' electrical hypothesis of central inhibition. [BJ, BQ]

In this hypothesis, a Golgi cell, **G**, is interpolated on the inhibitory pathway. Thus, we have the excitatory reflexo-motor collateral, **E**, ending in a synaptic knob directly applied to the motoneurone, **M**, while the synaptic knob of the inhibitory fibre **I** (also a collateral of a dorsal root fibre) ends on **G**, which in turn has its knob on **M**. Many such knobs as those shown may be imagined covering the somas and proximal dendritic regions of cells **G** and **M**.
From Brooks & Eccles (1947) [1A-079], p. 761, fig. 1.

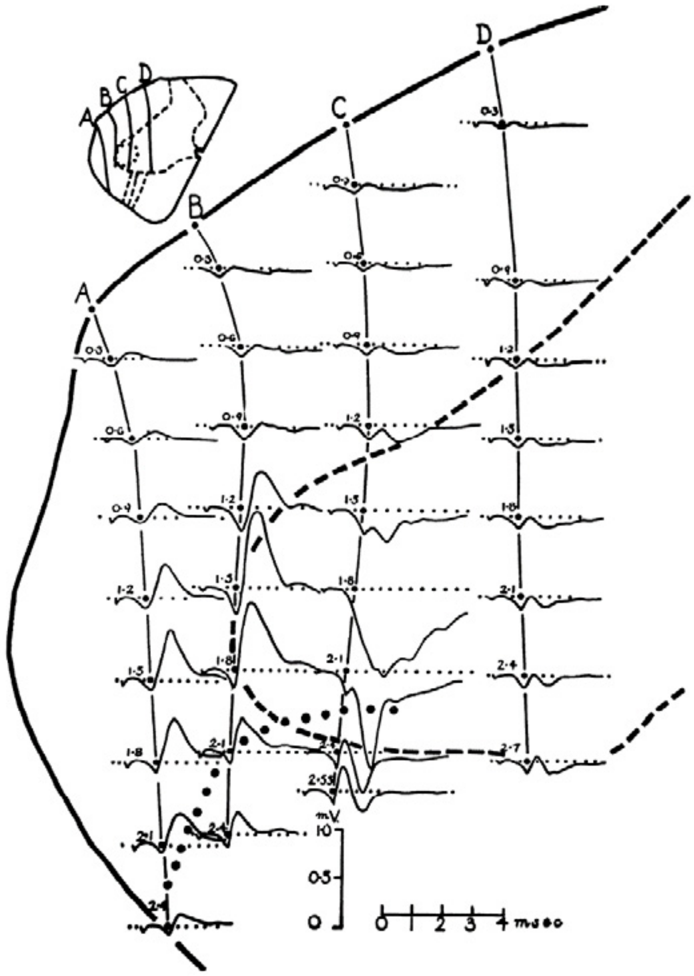


Fig. A42. Left ventral quadrant of spinal cord with the courses of four needle tracks. [BK, BP]

Inset shows outline drawing of microphotograph of transverse section of spinal cord (left half) in upper part of 6th lumbar segment, grey matter being outlined by broken line. Observed courses of emerging bundles of ventral root fibres are also shown by broken lines. Four micro-electrode tracks entering dorso-lateral aspect of cord are labelled **A**, **B**, **C** and **D**, and approximate site of *quadriceps* nucleus is ringed by dotted line.

Main figure shows enlargement (rather more than 8 times) of the courses of the four micro-electrode tracks, with corresponding antidromic potentials plotted thereon as described in text. Each plotted curve is mean of two closely similar records, and has its depth in millimetres indicated. Potential scale and time course applies to all records. Note that straight medial line of inset gives dorso-ventral direction for main map.

From Barakan, Downman & Eccles (1949) [1A-089], p. 396, fig. 1.

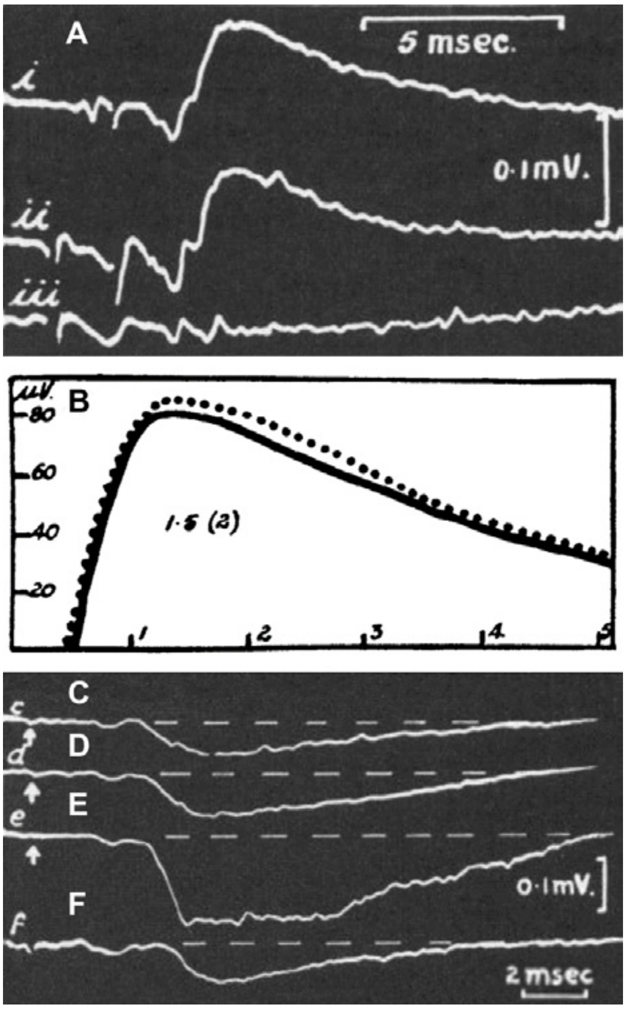


Fig. A43. Focal synaptic potentials of inhibited motoneurons. [BK].

A. Focal synaptic potentials set up in *quadriceps* nucleus by *quadriceps* (E) and hamstring (I) afferent volleys, (i) E alone, (ii) I 1.5 msec. E, (iii) I alone. **B**: Plotted records of averaged curve obtained by subtracting several I curves from several IE curves of the focal potentials illustrated in A, showing the small depression of synaptic potential that is effected by "direct" inhibition of the *quadriceps* motoneurones by the hamstring volley.
From Brooks, Eccles & Malcolm, 1948 [1A-086], p. 420 fig. 5a and p. 421, fig. 6a.

C. to **E**. Focal potentials set up by a volley in posterior tibial nerve with strengths of stimuli respectively 1.0, 1.25 and 2.5.

F. same experiment, but after an additional 90 mg. Nembutal per kg., the stimulus strength on the same scale being 1.67.
From Brooks & Eccles (1948) [1A-085], p. 411, fig. 9.

a

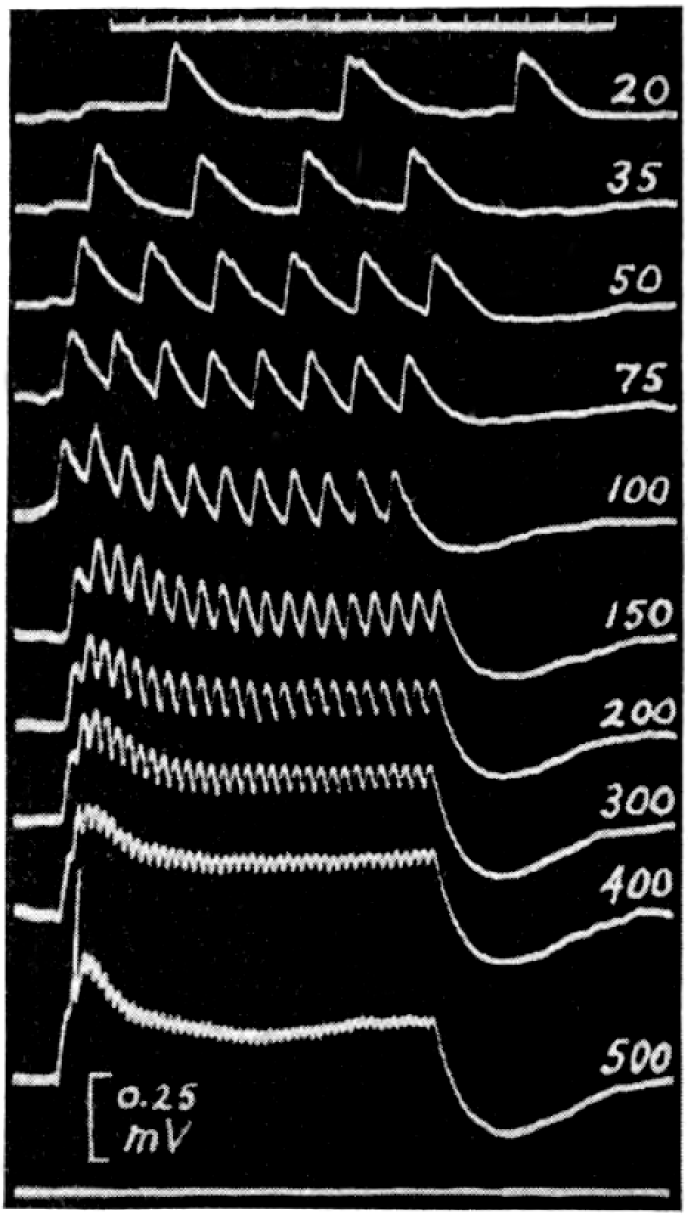


Fig. A44. Repetitive synaptic potentials recorded in emerging ventral root. [BM, BQ]

Numerals give approximate frequency of stimulation per sec. Records from rostral part of L_6VR; volleys were set up in the *quadriceps N* and stimulated at strength 6 times group **I** threshold. Time, 100/sec.

From Eccles & Rall, (1951) [1A-100], p. 478, fig. 1 [only frame ***a*** is shown here].

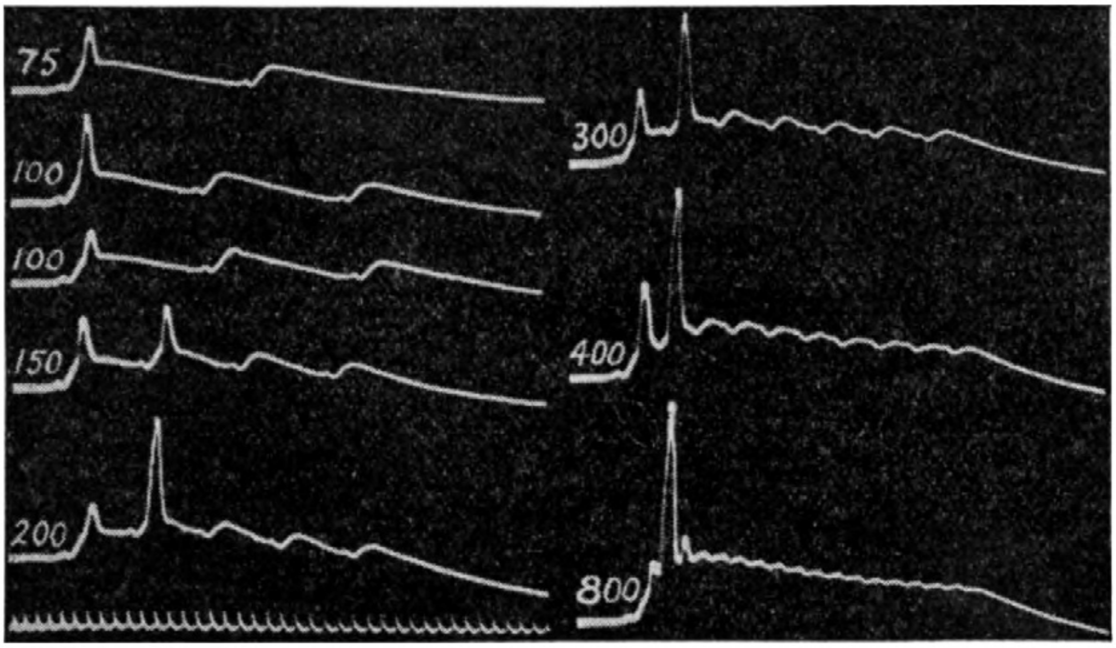


Fig. A45. Repetitive synaptic potentials with reflex spikes. [BM]

Records from rostral part of L_6VR; *quadriceps N* stimulated at frequencies shown by numerals; time in msec.

From Eccles & Rall, (1951) [1A-100], p. 487, fig. 7.

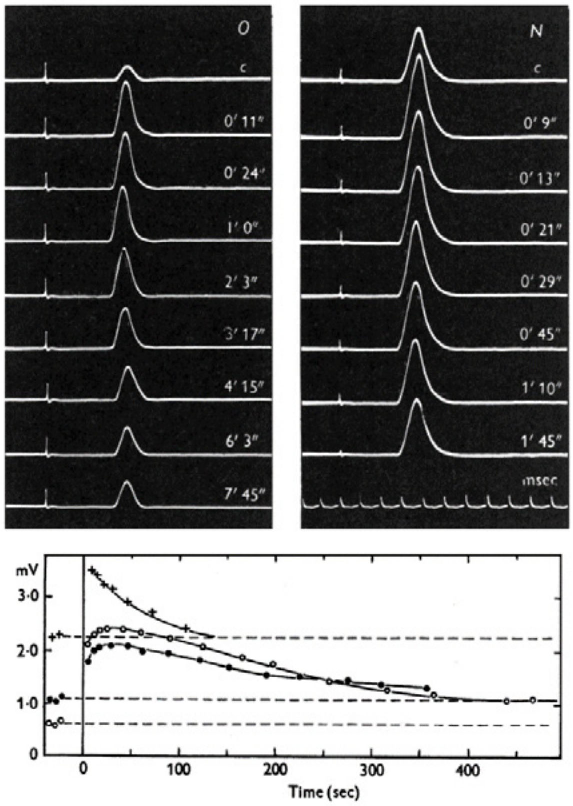


Fig. A46. Time course of monosynaptic reflex discharges. [BM, BR]

Upper frames (series O and N): Discharges, evoked as in Fig. A36A, and recorded in *gastrocnemius* ***N*** 40 days after extra-ganglionic operative section of the dorsal roots stimulated in the ***O*** records. Record (***c***) of both the ***O*** and ***N*** series is the reflex response before any tetanic conditioning. The remaining series show potentiated responses after a conditioning tetanus of 6,000 volleys at 400/second (cf. Fig. A44). The figures above each response show the time, in minutes and seconds, at which it was elicited after cessation of the conditioning tetanus. Amplification same for ***O*** and ***N*** responses.
From Eccles & McIntyre (1953) [1A-113], p. 495, fig. 1.

Lower frame. The crosses plot the ***N*** observations and the open circles the ***O*** observations. The vertical line marks the end of the conditioning tetanus, points plotted to left being preliminary controls (***c***). Horizontal broken lines give respectively mean control heights of reflex spikes. The filled circles are also ***O*** responses some 2 hours later than the open circles. Note that initial control level is same as level of residual potentiation surviving at end of first potentiation (open circles to right). Abscissae, time after end of conditioning tetanus.
From Eccles & McIntyre (1953) [1A-113], p. 501, fig. 4.

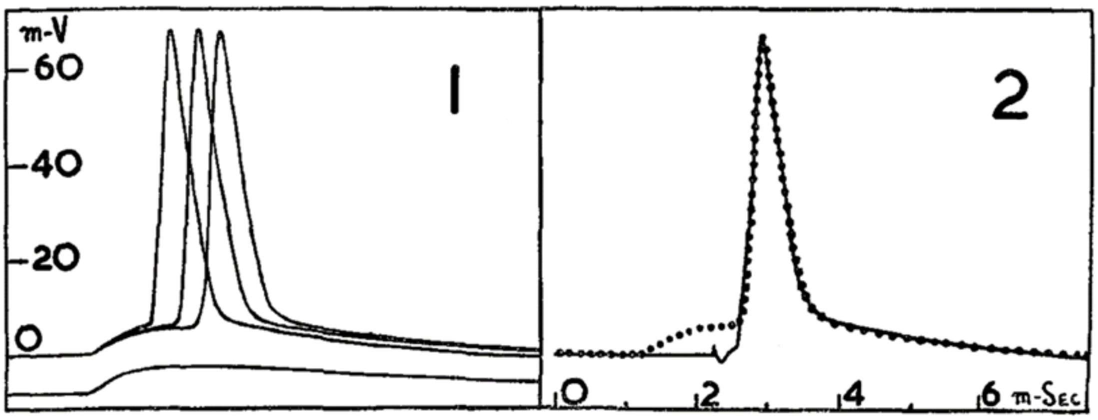


Fig. A47. Intracellular (EPSP) action potentials of cat spinal cord motoneurones. **[BQ, BR]**

Frame 1: Four successive responses shown of a motoneurone, stimulated monosynaptically by an afferent volley in the group **I** fibres of the appropriate muscle group. In the three superimposed records a spike of 68 mV with duration of 1.0 msec. (rising phase 0.3 msec.) rises from an initial synaptic potential that is seen alone in the lower record.
The larger the EPSP, the earlier the spike occurs.

Frame 2: Motoneurone excited by an antidromic impulse in its own axon sets up a spike potential (continuous line). The dotted line shows a superimposed spike response generated by monosynaptic excitation (cf. frame 1) Potential and time scales are common to both figures.
From Brock, Coombs & Eccles (1951) [1A-098], p. 15, figs. 1 & 2.

Experiment 20.08.1951

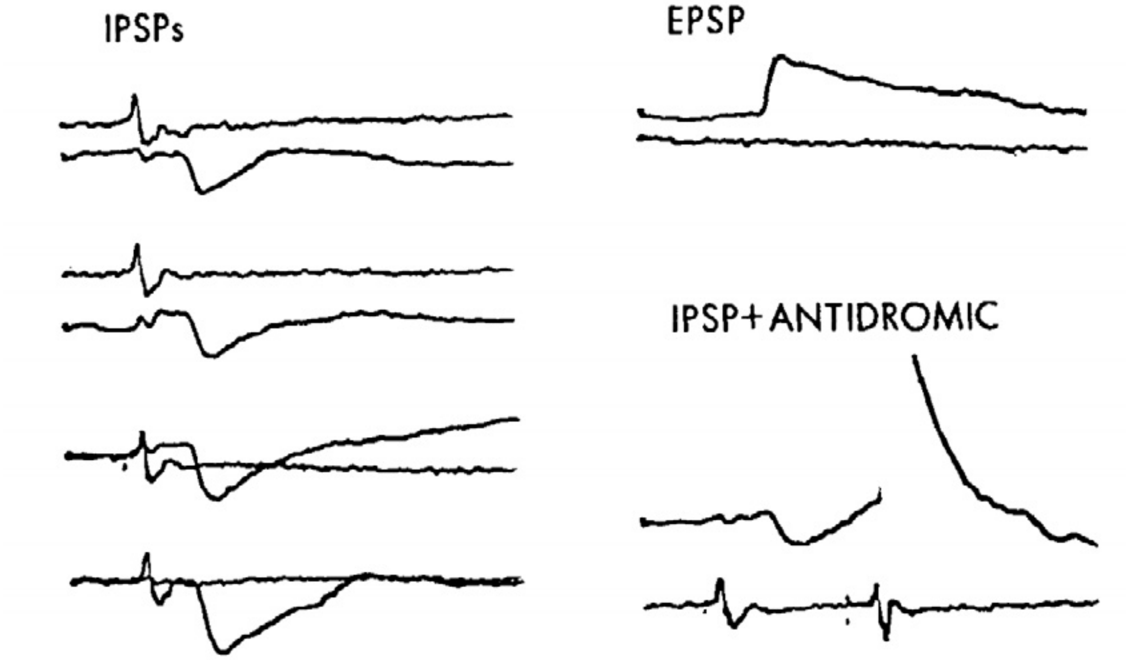


Fig. A48. **Intracellular recordings of EPSP and IPSP traces**. [**BQ**]

Left: From a *posterior-biceps-semitendinosus* neuron showing IPSPs generated by a group **Ia** *quadriceps* volley as downward (negative) deflections about 10 msec in duration.

Right upper: The other trace shows the action potential generated by this volley in the L_5 dorsal root. The EPSP is generated by a group **Ia** afferent volley in the *semitendinosus* nerve.

Right lower: The antidromic potential (truncated) is produced by stimulation of the L_7 ventral root.

From Eccles (1982) [1A-507], p. 335, fig. 3.

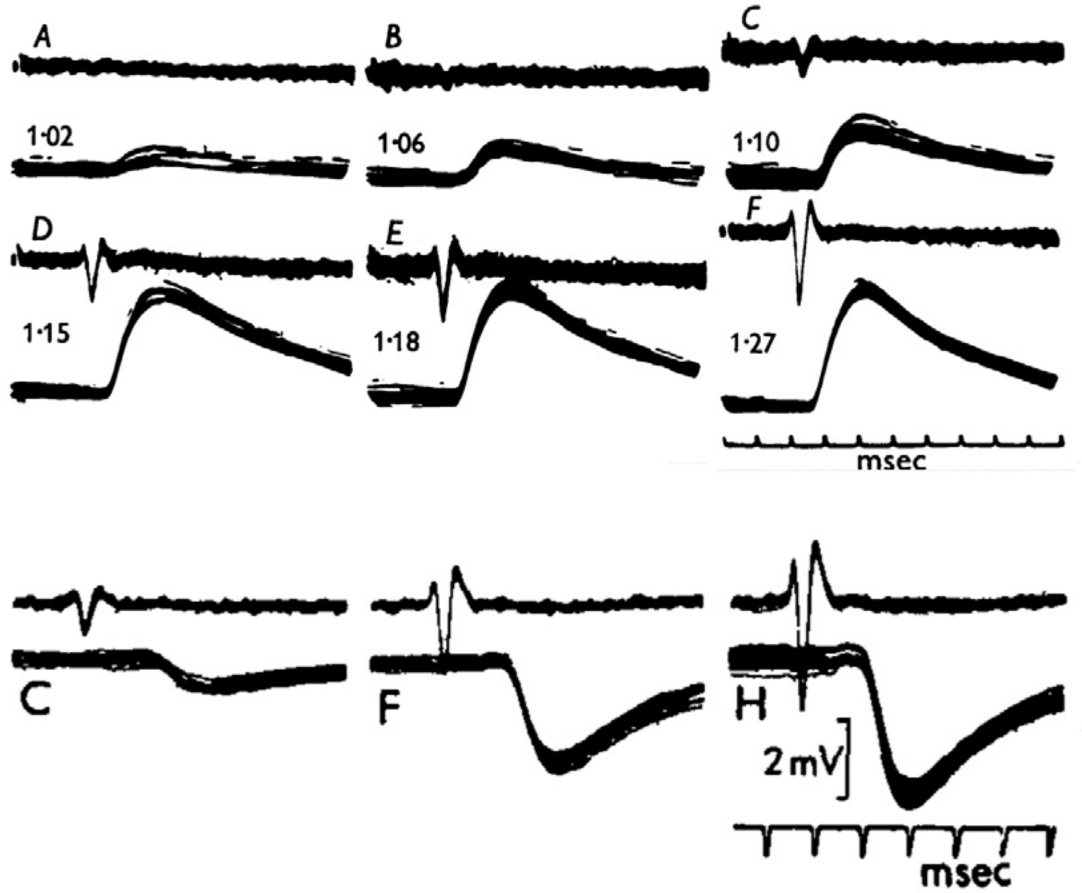


Fig. A49. Multiply superimposed traces of EPSPs and IPSPs. [BQ]

Upper series (monosynaptic EPSP), With progressively stronger stimulation applied through the stimulating electrode (from 1.18 to 1.27 times threshold in ***A*** to ***F***) the intracellularly recorded response increased to its maximal value in ***F***.

From Eccles et al (1957) [1A-140], p. 537, fig. 8;

[see also McGeer et al., (1978) [1B-a16], p. 105, fig. 4.2, traces B to G]

Lower series (IPSP). Here, a single volley in the afferent fibres from annulospiral endings in *quadriceps* muscle evokes an inhibitory postsynaptic potential (IPSP) in a motoneuron of the (antagonist) *biceps-semitendinosus* muscle. With progressively stronger stimulation applied through the stimulating electrode from traces ***C*** to ***H*** the intracellularly recorded response increased to its maximal value in ***H***. Traces were superimposed (ca. 40x) to give precision to EPSP and IPSP time courses.

From Eccles (1958) [1A-154], p. 38, fig. 5; traces C, F, H. [traces D, E, G ae not shown here]

[see also McGeer et al., (1978) [1B-a16], p. 114, fig. 4.7, with traces renamed A to C]

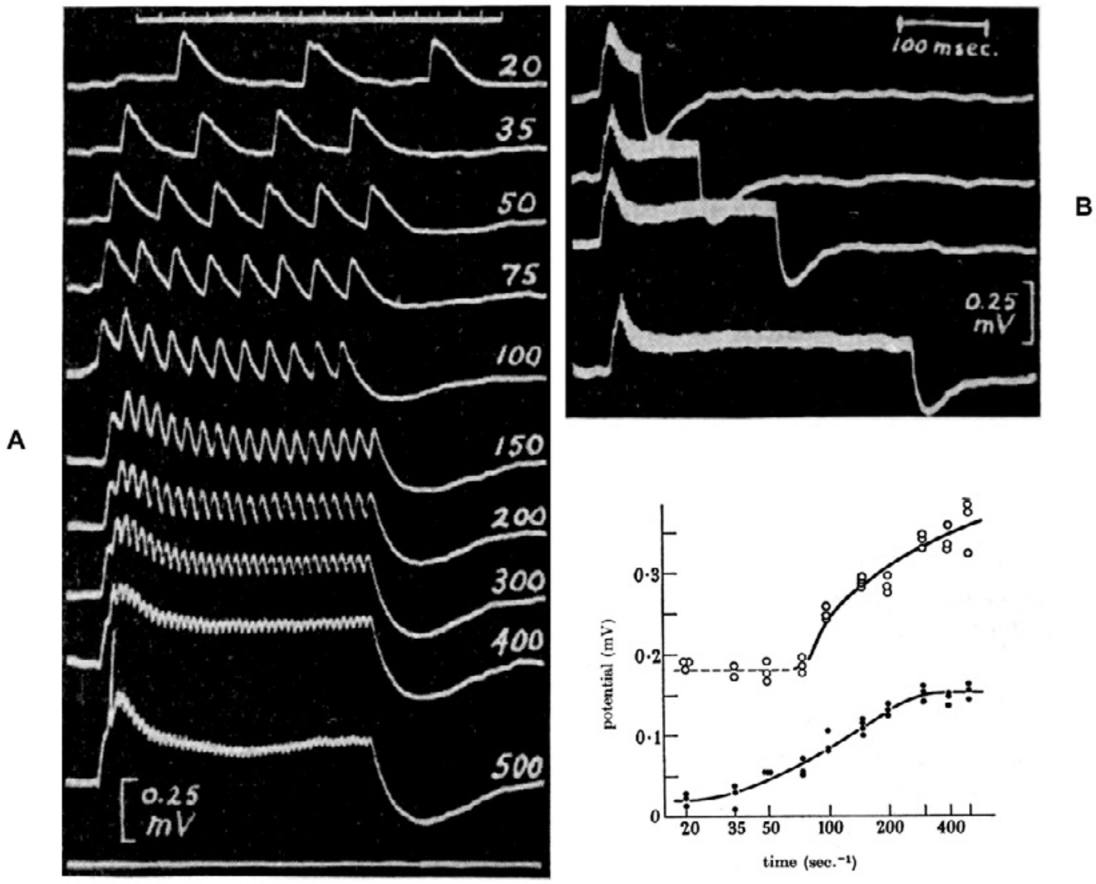


Fig. A50. Repetitive synaptic potentials; ventral root recording from rostral part of L6VR. [BQ]

A. Recorded with *quadriceps N* stimulated at strength 6 times group **I** threshold. Time-bar in 100/sec. Numerals give approximate frequency of stimulation per sec.

B. Slower records from *quadriceps* stimulated at 300/sec.; strength 6 times group **I** threshold.

From Eccles & Rall, (1951) [1A-100], p. 478, figs. 1a & 1b.

Insert lower right. Effect of frequency of stimulation on the build-up of negative potential (open circles) and after-positivity (solid circles) in ventral root records of **A**.

From Eccles & Rall, (1951) [1A-100], p. 482, fig. 4a.

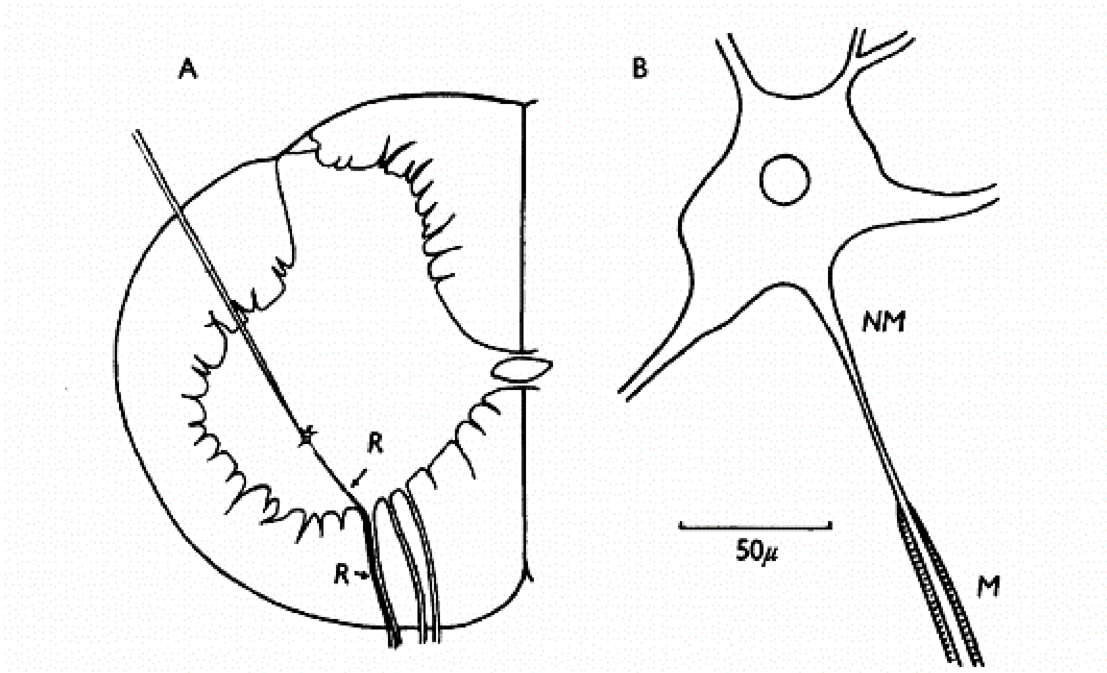


Fig. A51. Drawings of antidromic impulse pathway invading motoneurone. [BP, BQ, BR]

A: transverse section of spinal cord showing typical path of axon to motoneurone in the *biceps-semitendinosus* nucleus and the nodes of Ranvier, ***R*** (shown in exaggerated form) that occur in its medullated segment, which is shown penetrating the grey matter and ending within 100μ of the axon-soma junction. Note also micro-electrode in position.

B: tracing from a photomicrograph of an actual motoneurone; which shows in particular the beginning of the medullated segment, ***M*** (shown stippled), the non-medullated segment, ***NM***, with the thin segment and the axon hillock.

From Brock, Coombs & Eccles (1953b) [1A-115], p. 431, fig. 1.

[The photomicrograph referenced in **B** can be seen in Brock, Coombs & Eccles (1952a), [1A-103], p. 434, fig. 1A]

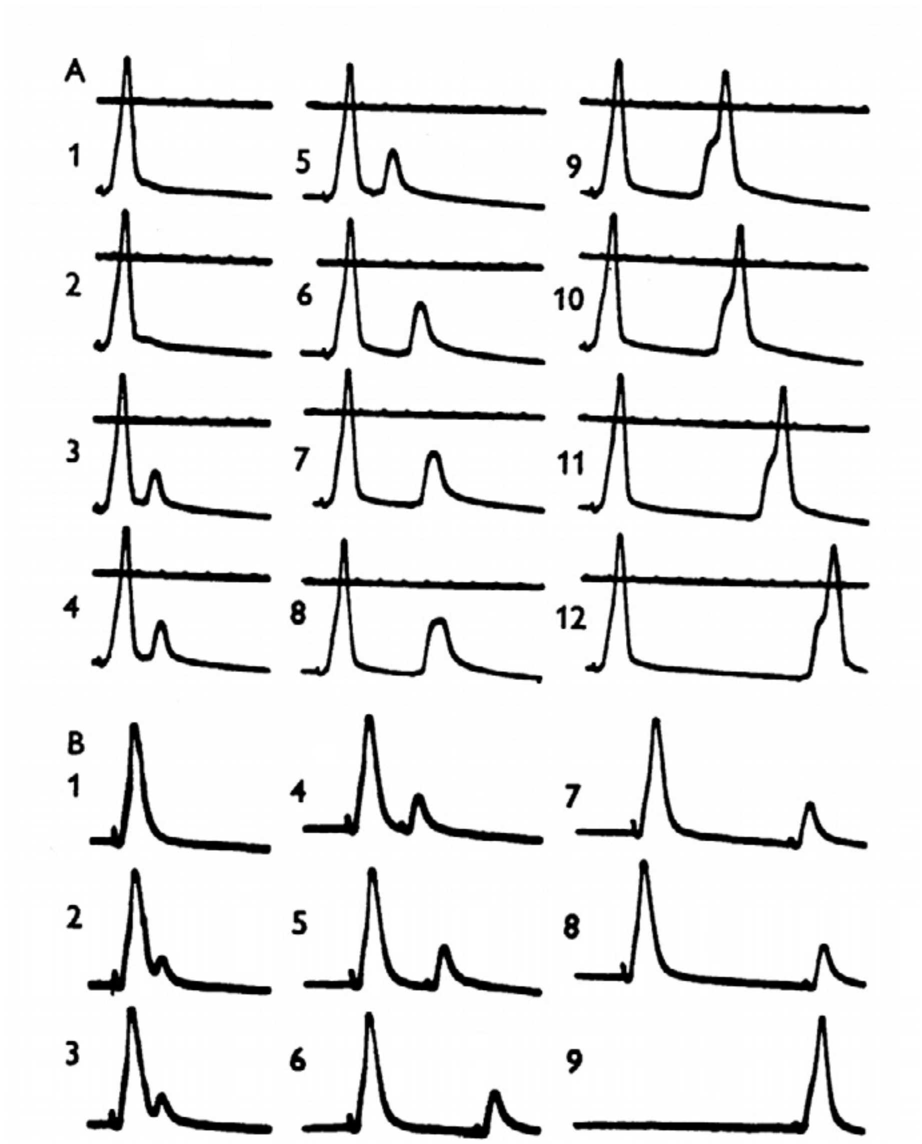


Fig. A52. Action potentials set up by double stimulation of the ventral root. [BQ, BR]

A: two antidromic stimuli at various time intervals. Time (in milliseconds) on the reference potential line for zero membrane potential. Resting potential, 72 mV.

B: as in **A**, but in another experiment, the last record (9) showing the control response to the second impulse alone.

From Brock, Coombs & Eccles (1953b) [1A-115], p. 438, fig. 5.

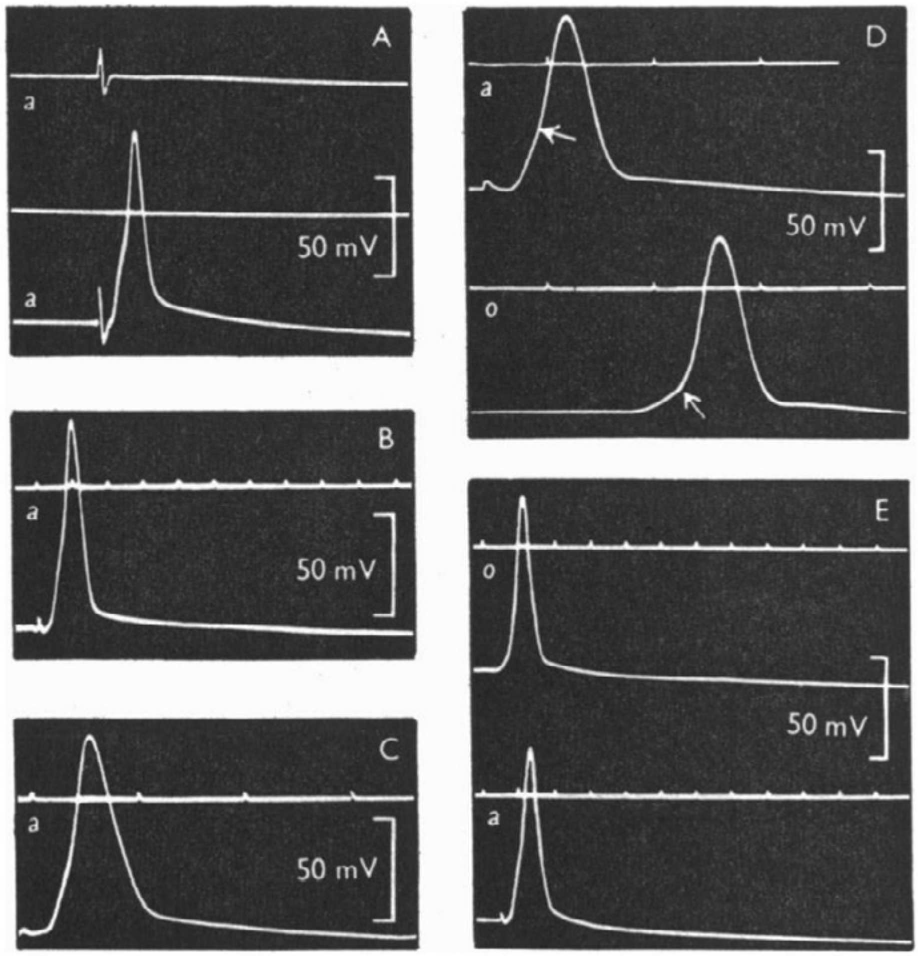


Fig. A53. Spike action potentials from motoneurones with an intracellular electrode. [BQ, BR]

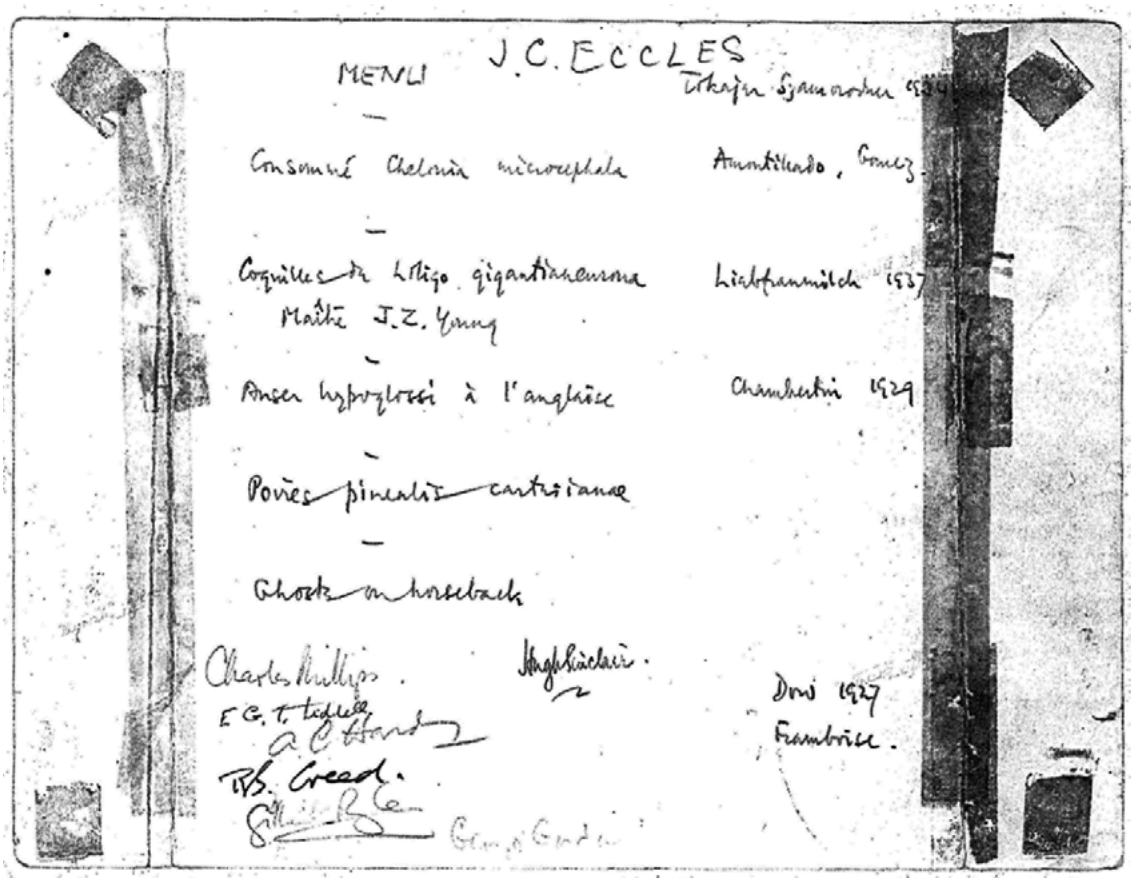
A. *gastrocnemius* motoneurone showing at top virtual zero response to a stimulus a few per cent weaker than the threshold.

B & **C**, as in **A**, but for motoneurones of muscles of sole of foot and *biceps-semitendinosus* (BSt.) respectively.

D & **E**, antidromically and orthodromically evolved spikes for motoneurons BSt. and *gastrocnemius* respectively. In **D**, arrows mark inflection at commencement of soma spike. (**a**) indicates antidromic responses evoked from a single stimulus to S1 ventral root, and (**o**) orthodromic responses evoked by a single afferent volley from appropriate muscle nerve.

(Note; in all records the reference line for zero membrane voltage with the time scale in milliseconds marked thereon except in **A**, where time scale as in **B**.) The time scale in msecs is the same for **A** and **B** (**C** and **D** have a faster time base).

From Brock, Coombs & Eccles (1952a) [1A-103], p. 439, fig. 3.



J.C. ECCLES

MENU

Tokaji Szamorodni

Consommé Chelonia microcephala — Amontillado, Gomez

Coquilles de Loligo gigantineurona Maître J.Z. Young — Liebfraumilch 1937

Anser hypoglossi à l'anglaise — Chambertin 1929

Poires pinealis cartesianae

Ghosts on horseback

Charles Phillips. Hugh Sinclair. — Dow 1927

E.G.T. Liddell — Framboise.

R.S. Creed.

Fig. A54. After the Waynflete Dinner at Oxford, 1952. – J. C. Eccles' signed "menu". [BT]
Signatories (below the menu); Charles Phillips, Hugh Sinclair, E.G.T. "Pat" Liddell, A.C Ward, R.S. Creed, Gilbert Ryle. (Present, but not a signatory: Tom Boase)
From Sir John's private memoirs.

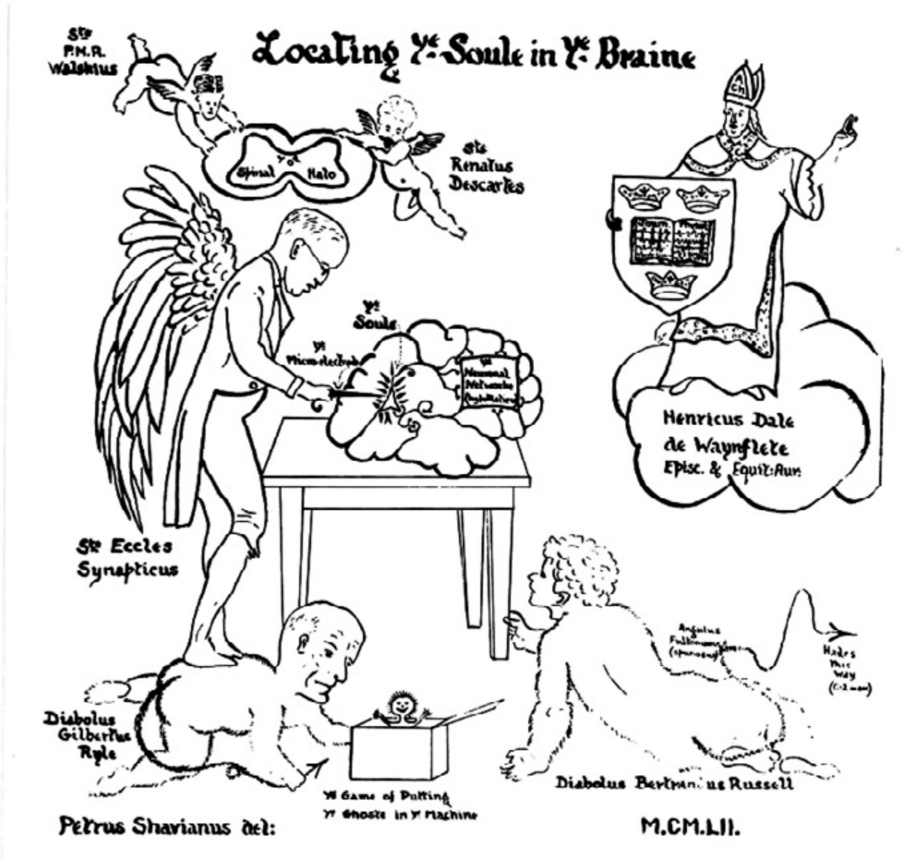


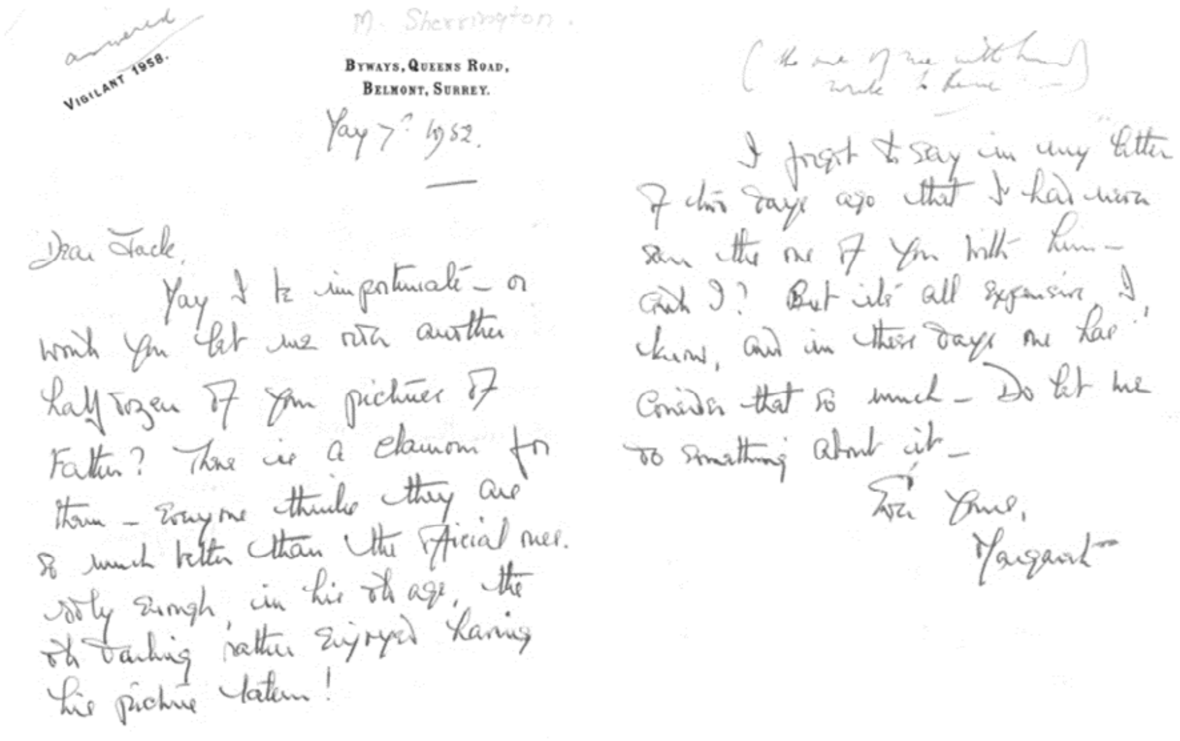
Fig. A55. Cartoon by Peter Shaw, shown at Eccles' Waynflete lecture by Hugh Sinclair [BT]

In Medieval English and entitled: ***"Locating ye Soul in ye Brain"***, and including the characters: St. F. M. R. Walshius[340] together with St. Renatus Descartes as cupids placing "ye spinal halo" on St. Eccles Synapticus; Henricus Dale of Waynflete, Episc. & Equit:Aur: (with opened "Journal of Physiology" on his shield); St. Eccles Synapticus with ye microelectrode and brain on the table, seeking ye Soul in ye Neuronal Network (hypothetical) and standing on the rump of Diabolus Gilbertus Ryle who is playing "ye game of putting ye ghost in ye machine"; Diabolus Bertrandus Russell[341] and the Angulus Fultoneous (spuriosus) of Fulton. The last three are roped together and connected with the signpost "Hades this way - (0.2 msec.). The cartoon is signed below by Shaw[342] as Petrus Shavianus and dated 1952.
From Sir John's private memoirs.

340 Walshe, Francis Martin Rouse (19.09.1885 – 21.02.1973) UK Neurologist. "Human reflexes".

341 Russell, Bertrand Arthur William (18.05.1872 – 02.02.1970) UK logician/philosopher. (NP 1950).

342 Shaw, Ivan Peter (1914 – 01.04.1993) UK history lecturer and secretary of Kings College London.


M. Sherrington.

answered

VIGILANT 1958

BYWAYS, QUEENS ROAD,
BELMONT, SURREY.

May 7th 1952.

Dear Jack,

May I be importunate – or would you let me have another half dozen of your pictures of Father? There is a clamour for them – everyone thinks they are so much better than the official ones. Oddly enough, in his old age, the old darling rather enjoyed having his picture taken!

(the one of me with him would be lovely)

I forgot to say in my letter of three days ago that I had never seen the one of you with him – had I? But it's all expensive, I know, and in these days one has to consider that so much – Do let me do something about it –

Ever Yours,
Margaret

Fig. A56. Request for photograph of Charles Sherrington by his stepdaughter Margaret. [BU]

Unfortunately, the referred-to photograph (taken by Jack Eccles) has not yet been located. From Sir John's private memoirs.

STAGE 5: Research in Canberra: 1952–1966
(Sections CA to CH)

CA. Deciding on a new location for my future research

A special feature of my return to England was that I came as a neophyte with my newfound enthusiasm for chemical transmission at both excitatory and inhibitory synapses in the central nervous system. In February 1952 there was a Ciba symposium on the spinal cord and also a Royal Society Symposium. At the Royal Society I had the pleasure of signing the Fellows Book some eleven years after my election in 1941-still the same book that Newton[343] had signed. It was a strenuous period with my travel around England and much entertainment and good discussion. I had the feeling that England was at the beginning of a magnificent new post-war era. Certainly, I was not misled in my estimate of the great scientific successes. Hodgkin, Huxley, and Keynes[344] in Cambridge and Fatt and Katz in London were leading the world in neurobiology, and that lead has been maintained -as evidenced by the Nobel awards to Hodgkin, Huxley, and Katz. But, as a power in the world and as a great industrial country, England has declined in a way not anticipated in 1952.

I would have liked to return to England at that time, because the Antipodean prospects were, as yet, a matter of faith and hope. There were by then some centres of achievement in Australia, in particular in radio astronomy and in microbiology, but Australia was at a provincial level in other sciences. This had motivated Florey to work for a research university that was entirely postgraduate, giving only doctoral degrees. So, in June 1952 I returned to Australia after a brief interlude in America attending the Cold Spring Harbor Symposium on the neuron. There was much discussion on intracellular recording. Woodbury[345] and Patton had also succeeded with motoneurons, but Lloyd was severely critical of the whole project, which he thought could only lead to a vast and misleading literature on damaged and dying neurons! This attitude of Lloyd's was more than I could have hoped for, and aroused Bob Morison[346] to compose two limericks which were regarded as unprintable in the published symposium! I realised that, with his superb technique and penetrating insight, Lloyd could have made great progress in intracellular recording in the study of excitatory and inhibitory synapses during the long latent period which necessarily would occur in the resumption of my research career.[A] It was to take much time and travail before I could establish laboratories in the temporary buildings then being constructed in Canberra. Meanwhile, I had brought from New Zealand four

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343 Newton, Isaac (25.12.1642 – 20.03.1726) UK physicist astronomer. Book 1687: "Principia Mathematica".

344 Keynes, Richard Darwin (14.08.1919 – 12.06.2010) UK physiologist. Na/K flux in nerves, electric eel.

345 Woodbury, J. Walter (07.08.1923 – 29.11.2017) US Univ. of Utah pioneer physiologist/biophysicist.

346 Morison, Robert Swain (25.11.1906 – 3.12.1986) US Head of Life Sciences Div., MIT. "EEG"

magnificent electrical stimulating and recording units (ESRU), designed by Jack Coombs and built in New Zealand.**B** At that time and for many years to come-in fact until the transistor era-they were the best general research instruments for electrophysiology in the world. Some were still in use in David Curtis's department until 1976, and I used the original ESRU until 1968. Without doubt the successes of our department in the Canberra period were dependent on the excellence of the ESRU's. For me it was very frustrating to have to wait month after month before I could resume the intracellular studies on motoneurons that had been interrupted in December 1951 on my departure from New Zealand. Paul Fatt had come to Canberra in the latter part of 1952 to continue with motorneurons the intracellular recording that had been such a success in the study with Bernard Katz on the neuromuscular junction.**C** In the first months before the laboratories were ready, he was intensely occupied in a critical appraisal of the literature on spinal motoneurons and came up with challenging ideas that helped to guide our research in those early Canberra years.

CB. Setting up my laboratory in Canberra

So, in March 1953 the active Canberra phase of my life began and continued for over 13 years. Without doubt it was the high point of my research career. Koketsu[347] from Japan joined Fatt and me in our study of Renshaw cells, which was one of my most satisfying research projects.**A** The cholinergic excitation of these cells by collaterals from motoneuron axons was a striking vindication of Dale's principle (c.f. Eccles, 1976, [1A-420]), namely that for the synapses formed by all axonal branches of a neuron there is the same chemical transmitter.

Other members of our research team during the first five years were Jack Coombs from New Zealand, Sven Landgren[348] from Sweden, Bill Liley from New Zealand, my daughter Rose, Vernon Brooks[349] from Canada, David Curtis[350] from Melbourne, Anders Lundberg[351] from Sweden,**B** Ben Libet[352], Bob Young[353],**C** and Kris Krnjevic[354] from the United States, Ricardo Miledi from Mexico, and Arthur Buller[355] from England. Already the department was taking on the international complexion that was to become so characteristic in later years. During these earlier years we

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347 Koketsu, Kyozo (1922 -) JP physiologist. Later professor of Kurume University.

348 Landgren, Sven Olof Esbjörn (05.05.1921 – 26.05.2016) SE Veterinary physiologist. In Canberra 1953-54.

349 Brooks, Vernon B (10.05.1923 – 04.10.2017) DE/CA(J) neurophysiologist. "Botox" action.

350 Curtis, David Roderick (03.06.1927 – 11.12.2017) AU pharmacologist & neurobiologist.

351 Lundberg, Paul Anders (10.09.1920 – 18.05.2009) SE neurophysiologist. In Canberra 1950s. Eccles Obituary.

352 Libet, Benjamin (12.04.1916 – 23.07.2007) US(J) scientist in the field of human consciousness.

353 Young, Robert Rice (?-?) US neurophysiologist.

354 Krnjevic, Krešimir "Kris" (07.10.1927 – 16.04.2021) HR Croatian physiologist. Prof. at McGill University.

355 Buller, Arthur John (16.10.1923 – 09.05.2019) UK Bristol physiologist. "Muscle twitch contraction speed".

worked in the rather limited facilities of the temporary hut. The grandiose permanent building was longer in coming than we had hoped, but somehow much research was accomplished in the three research rooms.**D**

I felt very much the urgency of showing by our achievement that this extraordinary foundation by the Australian government and by the Prime Minister, Sir Robert Menzies, was delivering the academic goods. Menzies was one of the really great men I have been privileged to know. Canberra in those early days was a very small "city" for a capital, and very short on social amenities. Menzies advised that the first permanent building to be erected would be the residential college and faculty club, called University House. He rightly sensed that a university is a community of scholars and that there had to be good facilities for cross-cultural meeting in a faculty club. University House provided faculty club facilities rivalling any other such club in the world. I spent much time in those earlier Canberra years on the governing body of University House. Two Cambridge associates, Trendall[356] and Oliphant, and I tried to give University House the style of Cambridge and Oxford, but appropriate for an entirely postgraduate college and in harmony with the international culture that was the hope of the post-war world. It was quite a challenge to mould the style and tradition of the past so that it would be assimilated by the young academics. Some were very raw material on arrival, but most became civilized without appearing to notice the transformation. We kept our satisfaction confidential. I have dwelt long on this aspect of Canberra because I believe most American universities, particularly those financed by state governments, are miserly in their appropriations for cultural amenities for faculty. By contrast the student body is well catered for. The state university system of New York is a notable example of this absurd unbalance. As a consequence, I spent the last seven years of my academic life in Buffalo in virtual isolation from my colleagues in other departments. The university was more like a trade school-and much of it was so oriented.

CC. Birth of the Australian National University in Canberra

A remarkable feature of the Australian National University was its international orientation. No preference was made to Australians, and there were unrivalled facilities for overseas scholars. For example, if appointed to a research scholarship, the travel to Canberra of the scholar plus wife and children was fully paid and his emoluments dated from the time of departure. The emolument and the scholarship were about twice that for basic living and housing costs in Canberra, and furnished houses were provided for scholars with children. Married and single scholars lived in University House. There were no university or degree fees, and the return journey was also fully paid. The more senior staff had fellowships at appropriate levels, again with all travel costs paid and housing provided. These generous arrangements explain why there was such an international complex in this remote Australian university.

356 Trendall, Arthur Dale (28.03.1909 – 13.11.1995) NZ classical archaeologist “Italian pottery”.

This international generosity was encouraged by Menzies, who remarked that at last Australia was in the position to pay off some of the "academic debts" incurred during its growing and maturing stages, when Europe and America had been so extraordinarily generous in their help to young Australian scholars, as I for one well remembered from my years in England. Cynics may remark that it was an attempt to attract scholars from abroad to settle in Australia, but very few did outstay their appointments in Canberra. However, Australia did gain enormously in two respects. First, there was a transformation from the academic isolation of the pre-war years that I had experienced on arrival in Sydney in 1937, and many Australian scholars returned to Australia, often after long sojourns overseas. Second, the new generation of young Australians had the great advantage of association in Australia with scholars from overseas. The academic renaissance spread through the whole university structure of Australia. Australian science is now in top world class, a remarkable achievement for a middle-sized country (13 million) so remote from the great centres of the world.

CD. Establishment of Australia's Prestigious Scientific Body

At this stage I should make reference to another of the activities to which I devoted great enthusiasm in those early Canberra years. Despite the existence of many scientific societies, Australia had been lacking a prestigious scientific body that could speak with authority to the government, to industry, and to the country. What we needed was a foundation playing a role in Australia equivalent to that of the Royal Society of London. Sir Mark Oliphant was the leading spirit in furthering this project. In order to give the new foundation adequate credentials, the Fellows of the Royal Society resident in Australia, together with a few senior scientists they nominated, petitioned the Crown for the foundation of the Australian Academy of Science, which would be modelled on the Royal Society of London. In this project we were most enthusiastically supported by the Royal Society. All went well, and in 1954 Her Majesty Queen Elizabeth II founded the Australian Academy of Science in Canberra. It was the second time in history that a British monarch had founded a scientific society, the first being the Royal Society of London by Charles II in 1660! Oliphant was the first president from 1954-1957, and I succeeded him in 1957-1961. Those were early creative years with many problems in the travail of birth pains. But the Academy has flourished and has contributed notably to Australian scientific advancement and to the influence that science plays in Australian affairs.

A striking symbol of Australian science was the remarkable edifice of unique style, built by the Academy for its headquarters in Canberra. Oliphant initiated this project with great insight and courage and, in my period as president, the building was completed to the great joy of the Fellows and the amazement of the local inhabitants. It displayed an extremely simple geometrical form, an enormous copper-covered dome, a section of a sphere, broken only by the arches rising in scalloped form from some 16 "feet" immersed in a circular moat. I think the design was superb and the interior had excellent facilities, particularly the central meeting hall. I have most happy memories of the many great occasions associated with those early years of the Australian Academy of Science. [Fig. F20]

CE. Setting up my new Department in Canberra

But I should return to the Australian National University with the department of physiology as an integral part of the John Curtin School of Medical Research. At last, in 1957 the grandiose new building was completed. We had done so well in the temporary hut that I was somewhat overawed by the new magnificence and the greatly extended facilities. I had only one floor of one wing, but managed to plan the space so that there were six research laboratories and at least 12 studies. It was my belief that each research worker should have his own study, no matter how small, in order to have the privacy for working up his data, measuring, writing, and typing. The alternative of having several junior research workers sharing a larger space is almost universal. At Oxford I had this experience in my first year, 1928, where Denny Brown, Granit, Olmsted, Marcu, and I shared a large disused laboratory; but in 1929 I managed to acquire my own study, and since then I have almost always been able to provide separate studies for all of my associates. The increased accommodation of the new laboratories and the many applicants, particularly from overseas, resulted in a large expansion of research staff, particularly during the last half of my Canberra period-1959-1966. It was quite an organizational task to arrange for the coming and going so that there would be maximum occupancy and yet no overcrowding. In those years there were always more than 20 research workers and as many technical and support staff. Of course, I did not personally supervise so many. I had by then a semi-autonomous section. Macfarlane had developed his own research group in endocrinology and climatology. Curtis had his group in neuropharmacology and neurochemistry, and Hubbard had a group in the biophysics and electron microscopy of neuromuscular transmission.

My own research interests had developed far from the initial intensive study of the biophysics of the motoneuron and the action of excitatory and inhibitory synapses thereon. There was so much that this new technique could be used for at the spinal level that I stayed almost a "prisoner" in the cat spinal cord for many years -in fact until 1962.[A] As I look back on those years, I can hardly imagine how we dared to attempt so much! The opportunity to present in an integrated form the initial stages of our work at Canberra was provided by the invitation to give the Herter[357] Lectures at Johns Hopkins Medical School in 1955. These lectures were eventually published as The Physiology of Nerve Cells (Eccles, 1957) [1B-a03] by the Johns Hopkins Press.

Patterns of organization in the spinal cord provided the challenge for studies that Lundberg in part developed independently in 1956 and 1957. The inputs from muscle receptors by groups **Ia**, **Ib**, and **II** were studied in detail, particularly in relationship to

357 Herter, Christian Archibald (03.09.1865 – 5.12.1910) US physician & pathologist, “celiac disease”.

the functions of the muscles supplied by the motoneurons-those that are homonymous or heteronymous and synergic, and those that are heteronymous and antagonistic. In this study we were carrying the pioneering work of Sherrington to the new level of enquiry made possible by intracellular recording.

In 1957 my colleagues, Ben Libet and Bob Young from America and I utilised intracellular recording from axonotomized motoneurons to account for the enigmatic reflex responses of these chromatolyzed motoneurons that had been observed many years earlier.[B] It was of special interest because of the finding that synaptic excitation resulted in dendritic spike potentials that were transitional to the generation of impulse discharges down the motor axon.[C] There was also an investigation of the electrical properties of the chromatolyzed motoneurons and a full explanation of the earlier observations on reflex responses. I mention this paper because it has been undeservedly overlooked by later investigators and reviewers. These later papers have very little additional to report and the illustrations and measurements of our 1958 paper are superior to those of the later papers published in the 1970s. It seems that papers published more than a decade ago are ignored, regardless of content or merit!

Cross-union of various peripheral muscle nerves was attempted in 1957 in order to discover if it would result in some central reconstruction of connectivities by a kind of plastic response. Sperry[358] had failed to find any significant changes many years earlier but intracellular recording made it possible to do a more refined and quantitative study.[D] Already we had amassed control studies on monosynaptic inputs using intracellular recording from many hundreds of identified motoneurons. However, the first experiment completely changed our plans. I had cross-united in young kittens the nerve to the pale flexor, *gracilis*, with that to the red extensor, *crureus*. After a period of several weeks in order to allow time for regeneration, we proposed to see if there were changed connectivities to the respective motoneurons in the light of their transposed functions. For example, did *crureus* motoneurons now supplying *gracilis* muscle receive some connectivities appropriate to knee flexors? But, on exposing the muscles, there was an incredible display. The pale *gracilis*, now innervated by *crureus* motoneurons, had become bright red, the other *gracilis* showing the normal pallor. So, we immediately set up mechanical recording and found to our delight that the red colour of *gracilis* was matched by its much slower contraction. And, complementarily, the slow *crureus* innervated by *gracilis* motoneurons had become much faster relative to the control muscle on the other side. Arthur Buller had just arrived from England, so there was one year of intensive study on the influence of motoneurons in determining muscle contraction time. Not only did we study cross-union of various muscle nerves after a wide range of post-operative times, but we also studied the time courses of muscle contraction from birth onwards. Investigations in many laboratories have stemmed from these initial studies,

358 Sperry, Roger Wolcott (20.08.1913 – 17.04.1994) US neuropsychologist/neurobiologist. (NP 1981).

not only mechanical (Buller, Close[359] and associates), but also electrophysiological, biochemical, histological, and pharmacological.**E** The aborted study on central connectivities and cross-union was later taken up. Some changes were found, but even just after birth there was little evidence of the plasticity in the spinal cord that has now been shown to be so prominent at higher levels of the central nervous system.

Another good story began in 1959, when following up preliminary reports by Frank and Fuortes [1957] on presynaptic inhibition. The dorsal root potential and the dorsal root reflex had been known since the work of Barron and Matthews and Tönnies[360] in the 1930s and was studied by us in Dunedin in the 1940s, but the functional significance had remained an enigma. An intensive study for some two years in collaboration with Krnjevic, Schmidt[361],and Willis[362] revealed the story that has been corroborated and enhanced by much subsequent work in other laboratories. It was postulated that there are special axon-axonic synapses on presynaptic terminals that act to depolarize these terminals and so to reduce the action potential and thus the emission of transmitter. Electron microscopy, first by Gray[363] and later notably by Saito[364], has displayed these axon-axonic synapses much as we diagrammed them,**F** and recent work by Niznik[365], Nicoll[366], and associates has corroborated our suggestion that GABA is the transmitter.**G** The main thrust of these investigations was a systematic topographic and modality study in the effort to define the way in which presynaptic inhibition was employed physiologically.

I was only partially associated with the refined biophysical studies that were carried out in 1959-1963, largely by the Japanese team of Ito[367], Araki[368] and Oshima[369].**H** I was particularly happy at the finding that in an investigation of 34 species of anions the inhibitory transmitter was found to open up in the postsynaptic membrane gates that allow the passage of all anions regardless of species, provided that in the hydrated state their diameter is smaller than a critical size (2.9 Å). The only exception was formate, that passed through despite being slightly larger than this critical size for the other 10 species of anions. It looked as if we had a simple model

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359 Close, Russell Ian (?– ?) NZ neurophysiologist Research Fellow Canberra. “Nerve/muscle-fibre relationship”.

360 Tönnies, Jan Friedrich (10.10.1902 – 24.12.1970) DE Physiologist/inventor with Oskar Vogt, Herbert Gasser.

361 Schmidt, Robert Franz (16.09.1932 – 13.09.2017) DE Physiologist & textbook author. “Human Physiology”.

362 Willis, William D. Jr. (19.07.1934 – 15.09.2015) US neuroscientist & author. Transmission/reception of pain.

363 Gray, Edward George (11.01.1924 – 14.08.1999) UK TEM-neuroanatomist. “Synapse types 1 & 2”.

364 Saitō, Kiichirō (1940 –) JP electron microscopist. Univ. of Tsukuba. “Atlas of neuron ultrastructure”.

365 Niznik, Hyman B (?-?) CA Prof. Univ. Toronto of psychiatry & pharmacology. “Dopamine”.

366 Nicoll, Roger A (15.01.1941-) US Prof. Cellular & Molecular Pharmacology. Univ. of California.

367 Itō, Masao (04.12.1928 – 18.12.2018) JP Neuroscientist. Director of Riken Brain Science Institute.

368 Araki, Tatsunosuke (?-?) JP physiologist, Kyoto University

369 Oshima, Tomakazu “Kasu” (?-?) JP Dept Neurobiology, Tokio Metro. Inst. for Neurosciences.

for the mode of action of the inhibitory transmitter. Unfortunately, the investigations on cationic permeability of the inhibitory postsynaptic membrane were much more enigmatic, and the question of potassium permeability is still debated. Parenthetically, it may be noted that the ionic mechanisms of postsynaptic inhibition in hippocampal pyramidal cells was my last experimental study (until May 1975).

CF. My Nobel Prize

It was at this stage of my Canberra life that I received the Nobel award (1963) for the ionic mechanisms of synapses, and my Nobel Lecture was on the ionic mechanisms of postsynaptic inhibition.[A] Earlier in that year I felt that the time was ripe for an extensive review of the whole field of synaptic mechanisms. This proved a heavier task than I had anticipated, but it appeared as The Physiology of Synapses that was published just in time to be on display in Stockholm at the time of the Prize festivities in December 1963. The publishers (Springer Verlag) made an unprecedented effort in speed of publication in order to effect this felicitous timing. All was finally printed and in order for binding except for the subject index. The typescript reached the Heidelberg office on Monday, December 2. On Sunday December 8, I received in Stockholm some six bound copies by airmail special delivery, and, on Monday, the booksellers of Stockholm had display copies, and copies for sale were available on December 10, the day of the Prize award.[B]

CG. Our Research Attention becomes focussed on the Cerebellum

After some ten years of intracellular recording in the spinal cord I was happy to move into the much more complex and challenging problems presented by higher levels of the nervous system. The change occurred gradually. At first there were investigations led by Olov Oscarsson[370] on the cells of origin of the spinocerebellar tracts. Cells of origin of another ascending pathway were also studied. Meanwhile Tom Sears[371] was carrying out his refined studies on the control of respiratory movements by employing intracellular recording from motoneurons supplying intercostal muscles. At this time also stimulation of the motor cortex was shown to produce presynaptic inhibition in the spinal cord. However, the decisive change occurred with studies on neurons of the brain stem under the leadership of Per Andersen.[372]

Firstly, there was synaptic transmission in the cuneate nucleus with ascending actions from the spinal cord and descending from the cerebral cortex. The neuronal machinery involved in these actions was studied in detail. Next came the ventrobasal

370 Oscarsson, Olov (1931 – 19.07.1996) SE Prof. physiology at Lund University.

371 Sears, Thomas Anthony (05.1928 –?) UK Sobell Prof. Inst. of Neurology Queen Square.

372 Andersen, Per Oskar (12.01.1930 – 17.02.2020) NO Physiology prof. IMB, Univ. Of Oslo. "LTP".

nucleus of the thalamus on the projection line to the cerebral cortex from the cuneate nucleus. There was study of the neuronal machinery and the role of inhibition in setting the rhythmic activity of the thalamocortical circuits, a theme that Andersen was later to develop so well.[A]

The most important study was on the hippocampus, using the new techniques of intracellular recording and field potential analysis. Andersen already had extensive experience on the hippocampus, so good progress was assured. The most interesting discovery was that the basket cells of the hippocampus gave a very large and prolonged inhibitory postsynaptic potential of the hippocampal pyramids. It had been known since the time of Ramon y Cajal that the basket cells formed a dense terminal plexus (or basket) around the somata of pyramidal cells, which he believed to exert an intense excitatory action. The combination of depth profile and intracellular studies convincingly demonstrated that the action was an intense inhibition. So, for the first time an inhibitory cell with its synaptic terminals had been identified histologically. At that time Renshaw cells had not yet been recognised histologically.[B]

Having accomplished that identification so satisfactorily, I asked: where else are there basket cells? The answer being the cerebellum, we (Andersen, Voorhoeve[373], and myself) immediately in early 1963 changed our attention to the cerebellum. It was a more complex study than the hippocampus; nevertheless, the clear answer came that the basket cells there are also inhibitory, this again being shown by depth profile and intracellular recording. Per Andersen had to return to Norway, so we made a pact. He was to have the hippocampus for his field, and I and my associates, the cerebellum. I regret to report that in 1975 I broke the pact by again working on the hippocampus, in a final electrophysiological study on the ionic mechanism of postsynaptic inhibition. It was an appropriate and very successful termination of my experimental life with my colleagues Allen[374], Nicoll, Oshima, and Rubia[375].

The beautifully organized structural pattern of the cerebellum was a great opportunity for an analytical study of the mode of operation of the two input lines, by mossy fibres and by climbing fibres, and of the five species of neurons. Of particular importance was Szentágothai's[376] evidence for the origin of climbing fibres from the inferior olive. Remarkably clean results were obtained by stimulating through an electrode inserted into the inferior olive. The mossy fibre input gave a more complex picture, but by utilizing various sites of stimulating together with depth profile recording and intracellular recording from Purkinje cells, a satisfactory picture emerged that enabled us to make models of the mode of operation of the neuronal machinery in the cerebellar cortex. With but minor variations this model still holds, so the comprehensive book published in 1967 with Ito and Szentágothai, The

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373 Voorhoeve, Paul Eric (18.07.1927 – 13.07.2010) NL neurophysiologist.

374 Allen, Gary I (07.04.1942 –) US physiologist at Univ. New York Buffalo. "Cerebrocerebellar studies".

375 Rubia Vila, Francisco José (01.02.1938 -?) ES Medical Prof.at Universidad Complutense de Madrid.

376 Szentágothai, János (31 10 1912 – 08 09 1994) HU anatomist. Semmelweis University. "Cerebellum".

Cerebellum as a Neuronal Machine still does not need extensive revision.**C** This analysis of the neuronal operation in the cerebellum was greatly aided by a principle that I had proposed as early as 1954: that all the synapses formed by a neuron in the mammalian central nervous system have not only the same transmitter (Dale's Principle), but also the same action, either excitatory or inhibitory, there being no ambivalent neurons. So, we could generalise from our analytical experiments and propose models of circuits that displayed the essential features of operation in all the complex interactions of the neuronal machinery.**D**

CH. I am forced to face the Spectre of Forced Retirement

Troubling me in my later years at Canberra was the early retirement age of 65 that was soon to overtake me. I had hoped to get this age extended to 68, but the administrators prevented this.**A** I already knew the very impoverished conditions that would be my lot after 65 - half salary renewable year by year and one laboratory with almost no support for staff or assistants. So, I realised that soon my odyssey would take me from Australia across the Pacific. There were only two choices at that time: The University of British Columbia and the newly established Institute of Biomedical Research in Chicago. Both offered far more generous support than I would have in Australia, and there was provision for extension of my position for up to 70 years and even beyond. I was impressed by the grandiose plans for Chicago, and so, unwisely as it turned out, I accepted this position, which was the first I had ever been offered in the United States.

This decision relieved the Australian National University of what was clearly an embarrassment-to have me there as an impoverished worker-and there was much ceremony on my departure, including an attractive portrait of me by Miss Judy Cassab[377] and a witty cartoon by Frith.[378] Both were unveiled at the farewell banquet,**B** and there was a most generous speech by Lord Florey who was in Canberra on one of his numerous visits as Chancellor of the Australian National University. In my reply I alluded with approval to his frequent public statements that the value of the John Curtin School of Medical Research was not to be judged by the kilograms of publications, but by the value of its scientific discoveries for the people of Australia and of the whole world. Just to emphasise the point I displayed an official document prepared by my head technician, Lionel Davis, who was a Justice of the Peace, to the effect that the total publications of the department of physiology over 13 years weighed 10.8 Kg! The cost per Kg certainly would be discouragingly high for a business man.

Some more statistics for my 14 years at Canberra are that there were in the department of physiology 74 research workers from 20 different countries, and 411 scientific papers and 4 books were published. This is a tribute to the Australian

377 Cassab, Judy (Judit Kaszab) (15.08.1920 – 03.11.2015) AT(J) Viennese artist. Emigrated to Australia in 1951.

378 Frith, John Eric (1906 or 1908? – 21.09.2000) GB Cartoonist: Melbourne, Gerald & Weekly Times.

government for supporting the Australian National University so generously, particularly in respect of overseas visitors. Another "human dividend" from this Canberra period were the excellent personal relationships that developed between the families of my visitors, no doubt fostered by the isolation in Canberra. After all these years they still feel members of a supranational society of Canberrans who had dared to adventure to the Antipodes!

STAGE 5: – Fig. A57

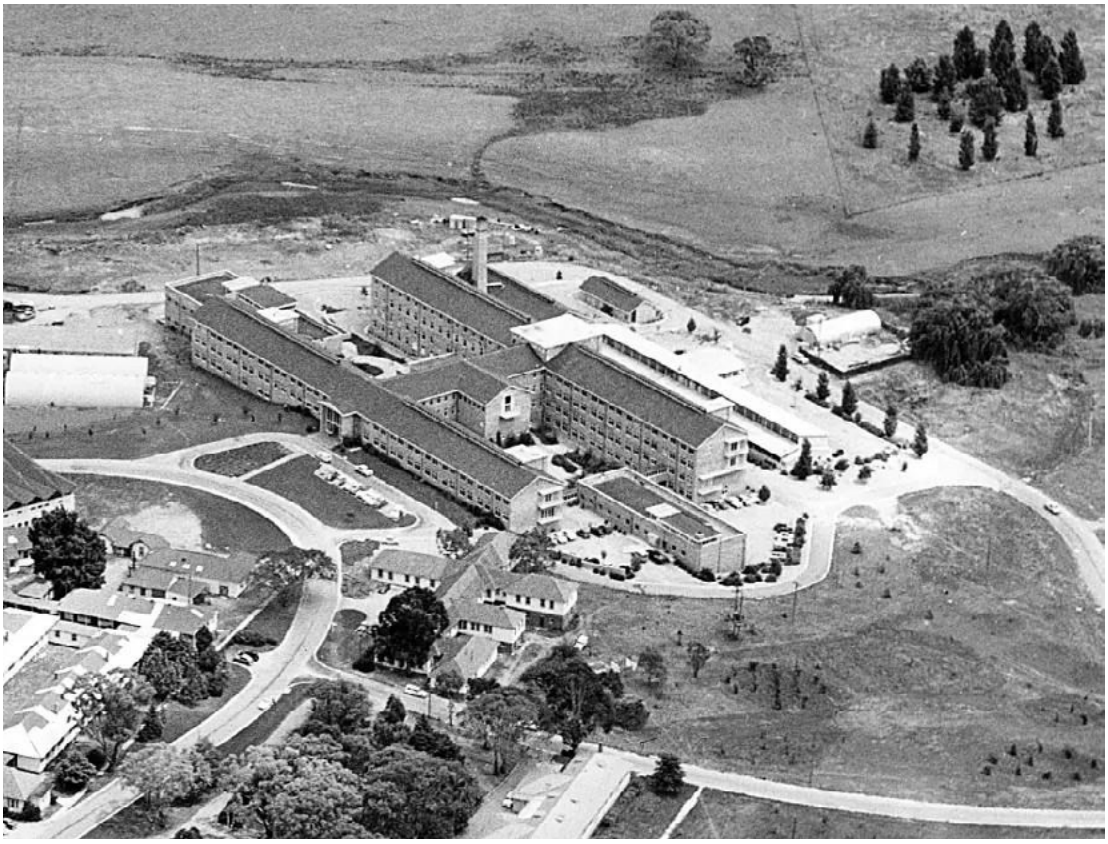

Fig. A57. The original ANU Research Institute's buildings in Canberra A.C.T. [CA]

An early view (on January 1, 1960) of the John Curtin School of Medical Research. This Aerial photo was taken during Sir John's research years as Physiology Professor at the School. [The original buildings were replaced in 2007 by new ones featuring a "DNA-Strand" concept.] From the Canberra Times archives.

STAGE 6: Research in America: 1966–1975
(Sections DA to DD)

DA. An Unfortunate Career Interlude in Chicago (1966-1968)

The next stage of my wanderings was the briefest, the least successful, and the most unhappy of my research career.[A] There were several reasons. Although at the start there was good material support in Chicago and a most prestigious governing body, it quickly became evident to me and to the Director of the Institute for Biomedical Research, that the American Medical Association was not enthusiastic - quite the contrary. When the retirement age was lowered to 68 years, contrary to our agreement, I realised it was time to look elsewhere. But there were severe internal problems within my own group, as well.[B] It was time to go, and fortunately I had one chance. It was an invitation from the State University of New York at Buffalo with very generous financial support of a unit to be created for me as a Distinguished Professor of Physiology and Biophysics.

DB. A New Start in Buffalo

So, the next stage in my journey was across land, not strictly Odyssean, across the ocean as heretofore. I have been often asked why I chose to go to Buffalo. The answer is very simple - I had nowhere else to go. My age of 65 was not encouraging to universities who may have been considering me as an associate. But in any case, the Buffalo appointment was very generous so far as support and salary were concerned and President Meyerson and the University agreed to retirement at 70 to be revised upward from year to year thereafter. So, everything started well, again in a temporary building, pending the construction of the grandiose new university. I was happy with the temporary accommodation which was soon fitted with the best research facilities I had ever had. It was of course on a much smaller scale than Canberra, which was a good thing. The unhappy experience of Chicago had warned me of the problems of personality. So, I had a small carefully-selected group of research associates and some of my associates of former times came back to join me for periods in Buffalo with the happiest results: Robert Schmidt from Germany, Tomakazu Oshima (for two periods) from Japan.

After the debacle of Chicago, I had begun to wonder if I had lost the personal touch that had given me such good relationships with all my associates at all previous "ports of call." So, it was very reassuring to find that at Buffalo I was again associated with a delightful group, not only the scientists and their families, but also the secretarial and technical staff. In all, counting my wife [Helena] and myself, there were 30 scientists from 11 different countries.[A] As this seven-year period came to an end with my voluntary retirement in 1975 at the age of 72, it was with great sadness that my wife and I said farewell. So, the happiest group of my research career was dissolved, with tears from the ladies!

But of course, outside our charmed circle we had had all the turmoil of the University revolt with threatened destruction by dissident students.[B] Buffalo was one of the centres of the storm, and lacked leadership at a critical juncture. I felt that the only course of action was to continue actively in research, come what may. And that we did, being helped by the isolation of our temporary laboratory from the main campus.

DC. Our Continuing Research on the Cerebellum and Cerebral Cortex

At the end of the Canberra section of this story I told briefly of our success in being able to construct models for the mode of operation of the neuronal machinery of the cerebellar cortex. But such models have to be built into the wider picture of the input and output paths if they are to be used in providing explanations of the mode of operation of the cerebellum in the control of movement. Despite the emotional troubles we already had some good successes in this study when at Chicago. But at Buffalo we were much better equipped for this ambitious task, with on-line computers, digitimers,[A] and, most importantly, a most versatile mechanical stimulator.[B] This latter instrument was of the greatest importance in the study we made on the role of cutaneous sensing in cerebellar control. Robert Schmidt's experience with cutaneous receptors was of vita! importance in this systematic study of cutaneous inputs onto cerebellar Purkinje cells. Hitherto it had been generally believed that muscle receptors were of more importance for cerebellar inputs than those of skin. In previous studies cutaneous stimulation had been crude: touching, brushing, squeezing, etc. With the instrumentation provided by our stimulator and an averaging computer, there was revealed the remarkable effectiveness of the cutaneous inputs particularly by the foot pads. Muscle receptors were much less effective, but the study of joint receptors awaits the development and application of good instrumentation. Suffice it to say that we were much impressed by the effectiveness of cutaneous inputs, and began somatotopic studies in the attempt to define better the way in which the cerebellar machinery was employed in controlling movement. This study on the vermis and pars intermedia of the anterior lobe of the cerebellum led on to sequential studies of the pathways from the cerebellum through the cerebellar nuclei and then by the next relay nuclei (the red nucleus and the medial reticular nucleus) on the pathway down the spinal cord to motoneurons. Our work was of course closely related to the comprehensive anatomical studies of the Norwegian school, but in conclusion it must be stated that as yet we are far from understanding the mode of operation even of the cerebellar anterior lobe onto spinal motoneurons.

In the latter two years I had encouraged Gary Allen to attempt the very difficult task of relating cerebral cortex to the cerebellar hemispheres. He had good success with the cat, and then proceeded to the primate, where these studies would be of the greatest importance attempting to understand how in man the cerebrum and cerebellum interact in the control of movement. About 88% of the human cerebellum is oriented exclusively to the contralateral cerebrum. Allen and his associates had made very good progress, and there was a good report of the whole project in Physiological Reviews (November 1974), yet his application for a National Institute of Health grant in 1975 was not funded. Since I was to continue as an adviser with frequent visits to Buffalo for this purpose, my plans for the continuance of my American association were thus terminated. This project of Allen's was almost unique in the world. Only at Kyoto is there the beginnings of a comparable study by Sasaki of the detailed topography of the cerebro-cerebellar connectivities in the primate, with a study also of the relay nuclei involved in this cerebro-cerebellar transaction.

DD. Reminiscences on my time in America

So, my active scientific life came to an end in 1975 and to my regret I feel that, after nine years of intense scientific effort in America I have left there no successors who would be continuing in the projects that we opened up. There was considerable scientific achievement as can be recognised from the more than 140 papers published from the Buffalo laboratory. But I was disappointed that so few young Americans came to work in Buffalo in the seven years I was there, altogether only five. Fortunately, I had many co-workers from other countries; eight from Japan, four from Germany, two from Canada, two from Italy, two from England, and one each from Australia, Czechoslovakia, France, Lebanon, and Sweden. I have the feeling that the scientific fashion is for analytical work, and that there is far too little interest in synthesis, particularly when it involves the complex neuronal machinery of the brain. But, in biology, the findings of analysis achieve scientific meaning only when they are synthesized into principles of functional operation. In the final synthesis, models can be constructed that provide the basis for understanding some performance of the whole organism. For example, the analytical success in disclosing the mode of operation of the neural machinery of the cerebellar cortex requires level after level of synthesis before it can provide a basis for understanding the cerebellar control of movement and posture.

STAGE 7: Retirement in Switzerland: 1975–1997
(Sections EA to EB)

EA. My Attention focuses again on the Mind-Brain Problem

The last journey of my odyssey is now ended, again across the ocean to Europe, where I live in Switzerland in idyllic mountain surroundings; I have here all my books and journals-many thousands of volumes and a large collection of reprints, so that I can continue my academic life, concentrating on the field that lured me into neurophysiology over 50 years ago-the mind-brain problem.[A] I believe that the great successes of recent years in the study of the brain, and particularly of the human brain, have opened up exciting new prospects for limited successes in this problem that has perplexed mankind since the Greeks, and particularly since Descartes. I have had several attempts in this field since my Waynflete Lectures in 1952, but now realise their inadequacy. Surprisingly I was too timid! I have now developed a much stronger dualistic-interactionist philosophy and it is incorporated in a book that is being published conjointly with Sir Karl Popper, The Self and Its Brain.[B] This is the first fruit of my life of retirement. I have much more planned because I realise that the present predicament of mankind results from the continuous process of denigration that has proceeded too far - far beyond the limits justified by our scientific understanding of the cosmos, of evolution, of genetics, and of the brain. Scientists and philosophers share the guilt of being dogmatic in promulgating claims to a knowledge and understanding that devolves from their inflated self-esteem. Mankind has been misled by these spurious claims. I see my task as twofold:

To deflate this dogmatism, based not upon science, but on a "this-worldly" religion of materialist-monism often allied with Marxism;

To help in building a new philosophy of man which recognises that he is a creature that has transcended his animal origin through the building of culture and particularly of language, the World 3 of Popper.[C]

We academics have to be humble in our discussion of the nature of man, recognizing the ultimate mystery of the personal existence of a conscious self.[D]

Editorial note: Sir John Eccles died in Contra (in the Swiss canton of Ticino) on the 2nd of May 1997 at the age of 94 years, survived by his second wife, Helena.

EB. Posthumous events relevant to the life and work of Sir John Eccles.

On 7th October, 1997 there was a meeting in the University of Bonn arranged by Professor Hans Biersack entitled “In Memoriam of Sir John Eccles”.

The contributions (with other added items) were later published as a book by Lady Helena Eccles and Hans Biersack: see Eccles & Biersack, (2000).
The book contains meeting contributions by Filenz, (2000); Ito, (2000); Strata, (2000); Nicoll, (2000); Stotz-Ingenlath, (2000); Feinendegen, (2000); Schmolke et al, (2000); Biersack et al. (2000); Beck, (2000); Mombelli & Monotti, (2000).

FAMILY REMINISCENCES:
(Sections FA to FM & Figs. F01-F41)

"Happy families are all alike; every unhappy family is unhappy in its own way."

From Tolstoy's[379] novel "Anna Karenina", (1878)

The following sections describe the childhood of John Eccles' life and later events in his life as recorded or remembered by family members; mainly by his wife Irene "Rene", son Peter and daughters Mary and Rose.

These have been added to the autobiography to provide the necessary human family background, complementary to his scientific life. (Several minor duplications of textual material with those in Eccles' autobiography have nevertheless been retained to preserve continuity here).

As a result of divorcing Rene, contact between him and his family abruptly and almost completely ceased, except for occasional visits by him to son Peter in America and a few visits to him and his second wife Helena in Switzerland by children Richard, Mary and Rose.

The accompanying figures (which are mainly of a domestic nature) are interspersed within the text and labelled F01 to F41.

More-detailed reminiscences concerning Sir John as well as the Eccles family history can be found in Mary Mennis' two books; Mennis, (2000) and Mennis, (2003).

379 Tolstoy, Lev "Leo" Nikolayevich (09.09.1828 20.11.1910) RU Great & influential writer; religious thinker.

FA. Childhood and adolescence (1903 – 1924)

Fig. F01. John Eccles's parents' family in Jumbunna, south Victoria, Australia

Young John with his sister Rose[380] and parents, Mary and William Eccles (Nan and Pa) ca. 1910.

From Mennis (2000), p. 74.

380 Howells, Rosamond Mary née Eccles (26.11.1904 – 07.08.1995) AU Schoolteacher; sister of J. C. Eccles.

Family Reminiscences of Jack

John Carew Eccles was born in Melbourne, Australia, on January 27th, 1903. He owes much to his early training by his father, William James Eccles[381], who was a teacher in Jumbunna in the Gippsland outside of Melbourne.

His father married Mary Carew[382], a fellow teacher. Their house in Jumbunna had two acres of land with a road around two sides. It had four rooms with a passage down the middle and a veranda on the front. As the front was higher, there was storage space underneath for apples, plums, cherries and peaches from the orchard. In this dark space, hiding from the heat of the day, lurked snakes, tiger, copperhead or black, and also large black scorpions which had a nasty bite. The two acres of land were divided into an orchard, a vegetable garden and a paddock for the horse and cow. The buggy, harnesses and saddle were stored in a shed near the house. William liked to keep his horsemanship up and rode over to visit the neighbours. Mary was a busy housewife who, like the other pioneer housewives, preserved the fruit for the winter, made jam, baked the bread and boiled the laundry in the big copper. She was very musical and taught at the school on a voluntary basis.

John Eccles' first teacher was his aunt, Maggie Carew[383], who came to the Jumbunna School in January 1907 and lived with the family until 1910, when she was transferred to Fern Tree Gully. Young John and later his sister, Rose, thrived under the tutelage of Auntie Maggie. With three teachers in the house, all keen to educate them, they could not fail to progress.

The family lived at Jumbunna until John was 8½. Early in 1911, William Eccles was transferred to Koroit, near Warrnambool, west of Melbourne. The Koroit area had rich volcanic soil from the nearby Tower Hill Volcano which was now dormant. It was an agricultural area where potatoes, onions, maize and oats as well as dairy products abounded in the green pastures. Many were Irish settlers who had escaped from the dire straits in Ireland.

John Eccles remembered his time in Koroit as follows:

We lived at the school-house which was enlarged for us. The two-acre grounds were also the feeding grounds for our horse. We had a buggy to get around in and we had an excellent vegetable garden, often getting prizes in the Koroit Show in vegetables and pastry making. I came home for the weekends during the 4 years I was at Warrnambool High School. In 1919 I moved to Melbourne High School for my final year before the University in 1920 where I did medicine, getting a Rhodes scholarship in 1924.

The Rhodes Scholar (1925).

The following article from "The Speculum" (The Journal of the Melbourne Medical Students' Society), sums up John Eccles' excellent record at the University.

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381 Eccles, William James (1866 – 16.03.1948) AU Schoolteacher.

382 Eccles, Mary née Carew (1869 – 1952) AU Schoolteacher, later housewife; mother of J. C. Eccles.

383 Carew, Margaret "Maggie" (1876 – 05.01.1965) AU Schoolteacher; aunt of J. C. Eccles.

Once again, the honour of providing the Victorian Rhodes Scholar for the year has fallen on the Medical School in the person of Dr. J. C. Eccles. And one is inclined to think that the selectors might have gone farther and fared considerably worse.

As a scholar, his record is an amazing one. To leave out the numerous scholastic distinctions of his school days, and trace an outline of his career at the University, we find that in his first year he took three exhibitions and a second-class honour. In his second year he was head Apostle and second Prosector [a person who dissects dead bodies for examination or anatomical demonstration]*, which slip he recovered in third year by taking the exhibitions in both anatomy and physiology. Fourth year was a lean one. He did not get the exhibition in pathology, but he got first-class honours in pathology and everything else, and all the other prizes and exhibitions there were. At finals, space does not permit of a detailed account of his achievements. Suffice it to say that he shared one exhibition and two prizes, obtained first-class honours, and headed the class list. And the above is but a resume.*

On the athletic side we find the same sort of thing. At tennis and athletics, he was no mean performer while at school, and at the University he was a prominent member of the athletic team, broke records for pole-vaulting, and gained his Blue. But even this did not exhaust the energies of this remarkable young man. He was a member of the committee of the University Athletic Club, he was the St. Vincent's Hospital representative on the M.S.S. executive, and last, but by no means least, he was a member of the Speculum Board.

In view of the evidence, there is no need for us to attempt any further proof of our original statement. Dr. Eccles leaves for Oxford in August, hoping to enter Magdalen College, where he proposes to do the final honour course in physiology from which he hopes to proceed to research work for his Doctorate of Philosophy. (The Speculum No. 116, June 1925, Eccles' photo and his achievements appear on pages: 8, 22, 57, 58, 71).

[Note: William Alexander Osborne (1873-1967), professor of physiology, man of letters and broadcaster was appointed professor of physiology and histology at the University of Melbourne in 1903. The range of 'Ossie's' lectures, his wit and anecdotes, opened up new worlds to his students; he was especially generous of time to his '*apostles*', the best dozen students each year. Over the years the apostles included Sir Macfarlane Burnet[384], Dame Kate Campbell[385], Sir John Eccles, Charles Kellaway, G. C. McK. Mathison (killed at Gallipoli) and Sir Douglas Wright. Osborne was dean of the faculty of medicine from 1929, president of the professorial board (1919-21) and council-member (1919-22, 1924, 1928). Ossie retired in 1938. Apart from reference to the biblical apostles of Christ, the Twelve Apostles is also the name of a set of coastal limestone stacks off the shore of Port Campbell National Park, situated between Melbourne and Warrnambool].

384 Burnet, Frank Macfarlane (03.09.1899 – 31.08.1985) AU virologist & immunologist (NP 1960)

385 Campbell, Kate Isabel (22.04.1899 – 12.07.1986) AU physician/paediatrician. "Premature baby blindness".

Fig. F02, The successful sportsman and scholar
John Eccles was a champion pole-vaulter at Melbourne University.
From Mennis (2000), p. 79.
His "Ernst Leitz" microscope from the 1920's has unfortunately since become lost.
From M. Mennis, personal archives.

FB. Oxford (1927 – 1937)

John Eccles graduated from Melbourne University in Medicine with first class honours in 1925, and as Victorian Rhodes Scholar for 1925 entered Magdalen College, Oxford, as an undergraduate in order to study under Sir Charles Sherrington in 1927, with first class honours in Natural Sciences, the Christopher Welch Scholarship and a Junior Research Fellowship at Exeter College, Oxford, he commenced research on reflexes with Sherrington's colleagues. Later from 1928 to 1931 he was research assistant to Sherrington, there being eight papers published conjointly; and he also collaborated with Ragnar Granit on two research projects. He was awarded an Oxford D. Phil. degree in 1929 for a thesis on Excitation and Inhibition. Later Oxford appointments were to a Staines Medical Fellowship at Exeter College in 1932, a tutorial fellowship of Magdalen College, and a University Demonstratorship in 1934.

During this Oxford period research was largely on synaptic transmission both in the central nervous system and peripherally in sympathetic ganglia, smooth and cardiac muscle, using the newly developed techniques of electrophysiology – amplifiers and cathode ray oscilloscopes. It was the period of controversy between the exponents of the rival chemical and electrical theories of synaptic transmission with Eccles in particular resisting many aspects of the chemical transmitter story that was being developed so effectively by Dale's group. In retrospect it can be appreciated that this controversy had the effect of defining problems and stimulating much good experimental work, but the decisive victory of the chemical theory had to await the intracellular recording both from neuromuscular junctions by Fatt and Katz and from nerve cells that was made possible by the technique of the microelectrode with cathode follower amplification. And now, as a final stage of this drama, electrical transmission between nerve cells is being demonstrated in many specialized synapses, not only in the invertebrate, but also in the vertebrate nervous system. These recent developments have served to increase still further the assurance with which we can accept the chemical transmitter hypothesis for an overwhelming majority of both central and peripheral synapses.

Fig. F03. Magdalen College Second Eight rowing crew.

John Eccles is sitting sixth away from the Cox (at the right-hand side, facing the crew). From Mennis (2000), p. 84.

Jack married Irene Miller in Oxford in 1928

A year after Jack and Rene were married, their first child, Rose, was born. Rose's godfather was J.R.R. Tolkien, a close neighbour, who worked at Oxford University and who later became a famous writer. Tolkien had a daughter, Priscilla[386], the same age as Rose and, as they grew up together, Rose played with her and was invited to birthday

386 Tolkien, Priscilla Mary Anne Reuel (18.06.1929 – 28.02.2022) UK social worker and book publisher

parties at the Tolkien house. Rose also enjoyed sitting in Tolkien's study, listening to him read stories. Another friend of the family was Ragnar Granit and his wife, Daisy, who lived opposite.

Fig. F04. First daughter Rose's christening.

Rose is held by her godfather, J.R.R. Tolkien (author of "Lord of the Rings"). The Tolkiens were the Eccles' neighbours in Oxford. Jack's research colleague E. G. T. Liddell is also present (top left).

From M. Mennis, personal archives.

Jack Eccles (in a letter to his parents):

Rene's typing has been a great help, for I don't think that I could ever have finished the task of copying it all out each time. She has typed the whole thing through at least twice from my pencil notes, which were much too rough for any of the typewriting firms to tackle. The papers will be published about March, but before then Sir Charles and I are going up to read them before the Royal Society.

Mostly I am very pleased with the whole contribution and think that it puts us years ahead of anyone else in the world. The only difficulty is that I hope people will be able to understand it. Of course, it is only the beginning of the story and there are immense *possibilities for further developments. We have now to wait and see how it is received. Sir Charles told me that he is not going to work so much in the future. I am going to carry on with Hoff who is now quite an able assistant. I think that it is wise for Sir Charles to take things more easily now. He is almost 74 and it is surprising that he still so active. I don't know how long he will continue as Professor. I don't think he has any thought of retiring - he is the sort of man that will die in harness. If he carried on for two or three years, it has been suggested that I would be his most likely successor - but don't tell anybody about that. If for less, McSwiney is probably the most likely man. The laboratory at present is in its most flourishing condition and will become more famous than ever when the present papers and the book are published.*

At present we are having a cold spell with a temperature not rising above freezing point all day. The baby (Rose) is not at all keen on being shut up inside, but it is a bit cold for her out of doors. Some of the people who were away on holidays are now returning for it is just over a week till term begins. I have had no real spell at all, but hope to have some time off when Ted and Leo arrive. I have not been able to get away because of course Rene is getting near time and I do not wish to leave her in case things happened prematurely. She is in quite good health and except for breathlessness gets around normally. [Peter was born on 28th January 1931].

Sir Charles has heard about the papers we sent in. They have all been accepted for publication as they stand and are coming out as a whole number of the Proceedings of the Royal Society at the beginning of March. I think that is quick work considering the size of the budget. It is almost a record to fill up a whole number of a journal.

Fig. F05. John Eccles conversing with his mentor, Sir Charles S. Sherrington.
Photograph taken at Ipswich, England in 1936.
From Mennis (2003), p. 10.

Jack Eccles; (many years later):

England, in my thirteen years there (1925~1937)*, was a delightful and stimulating place for a young academic, although by present standards the laboratory facilities were primitive. There were almost no research grants and no secretarial assistance even for Sherrington. We had to type our papers and service and organise our equipment which gradually became more complicated with string galvanometers giving place to cathode-ray oscilloscopes in 1933, and valve amplifiers. But in research the competition was not severe. The world literature was unbelievably small, so that one could easily survey the total publications, not only on the nervous system, central and peripheral, but also on all types of muscle and all types sensory systems. Furthermore, one met personally almost all the great figures for they came to visit Sherrington at Oxford.* (Eccles 1977, p. 3)

In 1934 Jack Eccles had achieved a permanent position at Oxford with a Tutorial Fellowship at Magdalene College and a University Demonstratorship. Then in the late 1930s there was the ominous rise of Hitler against the unprepared western alliance. Jack's position at the University was coming to an end and he was seeking a new job. In 1935 the problem arose of election of a successor to Sir Charles Sherrington. It was considered then that Jack was too young at 32 and an older man was elected to the position. Jack was unhappy in missing the chair of physiology at Oxford and at the decline of the department. Furthermore, there was the threat of war in Europe with the aggressive attitude of Hitler.

Peter Eccles (1931 – 2005) memories:

The second time Nan and Pa came to visit us and to continue with their research of the Eccles' history, was when I was about five, 1936. Apparently, Pa was very keen on tracing his roots, our roots. I wonder if he ever thought that his own autobiography would interest us. I can remember Pa as seeming very strong. When we were hitting tennis balls, I couldn't get any past him, and they came back at me as if they were rocket-powered. His parents' visit was an occasion for Dad to show us what he did and where he did it. He showed us around Oxford University, and took us up a tall curving staircase to the top of Magdalen Tower. But best of all was his laboratory. There he had a very interesting method of doing things. First of all, he had a big cage made out of copper mesh stretched over a big wood frame. He said that that was a "Faraday Cage" and that it kept bad signals and voltages out. To get inside this we walked in a door, which he carefully shut. Then he had a weight on a stiff pendulum arrangement about 60 cm diameter, that swung a set of contacts through other contacts. At a specific time after he released the weight into its swing, it released a linear paper chart to travel at a constant speed. This way, the contacts on the pendulum arrangement stimulated a live nerve fibre, and set the chart to record whatever his experiment required, from another set of contacts on the nerve fibre. The weight was caught at the top of its swing and could be set to run again as required. The whole thing looked like a Heath Robinson setup, yet it was this work with this gadget, together with his then *collaborators, Hodgkin (who worked developing radar during the war) and Huxley, which won Sir John Eccles his Nobel Prize. As a boy I was most impressed with this great arrangement, but I also met his staff, who looked after this elaborate mechanical timer, and prepared his nerve fibres, a Mr. Chapman. Dad always referred to him as Chapman, and Chapman was his faithful technician throughout Dad's experimental career, all the way to Buffalo, New York in the 1970's.*

FC. Voyage to Australia (1937)

Jack wrote:

In 1937, on the advice of Kellaway, I accepted the Directorship of the Kanematsu Institute at Sydney Hospital. In retrospect I feel I should have stayed in England and weathered the storm, but instead I embarked on my Odyssean journeys, never to return to my beloved England. It was a fateful choice. I had only to exercise general supervision of the clinical sections of the Institute that were fully housed in the three lower levels of the fine new Kanematsu Building that had been built as a Memorial to Fusajiro Kanematsu, a Pioneer Japanese Merchant in Australia. It was long before Pearl Harbour and I was gifted with great energy and enthusiasm as well as a wide range of research experience for my challenging new position. (Eccles 1977, p.3)

Peter Eccles:

I can remember the first time I heard Dad say that we were going to Australia - that fairy-tale land. We'd heard about it from Nan and Pa, who lived there, Mum and Dad who had lived there and we had some books. It was warmer. There were lots to explore. There was lots more sun, and we liked that thought. But would I turn black? Like the Aborigines? How much Aborigine was in me? I was full of questions. Rose and Alice were full of questions. William was just a baby. But best of all, "Kids, you will be going home." Dad had accepted a position as Director of the Kanematsu Memorial Medical Laboratory in the Sydney Hospital. He was going to be the head honcho there. Here he was a fish in a big pond; there he would be a shark -- the BOSS. We had wonderfully romantic notions of Sydney and what it would be like. But soon it was very serious. We could only take a few things.

I do remember the Tilbury Docks, London where we embarked for Australia, the loading of the holds using the ship's cranes, our clamouring for paper ribbons which tied us for the last time to the friends who had come down to see us off (Tolkiens, Liddells, McSwineys and others) and the breaking of these as the ship (SS Orford, Orient Line) steamed (real steam, real steam engines) out of the Thames. I think our first stop was Naples, where we had our first view of a lifestyle, particularly near a ship, which was totally different from anything we had seen before -- particularly the beggars, and street vendors.

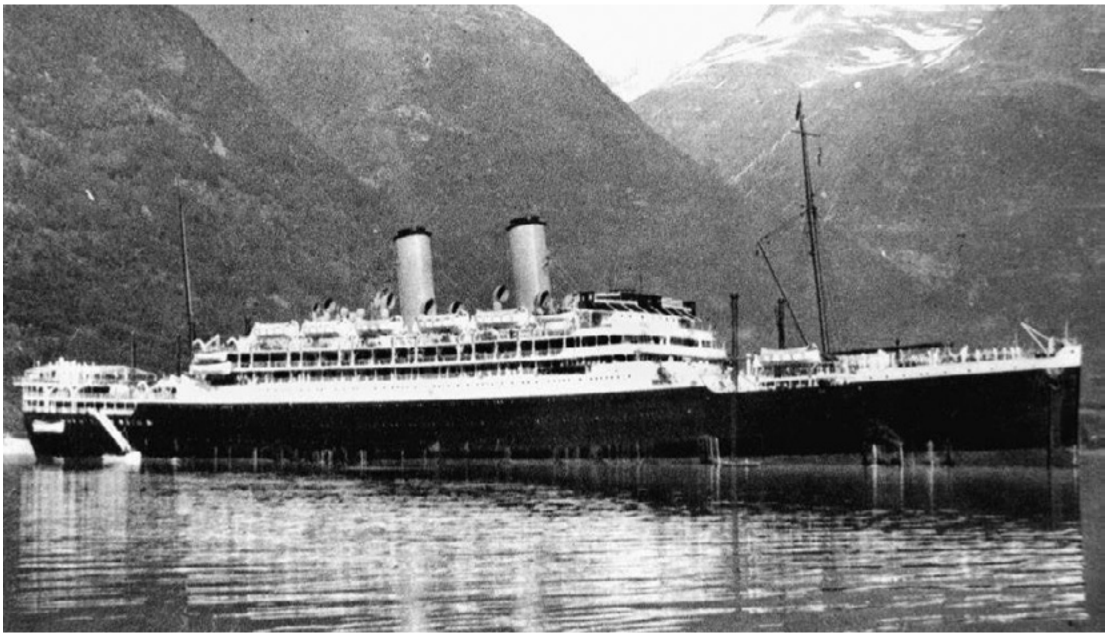

Fig. F06. The SS Orford.

The *Orford* was a 19,941 GRT steam ship, built at Barrow by Vickers Shipbuilding in 1928. She steamed as Orient Line passenger liner between London, Australia and New Zealand until 1939, when she was requisitioned as a troop ship. On the 1st June 1940 she was bombed and set afire off Marseilles. Later scrapped.
Item held by John Oxley Library, State Library of Queensland.
https://commons.wikimedia.org/w/index.php?curid=14489903

Mum and Dad took us on a tour of Vesuvius and Pompeii, where I was unimpressed with the dioramas of people who had been incinerated in their tiny houses. The next memorable stop was Port Said at the entrance to the Suez Canal. That was our first view of watermelons, and the fun the kids had eating these enormous end-to-end slices. All sorts of boats, rafts etc pulled up to the side of the ship so that the "street vendors" now were just at the end of a rope, selling clothing, fruit etc. One of the greatest sights was that of the urchins who would dive for the large British pennies. We'd throw one and a dozen youngsters would dive for it, one of them unbelievably getting it, perhaps 50 ft under the water, and would wave it victoriously to our cheers. We also stopped at Suez, at the south end of the Canal, to let the Suez Pilot off and to allow those (not us) who went on a tour of the Pyramids, Sphinx etc, to re-board. The Red Sea was interminably hot, so a swimming pool was fashioned for our comfort out of an enormous canvas sheet hung over one of the Hold Hatches.

The now infamous Aden was our next stop so that the Orford could coal up, and then onto Bombay then Colombo, where the ship side activity and the streets seemed a repetition of Port Said and Suez. Been there, done that. How about getting us to Australia? Our first sight of Australia was north of Perth, and we berthed at Freemantle. Our thrill at being at last in Australian waters dissipated on our departure *from Freemantle, because the enormously rough seas of the Great Australian Bight kept us all seasick until we reached Adelaide. But from there to Melbourne was smooth sailing. On the Orford we travelled second class -- but it was like today's cruise class on a cruise ship. There were great spacious dining rooms, white tablecloths, linen serviettes, real chinaware and silverware, waiters in formal wear and plenty of delicious food to eat. There were lots of places we could go to explore the ship, and lots we couldn't because they were for the First-Class passengers. One of the passengers was a professor of physics and meteorology from London, Dr. Harrie Massey*[387]*. He and Dad became good friends, and through that friendship I spent quite a bit of time with Harrie Massey on that trip.*

FD. Sydney (1937 – 1943).

Fig. F07. The Eccles house in North Shore, Sydney.
"Dunsfold", located at 14 Clanalpine Street, Mosman, NSW.
From Mennis (2000), p. 103.

Mary: *In Sydney Jack and Rene found a lovely house called "Dunsfold". It overlooked Sydney Harbour and was set in a lovely garden. There was a playhouse in the backyard which was subsequently called the Hobbit House after the famous book by their friend J.R.R. Tolkien*.

Because he was anxious to see his new working environment, Jack visited the Kanematsu Institute soon after his arrival and met Ritchie, the Senior Physician of Sydney Hospital, who became his friend and adviser through his Sydney days.

387 Massey, Harrier Stewart Wilson (16.05.1903 – 27.11.1983) AU mathematical physicist. Atmospheric physics.

New friends made in Sydney included: scientist Archie McIntyre; biochemist, Rudolph Lemberg and his wife Hanna, who enjoyed walks with the family in Kuringai Chase amongst the wild flowers;**[A]** Vincent (Victor?) Flynn, an old Oxford friend and now a wealthy lawyer often entertained the family with his wife in their magnificent home; Vincent's elder brother, James Flynn, an ophthalmologist. James' wife, Ranee became a good friend of Rene. During the war, James Flynn was a Surgeon Lieutenant Commander and researched sunburn of the retina that he detected in the gun crews of his ship (*HMAS Australia*) after the Dakar engagement.

They also made friends with members of the Grail including Frances van der Schott[388] and Judith Bouwman[389]. The Grail Movement was a lay organisation for young women, and had originated in Holland. Through the Grail movement, widespread friendships developed between a growing group of Catholic intellectuals. These Ladies of the Grail believed in making religion a source of joy to the young.**[B]** They wore attractive street clothes and fostered music, dancing and drama. The Eccles family often went to their weekend religious festivals, and Jack taught them English Folk Dances that he had learned at Oxford.

Peter:

For my joy and bliss, Dad bought the biggest and fastest (speedometer to 100 mph) available car in Australia: a cream coloured, four-door, leather upholstered, 85 hp 1937 Ford V8 from Hastings Deering south of the harbour, instantly called Matilda. He had it fitted with an interior bed, so that the front seat laid back on a special hinge, almost flat with the back seat for camping trips for he and Mum -- an instant tent, anywhere. Eventually, he took this not only to New Zealand, but also back to Australia in 1952. holidays were at Bawley Point, 150 miles south from Sydney. The beach we went to was another few miles along that road as it hugged the coast, through a gate and a half-mile across a rabbit-infested meadow. On one occasion the Ford broke a rear spring in a rabbit burrow, and Dad had to "limp" Matilda into Milton, about 20 miles north to get it replaced. The beach was unfrequented. We left the car behind the expanse of white, grass-laced dunes, and walked across these and along a beautiful beach. The only people beside ourselves we saw on it were surf fishermen in the days before dune buggies, so they were all walking. The surf was generally light so we body surfed and played in the shallow water. We were always aware of sharks "out there" and kept close to shore.

388 van der Schott, Frances (? –?) NL a founder of the Australian Grail Movement.

389 Bouwman, Judith (1900– 1940) NL Grail Movement President in Australia. Died in car accident.

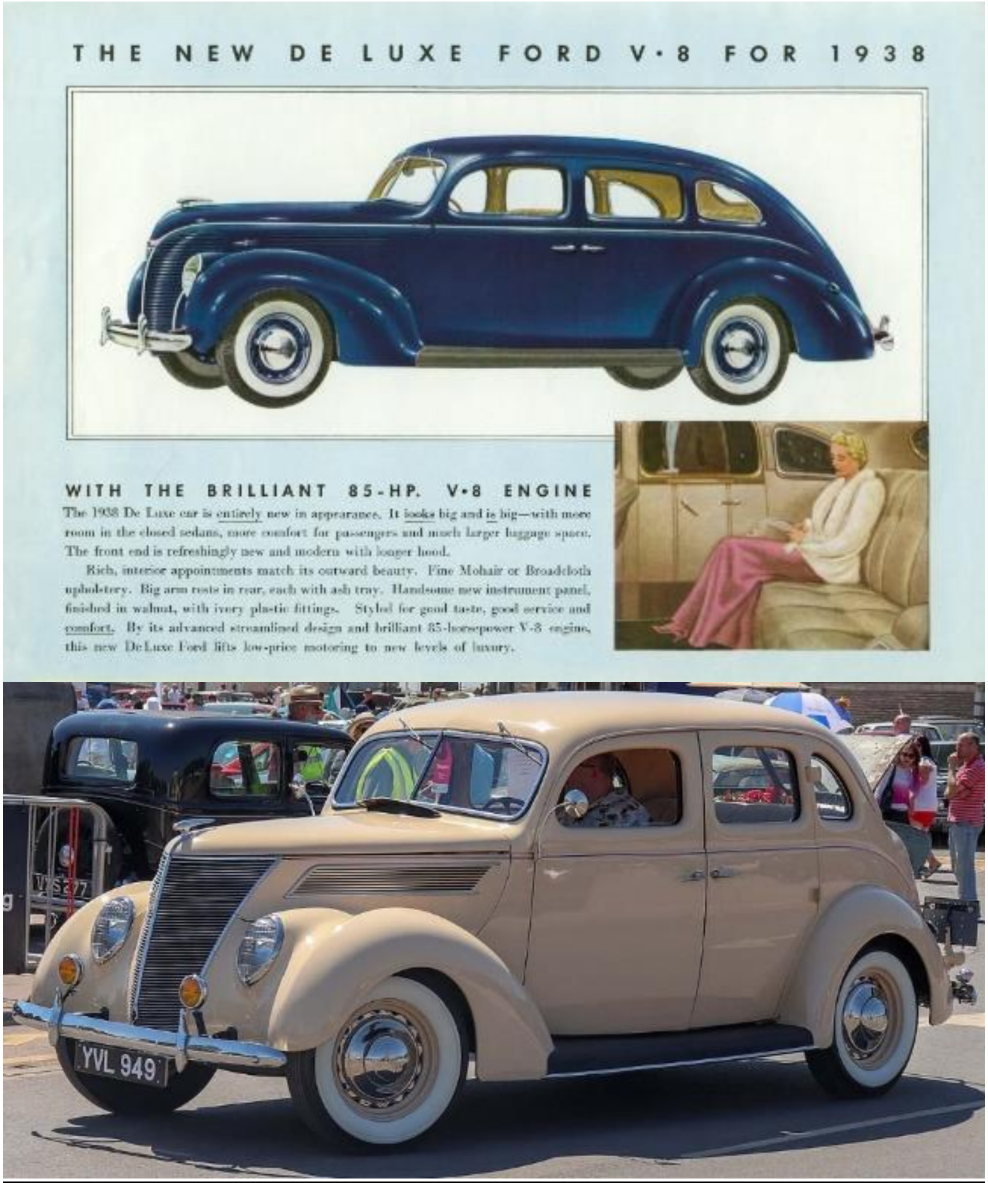

Fig. F08. The 1937/8 Ford 4-door 85 HP V8 De Luxe “Fordor” Sedan.

Above. Ford’s advertisement of their luxury model. This had over 7 times the rated horsepower of a typical family car at that time, e.g. General Motors’ Vauxhall 12.

Below. A more recent photo of this Ford model – now a collector’s item and a favourite with “hot-rod” enthusiasts.

<u>Mary:</u>

One good friend was Father Richard Murphy, a Jesuit priest and an intellectual. Towards the end of 1938, Father Murphy met an Austrian refugee, Dr. Steve Kuffler, who was interested in doing research. Fr. Murphy contacted Jack Eccles who arranged *for them both to come over for a Saturday tennis afternoon. Jack was keen to meet Steve as he had been the Austrian Junior tennis champion. The afternoon was very successful and Steve Kuffler was duly appointed as an associate member of the Kanematsu and moved into an apartment in Mosman. Father Murphy was also friendly with Damien Parer*[390]*, a photographer who was gaining quite a reputation and was later to become famous for his wartime photographs, both still and movie. Through his interest in films, Damien met up with Elizabeth Cape of the Grail and thus the Eccles family. With his cousin, Ray Triado*[391]*, Damien spent many a pleasant day at the family home playing tennis.*[C] *These young people were all members of the Campion*[392] *Society, a serious group of intellectuals who met to discuss religious books and issues. Jack Eccles was invited to give some of the lectures and he enjoyed the philosophical discussions. Eric Gill*[393]*, sculptor/philosopher became another good friend.*

Jack Eccles:

Sydney was of course a lovely place to live, but the academic isolation was severe. The Sydney University Medical School was a very dim place, being little more than a teaching institution. Unbelievably, it was completely locked up by guards at 5 PM, even the professors had to scurry out to avoid imprisonment for the night! The Institute I was to direct was simply the routine pathology department of a large general hospital in the city some three miles from the University. Nevertheless, with good help from the Institute Committee and the Hospital Board, I was able to construct research laboratories on the top floor, utilizing for a start the equipment that Professor John Mellanby had kindly allowed me to bring from my two research laboratories at Oxford. I decided to study the electrophysiology of neuromuscular transmission in muscles of the cat hind limb because I thought that it could lead to results of clinical interest.

The academic wilderness soon blossomed. In 1938 Stephen Kuffler arrived in Sydney as a refugee from Austria, and by good fortune I heard of this young pathologist in search of a position. So, he became a neurobiologist in the Kanematsu Institute, a novice with almost no background knowledge of the nervous system! In 1939 I managed to attract Bernard Katz from England on a Carnegie Fellowship. Thus, in this way, through the machinations of Hitler, we three were sheltering securely in remote Australia and studying neuromuscular transmission in cats and frogs. (Eccles 1977, p. 4)

Each morning, Bernard, Steve and I would travel by ferry across the harbour to work. If we worked late, we would have dinner at an Italian restaurant, then dash down Sydney streets to catch the last ferry at midnight. Lunches would be eaten sitting on the grass at the nearby Botanic Gardens and at the weekends, we played tennis on the

390 Parer, Damien Peter (01.08.1912 – 17.09.1944) AU WW II war photographer. Killed in Action.

391 Triado, Raymond Joseph (17.07.1910 – 04.07.2005) AU lawyer. Established "Whitlands" community.

392 Campion, Edmund (25.01.1540 – 01.12.1581) UK Jesuit priest and martyr.

393 Gill, (Arthur) Eric Rowton (22.02.1882 – 17.11.1940) UK controversial Catholic sculptor/philosopher.

grass court at 14 Clanalpine Street. It was a good life. In 1941, I was elected to a Fellowship of the Royal Society. Sherrington had submitted my name as early as 1935 but it was not until March 1941 that I received a telegram of congratulations, "Heartiest congratulations Royal Society Election, Adrian." There was a great celebratory party at the Mosman house. I was pleased to hear that my former Chemistry lecturer, Dr David Rivett, was another Australian to be elected that same year to the Royal Society.

Meanwhile, the war was coming closer. A Japanese attack was expected at any time. There were blackouts at night and inspections. Cars had to have hoods over the lights with slats to focus the light on the road only. When the Pacific War broke out the soldiers marched past down one of the main streets in Sydney. They were the soldiers of the 6th and 7th Divisions who had returned from the Middle East and were now on their way to New Guinea and Darwin to defend the country against the advancing enemy. Since Jack Eccles was a scientist, he was not called up, but worked on wartime experiments such as artificial fogging so the planes could swoop in and attack before the enemy on the ground could detect them. It was being designed for a place in Papua New Guinea called Rabaul.

Fig. F09. The Eccles family in 1940.

Rene and Jack with children Alice, Mary and Bill; in front, Rose and Peter.
From Mennis (2000), p. 106.

<u>Jack</u>:
For two years I was deeply involved in various wartime projects, and the Kanematsu Institute became the Australian centre for blood serum preparation and for applied research on such acoustic problems as noise protection and communication in the high noise levels of tanks and planes. Bernard Katz was chosen to become a radar expert and rendered most distinguished service. (Eccles 1977, p. 4)

According to the Official War Records, on 31st May 1942, two midget Japanese submarines entered Sydney Harbour from a mother submarine outside the Heads. For some strange reason no sirens went off. The crew blew the subs up rather than be captured. Another night the sirens were blaring warning signals and the family hurried down to the basement where there was a supply of drinks and food.

Jack was once summoned by Archbishop Gilroy who was an important figure in the Church (later ordained in 1946 as the first Australian-born Cardinal). It was probably the time he was called to heel by the archbishop for some of his statements published in a Catholic paper. He had given a talk to the Campion Society presenting an evolutionary account of human origins but still maintaining the separate creation of the self as a divine mystery.[D] The archbishop refused to listen to Jack's side of the argument or understand that in many ways his beliefs coincided with the Church's teaching. John Eccles received the censure of the Church. Yet he never lost his belief in God; in the separate creation of the soul; and in an after-life. This was in spite of being criticised by the materialists and some modern-day scientists. In a way he fell between two stools and to his dying day he wished the Church had taken more notice of his work.

Jack Eccles was ahead of his time and appreciated other people who had ecumenical views like his own. There was Rev. Alan Tory of the Presbyterian Church in Sydney. He once preached a sermon from the pulpit of Alan's Church, but this did not help his case with Archbishop Gilroy. As he was still a practising Catholic and had many Catholic friends, it did not change anything.

FE. Voyage to New Zealand (1943)

The family members were sad when they learned that they were leaving the house in Sydney as it had always seemed so light and happy. According to Jack, it had to be sold for just what he paid for it plus the reconstruction costs because of the government war-time regulations. World War II was still on when they left Australia at the end of December 1943. They could travel by ship to New Zealand, but it was very secretive and the family had to travel to Melbourne with only a few days' notice.

Rene Eccles:

We had a very busy time getting away from Sydney, we brought all our household goods with us (Grace Bros. Packers) we re-stocked the china supplies; some linen. There was so much to plan – Jack was more than equally busy at the Lab – much of his stuff – apparatus etc. was packed with the furniture – he was sorry later that he had not brought more things. And then there were the "parties" to attend some at home and others the length and breadth of Sydney – people we hadn't seen for ages demanded to say goodbye to us! (The shortage of petrol had cut us off from several of our friends) The University Catholic group landed at our place on Saturday – it was such a surprise. They brought a magnificent afternoon tea with them!! Then we had a special Sunday put aside for a 'Grail Day' at our place. It was a lovely Day. We had lunch out on the front lawn and singing and folk-dancing and play acting.

The last party for as many friends as could come, we had on Sunday 19th December 1943. About 40 to 50 of them did come and some remained to help strip the house of curtains, rods, stair carpet etc. The family then went to Melbourne by car, arriving there in for tea on December 24th, 1943. We thought that we'd perhaps have weeks to spend with Nan and Pa but we were aboard the Mooltan (20,000 tons) in a week's time!

The week went so quickly, and we were aboard the Mooltan before we had time to realize that we were really off. It was still hot and breathless and seemed more so, on the boat. We left early next a.m. – the boat had a few passengers but many soldiers returning from the Middle East, Italy. Etc. We had a strict lifeboat drill every day. The boat was well gunned – anti-aircraft as well as long rangers – they practiced one day. Peter was anxious to be with the gunners, but no one was allowed on top deck of course and when the practice began hardly anyone wanted to be on the lower deck.

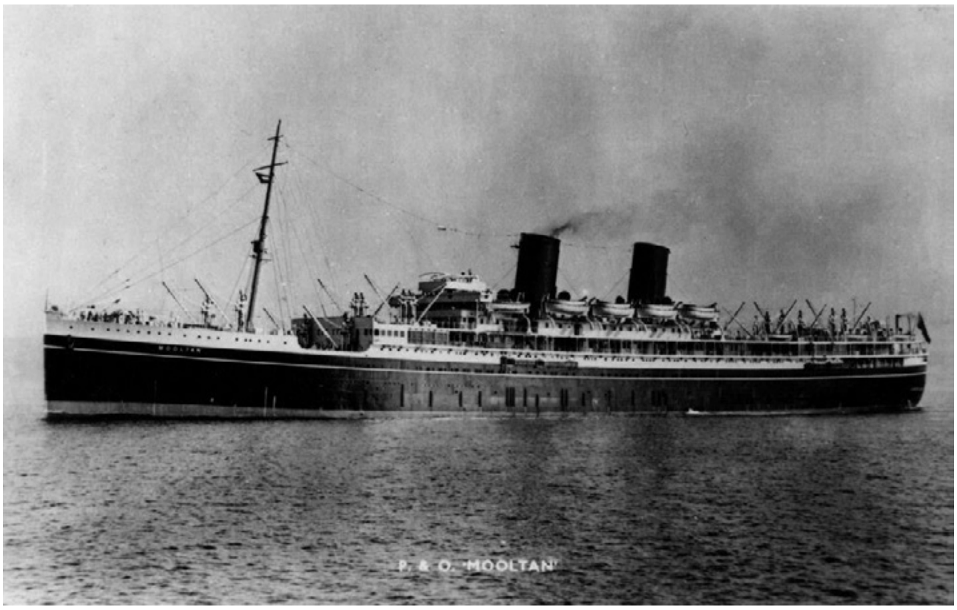

Fig. F10. The RMS Mooltan.

This P&O ocean liner and Royal Mail ship was in service from 1923-1954. It served during WW2 as HMS Mooltan, an armed merchant cruiser.
Photo held by John Oxley Library, State Library of Queensland., Public Domain.

We were escorted by planes on the 1st day out of Australia and part of the 2nd – the mine detectors - one on each side of the front of the boat, caused a chill when they were put out. A constant alert lookout was kept from the Crow's Nest and by gun crews – strict blackout at night. We were met by planes off the New Zealand Coast and escorted into Wellington Harbour – January 6th 1944 (Three Kings Day/Epiphany). Photographed by the press. Jack had a great effort to get berths for us all on Wahini and won his case after two visits to the shipping office. That same little tub, with all its vibrations, cramped accommodation and hardly any blackout restrictions, has several times done the trip across the Tasman to get N.Z. people home again! (Two life-boats only).

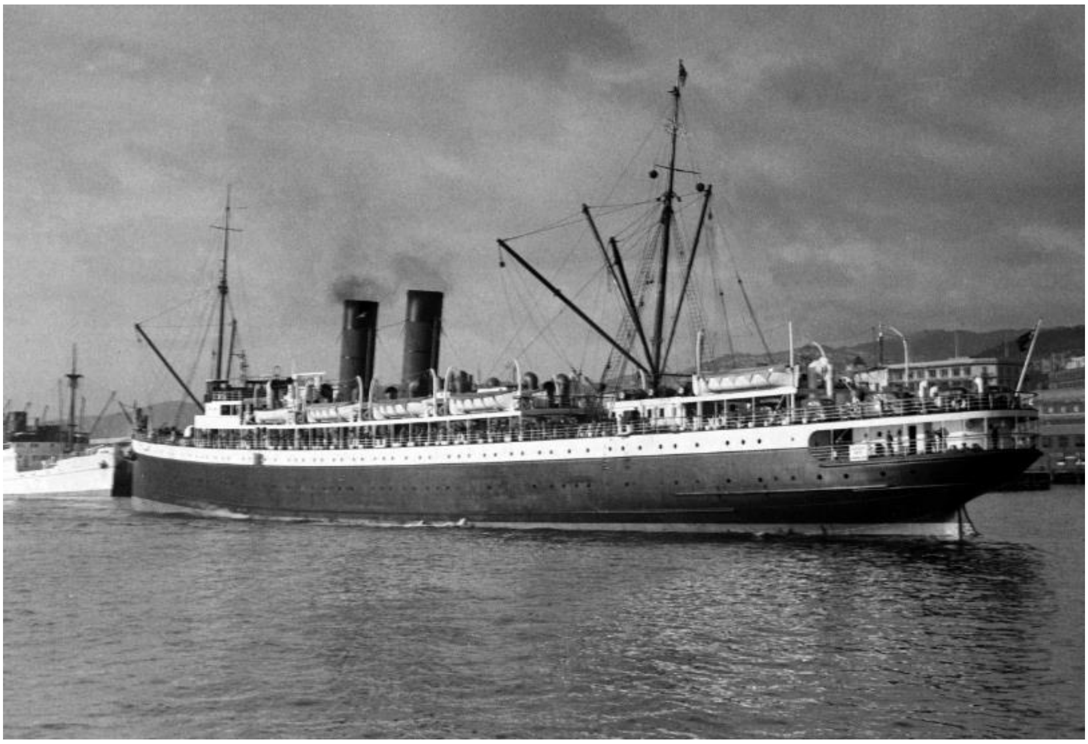

Fig. F11. The TSS Wahine.

Union Steamship Co. New Zealand interisland passenger ferry between Lyttleton and Wellington. In service from 1913-1951. Used also as a troopship during WW 2. Sank near PNG after striking a reef.

<u>Rene:</u>

We got into Lyttleton Harbour half-hour before time – we weren't told, so nearly missed the train to Christchurch. It was moving when we arrived – some soldiers helped us on!! We enjoyed the rest of the train trip and got to Dunedin about 4 pm and were met by Charles Focken, Professor Edson, Dr McIlray[394]. They soon got us up to Dr Hercus' House – they were away but lent us their house in the meantime. We saw Professor Bell's house but it seemed too small – we then toured 'houses for sale' and eventually went back to Bell's, measured and fitted (imaginarily) our furniture - and then bought it.

394 McIlroy, Neil Joseph (08.10.1912 – 1997) NZ Otago Med. graduate 1940. G.P. Invercargill & Christchurch.

Fig. F12. The Eccles' house at 84 Cannington Road, Māori Hill, Dunedin.
In the 1940's. The house with family group; photographed from the back garden.
From Mennis, (2000), p. 119.

FF. New Zealand (1943 – 1952)

Jack Eccles was to be professor of Physiology at the Otago University for nearly nine years and initially got busy setting up his labs. He wrote to his parents about the challenge it was. *"And so, my odyssey continued to the remote university in the south of the South Island of New Zealand, the closest university to the South Pole.*[A] *Even there, I found stimulating challenges and the opportunity to develop scientifically*".

Jack:

My Scientific Odyssey, was across the ocean to an even more remote home. But the war was still on; and there was an attraction in this remoteness in the age of atomic weapons.

One of his students, Marianne Fillenz remembers his teaching:

*In 1944 I was a medical student at Otago Medical School. Professor John Malcolm has just retired from the chair of physiology and I and my other contemporaries were anxiously waiting to see who would be appointed as his successor. Rumors were circulating that a Dr Eccles from Australia had been appointed, about whom we medical students knew nothing at all. --- We soon discovered how extraordinarily lucky Dunedin and New Zealand were. Eccles came with a strong recommendation from Sir Charles Sherrington; 70 papers published or in Press and a Fellowship of the Royal Society awarded when he was only 38 (*Fillenz 2000, p. 11).

The Otago University was founded in 1869 by the Presbyterian Church that created and paid for the first four professorships, Philosophy, English, History, Physics. The Medical School was begun in 1876 when Dunedin was the largest city and was also the commercial centre because of its gold wealth. By 1943, when the Eccles family arrived, the situation had changed greatly with Auckland, Wellington and Christchurch all being much larger. However, the Otago University had the only Medical and Dental School in the country and its student population (2500) was well maintained. Despite this, the city population of 85,000 was not sufficient to provide the clinical teaching facilities for a large medical school with 120 students a year. So, the 6th year was held in the Hospitals of the three northern cities.

John Eccles arrived in Dunedin, bringing Irene and their family of 7 children (3 sons and 4 daughters) into the rigours and travel restrictions of wartime New Zealand. At that time food and petrol rationing measures in New Zealand were in full force, not becoming completely relaxed until 1950, (Oulton, 2011). The less draconian rationing in Australia was restricted to foods and abolished in 1948, (Butlin, 1977).

In 1944, Eccles was one of the first Catholics on the staff of the Otago University. One other was the Students' Guidance (Liaison) Officer, Dr. Basil Howard[395]. The family got to know the Howards well and some of them spent holidays at their 'castle' on the hill - a cabin overlooking the Taieri River Bridge. It was good to get away with the Howards to the Taieri River when it was our turn.

Mary:

"They arrived in Dunedin and, within a month, Rene and Jack bought the house at 84 Cannington Road, Māori Hill. It had an outlook onto the hills, Mount Cargill in front and Mounts Flagstaff and Swampy on the sides. Often snow-covered in winter, Flagstaff and Swampy were both climbed by the family. It was a matter of honour to climb the peaks that you saw so often". The house, at 84 [now 82] Cannington Road, Māori Hill, was a lovely Tudor style house which had previously belonged to Professor Bell and his family. It was supposedly a replica of a house in England, including a priest's hole and a secret passage from the cupboard in the bathroom, where a panel hid it.

Rene:

We got into our home and the furniture was moved in as planned. Jack was at the university and I directed the packers and everything was quickly in its place. It all took a little bit of getting used to! But now we are very happy there and are on our way to loving it more than any of our previous houses. The outlook onto the hills of 2,300 ft is soothing and exhilarating. The walks around about we love, especially the short evening one to the Balmacewen Golf Course. We have also climbed to the top of Flagstaff.

395 Howard, Basil Hillyer (1898 – 1974) NZ book author. In 1940: "Rakiura, A history of Stewart Island, NZ".

Mary:

Life revolved around the kitchen/scullery where meals were prepared and eaten and the washing up done. The drawing room was next to the kitchen. It had the piano in it and the round table, which had followed the family since Oxford days. Next to that was a small sewing room still with the Singer sewing machine bought in Oxford. Next to the sewing room Dad had quite a large study with a fireplace and big desk where he spent long hours working on lecture notes and writing. Bedrooms were upstairs, all six of them, with good views of Flagstaff (668 m.) and Cargill 676 m.) mountains from the windows

Friday nights were folk-dance nights when dad played country-dance records. Some of his university friends would join in for a good evening and we children were all involved with preparation, dancing and supper. The folk-dancing was held in a large basement which had been excavated under the house and cemented in by dad. It was an informal occasion every Friday night. Horace Smirk was an enthusiast as also the Sopers, the Howards and the Passmores. There was also the three-quarter size tennis court at the side of the house for tennis afternoons.

Marianne Fillenz, then on the staff of the Physiology Department, spoke of the folk dancing which she took part in on Friday nights at the Eccles family home.

On Friday nights we all gathered in the Eccles family home for folk dancing. This became a firmly established tradition which Eccles enjoyed, for its conviviality a well as the vigorous physical activity. There was a large basement room in the house where the dancing took place. In the intervals there was time for conversation and this is when Eccles reminisced about his time in Oxford. On the wall of his study, he had the oar he had won during his rowing days there.

Marianne also remembered the physiology department *"It was a very happy, stimulating community where social, personal and scientific interaction all merged seamlessly.*" (Fillenz, 2012, p. 218)]

Peter Eccles:

Mum and Dad selected 84 Cannington Rd as our house. It was about an acre, about three hundred feet deep. It had a tarmac tennis court, less than a full competitive size, because the runouts beyond the court were small to save space. There was an extensive vegetable garden and an orchard of apple and pear trees in the back yard. Beyond the vegetable garden (north) was a small wilderness area, containing a creek fed by street drainage water from Cannington Rd., bordered by some tall pine trees, which provided most of the wood we needed for the fires in the house (once I had harvested it and chopped it up.) The west side of the garden was a berry fruit patch of red and black currants and gooseberries. These required little maintenance apart from their annual pruning. Dad used to say "A good garden thrives on neglect" and this berry patch was a great example of that. The fruit trees were always requiring spraying, the garden always needed weeding, the lawns required mowing with a push mower, the *raspberries and strawberries needed protection from the birds, the fowls (chickens) required care and feeding, but the berry patch stolidly produced more than enough berries for the growing Eccles family year after year. The garden was surrounded by a twelve-foot-high hedge, which I trimmed using manual hedge cutters. Getting the high parts of this hedge trimmed was a real effort. North of the garage was the hen house and their yard. This was our own source of eggs and chicken meat. I was the designated butcher, and I became expert at getting the "chooks" ready for the oven. We were not supposed to make pets of them, and since they were all white leghorns, they were hard to tell apart. But some were distinctive so Mum sometimes had explaining to do when a "pet" disappeared, and chicken soup followed. The other pets that seemed to have a short life were cats. Cats found us. We never sought them out. We never had a dog, so cats found our house and garden peaceful. And many of them used to become lap cats. But a probable explanation for cat disappearances was that Dad did all of his research on cat spinal cords, and that this research was always fatal to cats. Perhaps they ran short of their regular source at the Medical School? I don't know if the other siblings made any accusations. I never did.*

Mary:

Following their parents' training, both mum and dad were keen gardeners. About quarter of an acre was under cultivation with potatoes, onions, parsnips, carrots, spinach, cauliflowers and Brussels sprouts and all types of beans and peas. Some fruit trees did well in Dunedin such as pears and apples. Canes of black and red currants, raspberries and gooseberries were down the back of the vegetable garden and were a favourite place for the hide and seek games which we played in spring and summer amongst the flowering rhododendrons. Usually, the boys did the outside work, gardening, chopping the wood etc while we girls did the housework and cooked large meals. After working outside, dad and the boys ate hungrily.

Evening meals were eaten in the kitchen with all of us sitting around the large table. Dad usually dominated the conversation and talked science or physiology with those who could understand. Sometimes the teacher in him would come out and he would spend the mealtime giving us a geography lesson, getting a geographic magazine or an encyclopaedia out and explaining different things to us. He had a great wonder about the world and tried to hand it on to us. Dad had quite a sense of humour and we would have many a laugh. Later, Mum would read from the Bible with her lilting voice and we would have family prayers. After this time, dad would retire to his study where he would work until all hours while listening to classical music.

In the winter, the clothes were hung to dry on a bamboo raft ["pulley airer"] *and hoisted up to the ceiling of the kitchen, rather like a Chinese laundry above our heads. The wood stove in the corner gave off enough warmth for that room but the rest of the house was cold. Winters were just cold with chilblains on fingers and toes.*

On Sundays, if we had to walk to Mass, it was 110 steps down a very steep pathway and then across a steep road which could be icy in the winter time. Then, at last, one *would be down on the flat and rush past Edson's house and along a few blocks to Holy Name Church, opposite the Otago Museum.*

Glimpse of the Eccles Family in Church, written by Mrs Herbert of Dunedin:

"I had to tell you about the lovely sight of Dr Eccles and his entire family at Mass last Sunday. Mrs. Eccles came first carrying the baby (about two weeks) then two small girls and then the rest of the family - altogether five girls and four boys. They took up the whole seat. It was really a picture. I would have loved to have taken a photo. They are such a good, holy family. I have not spoken to the Dr yet. I must really as I admire the family so much."

Mary:

With the whole eleven of us in the front pew it must have been unnerving for the Parish Priest to give a sermon, especially with dad listening in. Once Fr. Mee[396] *was startled to see dad suddenly turn and stare at him. He thought over what he had just said, then he said it again just to make sure. Sometimes, after we had been to church, we would go to the Botanic Gardens. In the autumn the colours were beautiful but in spring they were a picture with daffodils by the acre and azaleas of all colours.*

Fig. F13. The nine Eccles children in Dunedin.

From left to right: Judy, Alice, William, Peter (holding Richard), Mary, Rose (holding Frances) and John.
From Mennis (2000), p. 131.

396 Mee, Peter (? – 11.10.2003) NZ? Ordained as Catholic priest in 1949. Later Monsignor.

<u>Mary</u>:

Other memories include the botanic gardens where we went for walks in the azalea time; trips to the beach at St Kilda; bushwalking and mountain climbing as a family and rosehip picking out in the fields. There was plenty of work to do and we were all allocated jobs. Quite often, in the summer months, we would go for walks down to the golf links with views of Mount Flagstaff and Cargill. Later the family (eleven of us), would gather around the large table in the corner of the kitchen with the wood stove burning and dad would talk about his work and try to give us general knowledge from the encyclopaedia or atlas. Our general knowledge was good. But it was no good taking homework into dad when we were in high school. He would get his slide rule out - I never did learn how it worked - and he would give you the answer just like that. You would go off with the answer, but no knowledge of all the steps involved. That was the trouble, he was far brighter than us, and had difficulty getting down to our level. He was so caught up in his own work, that he had little time to encourage us. In many ways we helped each other with homework. I have lasting memories of Alice and me doing our home-work on the kitchen table late at night after a long session washing the many dishes after the meal we had helped prepare – even down to digging up the vegetables from the garden after a long day at school.

<u>Rene:</u>

Jack is very happy to be with students again – he worked out practically a new course for them – read volumes of books of Physiology to make himself up-to-date and was worn-out at the end of the Term I. He went back refreshed at the end of Term II.

<u>Jack</u>:

After my ten years of teaching at Oxford, I was enthusiastic to attempt a similar program of years of lectures, practical classes, and discussion classes despite the greatly restricted facilities. In this I was fully supported by Norm Edson, an inspired teacher of biochemistry in the modern form that he had learned from Krebs. So, the medical students were subjected to this intensive modernization of physiology and biochemistry. In my first year in Dunedin, I lectured to the second-year medical class in the whole of physiology- 75 lectures in all, and I also did much of the first-year course. With the practical and discussion classes I found my total teaching time was 20 hours a week for 25 weeks. In addition, I had to spend many hours each week learning the whole of modern physiology, so that I could lecture on it with authority.

My research virtually came to an end during the first year when I was learning physiology for my lectures and also creating a completely new practical course with its specialized equipment. But this extreme operation has to be evaluated against the world situation; in 1944 and 1945 research had virtually come to an end for all except a few who were fortunately sheltered. (Eccles, 1977, p. 5, [1A-436])

Karl Popper, the Philosopher.

In 1944, Jack Eccles became friendly with Karl Popper who was then an academic in Christchurch and later a world-famous philosopher, with revolutionary ideas on the philosophy of science. Jack was delighted to find an academic of his calibre in such close proximity as he regarded himself as an academic exile after his many years at Oxford.

Jack:

The year 1944 was important in my scientific life above all my post-Sherrington life dates from that time. I had heard from Edson about the great stir that Popper was making among the scientists at University College about 200 miles to the north in the city of Christchurch, so we invited him to give five University lectures on the philosophy of science. They were an enormous success among the staff and student body, and there were also two special seminars, one to physical scientists, the other to biological scientists. Many people, including myself, had our scientific lives changed by the inspiring new vision of science that Popper gave us.

Briefly the message we got in those memorable lectures was that science is not inductive, but deductive. A scientific project starts as a problem, for example with a theory that appears deficient or inadequate. New Hypotheses are developed and tested experimentally either to be falsified or corroborated, but the claim of verification should never be made. (Eccles, 1977, p. 6, [1A-436])

Mary:

According to Encyclopaedia of Biography [Vol 5: p. 195]*, Jack Eccles, "actually disproved his own hypothesis about the electrical nature of synaptic transmission, and henceforth championed the alternate theory of chemical neurotransmission.". Because Popper showed him that it was acceptable to disprove his own theories, Jack Eccles put Karl Popper on a level with Charles Sherrington as men who influenced him in his life.*

Both Karl and his wife came and stayed with us on a few occasions. Mrs Popper had been to school in Austria and one of her class mates was Maria von Trapp of the Trapp Family Singers. [Later, their story was incorporated in the musical production "The Sound of Music".] *Mrs Popper still kept in touch with Captain and Mrs von Trapp, and was very taken with our family, which she said was just like the Trapp Family. Not that we could have put a choir together but perhaps because we were a large Catholic family who lived on acreage and spent much of our home time on chores to run the establishment. Maria was a great organiser like my mother. Anyway, mum got to read the Trapp family books and through Mrs Popper, mum corresponded with Maria von Trapp*[397]*. We were fascinated by their story.*

Years later in Papua New Guinea, I met Maria von Trapp[398], one of the daughters, and she became a close friend.

397 Trapp, Maria Augusta von (26.02.1905 – 28.03.1987) AT Stepmother & matriarch of Trapp Family Singers.

398 Trapp, Maria Agatha Franziska Gobertina von (28.09.1914 – 18.02.2014) AT Singer & PNG missionary.

As we lived up on Māori Hill the approach from school was up a steep road called Rattray Street which ran beside the St Joseph's cathedral. Our school St Dominic's was behind the cathedral. Access to the bus on the top of the steep road was by cable car which was an amazing machine.

Fig. F14. The Roslyn cable car line (in service 1906 to 1951) in Rattray Street, Dunedin.
Dunedin was the second city in the world to adopt the cable car (after San Francisco). Cable Cars served three lines: the Mornington line (1.6 km), from High Street to Mornington; the Stuart Street Line (1.9 km) from the Octagon to Stuart Street and the Roslyn/Kaikorai line (2.3 km) via Rattray Street with world's first "pull curve" in front of St Joseph's Cathedral, which can be seen here in the background. The cable car line system operated from 1883 until March 4, 1957, however this discontinued historic service is planned to be reinstated.
From M. Mennis, personal archives.

<u>**Mary:**</u>

I would make it down the steep track beside the cathedral and out on to Rattray St, where I would wait for the cable car to come up the hill. Around the bend it would come and creak to a stop. On we would pile, after throwing our bags on the front luggage container. We might only have four inches of foot space and a rail to cling to and then *with a "clang - clang" up the hill it would go, stopping at the Boy's High school. The boys would push and shove to get a place, hanging on outside us with the ground swirling past underneath. Clang! Clang! Clang! Another cable car would be coming the other way and we would all press into the middle so that we were not hit by the passengers on a downward cable-car - dangerous stuff going home in those days. Rattray Street is one of the longest, steepest streets in the world according to the tourist brochures.*

Rene:

And now at the end of 3rd term Jack's very tired - examining starts soon and then – "hooray for the long Vacation!" We think that we'll stay at home for a long time! At the end of Jack's last lecture an unheard-of thing happened – the student representative got up and thanked Jack for all of the effort that he had put into the course and then the staff for their herculean efforts. Jack was so pleased because he wasn't sure that the students realized how good the course really was!! (Vain man) It's grand to know they do and are willing to profit by it – it makes everything seem so much worth-while. Jack went to America last January – left home a week or so before his birthday (January 17th 1946), and returned March 17th 1946. [Jack Eccles had received a cabled invitation from the New York Academy of Sciences to partake in an International Congress on Neurophysiology.] *He had a rushed but profitable time with continental and American scientists – he went to Hawaii in a small boat and flew to New York arriving ½ hour late for the 1st dinner.*

Mary:

When he came back, he told us what had happened. He arrived in New York on the very eve of the congress after many delays and strange methods of transport. There were no passenger ships because they had been sunk in the war. He left Wellington on a slow American Navy cargo boat, The Sword Knot of 2,300 tons, which was delayed by head winds. However, he made the connection with a flying boat, an old China Clipper. It was an enormous aircraft with a fine dining room, bathing facilities and sleeping bunks [Fig. F16]. *When he arrived at San Francisco, he had to use the name of the Rockefeller Foundation and the New York Academy of Sciences to get his ticket for the final leg of the journey, which he did on a TWA DC-3. The cost of the whole trip was covered by the Rockefeller Foundation. On the return, the Pacific flight had stopovers at Honolulu, Canton Island, Fiji and landed in Melbourne. It was not a passenger flight, but was a delivery flight for a DC-4 for Trans Australian Airlines, a newly formed Australian domestic airline. It carried 20 passengers by special arrangements, with a steward, who was recruited in San Francisco and who arranged for the provisioning. The pilot and navigator had not flown that route before. They used a National Geographic map of the Pacific Ocean that they had bought in San Francisco for this first flight by a commercial company across the Pacific. Dad's immediate task was to get back to Dunedin, a few days late for the term!*

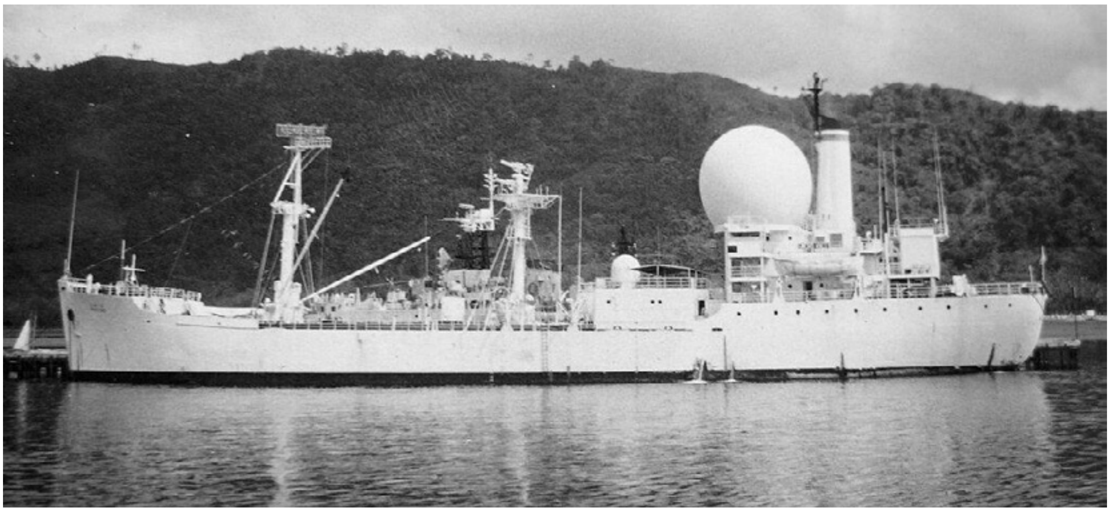

Fig. F15. USNS Sword Knot (shown in 1966, after missile range instrumentation alterations).

The "small boat", a type C1-M-Av1 MC hull 2466 diesel, single propeller ship; speed 11.5 Knots (21.3 km/h) was first placed in service under a US War Shipping Administration agreement with Lykes Bros. Steamship Co. on 30th May 1945 and returned to the US Maritime commission, 1st May 1946 (soon after John Eccles' Auckland to Hawaii voyage). The vessel was later modified (as seen here in Trinidad) for use as a tracking ship by the US air force 1957-1964 and scrapped in 1971.

From: Wikimedia
https://upload.wikimedia.org/wikipedia/commons/thumb/8/86/USNS_Sword_Knot_%28T-AGM-13%29_in_Trinidad_%28crop%29.jpg/1024px-USNS_Sword_Knot_%28T-AGM-13%29_in_Trinidad_%28crop%29.jpg

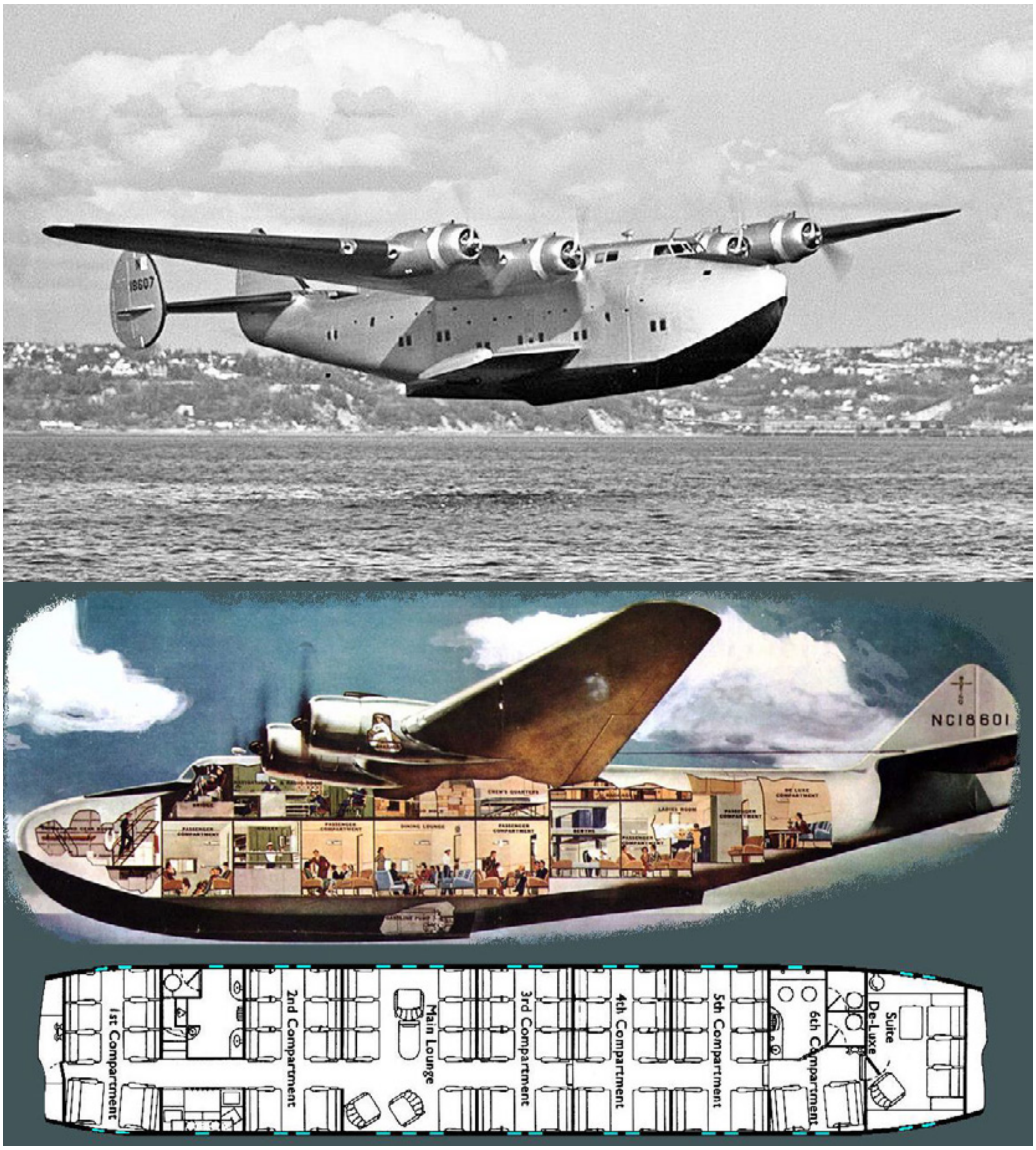

Fig. F16. A "China Clipper" flying-boat from the Pan Am airplane fleet.

Upper: In 1946 John Eccles flew from Honolulu to San Francisco an aircraft such as this. China Clippers were in regular passenger service from 1939 to 1946.

Lower: This flying-boat provided the greatest luxury available in those times, as shown by the internal profile and the seating/sleeping area plan of its passenger floor.
From: https://sierrahotel.net/blogs/news/boeing-314-clipper

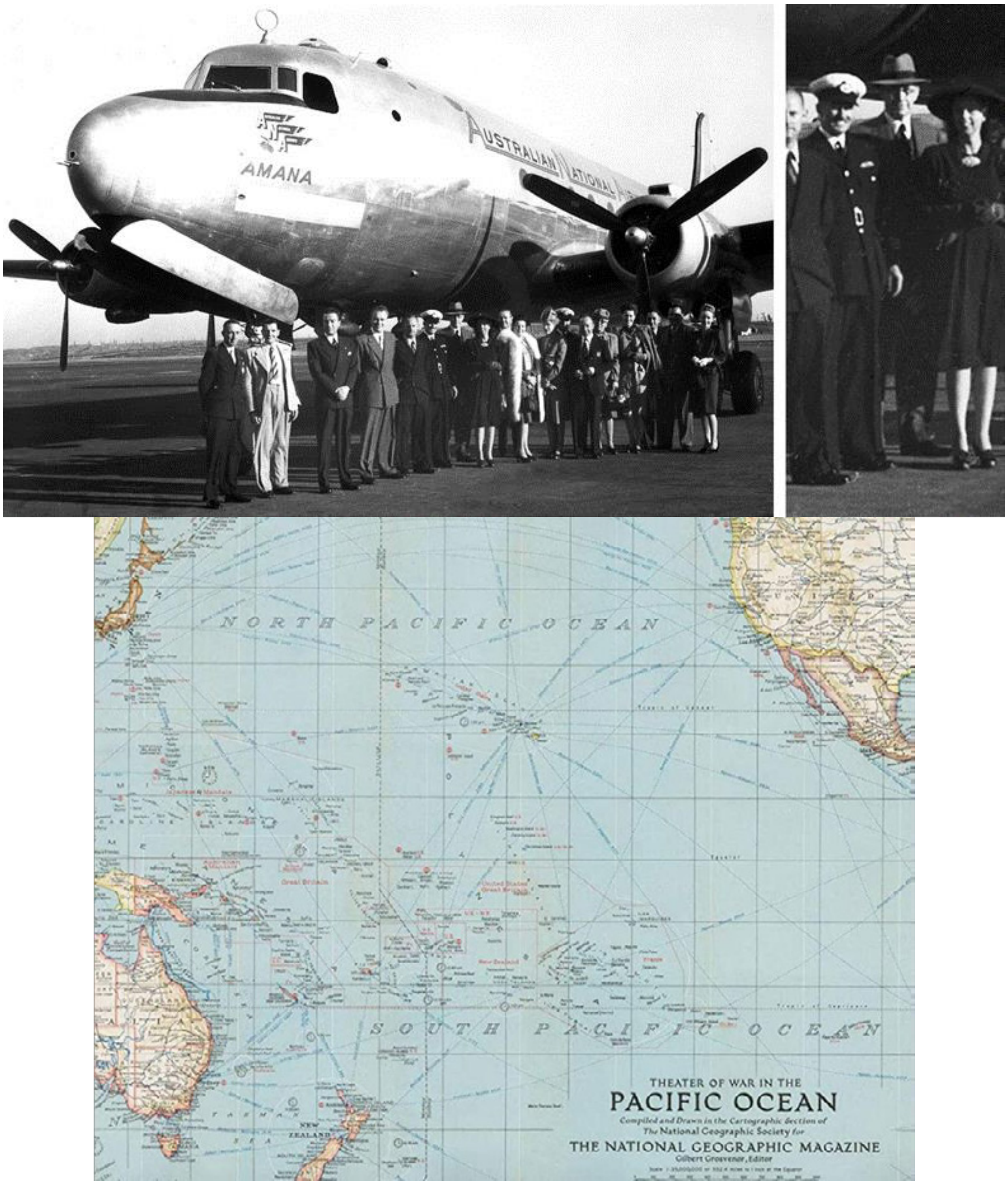

Fig. F17. TWA DC-4 delivery flight in February 1946: The plane, its passengers and map used.

Upper: Amongst the passengers and crew John Eccles can be recognised (tall with hat) 7th from left, standing behind the captain and a woman passenger (See also enlargement on right). From R.N. Smith's photographic collection "AussiAirliners, #125.105".

Lower: The aircraft crew were forced to use a National Geographic Magazine map (like this one from 1942) as substitute for official navigational charts, which were unavailable at the time of the flight.
From the National Library of Australia. See https://nla.gov.au/nla.obj-594453677/view

Fig. F18. Family Photograph (1946).
John Eccles (holding Richard) with visitor Ralph Gerard. Other children (from left) are Alice, Mary, Frances, Judith and John.
From Mennis (2000), p. 139.

Rene.

This year (1946) Jack and I spent Easter away from home and left the children in Rosamond's care with Betty Wilkinson coming at night to sleep. They managed very well. The original Ford V8 car was still with us and it could be converted for sleeping and there were wonderful sites on the inland lakes for a few days of recovery. We went up central and enjoyed the Lakes, Wanaka, Hāwea, Wakatipu but Hāwea came first – it was more isolated and unspoiled than the others – we found Queenstown disappointing, though we enjoyed the view from Crown Range. We climbed to the top and saw a grand panorama and, during the night spent up there, saw the Aurora! Jack ran the engine during the night – just to make sure that it didn't freeze. There was ¼ inch of ice on our wash bowl this a.m. We were warm and cozy in the car. We then went via Milton, Laurence, Beaumont, Alexandra, and returned to Alexandra and then Wanaka, Ranfurly, Middlemarch (the 4- or 40-mile road – so bumpy).

We camped outside Alexandra – high above the Clutha and in pine forest – good spot – then to Wanaka – lovely scenery all the way – the golden poplars were breathtaking and rose-hips – just miles of them! We camped at Glendhu Bay (not at the camp!) and next day drove up to Niger Hut and walked for miles past it – in search of Mt. Aspiring – which was looking at us all at the time – only we didn't know, as we had no map showing it. After 3 days went on to Hāwea for one night and then on to Moke

Lake – delightful spot – bad road, camped at Wakatipu and home by Kawarau Gorge saw 'Roaring Meg', back to Alexandra and home via this dry and barren part.

Jack.

During my latter years in Dunedin, I had come to realisation that the heavy teaching program seriously handicapped me in competition with the new wave of intensive neurobiology that was developing, particularly in America. There, the teaching loads were much lighter and the financial support of research much greater. Dunedin was an acceptable home for me during the war and in the period of world-wide disorganisation and reconstruction that followed, but I could foresee my failure in world class if I continued there. (Eccles, 1977, p. 7, [1A-436])

Mary:

During the late 1940's, Jack began to hear of plans in Australia to begin a University in Canberra. The aim was to attract world-class people in their fields to establish a research university, later to be called the Australian National University. Already Mark Oliphant had been chosen to be Professor of Physics. Prime Ministers Chifley, Curtin and finally Menzies all gave generous support. Canberra at that stage was not much bigger than a country town of 25,000 people with sheep grazing around the parliamentary buildings. John Eccles was happy to accept the Professorship of Physiology at the Australian National University in Canberra.

FG. Voyage to Australia (1952)

Mary:

Our family was delighted at the prospect of returning to Australia. I remember sitting at table in Dunedin when dad announced that he had accepted a position in Canberra and being overjoyed. "You just ***want*** *a change of scenery," he teased, but, no, we wanted to hear the kookaburras and smell the gum-trees again. Dad and Mum, Bill, John, Richard and the three girls stood together on board the Monowai and watched New Zealand gradually fade from view. We girls were wearing our old school navy coats and berets and tartan skirts underneath.*

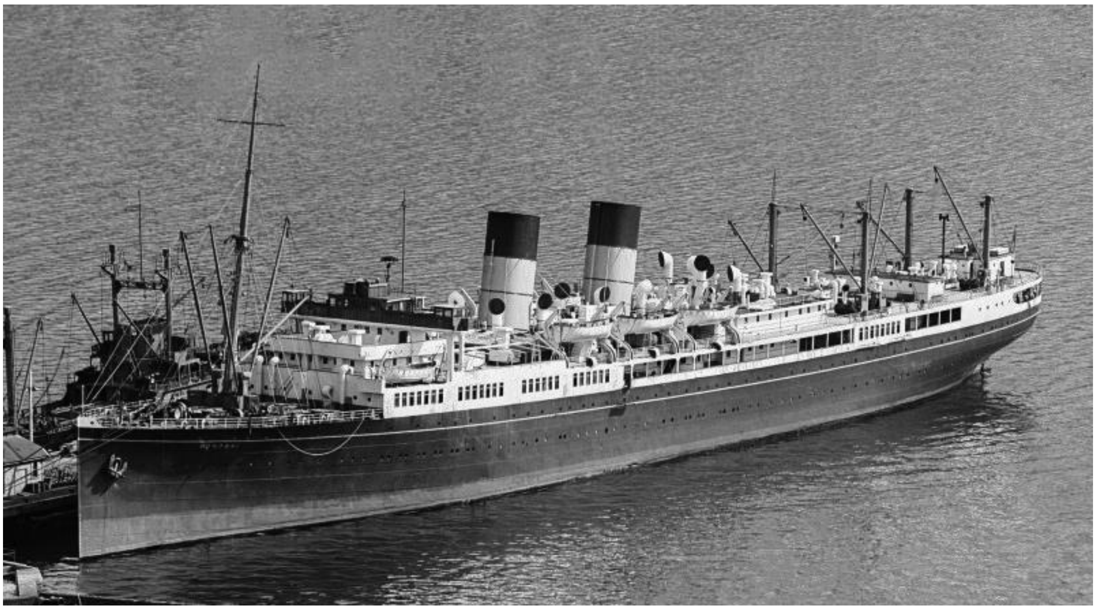

Fig. F19. The T.S.S. Monowai.

This vessel (the second ship bearing the name Monowai) was in trans-Tasman ferry service from 1949 until 1960.

http://ssmaritime.com/Monowai.htm

From https://commons.wikimedia.org/wiki/File:Monowai_In_Milford_Sound_Feb_1933.jpg

When we first saw the new house in Canberra, it stood in an empty paddock with a few seedlings planted at intervals. It was different from the former houses in Oxford, Sydney and New Zealand, which were already established and had a character of their own with their gardens flourishing. In Canberra, we were the pioneers again just like our forebears in the Gippsland. The old idea from the Gippsland of the children providing the labour still held and there were plenty of jobs to be done. In the summer months, there was endless watering of the trees, which were to become the tree belt. The soil was an orange red colour and rather rich in what it could produce.

The Council of the ANU considered his acceptance as a 'brilliant catch' considering he could have accepted positions in England and the United States. It was Sir Howard Florey's decision to tempt Eccles across the Tasman to Canberra as he considered Eccles as "one of the best living neurophysiologists". Eccles himself thought that the ANU would 'give him exceptionally favourable opportunities' for pursuing his research interests and a release from his current burden of teaching at Otago [Foster & Varghese, 1996, p. 60]). Jack Coombs, a physicist and instrument designer, had been with dad in Dunedin. When he was transferred to Australia, it was lucky that Jack Coombs could transfer also, bringing with him the highly specialised equipment he had designed and made in Dunedin, "This included four electrical stimulating and recording units which were critical to Eccles' research during his fourteen years in Canberra" [Foster & Varghese, 1996, p. 91]. Setting up his new Department in the John Curtin School of Medical Research was a real challenge to him. His first laboratory was in a temporary building but a larger building was promised. However, even the temporary laboratories were not available until February 1953. Dad filled in his time working on the final drafts of his book. At last, the book was published in 1953 and he proudly showed us a copy, the title being *The Neurophysiological Basis of Mind.*

FH. Overseas travel (1951-1952)

In the transition period from Dunedin to Canberra, Jack Eccles travelled to the United States in 1951-52 to meet with colleagues including Chandler Brooks and then to England where "*Hodgkin, Huxley, and Keynes in Cambridge and Fatt and Katz in London were leading the world in neurobiology"* (Eccles, 1977, p. 7, [1A-436]).

In 1951, at a meeting of the Physiological Society, he suddenly revealed that he had proved himself wrong in his previous theory when he believed that it was electrical rather than chemical transmissions between the synapses that causes the neurons to be fired. The physiologists were astounded because Eccles had previously debated his views with Dale who had always held that it was a chemical transmission. He was able to do this without too much loss of face because of the influence of his friend, Karl Popper, who always said that, in science, it is acceptable to disprove your own theories.

In 1952, he spent five months in residence at his old college, Magdalene College, preparing the Waynflete Lectures. Back in 1950, he had received an invitation from the President of Magdalen, Mr Tom Boase, to give the 1952 series of lectures named after the founder of the College in 1458, William of Waynflete, Bishop of Winchester. The title of the lectures and the subsequent book was *The Neurophysiological Basis of Mind, Principles of Neuro-physiology*. While he was there, he visited his mentor and friend Sir Charles Sherrington.

Back in 1951, Professor Mark Oliphant and D.F. Martyn[399], a scientist from the CSIRO, mooted the notion of an Australian Academy of Science based on the Royal Society in London. It was formerly inaugurated in 1954 and opened by the Queen. Eccles wrote, "*It was the second time in history that a British Monarch had founded a scientific society, the first being the Royal Society of London by Charles II in 1660!*". (Eccles, 1977, p. 10, [1A-436]). John Eccles was made a Foundation Fellow of the Academy in 1954 and became the second president.

Because of Oliphant's involvement, he fittingly became the First President 1954-1957. John Eccles was the second one from 1957-1961. The actual Academy building was finished in 1958. "*A striking symbol of Australian Science ----. It displayed an extremely geometric form, an enormous copper covered dome, a section of a sphere, broken only by arches rising in scalloped form from some 16 "feet" immersed in a*

399 Martyn, David Forbes (27.06.1906 – 05.03.1970) UK atmospheric physicist. Radar. Aust. Acad. Of Science.

circular moat." (Eccles, 1977, p. 10, [1A-436]). The scientists were overjoyed at their symbol and the local population were agog with the sight. It promptly became part of the tourist circuit. Over the years, the Academy of Science has taken an increasing interest in science taught in school and has developed programs to teach science even at the primary level which is an excellent idea. So, the vision those pioneer scientists, like Eccles and Oliphant, had of developing a scientific centre where excellence could be recognised by the award of FAA (Fellow of the Australian Academy of Science) and a building where these scientists could congregate proved to be a great success. "Awards could be of immense value to institutions as proof of achievement" [Foster & Varghese, 1996, p. 253].

Fig. F20. The Academy of Science building in Canberra.

The "Shine Dome" (previously known as Becker House) is a well-known Canberra landmark, notable for its unusual structure, and colloquially referred to as "The Martian Embassy", an allusion to its shape and the fact that as the capital of Australia, Canberra is the home of foreign embassies. When completed in 1959 its 45.75-metre-diameter dome was the largest in Australia.
From Mennis (2000), p. 156.

It was not until 1957 that the new John Curtin School of Medical research was finished, and the scientists were able to vacate their temporary accommodation. Eccles wrote "*At last the grandiose new building was completed. We had done so well in the temporary hut that I was somewhat overawed by the new magnificence and the greatly extended facilities*" (Eccles, 1977, p. 10, [1A-436]). He planned 12 studies for students so they could have their own privacy, however small. Since Oxford days, when he had to share with Denny Brown, Granit, Olmsted and Marcu, he saw the need for individual space.

Fig. F21. Staff of the John Curtin School of Medical Research, 1960s.
John Eccles can be seen in the third row from front, fifth from the right. Arthur Chapman is standing fifth left from Eccles in the same row.
From Mennis (2000), p. 157.
Source: (ANUA15-115). Commonwealth News and Information Bureau, ANU.

FI. Knighthood (1958)

In 1958, John Eccles was honoured in the Queen's birthday list, becoming Knight Bachelor. The day of the ceremony was cold and windy. We assembled outside Government House and were greeted by the Governor General and his wife and the ADC. William Slim[400], the Governor General, looked stunning in his military uniform and knighted John Eccles and the others with all the pomp and ceremony he could muster.

400 Slim, William Joseph "Bill" (06.08.1891 – 14.12.1970) UK military commander, 13th Austral. G.G 1953-60.

Fig. F22. The accolade.
Sir William Slim dubs John Eccles in 1958, so conferring knighthood.
From M. Mennis, personal archives.

Fig. F23. John Eccles, here portrayed as "knight of traces", conquering the neuron.
Cartoon drawn for Sir John by Pam Macfarlane[401].
From Mennis (2000), p. 157.

401 Macfarlane, Pamela Sinclair (1926-1999) NZ artist (wife of physiologist W. Victor Macfarlane).

Jack had accepted the challenge to be one of the founding professors of the ANU. and subsequently helped establish the John Curtin School of Medical Research. He wrote of this time: "*Without doubt it was the highlight of my research career*". He saw it all as a challenge, a new venture and was enthusiastic. He attracted some famous researchers from overseas. He sought the best people wherever he could find them, so that Physiology quickly became the most 'international' department in the university. In the first five years the team comprised, besides Eccles, three Americans, two Australians, two New Zealanders, two Swedes and one each from Mexico, Canada and England. (Foster & Varghese, 1996, p. 91).

Fig. F24. John Eccles, standing before his new Canberra residence.
Located at 28 Monaro Crescent, Red Hill and largely designed by him – "this is the house that Jack built".

From Mennis (2000), p. 149.

The two Swedes were Sven Landgren and Anders Lundberg, Ricardo Miledo came from Mexico, Vernon Brooks from Canada, Ben Libet, Bob Young and Kris Krnjevic from the United States. Compared with the isolation he felt in Sydney and Dunedin, Eccles thought that the young people had "the great advantage of association in Australia with scholars from overseas". These overseas scholars were invited to the Eccles home for tennis parties at the week-end. Rene would cook her special scones with delicious home-made raspberry jam and thick cream from the Shoebridge's cow. David Curtis and his wife, Laurie, and their children would be frequent visitors in those days. Jack was trying to duplicate the Sydney days when he and Kuffler and Katz did the same on the tennis court in Mosman. Jack and Rene certainly knew how to create great gardens with flowers, vegetables, fruit and poultry providing all the necessities. If we had a visitor for a meal, Jack would say proudly "All this was produced on our place except for the milk and meat". Pumpkins were enormous as were also the carrots and beetroot. Rhubarb and spinach had prize-winning sized leaves. Along the fence, down the bottom of the vegetable garden, were boysenberries, which produced loads of fruit. These were collected and bottled or turned into jam. It was marvellous the work that he and the boys put into the garden. They sprayed and pruned the fruit trees and, when the fruit was ripe, the fresh produce was eaten or bottled.
One day as we children were preparing for school, dad arrived home from work! When I met him in the passageway, he said. "Mary, guess what I discovered last night?" I had no idea. "Well, I discovered how tetanus affects the nervous system." I was impressed by his discovery, but also impressed by the fact that he had worked all the day before and through the night without sleep. Of course, tetanus vaccination injections had been available as a treatment before this but it was not known how the disease affected the body. Subsequently, we were all lined up for a "tetanus" injection to be given by David Curtis, except for my brother, John, who climbed up a gum tree and refused to get down.

FJ. The Nobel Prize (1963)

In October 1963, Sir John Eccles received the Nobel Prize (with Alan Hodgkin and Andrew Huxley) for his discovery of the chemical means by which impulses are communicated or repressed by nerve cells. After all his hard work, he deserved it and we were all very proud of him.

He was not in Australia at the time but was in Venice with mum on one of their many overseas trips. Venice was a city he had heard about from his father when he was a toddler and he had had a love for it ever since. They were out on a gondola when the message arrived at the government office there. A gondola went out after them with the message and the gondoliers made much of him when the importance of the message spread.

Later John said:

"*I received the Nobel award (1963) for the ionic mechanisms of synapses, and my Nobel Lecture was on the ionic mechanisms of postsynaptic inhibition. Earlier in the year I felt that the time was ripe for an extensive review of the whole field of synaptic mechanisms. This proved a heavier task than I had anticipated, but it appeared as* The Physiology of Synapses *that was published just in time to be on display in Stockholm at the time of the prize festivities in December 1963. The publishers made an unprecedented effort in speed of publication in order to effect this felicitous timing*". (Eccles 1977, p. 13)

Fig. F25. Gondoliers cluster around Dad in Venice after giving him the news.
An impromptu photo, documenting the delighted couple, John and Rene.
From Mennis (2000), p. 160; [also used in Mennis (2003), p. 42]

Fig. F26. The Nobel Laureates for Medicine arrive at Stockholm Airport.

All three Nobel Prize recipients arrived at the same time in December 1963 and were pictured together. There was Alan Hodgkin and his family, Andrew Huxley and his family and John and Rene, but none of the Eccles' family of nine children were able to be present.
From M. Mennis, personal archives.

Fig. F27. King Gustav Adolf presents the Nobel Prize to Sir John Eccles in December 1963.

Presentation of the Nobel Prize is performed in the presence of other members of the Swedish Royal Family.
From Mennis (2003), p. 42.

Fig. F28. Sir John Eccles danced with Princess Désirée of Sweden.

Princess Désirée Elisabeth Sibylla (Baroness Silfverschiöld); the third child of Prince Gustaf Adolf and sister of King Carl XVI Gustaf of Sweden.

Sir John was seated next to a Swedish princess at the Nobel Prize dinner and later danced with another princess. It was a great occasion and he enjoyed it immensely. When he arrived back at Sydney airport on 17th December 1963, he displayed his leather-bound citation and his medal for the photographers. His share of the prize amounted to 7000 pounds ($14000).

From M. Mennis, personal archives.

Fig. F29. Sir John and Lady Rene Eccles, displaying the Nobel Medal and Citation.

Jack and Rene Photographed 1963 at Sydney Airport on his return from the Nobel Prize award in Stockholm.

From Mennis (2000), p. 161.

In January 1964, it was announced that Sir John Eccles was the Australian of the Year for 1963. The award was announced by Sir Norman Martin[402].

Fig. F30. The last photograph of the whole Eccles family, 11th January 1964.
From left: Dad, Mum, Rose, Peter, Alice, William, Mary, John, Judith, Frances and Richard, standing in front of their Canberra home.
From Mennis (2000), p. 162; [also used in Mennis (2003), p. 44]

Later in 1964, Sir John was responsible for a Study Week with the Pontifical Academy of Science at the Vatican from September 28th to October 4th. The purpose of the week was to relate Psychology to the Neurosciences. The title of the symposium was “Brain and Conscious Experience”.

In the preface he wrote:
The symposium was held in the Academy building in the most delectable spot in the Vatican gardens. The building dated from 1561 as a palace for Pius VI. The room in which we met had still the lovely tiled floor and the frescoed walls and ceiling of that period, and outside there was always the sound of the fountains in the marble paved court. in the evenings there were the pleasant social occasions of dinner and

402 Martin, Norman Angus (24.04.1893 – 08.10.1979) AU politician/patriot. Founded “Australian of the Year”.

gatherings thereafter. From a rather large experience of symposia in the last decade I am convinced that the most fruitful have been the most. enjoyable, because it is under these conditions that the human spirit (if I may use this phrase) operates most creatively in debate. (Eccles, 1966, p. viii, [1A-295W]).

Fig. F31. Meeting of the Pontificia Academia Scientiarum in 1964.

Pope Paul VI at the audience with scientists attending. Sir John Eccles is seated on the front row on right.
From Mennis (2000), p. 163.

FK. Voyage to the United States (1967)

In 1967, Sir John was 63 and he wrote:

Troubling me in the latter years in Canberra was the retiring age of 65 that was soon to overtake me. I had hoped to get this age extended to 68, but the administrators prevented this. I already knew the very impoverished conditions that would be my lot after 65. I realised my odyssey would take me from Australia across the Pacific. (Eccles 1977, p. 14).

The issue was much wider than the university. Across the country, his views were noted and he gave a lecture to the Australian Association of Gerontology where he said:

Today about two-thirds of men over 65 in Australia are no longer at work. Many of these have been retired when they were still very valuable with their skills, wisdom and knowledge. No doubt many should be retired. But the aim of society should be to introduce more flexibility in the whole question.

Rose:

On her father's dissatisfaction with the post-retirement future offered him by the ANU:

I think partly he either misinterpreted or decided not to understand what was being said to him. The ANU decided that he could have two labs downstairs, they had spent $10,000, which was a lot of money in those days, in fact it was my salary, to redo the labs. I know that both the Registrar and the Deputy Registrar have spoken to me about it: they felt that my father's interpretation had cast a bad light on the ANU. In actual fact, I think it was very generous and it was better than anybody else had ever got.

Rose comments on her father's momentous decision to leave the ANU and depart from Australia; influenced by increasing marital tension between him and Rene:

He could not have stood to not being professor and that somebody else was going to be professor over him and he wanted to be the one in charge and he always did.

Secondly, I think there was a lot of trouble between my mother and himself, they had drifted miles apart. My mother had become very religious and she went to religious meetings, she got up and went to daily mass and this used to irritate him because he'd get to bed at 2 or 3 and the alarm would go at 6 and you know, wake him up. Both were incompatible in many ways, their characters, and he was much more open, he loved meeting people. (Carleton 2003, radio transcript).

In the Canberra Times, the headline read: "U.S. position for Sir John Eccles".

In 1967 when Sir John Eccles was leaving Australia, he declared in an interview with the *Canberra Times* that:

"The fact that there is no arbitrary retiring age at the Institute, [in America] *has great appeal to me. It means I will be able to continue my work indefinitely as the head of a research team"* (Canberra Times, 17th February 1966).

At the Institute for Biomedical Research in Chicago, where he planned to continue his work on nerve cells and the brain, his research rooms occupied 5,000 feet of floor space in an impressive building, financed by the American Medical Association.

In spite of this euphoria over his new position, Sir John did not have a very successful time at the Institute because of friction between members of the research team. In 1968, he became the Professor of Physiology at the State University of New York, Buffalo, which was much better and his research thrived. Over the years, Sir John received many awards. In 1986 he was awarded the Order of the Rising Sun in Japan and in 1990, the Order of Australia, as well as 15 honorary doctorates from universities that included Melbourne, Cambridge, Oxford, Prague and Basel. He wrote 16 books about science and the philosophy of science including *The physiology of Nerve Cells* (Eccles, 1957, [1B-a03]); *The understanding of the Brain* (Eccles, 1973, [1B-a14]); *The Human Mystery* (Eccles, 1979, [1B-a17]); *The Wonder of Being Human* (Eccles & Robinson, 1984, [1B-a22]); *The Evolution of the Brain: Creation of the conscious Self* (Eccles, 1989, [1B-a25]) and *How the Self Controls its Brain* (Eccles, 1994, [1B-a29]) – the last when he was 90 years old.

FL. Second marriage and retirement in Switzerland (1968 – 1997)

In April 1968 Eccles divorced Rene and married his second wife Helena[403], a neurophysiologist who collaborated closely in the laboratory with him in America until he ceased experimentation in 1975. It was that same year they decided to move to Switzerland.

Rose:

Did I know about Helena? Well, it's interesting looking back. I do know that at one stage he and Mum were overseas, and he said he was going off to Paris for the weekend and she found an Italian sticker on his case, so there was a terrible row about that because he'd been untruthful, but he didn't then own up that he'd been down to see Helena.[A]

Fig. F32. Sir John with his second wife, Lady Helena Eccles.

Olov Oscarsson with Lady Helena (left) and Sir John Eccles and his wife, Gerd Oscarsson[404], photographed in Canberra in the 1960s. Courtesy of Gerd Oscarsson.
From Voodg (2010), p. 341, fig. 9. j.voogd@erasmusmc.nl.

403 Eccles, Helena Táboriková (09.02.1925 – 25.10.2017) CZ physiologist. Married Sir John in 1968.

404 Oscarsson, Gerd (24.09.1931 – 01.08.2018) SE Wife of Olav Oscarsson.

Mary:

Eccles loved the mountain scenery of Contra, near Locarno, but it had some drawbacks; he reminisced to his daughter Mary about the poor design of their house with its flat roof unlike the other houses which had inverted V-shaped roofs. This meant that in the depth of winter, the weight of snow on their roof threatened to collapse the house. There were times when he and Helena were up on the roof shovelling snow off to save the house. But the plusses were the wonderful spring with the wild flowers and the grape vines which covered their outdoor eating area. Like in most of his previous houses, he and Helena had a vegetable garden outside their back-door. The winding road up to their house passed little village houses and meadows where cows grazed in summer. In this majestic mountainous landscape, Eccles concentrated on the mind-brain problem. In spite of his considerable age, he continued writing on this and related themes. A long series of books, and articles flowed from his hands, all hand-written, until well beyond his 90th year. In all of this activity, he was efficiently and caringly assisted by his wife Helena.

Rose:

Helena was very protective of him, naturally. I felt that since he had written to me and indicated he didn't want contact, just to let him go in peace. So, I made no effort to contact him. Really, I just remember him when he was younger and I ignore the later years.[c]

Fig. F33. Pope Paul VI, being introduced to Sir Robert Menzies by Sir John Eccles.

At the invitation of Cardinal Norman Gilroy, the Pope made a special visit to Sydney only and celebrated Mass there at St. Mary's Cathedral (from 30.11.1970 to 03.12.1970), shortly after surviving an attempted assassination whilst in the Philippines. At this time, Eccles was living and working in Buffalo, but must have made a special journey to Sydney to partake in this event. The former Australian Prime Minister, Robert Menzies (a Methodist protestant but also "bridge-builder" to other faiths) was a good friend of John Eccles and they formerly dined together with their wives, Rene and Pattie.
From M. Mennis, personal archives.

Fig. F34. Sir John, enjoying outdoor activities during his retirement.
Photographed in a Swiss village in 1980.
From Mennis (2000), p. 165.

Fig. F35. Sir John and Lady Helena Eccles' abode in Contra; named "Ca' a la Gra".
Their house was later demolished and redeveloped by the new property owner.
From M. Mennis, personal archives.

Their house with address Via Falò 122, Contra (Locarno) Ticino CH 6611 in Switzerland was demolished after the death of Helena. It was located on a hill overlooking Lake Maggiore and surrounded by lovely spring flowers and the perfume of climbing roses. He wrote about his life there:

"*The last journey of my odyssey is now ended, again across the ocean to Europe where I live in Switzerland in idyllic mountain surroundings"*. (Section **EA**)

Peter wrote of his father's visits to USA from Switzerland.

My wife Margaret and I became part of a conference on theological issues supported and hosted by the University of Colorado as well as the archdiocese. I had proposed, and it was accepted, that Dad be part of the triumvirate of experts on these issues, so well before it, Dad accepted the invitation. He was always very careful to coordinate his visits from Switzerland, where he was living, to the United States with a large number of conferences and other academic events. So, we didn't have to pay every last cent for his presence. But his talks, and debates with the other panel members filled the Physics Department Auditorium, the largest in the University, to overflowing. There was tremendous interest in his message, and he was very generous in the time he spent answering questions from the floor. He spent some time with my little family and played with the children. But he didn't have time for much more than some long walks. From our home in the Rocky Mountain foothills, we could walk to them and climb about, but the real trails required us to drive, and he didn't want to get up in those mountains.

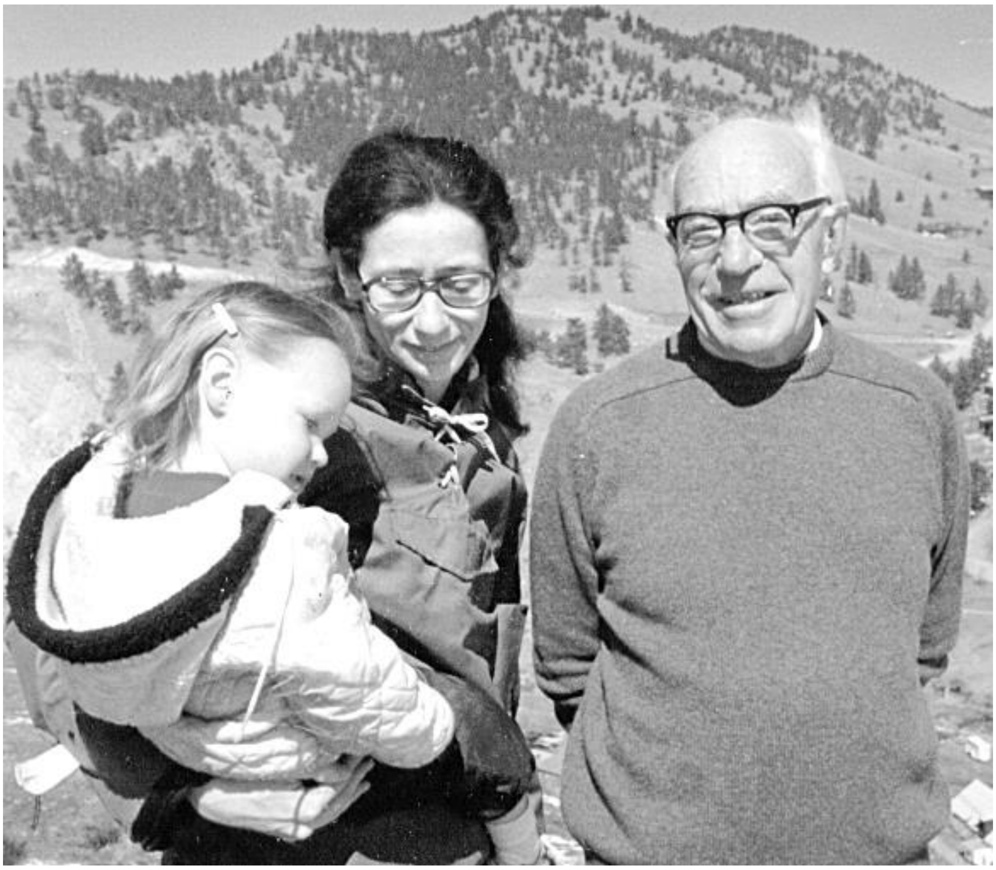

Fig. F36. Sir John Eccles with son Peter's wife, Margaret, and baby Alice in the US. From M. Mennis, personal archives.

The second time was on the occasion of his honorary Doctorate at Georgetown University, Washington, DC. Somehow or other, I believe it was through the good offices of Dan Robinson[405], Professor of Psychology at Georgetown, I was invited to various functions during this great event. Dan had been a co-author with Dad, and during that collaboration had hosted Dad at his home in the country, but near to Washington. Having found out that he was coming, I called him to ask if he would like to be a MITRE Distinguished Lecturer. Dad responded positively, figured out a title for his talk to a bunch of engineers and computer experts "The Neural Machinery of the Brain." Georgetown had hosted him at The Cosmos Club, a very exclusive club,

405 Robinson, Daniel N. (09.04.1937 – 17.09.2018) US psychologist and author. "Philosophy of mind".

so Dad did not need to take advantage of my offer of hospitality, though he did stay with Margaret and me for the best part of one day while he was in Washington. His talk was a great success; MITRE taped it and gave me a copy of it. I brought that to Australia when we had a memorial mass for Dad, and each of my siblings who were present got a copy of it. I also gave a copy of it to the John Eccles Memorial Library at the John Curtin School at ANU.

Letter October 1988 to his son, veterinary Surgeon Dr John Eccles
(Sent via Mary Mennis' postal address)

October 3th 1988, Sir John and Lady Eccles CH6611 contra (TI) Switzerland.

I don't know your address but Mary[406] will know.

My dear John,

I am trying to communicate to you all but time is a problem so here I go with a general letter. I am in surprisingly good health and able to write 80 hours a week. The last two years I have been deeply involved in a new book. Evolution of the Brain: Creation of the Conscious Self.[B] *I am a Darwinist for the first part and strikingly advocate the Divine Creation of the soul or self with the second part. Had difficulty in getting it published. The materialists realise that I am their greatest enemy but I struggle on and it was accepted by Routledge London in January. It's going well in the press but there is a terrible lot to do in the publishing details. It is probably my last book though many people want me to write an autobiography. A big book that I published on the Neurology of the Brain with my good friends the McGeers, has already sold more than 7,000 copies. It is certainly the best book in the world in this basic field.*

All this advertisement is to let you know that life is full of activity and success. In a few days Helena and I go to Rome where I have organised a study week for the Pontifical Academy of Science (see [1A-584] & [1A-585]). They look after us very well at the Vatican and the Vatican is at last getting interested in the brain with many professors of the Gregorian University attending as observers – about time.

Academically, this year has been far too busy - in the first half I gave 30 lectures in Europe and America. I hope for an easier time when the book is published. Already it comes out in English, German, Italian and Japanese.

You may remember Masso Ito from Canberra. He is the leading brain scientist in Japan. He will be at the Pontifical Academy conference. Two years ago, when we were in Japan, he arranged for me to be to be given the Order of the Rising Sun with gold and silver stars. It is very ornate but when will I wear it?

Helena enjoys all the style of our scientific life. Just for fun this envelope is from the last hotel we stayed at. We enjoy music and she has built up a wonderful artistic collection here at home. So, I live with beauty. We have good friends here and in

406 Mennis, Mary R. née Eccles (10.07.1938) AU Anthropologist in Papua New Guinea. Daughter of J. C. Eccles.

Europe and travel to visit them. I don't know how long I can go on in this way. Helena and I feel we should do what we can when we can. I read my poetry and am very religious in my life but I am of course on the fringe of the church. I think of you all with love, may God bless you,

Dad and Helena.

FM. Last days, family reconciliation and obituaries

Mary:

Visits to my father in 1980 and 1991.

I visited my father several times when he lived in Switzerland with his second wife, Helena. They had a lovely home overlooking Lake Maggiore in Contra near Locarno. In 1980 after I represented Papua New Guinea at a Women's Conferences in Hamburg, I was able to stay a week with my father while Helena was visiting her mother in Czechoslovakia. I stayed a week with him in their lovely home at Contra above Locarno. It overlooked a large lake, and the fields were full of spring flowers. Helena was away at the time visiting her mother in Czechoslovakia, so Dad and I explored the countryside and he told me stories of his youth.

It was a time to catch up after many years. Dad was interested in my work in New Guinea as an Oral Historian, studying canoes and culture. It was also a time to ask him about his childhood in Victoria, Australia. as I was becoming interested in our family history. He loved living in Switzerland – the mountains and the villages and people. He said that by law in Switzerland each house should have several months' supply of food stored. He opened a cupboard and pointed to the bottles of wine. 'At least we have six months' supply of wine and chocolates', he quipped. He liked to laugh at things like this. His lawn was full of colourful flowers that had just sprung up. There were flowers everywhere in the fields and beside the road. He had his usual vegetable garden. In New Zealand (1943 -1952) and Canberra (1953 – 19 66) our family had lived off his large vegetable garden and this was no exception. His front door had "Ca a la Gra" painted on it featuring several chestnuts. It meant the home of the chestnuts. A grapevine covered an arbour at the side, next to a small swimming pool. The house, having a flat roof, was a hazard in the snowstorms in the winter. He said that he and Helena had to go up on the roof shovelling snow off. The weight of the snow could cause the roof to collapse. Most nearby houses had inverted V shaped roofs for this very reason. Downstairs he had converted a garage into his study with shelves of books and papers. I did some typing for him, to help him. Then over two days we drove around the local area enjoying the local cafes. An American tourist took a photo of us.

Fig. F37. Sir John Eccles with daughter Mary during her visit in 1980.
From M. Mennis, personal archives.

In 1991 I was again visiting Dad and Helena and stayed in Locarno. It was during this time that my father gave me the copy of his autobiography. Helena was at the doctors' and my father, and I went to a photocopy shop, and he had his manuscript copied there. He presented the copy to me saying, 'Mary, take this autobiography back to Australia, it is important.' So, I took the autobiography back to Australia. Unfortunately, it finishes abruptly after we left New Zealand in 1952. My father seemed quite secretive when he presented me with the copy of his autobiography. He did not want Helena to know. She was very helpful to dad and worked with him, but when it came to our family it was a different story. We know he kept working on it until his death in 1997, but sadly all these copies were destroyed. Luckily, I did keep mine, as it turned out to be the only copy in the world to survive.[A]

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A poem (after meeting my father at Ascona, Thursday 19th September 1991)

He came to me with his new wife,
and spoke to me of their life,
together.

Helena is nice, I like her face,
she holds her hair in place,
with some pins.

We sat beside the Ascona Water,
father, wife and middle daughter,
laughing together.

My face glowed as he told me
how once I dangled on his knee,
and giggled.

There was a spiritual affection,
between us and the direction,
was inwards.

He spoke of the soul, the main
part of man with his mind and brain,
in the body.

The soul that will survive this life,
of endless laughter and some strife,
in the end.

I loved the gentleness in his eyes,
and the compassion as he sighs,
over his past.

I wonder what has kept him away,
for years and months and many a day,
from Australia.

The land of his birth and his childhood,
the land his ancestors understood,

And loved.

Is it enough to have sons and daughters,
and then depart across the waters,
Forever?

Perhaps I must sever the strings,
and let them get on with things,
In this life.

I said goodbye a while ago,
to dad and Helena and watched them go,
Into the distance.

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The last time I saw my father.

It was Easter 1997. I had not seen my father, Sir John Eccles for years as he lived in Switzerland with his second wife, Helena.

Helena was a scientist like my father, and they worked together in the United States before they retired to Switzerland where they had a good life together. However, over the years Helena increasingly cut ties between us. It was sad really as he had had nine children with our mother Irene who was still alive. Now he was dying in a Locarno Hospital. I had rung various hospitals from home in Brisbane to locate him and the doctor there said the if I wanted to see him, I should come soon. He also said that my father was a vegetable. Really a vegetable? I wanted to ask him whether he was now a pumpkin or a cabbage, but I kept my cool. As I was a teacher, I planned to travel to Locarno in the Easter holidays. I was hoping against hope that I would see him again. Since the divorce in 1967, I had kept in touch as mentioned already, but over the years the barriers were increasingly in place. It was a long flight from Australia to Switzerland, a long sleepless flight. When I arrived in Zurich. I decided to take the train ride across the snow-flecked landscape where Spring blossoms were beginning to show. I arrived at the Locarno station and took a taxi directly to the hospital, lugging my bags up to his floor. I was met by a hostile Helena who told me that my family belonged to his old life, and he did not want to see me. The doctor made us meet in his office privately. I gave Helena a hug and thanked her for looking after my father in his final years. This, however, did not change her attitude and I could see that it was a hopeless task. It looked as if I had come all the way for nothing. Should I return to Australia with these words ringing in my ears? To tell his family down the years, that my attempt was a failure?

The doctor's secretary was kind and took me under her wing. She took me along the passage and showed the room where my father was, and I noted the number on the door. She also helped me to book into the hotel across the small square. The hotels were booked out for the Easter season as from the next day, so I took off to France. To France where the daffodils were yellowing the countryside to stay with my friends Bob and Sue Deviana over Easter. I helped Bob harvest the gooseberries and Sue and I bottled them. That first night I let their son's cat out when it was meowing at the door. "Oh Mary, that cat is Dominic's, and he is leaving tomorrow. It must not be let out." We spent an hour outside finding the cat with the Hale–Bopp comet above us with its amazing long tail. If it hadn't been for the lost cat, I would never have had such a good view of the comet.

On Sunday Bob took us to the little church up the road where the Cure D'Ars[407] had been the parish priest a long time ago. He was now a declared saint. I said a prayer to him to help me see my father when I returned to Locarno. Sue was hopeful that I would see him again 'I'll come back with you, Mary" she offered. So, on the Easter Monday we boarded a train back to Switzerland, back to Locarno, back to the hotel and planned to visit my father again. On the way I suggested that we should buy a bunch of flowers, As I was purchasing them the lady asked me what greenery I would like. "You can even have eucalyptus leaves," she said. "Oh yes" I exclaimed, "Let's have them."

As we approached the hospital, we were guided by some invisible spiritual force to take the wrong way and went up and down a lift to the specialist offices. Funny, that, as I knew where the entrance was. But, because we did that, an extraordinary event occurred. When we finally approached the correct entrance, there was Helena leaving the hospital. Now I realised why we had been led astray by some invisible force. If we had not done that, I would never have got to see him. The timing was perfect. As soon as I saw Helena, I put the bunch of flowers in front of my face, and she kept going away from the hospital. The coast was now clear. Sue and I entered the hospital lobby, and I knew which floor to go to and the room number. I saw his doctor in the passage but there seemed to be a cloud between him and us and he did not see us. Tentatively I knocked on my father's door and slowly entered. There he sat on a chair in a very clean, antiseptic room. He was just staring into space. No music, no nothing...

I sidled over to the chair not wanting to tell him who I was in case he really did not want to see me. "Look" I said softly. "I have brought you some flowers." He looked up then, thinking we were just two flower women from the local florists. 'How come you speak English?" he queried. I felt like saying, "Well you taught me when I was a baby," but all I said was "Do you like flowers?" "Yes, I love flowers," he answered, "But who are you?" "Well, I am your daughter, Mary, and this is my friend Sue." He looked up right into my face and his expression softened. "Mary! Mary! How did you find me? How did you know where I was?" I gave him a hug "Well I rang all the hospitals until I found you."

Sue and I spent a happy hour with him. He wanted to know how all the family members were, and I gave him a card they had signed. He remembered his friend Sir Mark Oliphant because my father had been professor of physiology for years in Canberra, researching the brain and nerve cells. He still had his wits about him. He was

407 Vianney, Jean (08.05.1786 – 04.08.1859) Patron saint of parish priests "Curé d'Ars".

no vegetable, pumpkin or otherwise.

Fig. F38. The last meeting of Mary with her father, shortly before his death in 1997.
From M. Mennis, personal archives.

We turned our attention to the bunch of flowers and the eucalyptus leaves in the bunch. He rubbed them joyfully and smelt them "Oh Australia, Australia. How I have missed it." Tears came to my eyes remembering all the years we had spent together when I was growing up. Bundles of memories of his nine children; of Irene our mother, and the rest of the family whom he had not seen since 1967 apart from one nephew and two daughters, Alice and Judy who saw him once. The soul was mentioned, and I reminded him what Sherrington had said as he lay dying. "Oh Jack. All that is left is the soul." My father gazed to the ceiling, He agreed. "Yes, I remember Sherrington. It is true. All that is left is the soul."

Forgiveness came then and some prayers were said. "We all forgive you, dad, do you forgive us if for any reason our ties were broken?" "Yes, yes all is forgiven. Let us be friends, to the end". - These words were spoken.

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For You, My Father. A poem about the occasion.

For months when we rang Switzerland,
We got no answer from you.
They told us, you did not want to speak to us
That all ties with your family had been broken.

What had we done? What had we spoken?

I did not believe the cruel words were true,
I remembered the joyful time in 1992,
During our last meeting.
Was it true all ties were broken?
What had I done? What had I spoken?

When I heard that you might die
My love made me fly
Across the oceans to be with you.
Through the long night I sat bewildered
Was this a futile flight?
So little chance that I might see you.
You could die and all ties would then be broken.
What had I said? What words had been spoken?
That this would be?

Was it your mother and your father
Calling me from the next world?
Or was God himself prodding me to be at your side?
To be near before you died,
So that the ties would not stay broken
And all we could say, would be spoken?

My eyes ached and my bones were tired
When I landed in Switzerland.
But I took the long train ride,
Across the snow-streaked land.
I rushed to the hospital to be at your side.
"Please let me see him. Please let me just pass by".
Again, they told me the ties were broken.
"Your father does not want to see you".
But not from your lips were these words spoken.

Should I return to Australia
With these words ringing in my ears?
To tell his family down the years,
That my attempt was a failure?
For one long week I turned aside,
To France where the daffodils were yellowing the countryside.
I saw it all, but my heart ached to help your soul,
The Cure D'Ars was asked to help

In broken words, barely spoken.

Once again, I tried to see you, with my friend, Sue,
Armed with flowers and a card,
We turned into the hospital yard
With flowers aloft, hidden behind the yellow blooms
No-one stopped us, as we made our way past the rooms.
With trembling hand, I turned the knob.
Would the ties be really broken
'Ere a word had been spoken?

We decided we would not say who we were
It was not your daughter and friend at the door.
Just two hospital ladies doing a chore.
When we opened the door just a fraction
We saw you staring at the wall, no reaction.
There was no music, no books at all,
To fill the long, bleak hours.

I wanted to dance across the floor
Give you the flowers and fill the room with joy
But we pressed forward gently.
"Here we've brought you some flowers. Do you like them?"
Were the first words spoken.

You looked up, as if you had just woken, "You speak English!"
You said, amazed. Our subterfuge was blown.
In a hospital where all speak Italian
To hear English means, it was known
We were no flower women.

You glanced at the flowers and said
"Yes, I love flowers, but who are you?"
Now was the moment of truth.
Would you reject me outright, shaking your head?
Anxiously I whispered "I'm your daughter, Mary,
And this is my friend, Sue."
You turned to me in amazement and joy
And before a word was spoken.
I knew the ties had not been broken.

Your face lit up,
"Mary! Mary! How did you get here?

How did you know where I was?"
"I rang all the hospitals 'til I found you"
Holding your hand my tears began to spill
"I flew half way around the world
When I heard you were ill".
You nodded your great head slowly but did not say a word
"Are you happy I came so far dad?"
You smiled with joy, "Yes. Yes, I'm glad!"

My emotions were mixed.
Happy to be near you. Happy to be wanted.
But angry at the cruel words, that had been spoken.
"All ties with the family have been broken.
Your father does not want to see you."
Had anyone asked you did you want to see me?
All lies, all lies as far as I could see.

You studied the photos I'd brought with emotion
The faces of your sons and your daughters
And your descendants to the third generation.
And with none of them the ties were broken,
From your words that were spoken.
You were pleased with the card
The notes and the endearments,
"We're all proud of you and your achievements".

But a haunted look returned
A worried look that seemed burned
Into your memories.
The soul, the soul was mentioned
And the spell was broken.
Forgiveness came then and some prayers were spoken.
"We all forgive you, dad, do you forgive us?
If for any reason our ties were broken?"
"Yes, yes all is forgiven. Let us be friends,
To the end". These words were spoken.

The yellow daffodils brought in from the fields around,
Were admired in those short hours
And the spring air was full
Of the scent of the blue gum leaves
In the bunch of flowers.
Rubbed gum leaves and the scent of the eucalypt

Filled your nostrils. "Ah Australia!"
Memories of Australia, the land of your birth.
Came back with this smell of the earth.
Later when we were leaving,
Sue said "Go to him; he wants one more hug."
So, I danced across the room to your arms with a cry
Knowing sadly, it would be my last goodbye.

Within the month to the day your life was over;
Within the month your breath was still.
On a Friday you died and a Saturday buried,
Beneath the clover on the hill,
One day I will go there to the clear mountain air
To put gum tips and daffodils, on your last resting place.
In Contra, Tenero.

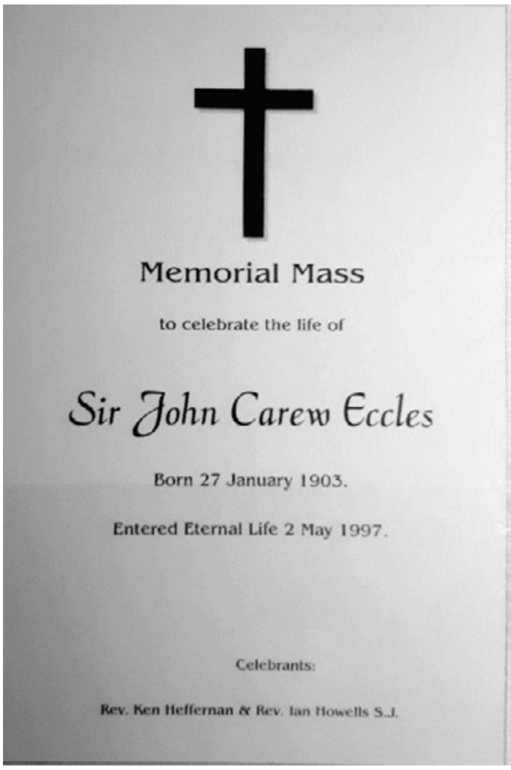
Now you're with your parents and sister, Rose,
Enjoying life in Heaven blest
The joy of meeting you continues,
Every time I go to rest.
For during that long hour with you, dad
While we said our last goodbye,
The ties were strengthened and not broken
And all the words needed were spoken.

Easter 1997. Mary Mennis (Eccles). Brisbane.
++++++++++++++++++++++++++

That was the last time I saw my father. I arranged for the hospital chaplain to give him the last rites of the Catholic Church. He died three months later in May 1997.

Some years later I visited his grave and laid some yellow flowers there. He is buried in a lovely site overlooking the lake.

Sir John Eccles died on 2 May 1997 in the Hospital "La Carita" in Locarno. He was buried on 3 May 1997, following his wishes, in Contra near Locarno, not far from his and Helena's house.


Memorial Mass

to celebrate the life of

Sir John Carew Eccles

Born 27 January 1903.

Entered Eternal Life 2 May 1997.

Celebrants:

Rev. Ken Heffernan & Rev. Ian Howells S.J.

Fig. F39. Memories: John's grandson at the grave, overlooking Lake Maggiore, August 2007.

Left. Card of Australian Memorial Mass held in his honour by Fathers Heffernan and Howells.
From M. Mennis, personal archives.

Right. Cemetery at Via Contra 718. John Eccles, son of veterinary surgeon Dr. John Eccles, was working as an engineer in Switzerland at that time. The name "John Eccles" has thus been passed on down to the next generation.
From Mennis (2003), p. 53.

II. Timothy 4; 7,8

7. I have fought a good fight,
I have finished my course,
I have kept the faith:

8. Henceforth there is laid up for me
a crown of righteousness,
which the Lord, the righteous judge,
shall give me at that day:
and not to me only, but onto all them also
that love his appearing.

SIR JOHN ECCLES, FRS, AC,

27. January 1903 - 2. May 1997

On the 2nd May, 1997, my dearest husband John left this world, he died in the Hospital La Carità of Locarno.
The following day, according to his special wish, he was buried in the small and picturesque cemetry of Contra, surrounded by the local Authorities and his closest Friends.
Sir John will always be remembered by all those who knew and loved him, and greatly appreciated by Scholars the world over for his tremendous and incomparable contribution to Medicine and Science.
The memory of my beloved John will live forever in my mind, and I shall mourn him for the rest of my life.

Lady Helena Eccles

Contra, 5th May 1997

Fig. F40. Memorial card of Sir John; used at his funeral service in Contra.
Card generously provided by Frau Dr. Monotti of Ticino, Switzerland to M. Mennis.
From M. Mennis, personal archives.

Obituario: Lady Helena Eccles 9.2.1925 – 25.10.2017
(Translated from: *Tenero in Contra Periodico di informazione* – Nov. 2019, p. 12-13.)

Helena Táboriková was originally from Prague where she was a medical laureate specialising in neurophysiology from the old university of Carlo IV. In 1963 during a scientific congress, she met Sir John Eccles, the Australian Nobel Prize winner for medicine. She followed him as a research assistant to the United States and in 1968 she became his second wife. In 1975 the couple decided to settle in Europe. They fell in love with Ticino and met a real estate agent who spoke the same Czech language as Lady Helena. He showed them a house near the locality of *el Faló*. They fell under the charm of the place, the landscape, and natural surrounds. It was the perfect location for Sir John to continue with his studies. Lady Helena collaborated with her husband's research. Sir John was totally immersed in his studies but could not express himself in Italian. This caused some problems with the local council because of his being naturalised as a Swiss citizen. In 2003, on the centenary of Sir John's birth, Lady Helena donated, in his memory, to the township, a beautiful round fountain which is now near the council chambers of the town of Contra.

Fig. F41. Sir John's memorial fountain at Contra, donated by his widow, Lady Helena Eccles.

The fountain, donated in 2003, is situated beside the local Casa Comunale di Contra at Via Contra 750.
From Google Maps (as seen in street-view mode in 2019).

Obituaries: Sir John Carew Eccles

Numerous obituaries (and also later reminiscences) of Sir John have appeared, including those of:

Andersen & Lundberg, (1997); Borck, (1998); Curtis & Andersen, (2001a); Curtis & Andersen, (2001b); De Sio, (2016); Fillenz, (2010); Fillenz, (2012); García de la Rocha, (2013); Iggo, (1997); Ito, (1997); Ito, (2000); Karczmar, (2001a); Karczmar, (2001b); Nicoll, (1997); Scott, (1999) & (2006); Todman, (2008b).

BIOGRAPHICAL NOTES & COMMENTS: (Sections GA to GF)

Science without religion is lame, religion without science is blind.

— Albert Einstein —
from an address presented at
The Conference on Science, Philosophy and Religion in 1940.

The notes are designed to complement Eccles' terse autobiography text with background information material, which could motivate serious readers (and historians) to indulge in further investigation.

Foreword. [A] Hoover: a well-known brand of household vacuum cleaner.

GA. Stage 1 career notes (for sections A to H)

A. [A] Fabio De Sio has contrasted the complementary scientific importance of research by Eccles and Young (De Sio, 2018). See also a review of Eccles' genius in Burke (2006).

B. [A] After primary school education at the school run by his father in Koroit, Eccles attended for four years the High School at the nearby town of Warrnambool and for his last school year (1919) the Melbourne High School (formerly named Melbourne Continuation School), then situated in Spring Street with Joseph Hocking as its Principal from 1912-1923. (Mennis, 2000, p. 76-77). The Spring St. school site is presently occupied by the Royal Australasian College of Surgeons.

B. [B] The geometrical problem solved so elegantly by Eccles was not indicated. Examples of quadrilateral proofs as presented to senior students can be seen in: https://www.ck12.org/book/ck-12-geometry-concepts-honors/section/4.7/

B. [C] Eccles' usage here of "just" can be interpreted in several ways. The word, "just" is probably best interpreted in the sense of "morally fair and reasonable" rather than its more common usage as "simply" or "merely". [Ed.]

C. [A] Because the Christian Church in Rome, the English (Anglican) Church, the Old Catholic Church and some Protestant Churches all claim to be catholic (universal) churches, the Church based in Rome is thus often referred to as the Roman Catholic Church in English-speaking countries. In this book, however, use of the word Catholic refers solely to the Roman Catholic version of the Christian faith.

C. [B] See Darwin, (1859).

C. [C] As a devout Catholic, Eccles' dilemma would have been to reconcile the Darwinian concept (of seamless evolutionary transition over eons from primitive organisms to humans) with the Church Catechism's teaching that *endowed with "a spiritual and immortal" soul, the human person is "the only creature on earth that God has willed for its own sake."* "*From his conception, he is destined for eternal beatitude*" [exalted happiness]. See *The Dignity of the Human Person, Man: the image of God,* in *Catechism of the Catholic Church*, second edition (1997) §1703, p. 425.

Eccles might also have taken seriously school teacher Nessy's humorous connection of his surname to a practitioner of ecclesiastical (Church-related) duties. Could he have believed that research into the working of the brain might lead to a breakthrough for the Church in matters spiritual? If so, the rewards from such a momentous discovery would certainly dwarf attainment of the Nobel Prize into insignificance!

The newly-developing concept of electromagnetic waves in the early 20th century might also have been a factor influencing Eccles' choice of career. Apart from his already deeply-rooted faith in the teachings of the Church, young Eccles' brilliant intelligence and wide-ranging interests would certainly have encompassed fundamental understanding of Oersted[408]'s experimental discovery (published 1820) confirming direct relationship between electricity and magnetism followed by Ampère[409]'s development of the corresponding theory, also Fresnel[410]'s theoretical proposal in 1818, (widely accepted until the mid-20th century) of an all-permeating "aether" to mediate conduction of (electromagnetic) light waves. The experimental findings of Michael Faraday[411] concerning electricity and magnetism, *Experimental Researches in Electricity, 3 vols., 1839-55* (see Tyndall, 1914), had been followed by their extension and refinement into beautifully-formulated mathematical equations linking electricity with magnetism (Maxwell[412], 1873). https://oxscience.com/maxwells-equations/

These were soon followed by successful transmission and reception of electromagnetic signals for wireless electrical communication in the early 20th century by the Nobel Prize recipient, Marconi[413], (Marconi, 1909). The young Eccles would surely also have been influenced from the widely-disseminated spiritualist literature of "séances" claiming contact with the "spiritual world" and the then-popular publications by the renowned experimental physicist and Christian spiritualist, Sir Oliver Lodge[414] (Lodge, (1905); Lodge, (1907); Lodge, (1908).

408 Oersted, Hans Christian (14.08.1777– 09.03.1851) DA Physicist & chemist.

409 Ampère, André-Marie (20.01.1775– 10.06.1836) FR Physicist & mathematician.

410 Fresnel, Augustin-Jean (10.05.1788– 14.07.1827) FR Engineer & physicist.

411 Faraday, Michael (22.09.1791– 25.08.1867) GB Scientist and inventor in many fields of endeavour.

412 Maxwell, James Clerk (13.06.1831– 05.11.1879) GB Scottish scientist, pioneer in mathematical physics.

413 Marconi, Guglielmo Giovanni Maria (25.04.1874– 20.07.1937) IT Inventor and electrical engineer.

414 Lodge, Oliver Joseph (12.06.1851 – 22.08.1940) UK Physicist and philosopher.

C. **D** Many years later (Popper & Eccles, 1977, [1B-a15], p. 357) Eccles referred (using 3rd person form) to his own adolescent experience, in terms of an earlier description of an apparently identical experience by the Catholic, Blaise Pascal[415]:

"*One of us (J. C. E.) - at 18 years old - had a sudden overwhelming experience. He wrote no account of it, but his life was changed because it aroused his intense interest in the brain-mind problem. As a consequence, he has spent his life in the neural sciences with some continuing involvement in philosophy. Years later he found that Pascal in his inimitable style had described the predicament of an unbeliever in words that expressed so well the poignancy of that adolescent experience.*"

> ***"When I consider the short extent of my life, swallowed up in the eternity before and after, the small space that I fill or even see, engulfed in the infinite immensity of spaces unknown to me and which know me not, I am terrified, and astonished to find myself here, not there. For there is no reason why it should be here, not there, why now rather than at another time. Who put me here? By whose order and design have this place and time been allotted to me? ... The eternal silence of those infinite spaces strikes me with terror".*** *(Pascal, translated by J. M. Cohen in 1961)* (originally from Pascal's posthumous 1670 publication: "Pensées").

D. **A** In the early years of the 20th century, British physiology research was dominated by the Oxford (Sherrington) and Cambridge (Lucas and Adrian) schools. In particular, Sherrington, Waynflete professor of Physiology at Oxford, achieved fame in neurophysiology with his ground-breaking book; *The Integrative Action of the Nervous System*" (Sherrington, 1906) based on his extensive experimentation on the nature of reflexes, using dogs and cats. Robert Burke has reviewed this important work 100 years later. (Burke, 2007).

The Waynflete professorships are four concurrent professorial fellowships at the University of Oxford, endowed by Magdalen College and named in honour of its (15th century) founder, William of Waynflete, who had a great interest in science.

Comprehensive biographies of Charles Sherrington can be found in the books by Granit, (1966) and Eccles & Gibson, (1979). A rediscovery of Sherrington's valuable histological slide collection has been published by Molnár & Brown, (2010).

D. **B** Eccles spent six months working as Registrar at St. Vincent's Hospital in Melbourne before travelling to Oxford. At St: Vincent's hospital he first met his future wife, Irene Miller, who was working there as a nurse. They later married in Oxford.

F. **A** Study of brain function began (at a much simpler level) with the unexpected, fascinating and puzzling electrical nature of frog muscle twitch, first discovered and

415 Pascal, Blaise (19.06.1623 – 19.08.1662) FR mathematician/physicist/inventor/philosopher/theologian.

investigated by Galvani and Volta[416] during the late 18^{th} century in their so-called "frog soup" experiments, involving electrical stimulation of frogs' legs. Matteucci[417]) further investigated the nature of this phenomenon in the 19th century - see Noad[418], (1849); Moruzzi, (1996); Piccolino, (1998, 2000). Later, the German, Helmholtz[419], measured the speed of "action potential transmission" - the nervous impulse travelling along nerves - using brilliantly designed experiments on frog legs with still-attached nerves (i.e., Galvani's "rheoscopic frog" - the first usable bio-electricity detector) and found it to be about 27 m/sec. (Helmholtz, 1850; Schmidgen, 2002). Experimental electrophysiology, initially restricted to single excised muscles with their attached nerves, was transformed and greatly enhanced in the mid-19^{th} century by usage of the "spinal animal"; a vertebrate whose spinal cord is severed at or near the base of the skull so that most of the cord can nevertheless remain functional; i.e., a placid but living body with still fully-functional members, but these now disconnected from its brain. The spinal animal, in particular the spinal cat, combined the advantages of displaying a remarkably large subset of reactions (reflexes) upon nerve stimulation with the docility of a body deprived of its characteristic "fight or flight" reactions. Charles Bell[420] and François Magendie[421] elucidated the distinct functions executed by the dorsal (sensory) and ventral (motoric) root ganglia spaced along the vertebra (Jørgensen, 2003).

Emil du Bois-Reymond[422] (regarded as "father" of the discipline of electrophysiology) developed his "astatic galvanometer" to new heights of sensitivity for measurement (quantification rather than mere detection) of the extremely faint bioelectrical signals (Lenoir, 1986; Finkelstein, 2003; Finkelstein, 2015), achieved with the help of the famous Alexander von Humboldt[423] who showed great interest in his experiments (Kettenmann, 1997). Nevertheless, a severe problem encountered in recording current impulses in the nerves during the era of electromechanical recording was the "trade-off" between improved current sensitivity and the resultant slower response time of the swinging needle of the galvanometer. The tedious method of sampling the electrical signal at different (fine) intervals following stimulation enabled piecemeal construction of the complete time-course curve (Hof & Geddes, 1957, p. 331-336). The earliest device for producing exactly interrupted pulses of electricity,

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416 Volta, Alessandro Giuseppe (18.02.1745 – 05 03 1827) IT Physicist. Discovered electrochemical series.

417 Matteucci, Carlo (20.06.1811 – 25.06.1868) IT Physicist/neurophysiologist. "Rheoscopic frog detector".

418 Noad, Henry Minchin (22.06.1815 – 23.07.1877) UK chemist; physicist, and textbook author.

419 Helmholtz, Hermann Ludwig Ferdinand von (31.08.1821 – 08.09.1894) DE physiologist & physicist.

420 Bell, Charles (12.11.1774 – 28.04.1842) UK/Scot surgeon/neurologist; distinguished sensory & motor nerves.

421 Magendie, François (06.10.1783 – 07.10.1855) FR Physiologist/neurologist - bitter rival of Charles Bell.

422 du Bois-Reymond, Emil Heinrich (07.11.1818 – 26.12.1896) DE Physician/physiologist. "Animal electricity".

423 Humboldt, Friedrich Heinrich Alexander von (14.09.1769 – 06.05.1859) DE geographer, naturalist, explorer.

originally termed an electrotome in analogy to the histologists' microtome, was later renamed rheotome by Wheatstone[424] (Wheatstone, 1843, p. 307).

Julius Bernstein[425] (Bernstein, 1868), using his "differential rheotome", managed to record accurate time curves of the electrical variations associated with the action potential of nervous propagation. He later developed his "membrane theory" by applying Walter Nernst's[426] equations (Ostwald & Nernst, 1889) to predict electrical potentials from ionic concentration gradients, which he then compared with the "injury or resting current" as measured in nerve and muscle (Bernstein, 1902). The rheotome's duty in Bernstein's laboratory as not only to provide either single or repetitive stimuli of a known duration and frequency but also to map out the action potential of nerve and cardiac muscle with high accuracy (Hof & Geddes, 1957, p. 338). Bernstein applied Ostwald[427]'s concepts to muscle and nerve fibres, and (correctly) treated the non-conducting fibre shell as a semi-permeable membrane, although the existence of pores in its sub-microscopic membrane was quite unknown at that time (Seyfarth, 2006). Keith Lucas, with his enlightened biophysical instrument engineering, demonstrated the "all or none" response of individual skeletal muscle fibres to electrical stimulation (Lucas, 1909). His student/successor Edgar Douglas Adrian, in research spanning many years, extended the synonymous "all or nothing" mechanism with respect to nerve response to electrical stimulation. (Adrian, 1914); (Adrian & Forbes, 1922); (Frank, 1994).

F. [B] In his autobiography Eccles usually refers to Sir Charles Sherrington as "Sherrie" or "Sir Charles" and Lady Ethel Sherrington (née Wright) as "Lady Sherrie".

H. [A] "Bumps race" is a type of rowing race (ideal for narrower waterways and mainly used in Oxford and Cambridge universities) where the boats chase each other in single file and attempt to catch and "bump" the boat ahead without being caught by the boat behind. "Catching a crab" occurs when a rower inadvertently loses control of his oar(s), resulting in a temporary loss of boat speed.

GB. Stage 2 career notes (for sections I to AF)

J. [A] The first paper published by Eccles was Creed & Eccles (1928). This publication is thus labelled [1A-001] to correspond with Eccles' own numbering system, adopted also by the Eccles Archive in Düsseldorf and used throughout this book to minimize uncertainties in locating references to Eccles' publications.

424 Wheatstone, Charles (06.02.1802 – 19.10.1875) UK scientist/inventor. "Stereoscope, Wheatstone bridge".

425 Bernstein, Julius (18.12.1839 – 06.02.1917) DE physiologist. Researched nerve conduction of impulses.

426 Nernst, Walther Hermann (25.06.1864 – 18.11.1941) DE chemist. "Nernst equation". (NP 1922).

427 Ostwald, Friedrich Wilhelm (02.09.1853 – 04.04.1932) DE chemist and philosopher. (NP 1909).

Eccles joined Creed in his first experimental work, which was on the subject destined to dominate his research life for over 40 years; the mechanism of inhibitory synaptic transmission. (Bennett, 2001, p. 29).

J. [B] In order to provide reliable shock impulses a generator was required. Originating from the discoveries of electrical induction by Faraday and others in the 1830s, the induction coil was investigated and adapted by du Bois-Reymond for this purpose during his investigations into animal electricity. Its principle of operating principle may be considered as analogous to the "water hammer" effect" of fast-moving liquids in closed pipes (as utilised in "hydraulic rams") when flow is abruptly stopped – resulting in a sudden peak of high pressure in the system. The resulting "sledge induction coil" (also known as an "inductorium") became an indispensable tool in animal physiology laboratory for many years (Fig. X01). By the 1920s, the development of superbly designed high precision electromechanical rheotomes for providing timed electrical shocks, as well as equipment for recording faint and ephemeral nervous or muscular responses had reached its zenith. Typical equipment included Sherrington-Starling smoked drum kymographs (Khilnani, Thaddanee & Khilnani, 2013); Bryan Matthews' mechanical moving-iron oscillograph (Matthews, 1928); Gabriel Lippmann[428]'s capillary electrometer (Stock, 2004) and the extremely sensitive "string galvanometer" (or "electrocardiograph") of Willem Einthoven[429] (1860-1927). See Moss, (1923), p. 271-272; Snellen, (1995); Rivera-Ruiz, Cajavilca & Varon, (2008). An important development was the ability to mark fine, calibrated time intervals directly on to the experimental records during the experiment using sine waves produced by vibrations of a musician's tuning fork of known audio frequency (Ellis, 1885). Although the successful application of electronics (thyratrons) and cathode ray tube (oscilloscope) displays (Gasser & Erlanger, 1922) had already begun, great reliance was still placed on classical electromechanical methodology, especially in Sherrington's lab, for two major reasons:

1) Signal traces displayed on the screens of early oscilloscopes were too faint to record photographically, except for repetitive results which could be averaged over multiple traces. Much easier to record were excursions of an intense and finely-focused light beam (emitted either from a carbon arc or from an Ediswan "Pointolite" lamp), reflected from tiny mirrors fitted to galvanometers or myographs. These movements could then be recorded on smoothly moving photo-plates or bromide paper lengths by means of the "falling plate" camera (Moss, 1923, p. 269-271).

2) In those early days, square wave pulses produced by rheotomes and other mechanical interrupters such as Sherrington's torsion wire device (Fig. X02) were better shaped than those produced by electronically-generated pulses.

Experimentation using the apparatus available in those times was not a simple procedure; especially in the case of the extremely sensitive and expensive but delicate

428 Lippmann, Jonas Ferdinand Gabriel (16.08.1845-13.07.1921) LU/J physicist & inventor. (NP 1908).

429 Einthoven, Willem (21.05.1860-29.09.1927) NL/J Pioneer cardiologist & physiologist. (NP 1924).

string galvanometers, where the string could be broken by unintentionally applied electrical potentials as small as 100mV (Whitteridge, 1982, p. 442).

Although the work from Sherrington's laboratory was highly regarded, the physiology laboratory facilities were poor, even in 1927. Eccles' older research colleague, the New Zealand physiologist Denny-Brown, had already inherited in 1925 the sole well-equipped room from American John Fulton. It had the only electrical recording system - a string galvanometer, and it had the other standard equipment of a falling-plate camera, optical myographs, and stimulating equipment built up of various key arrangements for single and repetitive stimulation using induction coils (Eccles & Gibson, 1979, p. 48). Also available was a massive wall-mounted antique pendulum for producing accurate timing for two induction shocks (to 0.1 msec). This device, used by Gotch[430] at Oxford and also by Bowditch[431] at Boston (but little used by Eccles) has been described (Whitteridge, 1982, p. 422-3).

JZ Young, after a visit to Frank Schmitt's[432] lab in at Washington University US, compared the Sherrington laboratory with those in the US as follows:

Frank and I first met in the spring of 1935 in Saint Louis. I remember very well the impression of entering that laboratory, where Frank was stimulating a frog's nerve repetitively to study its metabolism. What struck me was that the room was totally silent and quite uncluttered by wires. I came from Oxford, where in Sherrington's laboratory Denny-Brown, Eccles, Granit and others were beginning their careers. The equipment that they used was of course wonderfully effective for its time, but it was not silent, and each cubicle was a maze of wires so dense that you had to stoop to enter. The electronic revolution had not reached Oxford, and stimulation was by means of pendulums or rotating drums, which made a tremendous noise (Young, 1975, p. 17).

J. [C] More insight into activities in Sherrington's physiology laboratory can be found in Tansey, (2008b).

J. [D] The lives of medical laboratory technicians are illustrated by Tansey, (2008).

J. [E] Eccles in later years wrote:

In addition I had the advantage during my earlier years at Oxford of working with my very good friends: Ragnar Granit, who later received a Nobel Prize for his work on vision, though it could just as appropriately have been given for his later work on motor control; John Fulton, who soon left Oxford to accept the Sterling professorship at Yale, where he founded one of the great neurophysiological schools of the world; and Derek Denny-Brown, who later at Harvard built up a school of neurology distinguished by its integral relationship with neuroanatomy and neurophysiology (Eccles, 1975, p. 160 [1a-417]).

Interesting aspects of Granit's Nobel Prize of 1967 have been discussed in the (Finnish) thesis of Vilén, (Vilén, 2013); with English summary on pages 376-385).

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430 Gotch, Francis (13.07.1853 – 15.07.1913) UK neurophysiologist. Capillary electrometer, action potential.

431 Bowditch, Henry Pickering (04.04.1840 – 13.03.1911) US physiologist. Dean at Harvard Med. School.

432 Schmitt, Francis Otto (23.11.1903 – 03.10.1995) US physiologist. EM of nerves, muscle & collagen.

J. [F] A biography of Liddell is published in Phillips, (1983). The origin of his nickname "Pat" is not known: It was apparently used only by him, Eccles, Granit and Fulton in their postal correspondence. All of them became close friends during the late 1920's at Oxford and kept in touch ever since; visiting each other on a regular basis. [pers. com. to J.P.C. by Vilén in 2022].

J. [G] See "The Discovery of Reflexes"; Liddell, (1960).

K. [A] Eccles & Sherrington, (1930), [1A-006].

K. [B] Decapitation involves simple severance of the complete head (at or near the atlas vertebra) from the remaining body. In contrast, decerebration involves careful removal of head region and forebrain in such a way that most bodily functions of the animal remain intact. In this case the body, including its lower jaw and tongue, has swallowing ability and thus can be maintained alive (without further anaesthesia) for long term experimentation, if food is supplied.

Sherrington had shown that low transections of the brainstem in the cat render the muscles paralyzed and flaccid, whereas high transections, above the red nucleus, produce a state of tonic hyperactivity, called ''decerebrate rigidity.'' These differing states aided the analysis of spinal cord pathways and functions. (Shepherd, 2010, p. 145). For details of Sherrington's investigations into decerebrate rigidity see Granit, (1966), p. 52-54.

To perform the operation of decerebration accurately and consistently, Sherrington devised a special guillotine for cats (Fig. X03), see also Sherrington, (1919), Mammalian Physiology pp. 137-9. Davenport, a former student from the Sherrington laboratory described the procedure as follows:

English vivisection laws did not permit students to use anesthetized preparations, and consequently the junior demonstrator in the department had to get to the laboratory early to etherize and then decapitate the cats, that were then kept going by artificial respiration. For the reflex experiments he had to whack off the cerebrum by striking with an enormous mallet a huge knife like a paint scraper while the etherized cat was held in a Sherringtonian frame. (Davenport, 1993).

For a discussion on the history of animal usage in experimental neurology see Stahnisch, (2010). For some aspects concerning the use of the cat as an experimental animal see Scott, (1977), the Australian National Health and Medical Research Council (2013). The medical historian, Otniel Dror, (1999), has considered the affect on experimental results dependent on animal temperament and emotional state as noted already in the early 20th century, but this factor, described as "affective psychosis" in Sherrington, (1906), p. 251 for dogs, was apparently not investigated by Eccles when experimenting with his vagrant cats.

L. [A] In these experiments the cat *biceps femoris* and biceps-*semitendinosus* muscles were used.

L. [B] For a review of historical information on the muscle spindle, see Matthews, (1981). The discovery by Granit's student appeared as Leksell, L.: *The action potential* *and excitatory effects of the small ventral root fibres to skeletal muscle*, Acta Physiol. Scand. (Stockh.) 10, Suppl. 31 (1945) pp. 1-79.

L. [C] The Linacre Lecture was published as "Problems of Muscular Receptivity" in Sherrington, (1924).

M. [A] Sherrington's isometric mirror myograph (Sherrington, 1928) was a massive construction, featuring a table for mechanically fixing the experimental cat (or dog). Its main use was to investigate the contractile response of electrically excited muscle, but a "falling-table" variant was also used to investigate proprioceptive muscle reflexes in response to stretch (Liddell & Sherrington, 1924, p. 213). The free end of the muscle under investigation was hung vertically on a side-arm projecting horizontally from the myograph sensor – a rod or wire which responded to changes in tension by torsional rotation. To measure this rotation, one end of the sensor was rigidly attached to a massive support, the other end (just beyond the location of the hanging muscle under test) was a bearing allowing rotation, but resting on a horizontal plate attached to a second massive support which prevented downward bending from influencing the rotation measurement. The rotation angle of a projected light beam was greatly amplified by the optical system mounted above the torsion rod (Fig. X04) and excursions of the beam during experiments were recorded at the horizontal entrance slit of a falling plate camera. Although this system only approximates isometry, owing to the small muscular contraction required to tilt the mirror, this defect can in practice be neglected without invalidating the results. The previously undetected problem of rotational friction at the moveable bearing led to Eccles' construction of his frictionless myograph bearing. The principle employed is illustrated by Whitteridge (1982) with a comparison of conventional and frictionless bearings (Fig. X05).

M. [B] Eccles & Thompson, (1935), [1A-030].

M. [C] *Superposition of traces from the old and the new myograph traces showed that the spurious "angle" was caused in the old apparatus by friction "hold" at the summit of the twitch contraction which continued during the early stage of muscle relaxation until friction resistance could "hold" no longer; the sudden "give" being registered as the "angle".* (Eccles, 1977, p. 2, [1A-436]).

M. [D] Eccles & Sherrington (1929), [1A-004].

M. [E] Except for some experiments performed on the very fast eye muscles, Eccles worked with muscles of the cat's hind leg (Fig. X06).

M. [F] The repetitive break shock device was first described as "Separation Key" (Liddell & Sherrington, 1923, Appendix p. 154-156), (Fig. X02). The frequency-tuneable torsion wire interrupter produced continuous excitation volleys instead of the single or double-shot impulses produced by the Lucas pendulum and was used to investigate tetanic stimulation. This electromechanical device was later superseded in Eccles' experimental work by the neon-tube stimulator (Briscoe & Leyshon, 1929).

M. [G] Eccles' tribute to Forbes is shown in Eccles, (1970).

N. [A] Parallel to electrophysiology experimentation, a series of pioneering histological studies provided complementary morphological information leading to the concept of the synapse. The Italian physician and scientist Camillo Golgi[433] (1843–1926) developed in 1873 an effective silver impregnation staining method for microscopy which, for the first time, allowed microscopists to observe nerve cell structures with great clarity and to follow their fine cell processes over long distances through tissue. Golgi described the nervous system as a continuous single network of fused cells, in support of a notion called the reticular theory whereas Santiago Ramón y Cajal (1852-1934), using an improved version of Golgi's stain, managed to visualize this network more exactly (Cajal, 1888), and claimed that the nerve cells are not fused into a diffuse continuous network (syncytium) in the bird brain - but retain their individuality; i.e., they might touch each other but they do not fuse together. After years of heated discussion between Golgi's "reticulists" and Cajal's "neuronists" Cajal's finding finally became fully accepted as the "neuron doctrine" - Guillery, (2005), Glickstein, (2006).

The next question soon arose; if the neurons are separated entities, merely touching each other, how could electrical signals be passed between them? The subsequent long-lasting debate on chemical versus electrical neurotransmission began with Emil du Bois-Reymond, who, in the case of nervous stimulation of muscles, contended in 1877 that "*either there exists at the boundary of the contractile substance a stimulative secretion (in the form of a thin layer of ammonia, lactic acid or some other powerful stimulatory substance) or the phenomenon is electrical in nature*" (López-Muñoz & Alamo, 2009).

Sherrington (following advice from the classicist, Arthur Verrall[434]) named the morphological nexus between two touching neurons a "synapse" because of the "clasping" nature of the connection. The word "synapse" is from the Greek *synapsis* (συνάψις), meaning "conjunction", in turn from συνάπτεὶν (συν (together) and ἅπτειν ("to fasten"). He also suggested that the characteristic features of the reflex arc may be satisfactorily explained by the special properties of the transverse membranes that separate two neurons in regions of close juxtaposition (Eccles, 1964, p. 3 [1B-a04]). Eccles and his contemporaries used the term "bouton" when describing the connections observed in the light microscope. Some authors generalize the concept of the synapse to include the communication from a neuron to any other cell type, such as to a motor cell, although such non-neuronal contacts may be referred to as *junctions* - an historically older term. (Tansey, 1997).

For more information on Sherrington's conception of the synapse at the time when he introduced the new term, see the historical articles of Shepherd & Erulkar, (1997), Bennett, (1999) and Pearce, (2004).

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433 Golgi, Camillo (07.07.1843 – 21.01.1926) IT biologist and pathologist. (NP 1906).

434 Verrall, Arthur Woollgar (05.02.1851 – 18 06 1912) UK classics professor at Trinity College, Cambridge.

N. [B] EM (here used as an abbreviation for Transmission Electron Microscopy, TEM) is an electron-optical technique for studying biological cell structure (normally "fixed" with solutions containing glutaraldehyde and/or osmium tetroxide, embedded in polymerized epoxy-resin, sectioned into ultrathin specimen slices and "stained" with solutions of heavy metal compounds such as lead citrate or uranyl acetate). Such preparations can be viewed at much higher magnification and finer resolution than that attainable by using conventional light microscopy (LM) of paraffin-embedded sections.

The less commonly used freeze-fracture technique is a complementary TEM technique in which rapidly-frozen single cells or small pieces of biological tissues are cleaved after shock-freezing to liquid nitrogen temperature (-196°C). The resulting fracture "face" of the material is transferred in its deep-frozen state to a high vacuum evaporation apparatus and there "sprayed" with an ultra-thin layer of platinum, directed at an angle of 45° to partially cover and thus "shadow" the topographical relief revealed after fracturing. After carefully controlled chemical dissolution of all the original organic material an ultrathin metal replica of the cleaved fracture surface remains, which preserves the topography and can then be examined by TEM (Fig. X07). Because the splitting process during cleavage preferentially favours the (hydrophobic) lipid component of cell membranes this technique can provide detailed images of extensive membrane surface areas unobtainable by conventional ultrathin sectioning of cells for TEM. Both the complicated "Balzers" freeze-etch evaporation apparatus used in the technique of Moor[435] and the much simpler but equally effective Bullivant[436] freeze-fracture device were developed in the 1960s (Heuser, 2011).

O. [A] Helmholtz's pendulum rheotome represented a major development in electrophysiology. The device consisted of a pendulum with a heavy steel weight. When raised and released, the pendulum opened a first pair of contacts at the bottom of its descent (i.e., where the speed was maximum); then it opened a second pair of contacts along its path. The first pair constituted a short circuit. Convenient as it was, the Helmholtz pendulum rheotome could not provide a current pulse of adequate brevity for many investigators. Accordingly, Lucas improved it by constructing a pendulum 540 mm long, which operated the two pairs of contacts. With his rheotome, a distance of 5 mm along the arc of the pendulum was equivalent to about 1 msec. ("**σ**" in the early literature). This "Lucas Pendulum" rheotome permitted easy adjustment for a stimulus duration range of 2-20 msec. (Geddes, 1984, p. S37-S39). Lucas continued developing the pendulum rheotome until his tragic accidental aviation death during WW1 (Lucas, 1907, p. 313); (Lucas, 1908); (Adrian, 1921).

Two so-called "pendulums" were manufactured by Lucas's firm, Cambridge Instruments Co. Ltd.; a simpler horizontal "spring" version and a massive vertical gravity-driven model (Fig. X08). (The speed of the spring version could vary somewhat

435 Moor, Hans Jakob (11.06.1933 – 25.01.2009) CH botanist. Inventor & "freeze-etch" technique pioneer.

436 Bullivant, Stanley (26.03.1932 – 16.07.2006) UK biophysicist at Auckland University. "freeze-fracture".

with room temperature, whereas that of the vertical model depended on the more constant local value of the force of gravity). Eccles used the larger vertical Lucas pendulum (Fig. X09) throughout all his early experiments and most of the time while working in New Zealand but replaced it by the fully electronic “ESRU” (Fig. X21) just before he and his group moved to Canberra.

These mechanical instruments represented the peak of perfection for purely mechanical devices (Shepherd & Braun, 1989).

Horace W. Davenport, one-time student in Sherrington's lab, described operation and attendant hazards of the spring version in detail.

Duration was measured using a Keith Lucas spring rheotome. A heavy steel spring, bent to the right, was held in a catch. When the catch was released, the spring swung violently to the left, and one had to be sure one’s left hand didn’t receive a nasty smack. As it swung, the free end of the spring knocked over two pins; the first closed the circuit so that current could flow from the potentiometer to the electrodes and thence to the tissue, and the second opened the circuit. (Davenport, 1993, p. S18).

David Whitteridge, Sherrington’s last departmental demonstrator (and later his successor as Waynflete Professor of Physiology) described the vertical version:

For the exact timing of two stimuli, Eccles and Sherrington preferred the Keith Lucas pendulum which could deliver two stimuli timed reliably to 0.1 msec. for intervals up to 40 msec. A ‘square’ wave form from its two stimuli was much squarer than ‘square’ waves delivered by electronic stimulators until the middle 1950s. If the pendulum fell unexpectedly in the dark room, one’s fingers usually suffered. (Whitteridge, 1982, p. 423).

O. [B] The Paul Hoffmann publication referred to by Eccles was probably that (in German) by Hoffmann, (1921).

O. [C] Eccles & Pritchard, (1931), [1A-042].

O. [D] Transmission neurons are connected in neural nets so that they will conduct normally in only one direction. Transmission in the usual normal direction is called ***orthodromic*** conduction, while activity moving in the opposite direction (which, although abnormal, can be produced by experimental procedures) is referred to as ***antidromic***. (Uttal, 1975, p. 47).

Antidromic invasion of motoneurons represented a major advance in the early technology, as acknowledged by Eccles.

My greatest indebtedness was to Denny-Brown, who had had two years’ research experience at Oxford before I started in research in late 1927. Not only did I profit in countless ways from his criticisms of our experiments and interpretations, but I also inherited from him an experimental procedure with analytical power, the antidromic-impulse technique. I can still vividly recall my delight when he told me in 1927 that he had just been investigating the effects produced in a motoneuron by firing an impulse into it from its axon, i.e., antidromically. I was later to exploit this effect in many researches, the first being in collaboration with Sherrington. (Eccles, 1975, p. 160 [1A-417]).

O. [E] Eccles & Sherrington (1931), [1A-010], [1A-011], [1A-012], [1A-013] and [1A-014].

O. [F] There are several effects associated with the name of Nikolai Wedensky. (Wedensky effect, Wedensky facilitation and Wedensky inhibition) The last-named effect, referred to as Wedensky blockade by Eccles, is inhibition of muscle response as a result of a series of rapidly repeated stimuli to the motor nerve. The papers referred to by Eccles are probably Adrian & Lucas, (1912) and Forbes, (1912).

P. [A] Syndic: a representative or delegate of a university (in particular, Cambridge) entrusted with special functions or powers; Oxford used mostly the term "Delegate".

Q. [A] Lankidden Cove, near the SW Coast Path via road from Ponsongath, a few miles west of Coverack village. See also the family photo in Mennis, (2008) p. 94.

R. [A] Lord Adrian and his intelligent usage of several methods to study the nervous impulse has been examined in the historical article of Moruzzi (1982).

R. [B] Sherrington & Eccles were the pioneer researchers in CNS inhibition. The roles of both neurophysiologists in studying the concept of central inhibition in the spinal cord and brain have been reviewed by Douglas Stuart[437] and colleagues (Callister et al, 2020).

R. [C] For a condensed account of Eccles' experiences in Sherrington's laboratory see Eccles, (1982), [1A-506].

S. [A] "*The Summoning of Everyman*" is an English late 15th-century morality play which examines the question of Christian salvation following death. The cultural setting is based on the Catholicism of the era.

T. [A] The pioneering experiments of Eccles, Hebb and later workers on repetitive firing of neurones have been discussed in detail (Brownstone, 2006).

W. [A] The London company was established by Alfred Charles Cossor Sen. In 1859 and made its first cathode ray oscilloscope in 1932.

W. [B] Details of Eccles' sophisticated laboratory setup, including stimulation, recording and electrical screening precautions are described in Eccles (1935) [1A-033].

X. [A] The *sino-auricular node* is an old term, synonymous with (and now replaced by) the term *sino-atrial node*, the heart "atrium" being formerly named "auricle".

Y. [A] Eccles reiterated the importance of the vagal studies as follows:
In 1932 G. L. Brown and I joined in the cholinergic (as it was felicitously called by Dale) investigations in our study of the inhibiting action of single vagal volleys on the

437 Stuart, Douglas Gordon (05.10.1931 – 06.04.2019) AU physiology professor at Univ. of Arizona.

cardiac pacemaker of the cat. ACh mediation was demonstrated by the depressant action of atropine on the inhibitory slowing, and by its enhancement and prolongation by eserine. I well remember Dale's enthusiastic comments when we presented this paper at the Oxford meeting. ***There were two sequelae.*** *Partly as a consequence of this work, Dale invited Brown to join him at Hampstead, with the consequences you all know. The other consequence was that I was so impressed by the long latency, 0.1 seconds, and the slow time course, measured in seconds, of the action of a single vagal volley that I continued for many years to regard this time course of an indubitable chemical mediation by ACh as the paradigm for all chemical transmissions* (Eccles, 1976, [1A-420]).

Hank MacIntosh and William Paton[438] commented:

*But the analysis (of the vagal inhibition) may have helped by its very elegance to perpetuate the erroneous view that chemical transmitters are in general, or even of necessity, transmitters of long duration, acting for at least some tenths of a second after being released. A corollary opinion was that any briefer transmission process could not be chemical; thus, it was supposed that transmission at neuro-muscular and neuronal synapses, which in many cases is accomplished within a few milliseconds, must be mediated by the electrical currents associated with the nerve impulse (*MacIntosh & Paton, 1974).

Z. [A] see Heinbecker Bishop & O'Leary, (1932).

AA. [A] See Dale Feldberg & Vogt (1936) and the review by Eccles (1982) [1A-507].

AA. [B] Sherrington favoured the electrical theory for synaptic neurotransmission although his student Thomas Elliott[439] may have been the first to suggest that sympathetic nerves secrete adrenaline (Elliott, 1905). Elliott's concept, shared by the English pharmacologist Henry Dale (discoverer of bradycardic effects of acetylcholine on heart rate), was not accepted by Sherrington. This difference of interpretation, which continued for years, was described as "*the war of the soups and the sparks*" and has been examined in some detail by Whitteridge, (1993), Valenstein, (2005), Marcum, (2006) and Van der Kloot (2007) p. 3-38.

Many years later, Dale's main research colleague, Feldberg, made the following comment:

"*The idea of chemical transmission occurring at the ganglionic synapse or at the neuromuscular junction was against the views of the electrophysiologists working in this field. They were convinced, and able to convince their colleagues, that with electrical methods alone it would be possible to unravel the mysteries of these transmissions, taking it for granted they could only be electrical, brought about by the eddy currents of the nerve impulse*." (Feldberg, 1977, p. 67).

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438 Paton, William Drummond Macdonald (15.05.1917 – 17.10.1993) UK pharmacologist. "Submarine physiol."

439 Elliott, Thomas Renton (11.10.1877 – 04.03.1961) UK physician/physiologist. Nerve chemical transmission.

The US psychologist, Jerome Kagan commented:

The politics during the first decade of the 20th century had the neurophysiologists (the "sparks"), who worked with clean, gleaming machines, cast as the Brahmins, whereas the biochemists and pharmacologists (the "soups"), whose hands were dirty with blood and urine, were workers of a lower caste. The sparks' arguments were persuasive. Brain processes must occur rapidly to account, for example, for the speed with which the pupil of the eye constricts in response to a bright light or the hand is reflexively withdrawn from a hot surface. Electrons travel fast; chemical reactions are often relatively slow. Thus, it seemed obvious that the brain could not rely on chemistry to accomplish its missions (Kagan, 2005).

Further details defending Eccles's unshakeable initial belief in electrical transmission can be found in (Eccles, 1982, 326-327).

AA. [C] The Angstrom **Å** length unit, 10^{-10} m has been replaced by the nanometre, nm; with its length of 10^{-9} m. The micron length unit, **μ**, was replaced directly by the micrometre; μm. The sigma unit of time, **σ**, 10^{-3} sec was replaced directly by the millisecond; msec.

AA. [D] The remarkable working relationship between Eccles and Dale surprised many:

Bernard Katz, who came to England in the mid-1930s as a refugee from Germany, described his amazement at how violently the younger Eccles and the older Dale would attack each other during these meetings, and his further amazement at how they would then retire to sherry and a convivial dinner together (Shepherd, 2010, p. 91).

Katz, later a research colleague of Eccles in Sydney, himself commented:

"*To my great astonishment I witnessed what seemed almost a stand-up fight between J.C. Eccles and H.H. Dale, with the chairman E.D. Adrian acting as a most uncomfortable and reluctant referee. At that meeting (Cambridge Physiological Society in May 1935), however, what impressed me most was Dale's rebuttal of Eccles' criticism. Eccles had used a somewhat unfortunate form of words, I think it was "pace Dale" (meaning "with due respect" or possibly the opposite), which Dale interpreted as peremptory and considered more appropriate for a Hyde Park oration than for a scientific argument at a meeting of the Physiological Society. It did not take me long to discover that this form of banter led to no resentment between the contenders, it was in fact a prelude to much fruitful discussion over the years and indeed to growing mutual admiration between Dale and Eccles*." (Katz, 1996, p. 373).

AB. [A] The Oxford university year has three academic terms; the Michaelmas term (October to December), the Hilary term (January to March) and the Trinity term (April to June). These names come from major Christian Church feast days.

AB. [B] *Nitella* and *Chara*; large fresh-water green algae (family Characeae) are nevertheless popular subjects for electrophysiological studies of the cell plasma membrane because of their extremely long and accessible axial internodal cells. See review (Beilby, 2016).

AB. [C] One of the best senior pupils at Magdalen, Charles Phillips[440], recalled his outstanding tutor, Jack Eccles:

"I can hardly exaggerate the stimulus I received in my first two years at Magdalen from my tutor, J.C. Eccles (later F.R.S.) before his return to Australia in 1937, and from the lectures of Professor W. E. Le Gros Clark[441], F.R.S." (Porter, 1966, p. 343).

AB. [D] Several writers have speculated on John Eccles' failure to secure advancement at Oxford:

Sherrington is thought to have favoured Eccles' election as his successor in the Waynflete Chair but this did not happen (Smith, 2014, p. 263).

Eccles' dominant personality, seen as a possible stumbling-block, is succinctly described by Shepherd:

Sherrington retired in1935 (at the age of 75, having been granted a personal extension). Although Eccles was an obvious candidate to succeed him, his Australian brashness and pugnacity were a bit much for the Oxford scene and John Mellanby was appointed. (Shepherd, 2010, p. 91)

In 1936, instead of Eccles achieving his much hoped-for promotion

"the distinguished Sherrington was replaced by John Mellanby, a lesser figure" (Harrison, 1994, p. 329).

After Mellanby's premature death, E.G.T Liddell was elected to the Waynflete Chair, a position which he held from 1940 until 1960.

"Liddell must have been a candidate, and he may have either been anxious about his chances or disappointed when the electors picked John Mellanby over many better candidates including John Eccles. Mellanby died in 1939 and Liddell did get the Waynflete Chair and a brand-new building that, during his tenure, some called "The Physiological Dead Space" (Davenport, 1993, p. S19). ["*dead space"* is a concept encountered in respiration physiology texts; see Fowler, 1948].

AB. [E] See Cannon & Rosenblueth, (1933), Rosenblueth, (1937).

AB. [F] See Eccles, (1936), [1A-040].

AB. [G] See Davenport (1981).

AC. [A] See also Akert & Sandri, (1970), Fig. X07.

AD. [A] For references to nocifensor see Lewis, (1936), Lewis (1937) and Lewis & Pochin (1937).

AD. [B] See Liljestrand, (1972).

AE. [A] For a discussion of the relationship of the French neuroscientists Lapicque and Fessard with researchers in England, see Barbara, (2006).

440 Phillips, Charles Garrett (13.10.1916 – 09.09.1994) UK neurophysiologist. "Recurrent excitation".

441 Le Gros Clark, Wilfrid Edward (05.06.1895 – 28.06.1971) UK anatomist/primatologist/palaeoanthropologist.

AF. [A] The RMS Maloja, a British luxury ocean liner in service from 1923 to 1954, had a reputation for comfort and reliability. (It was "Sister ship" of the RMS Mooltan Fig. F9.)

GC. Stage 3 career notes (for sections AH to AS)

AH. [A] According to the Kanematsu company's home page (kanematsu.co.jp), construction of the Kanematsu Memorial Institute of Pathology, Sydney Hospital was begun in 1929 after receipt of a donation from Kanematsu, and completed in 1933. The history of Kanematsu is inextricably bound up with Australia, as company founder Fusajiro Kanematsu in 1890 established Kanematsu's predecessor company as a specialist Japan-Australia trading house by opening the Sydney branch office to commence direct trade between Japan and Australia. The company shipped beef fat, cattle hides and wool to Japan. The building, comprising five floors, was built on the south-east corner of the hospital property, facing the Sydney domain and directly over the site of the old pathology building. The ground floor was devoted to the pathology department, with mortuary and post-mortem rooms plus a small chapel for the use of relatives of deceased persons. The upper floors were devoted to laboratories and other rooms. Each floor had an area of about 2980 square feet (277 sq. m.).

AJ. [A] Also known as Fulminant Idiopathic Intracranial Hypertension (FIIH). See Thambisetty et al., (2007).
AJ. [B] For an historical review of the structure and function of the motor endplate see Rudolf et al., (2019).

AK. [A] See Kuffler, (1942).
AK. [B] The working relationship of Eccles with his two exiled laboratory colleagues has been examined in detail by Stahnisch, (2017).

AL. [A] The research trio of Eccles, Kuffler and Katz worked together successfully in the study of neuromuscular transmission, first using material from spinal cats, as pioneered in Oxford by Sherrington; later from frogs (owing mainly to Katz's profound dislike of experimenting on living felines). The neurophysiologist Bert Sakmann[442], who worked in Katz's London laboratory in the 1970s, elaborates further:
BK [Katz] was, in his own words, a 'frogman', whereas Eccles and Kuffler were 'catmen', initially working on the cat soleus muscle in vivo. BK preferred to work in vitro on the sartorius muscle of the Australian tree frog (Hyla aurea) an attractive green and golden bell frog (Sakmann, 2007, p. 191).

442 Sakmann, Bert (12.06.1942 –) DE cell physiologist. "Patch clamp", single ion channels in cells, (NP 1991).

The American neurobiologist, Dale Purves[443], noted that although the three researchers worked together, there were, however, differences of opinion:

Despite Eccles's contrary view, Katz and Kuffler provided strong evidence for the chemical nature of neuromuscular transmission during their collaboration in Sydney. In later years, neither Katz nor Kuffler expressed much affection for Eccles, who could be overbearing in the prosecution of his ideas. (Purves, 2010)

The Australian neuroscientist, John Carmody[444], commented also on the friction which arose occasionally between Eccles and his colleagues:

He [Katz] later acknowledged that at the Kanematsu Institute he and Kuffler also had "the occasional stand-up fight" with Eccles on this very question [electrical vs. chemical linkage between nerve cells] (Carmody, 2003).

Subtly implied critique of Eccles, surfacing from one of his two Sydney research colleagues, can also be detected in the reminiscences of Masanori Otsuka[445] (a later co-worker of Kuffler), made many years later about Eccles' 1966 lecture on "The Cerebellum as a Neuronal Machine" at the Harvard Medical School:

I remember a most memorable line of Steve [Kuffler] *when he was introducing Sir John Eccles before his lecture: "He has often been wrong, but always about important things"* [also quoted in (Hubel, 1990, p. 32)]. *I attended this lecture given at Harvard, and as I remember, Steve finished his introduction by saying: "Let's listen to what he is going to tell us today". Prof. Eccles was a little taken aback and said: "I have never been introduced in such a way." But the friendly atmosphere between the mentor (J.C.E.) and his pupil (S.W.K.) was not at all lost on that occasion* (Otsuka, 2007, p. 61).

Another (somewhat paraphrased) reference to Kuffler's curious statement in Hobson, (2004), instead associated it with Eccles' blatant disregard of contrary evidence from EEG and REM studies - which supported monism, not dualism.

Otsuka also made interesting comments about the necessity of taking every advantage when attempting to start a scientific career; using the famous Kanematsu trio as illustration:

If I were asked to give some advice to a young scientist, I would remind him/her of the title of a book by A.L. Hodgkin, "Chance and Design". Stephen Kuffler is an excellent example. He did not miss the chance of his meeting J.C. Eccles at the tennis court and subsequently B. Katz. He had mistakenly thought that he could not compete with these senior scientists on the intellectual plane, and therefore decided to take advantage of his manual skills, which led him to develop the first isolated nerve-muscle junction. Kuffler later paved the path from neuron to brain. (Otsuka, 2007, p. 62).

Katz's memoir of Kuffler, provides important biographical information, including Steve's time with Eccles at the Kanematsu Institute (Katz ,1982).

443 Purves, Dale (11-03.1938) US neurobiologist. Duke Institute for Bain Sciences.

444 Carmody, John (?-?) AU neurobiologist. Prof. in School of Medical Sciences, University of NSW.

445 Otsuka, Masanori (1929-?) JP Pharmacology prof., Faculty of Medicine, Tokyo Medical & Dental University.

AL. [B] Electrotonus refers to the passive spread of charge inside a neuron and between cardiac muscle cells or smooth muscle cells. (Wikipedia). It is the change of condition in a nerve or muscle during the passage of an electric current (discovered by physiologist E. Pflüger[446] in1859).

Electrotonic potential (graded potential) is a non-propagated local potential resulting from a local change in ionic conductance (e. g. synaptic or sensory that engenders a local current). When it spreads along a length of membrane, it becomes exponentially smaller (decrement).

Catelectrotonic potential is defined as the condition of increased irritability of a nerve in the region of the cathode or negative electrode when a current is passed through it (cf. anelectrotonic potential observed in the region of the anode).

AL. [C] This work was reported in (Eccles, Katz & Kuffler, 1942).

AL. [D] The later involvement of Japan in World War II resulted in the break-up of the team for wartime duties and Eccles faced increasing problems and resistance from the university administration. The Australian Neuroscientist, John Carmody, provided interesting background information on these times in his radio transcript:

"*The idyllic period of their collaboration on problems of neuromuscular transmission could not survive the animus of those doctors and administrators at the 'Rum Hospital' who considered that making plasma for the troops at the* [war] *front was far more important than scientific research. All three left prematurely; Katz and Kuffler taking Australian wives with them, while Eccles went to a Chair in Dunedin before later moving to Canberra*". (Carmody, 2001). Note:- The original Sydney Hospital was built cheaply (with the promise of profits from rum sales for the builders, who ended up importing 60,000 gallons into the colony) so it was jocularly referred to afterwards as the rum hospital.

Later, in an Australian radio broadcast, Carmody spoke in detail of the difficulties that Eccles experienced in Sydney:

"*Scientifically, it was a rich period but, apart from a formal introduction to the Hospital Board in September 1937 soon after his arrival, he was never again invited to meet them. This was either extraordinary rudeness or clinicians' indifference to research, but it was all the more remarkable because, in March 1941, Eccles was elected as a Fellow of the Royal Society of London, which the Board should have seen as an enormous accolade for their hospital; there were few enough of them in Australia then. Eccles did not last much longer* [than Katz & Kuffler] *either, thanks to deteriorating relations with the Board and some of the clinicians at Sydney Hospital, who simply did not understand the significance of the work being done at the Kanematsu and whose own egos found Eccles' overbearing. The essence of his discontent in Sydney is revealed by the minutes of the hospital Board which gave less attention to his letter of resignation than to the replacement of a hall carpet. In a letter to the Medical Journal of Australia soon afterwards, he wrote that the Board 'had complete indifference to the research activity of an institute which, nevertheless, they*

446 Pflüger, Eduard Friedrich Wilhelm (07.06.1829 – 16.03.1910) DE physiologist. Founded "Pflügers Archiv".

insisted on controlling so despotically'… Years later I learned that in 1943 the gate-keepers at Sydney Hospital had been supplied with photographs of Eccles and instructed that 'under no circumstances is this man to be allowed to enter the hospital grounds'" (Carmody, 2013).

AN. [A] Book: Evolution of the Brain: Creation of the Self. By John C. Eccles, 1989 [1B-a25].

Eccles' talk to a religious group which so disturbed archbishop Gilroy was probably that reported in the Catholic Weekly (Sydney, NSW) of 4.11.1943, Page 5.

His subject, "Nature of Man," was followed by an open discussion in which Eccles answered many questions about the Church's teaching, and the scientific view on evolution. (See also section **FD** of the family reminiscences.)

AN. [B] Biographical information concerning Cardinal Gilroy has been published; see Williams, (1971); Luttrell, (2017) and Henderson, (2018).

AN. [C] The Grail Movement came to Australia in 1936 with the arrival in Sydney of five Dutch Grail members They had been invited by the Catholic bishops who expected that they would build a youth movement of young women here as successfully as they had done in the Netherlands. The Grail movement has enjoyed international success.

AN. [D] Killalea Shell Cove, a popular surfing reserve situated south of Wollongong. Named after Edward Killalea, a former Irish convict deportee who settled and farmed there in the mid-19th century.

AN. [E] Panpsychism; the concept that all matter has consciousness.

AN. [F] A pun based on Plato's proverb: "Empty vessels make the most sound", i.e. those with the least knowledge and least talent are the ones who often speak the loudest and the most.

AO. [A] See Eccles, (1944) [1A-073].

AP. [A] Courtice also wrote of this wartime work (without acknowledging the contribution of John Eccles to the project):

"*Blood serum was first issued later in 1941 to the Armed Forces as far away as the Middle East and Malaya. The demand for serum for the troops greatly increased the work of the Red Cross Blood Transfusion Service. In June 1941, the Board of Sydney Hospital placed at the disposal of the Service one ward for the bleeding of donors and several rooms in the Kanematsu Memorial Institute of Pathology for the preparation of serum. After a considerable amount of initial trial and error, serum was prepared in large quantities. In February 1942, Sydney Hospital placed another ward at the disposal of the unit, and for many months more than 350 donors were bled each day. At this time 30,000 were on call for blood for the preparation of serum while a further 7,000 were held in reserve in the metropolitan area, Newcastle and Woollongong. Late in 1942, at the request of the Director of Pathology, Allied Land Headquarters, methods of whole blood storage were investigated. A technique for the aseptic collection of blood into the military-type Soluvac bottle was devised and an ice-box* *suitable for the transport of blood by air was designed and constructed. The first box of blood was dispatched to New Guinea in December 1942."* (Courtice, 1985).

AP. [B] A word-play joke, combining neurologist, Katz, cats and bats with the old saying: "Bats up in the belfry", i.e., strange human behaviour, suggestive of a psychiatric problem and an oblique reference to yet another saying; "genius is akin to madness" Another likely connection could be to the popular comic strip "Krazy Kat" by American cartoonist George Herriman, which ran from 1913.

AP. [C] Sunburn experiments were published by Eccles & Flynn (1943), [1A-069].

AQ. [A] The referred to research paper was (Bronk, Tower & Solandt, 1935).

AQ. [B] The stellate ganglion lies on the thoracic part of the *longus colli* muscle, which arises from the ventral surface of the first six thoracic vertebrae, and is inserted into the costal processes of the sixth and seventh cervical vertebrae. For illustrations of the nerves connected to the ganglion in the cat, see Holmes and Torrance, (1959), fig. 1, p. 272 and Fioretto et al., (2007) fig 1, p. 133.

AQ. [C] Eccles later commented: *Looking back on those days [at the Kanematsu Memorial Institute] one can see the irony of the situation because it was our work with the blocking agents of nerve-muscle transmission and the use of anticholinesterases for unblocking, which at least formed an important scientific base for the modern use of muscle relaxants in anaesthesia.* (Eccles, as quoted in Winton, 1997, p 45).

AR. [A] A mock-Latin expression originating in the early days of WW2 and appearing in several forms; more often being quoted as "Illegitimi non carborundum".

AR. [B] Sir John probably intended to use the word "denigrate" or "belittle" here.

AR. [C] A letter by Alan Canny (dated June 10, 1946) appeared in the Medical Journal of Australia issue of June 22, 1946 pages 894-896, entitled "Research at the Kanematsu Institute" and began:

SIR: "*The expressed anxiety of the Board of Directors of Sydney Hospital to reopen the research section of the Kanematsu Institute is in contrast to the haste and secrecy with which the decision to suspend research was made by the Board before the possibility of the decision becoming a matter of public interest was apparent. The explanation made by the Board in justification of its action is based on two major points: lack of funds and the disintegration of Dr. Eccles's research team…"*

Dr. Canny's letter ended (following a comprehensive list of complaints against alleged inexplicable actions of the Board of Directors) with:

"The Board ends its statement by the publication of certain selected letters. I suggest that in the interests of truth it publishes all the correspondence between the Board and the Hospitals Commission and between the Board and myself which relates to the events leading to the suspension of research activities, to my rejection of the offer of the directorship of the emasculated institute and resignation from the staff of the hospital, and to events subsequent to my resignation."

Yours, etc.,

16, David Street, A. J. CANNY.

Clifton Gardens,
New South Wales.

AS. [A] The growth stages of the Kanematsu building, prior to its unexpected demolition in 1982 can be visualised in photos (Fig. X10).

AS. [B] The demolished Kanematsu building was later replaced by a new structure but the loss of the original building has been lamented by many; see Storey, (2010).

AS. [C] For short histories of both the *Walter & Eliza Hall Institute of Medical Research* in Melbourne and the later-established *John Curtin School of Medical Research* in Canberra see Crocket (1958).

GD. Stage 4 career notes (for sections BA to BU)

BA. [A] Almost certainly Eccles' New Zealand born wife, Rene, played an important part in that decision. Some useful research connections relevant to his research future had nevertheless already been made during Eccles' years in Sydney.

BA. [B] Edson held a fellowship with the Travis Research Trust for Tuberculosis Research from 1940 to 1944.

BC. [A] The history of the Medical School, dating from its establishment within the University of Otago in 1875 to the year 2000, has been published as a monograph. (Page, 2008). Most of the settlers sailed in the ship "John Wicliffe" and the rest arrived soon afterwards in the "Philip Laing". The University was actually founded by the Otago Provincial Council, with strong support from the Presbyterian Church. The four professorships became established over the following years, with the last one (History) appointed in 1920.

The Medical School in Dunedin was housed in the grand Lindo Ferguson Building "LFB" of 1927, about which the then junior assistant in the physiology department, Norman Edson, remarked: "*The impression that remains with me is one of large empty rooms, many of which were seldom used*" (Page, 2008, p. 78).

The Medical School had already achieved some standing in the academic world via advances made in clinical medicine by its expatriate graduate, Derek Denny-Brown, who also studied and published together with Eccles in Sherrington's laboratory.

The previous long-serving professor of physiology, "wee Johnnie Malcolm", an active researcher, highly respected for his work in biochemistry and nutrition, was described by medical colleagues Hercus and Bell as "*an altogether delightful character, soft-spoken, modest and helpful*". (Page, 2008, p. 42).

BC. [B] Folk-dancing at the Eccles' house on Fridays (Fig. X11) became a popular pastime for some Otago medical students and staff members.

Every Friday night there was folk dancing at the Eccles home (see Figure) when he often reminisced about his days in Oxford, which were symbolized by the oar above his desk (Fillenz, 2012, p. 218).

BD. [A] Eccles had first to reacquaint himself with the whole of physiology in order to teach medical students, something he had not done for some years. Preparing 75 lectures for second-year meds, plus others for first-year meds, along with a completely new laboratory course and discussion groups, meant his research virtually came to an end during that first year. He did design some of the medical students' laboratory work to assist his research, as student Miles Hursthouse[447] explained:

"*The professor conducted many interesting experiments, some of them on us! At our practical sessions we had to endure having needles stuck into a muscle, then contract that muscle while measuring the electrical impulse and rate of propagation"* (Hursthouse, 2001).

Eccles later expounded his philosophy and experience regarding student experiments as alternatives to animal experimentation:

"Let us also consider allowable forms of human experimentation. Many such experiments are quite without risk. For example, during the final three terms of physiology, which I taught from 1944 to 1951 at the medical school of the University of Otago, New Zealand, the students performed 85 percent of the total experiments on themselves. I had three three-hour courses on the systematic study of pain – muscle pain, skin pain, all kinds of inflammatory pains and periosteal pain. Of course, a great many procedures like this can be performed on human subjects without any danger and with little discomfort. I designed these courses originally because we were so short of animals and I discovered that it was far better to use the students as subjects. They investigated their own muscle contractions, stimulated their nerves and tested their reflexes. This experimentation can be effectively and appropriately done by medical students on themselves in order to give them some feeling for their eventual work in neurology. Similarly, excellent experiments on respiration and urinary secretion can be carried out on human subjects.

I believe, then, very much in this kind of innocuous human experimentation, and medical courses should be developed along these lines. This may relieve the problem of providing large numbers of rabbits or other animals for medical students to use in experimentation.

There are also advanced levels of experimentation that require human subjects. I refer, for example, to the experiments on different kinds of perception, for example, color vision, color matching, problems relating visual perception to retinal pigments and their bleaching, and after-images. These experiments can be done only on humans experimenting on themselves. The necessity of human experimentation derives from the fact that no other animal can report to you what was seen. At best, an animal's behavioral performance is a very inadequate measure of its perceptual experience. This is true not only for vision, but for all senses, e.g., for investigations on touch and pain. Often this type of work is done on volunteers. A friend of mine subjected some volunteer medical students to an aseptic operation in which small cutaneous nerves in

447 Hursthouse, Miles Wilson (27.10.1919 – 22.01.2019) NZ Nelson general practitioner/dermatologist & author.

the forearm were dissected down until there was only a single fibre left. He was then able to test their sensory perceptions aroused by stimulating these single fibres in cutaneous nerves. I think this is about the limit to which one can ask students to participate!" (Eccles, 1971, [1A-356], pp. 286-7).

Eccles' student, Marianne Fillenz, recalled Eccles' revolutionary teaching and practical courses as follows:

"While expert engineering and electronic assistance set up his research lab, he transformed the teaching of Physiology by designing a program modelled on the Oxford system. He gave 75 lectures covering renal secretion, endocrinology, respiration, circulation reproduction, and the nervous system. He worked tirelessly to master the many advances that had occurred since his Oxford days. In addition to the lectures, Eccles designed a practical course with some animal experiments copied from Mammalian Physiology, A Course of Practical Exercises *that Sherrington had designed in 1919. These experiments were supplemented with experiments using students as the subjects. These included three experiments on pain - cutaneous, inflammatory anoxic muscle, and joint - as well as on vision, hearing, respiration, cutaneous sensing, voluntary contraction, and human reflexes. Another important feature was the weekly Socratic-style discussion groups made up of 30 groups of four students in each, in which problems arising from the lectures as well as review articles were dealt with"* (Fillenz, 2012, p. 217-8).

"*The experiments which left the most vivid memories were three on pain: one on anoxic muscle pain, one on the triple response and, most vividly, the deep pain produced by a subperiosteal injection of saline! Such experiments would not pass today's health and safety regulations, but they left an unforgettable memory*" (Fillenz, 2000, p. 13).

Although Eccles was irreverently referred to by some students as "Synaptic Jack" or "The Great White God", his herculean teaching efforts were well appreciated by most of his physiology students, especially in his first year (Fig. X12). When Eccles departed New Zealand to work in Australia years later, his Dunedin students presented him with an engraved silver dish (Fig. X13).

BD. [B] One of Eccles' first students, David Cole[448], said of his lectures:

"*JC was a fine thinker and ideas man, full of enthusiasms and constantly stimulating, His lectures were less structured, harder to get the key facts from and could trend towards philosophical issues, his last presentations each year being highly theoretical and involving abstruse postulates about how the human mind really works"* (Cole, 2002).

Another of his earliest students, Gavin Glasgow[449], was not quite so easily impressed and in a memorial lecture later stated:

448 Cole, David Simpson (1924 – 08.09.2008) NZ Dean Ak. Med. School. Pioneer thoracic "open heart" surgeon.

449 Glasgow, Gavin Lawrence (14.01.1924 – 31.10.2015) NZ neurologist Auckland Hospital & Ak. Med. School.

"My clearest recollection of undergraduate teaching is Eccles on glomerular filtration and tubular reabsorption in the kidney, which to me seemed like a revelation of clarity and biological beauty. I subsequently learned that this was partly because it was fresh in his mind as he kept only a few pages ahead of us in "Best and Taylor" (Best & Taylor, 1943) *the standard text of the time"* (Cole, 2002).

BD. [C] Eccles' experimental research projects for BMedSc students:

Eccles invited five of his best students to an optional fourth year towards a BMedSc Degree. The students were David Cole, Gavin Glasgow, Marianne Fillenz, Mary Hanafin[450] and Deryck Gallagher[451]). David Cole described in valuable detail (here in shortened form) the projects he and Gavin Glasgow embarked on during their optional research year in 1945 (following the normal three pre-clinical years).

Our project was in two parts. One [the clinical project]*, in the hospital neurosurgery ward, was supervised by the outstanding young NZ neurosurgeon Falconer. It involved study of intervertebral disc protrusion (PID) which had recently been proved to be the pathology behind sciatica. Pressure on the nerve roots in the spine led to partial blockage in the nerve function and hence the numbness* (Falconer, Glasgow & Cole, 1947).

The other laboratory experimental project, supervised by Eccles, involved trying to reproduce the effect of the protruding intervertebral disc on the nerve roots to the legs, essentially testing pressure effects on nerves ... We had to expose the cat's lower spinal cord and put small paraffin blocks under the nerve roots in the lower back after doing a laminectomy from behind, and then let the poor animals recover. Later they were anaesthetised (and finally destroyed before waking) and the nerve conduction through the 'blocked' area compared with the normal on the other side using some of the sophisticated equipment that Eccles had developed, for he was becoming a world authority on nerve conduction and transmission. The nerve root project, involved long hours of recording, often overnight in shifts [and] *in the end did not prove publishable. I regret to say that what we did to those poor cats would, these days, never get past first base with an animal ethics committee* (Cole, 2002, p. 114).

Eccles' biographers have noted the beneficial effect of his scientific experimental enthusiasm on many of his students:

Other Otago groups strongly influenced by Eccles were the undergraduate science (e.g., M. Fillenz, A. Iggo, R. M. Eccles) and medical student research trainees in the department. They usually completed a research project comparable in many respects to an MS thesis in the USA. These were of high quality (e.g., Fillenz & Hanafin, 1947) and a major step forward for neuroscience and academic medicine in the Antipodes (Stuart & Pierce, 2006).

BD. [D] The newspaper article referred to was published under the pseudonym "Hygeia" heading the front page of the magazine Critic "*Official Organ of Student*

450 Hanafin, Mary "Mary Coldham" (1923 – 01.10.2014) NZ general practitioner.

451 Gallagher, Deryck Joseph Austin (1924 – 04.2008) NZ general practitioner and geriatrician in Auckland.

Opinion at Otago University". Vol. XXIII - No. 7. Thursday July 10, 1947 and titled **Medical Education in Otago**.

The editors' introductory paragraph to the featured article read:

It would be unusual if a Medical student should arrive at the fifth year of his training without some very definite opinions on the material presented in the course and also upon the manner in which it is presented by its teachers. Although, however a long term of imprisonment gives a prisoner a clearer opinion of the ways of his gaolers, his written ideas on the subject are no more welcome because of it. On the other hand, nobody has studied more closely or lived in more intimate contact with the inside of the cell than the prisoner himself, and his observation of it is probably of some considerable accuracy. Thus, it is in the belief that a Medical student's opinions on Medical education are to be similarly listened to that this article has been written.

This major article, under subtitles; **Physiology and Biochemistry** & **Psychology** contained detailed criticism of the above courses. (Irrelevant text under further subtitles; Transitional Period, Pharmacology, Medical Jurisprudence, Psychiatry & Clinical Material has been omitted here):

PHYSIOLOGY AND BIOCHEMISTRY

It has been pointed out by Dr. D'Ath[452] *that the object of the medical course was to produce adequately equipped general practitioners to serve the New Zealand public, and that the Government pays at least as much towards the education of the student as he pays himself, i.e., over £1000. I have heard much higher figures quoted. Hence it is clearly a waste of time, and of private and public money, to burden the student in an already overburdened. and prolonged course with material which will not be of value to him, either in the practical work of his career, or in the making of his background of knowledge and in the shaping of a proper outlook to his work.*

A thorough training in basic physical sciences is of course required, first in physics and chemistry; then biology, followed by anatomy and physiology but it is my belief that there is material in the physiology and biochemistry course which will be of no value whatsoever to students in their forthcoming careers, whether they work in general or in specialist practice. A very small proportion will of course become physiologists and biochemists, but the vast majority intend to be practicing doctors. After all, that is what the degree is for.

Let me be more exact. On looking back on my second and third years I remember a considerable number of lectures on the experimental behaviour of nerve and muscle fibres, at least half of which will never be of value to me whatsoever. This over-teaching I remember more particularly in biochemistry, where the lectures on enzymatic reactions and tissue respiration were carried out most ably to the front line of biochemical research, to the bewilderment of unfortunate medical students. In those days I knew the entire workings of the Krebs Citric Acid Cycle. I regret to say that I still remember a little of it. On looking at my third-year biochemistry notes I see two

452 D'Ath, Eric Frederick (25.03.1897-18.06.1979) NZ Otago Univ. Prof. of Pathology & Medical Jurisprudence.

lectures on the theories of bone salt deposition and two on detoxification which were dealt with in a far too complex manner and confused rather than enlightened. There was a lecture on the experimental use of isotopes and another on the evolution of the chemistry of nitrogen elimination from the body. I wisely wrote in my notebook opposite this last lecture – "Don't read this lecture through."

The fact is that, in many of the lectures from a welter of experimental detail with which the student is afflicted, very few clear facts emerge.

Of course, it was well known that mainly fundamentals were required for first professional physiology. For those who are not yet disillusioned I recommend a glance at the paper of November 1946. Why teach a subject in such detail that one loses sight of the simple and is dazzled by the complex, where one cannot see the wood for the trees?

PSYCHOLOGY

There are in the medical course three lectures in psychology. There are several more than this on neuromuscular transmission, perhaps twice as many. There are also about the same number on the deposition of bone salt, and there are about a dozen on the mechanism of tissue respiration. The practical significance of these three latter subjects is, I believe, approximately nil. It is thus obvious that that the study of psychology is so little valued by the medical faculty that it is almost fortunate to have appeared at all. It is also obvious that since these three lectures are one of the duties of the Professor of Physiology, they may theoretically be given by a person who knows less of the subject than the students he is teaching.

The introductory remarks of the Professor on this occasion, in my third year, showed that the lectures were intended as a counterbalance to a purely physical conception of mental function, and to prevent such willing acceptance of the powers of the conditioned reflex that one should be satisfied with a purely behaviourist psychology. In other words, he wished to open before us the possibility of there being another plane on which the mind could be studied, the psychological as opposed to the physiological. These lectures were, I believe, in the nature of an apology, at any rate one was certainly necessary when students on the eve of their entry into the hospital, who had received about 2,7000 hours' instruction in physics and chemistry and their application to animals and to men, and were now to receive a paltry three lectures to tell them that, strangely enough, man could be approached from another direction. Surely here is the reason why so many doctors scarcely seem to realise that their duty is to treat men and women with disordered minds and bodies, rather than to regard them purely as a vehicle for the disease with which the doctor is at war.

The teaching of psychology should be carried out continuously in second and third years by a competent teacher in that field. In my opinion one lecturer a week would be sufficient, and the time could be made by eliminating irrelevant detail, particularly in biochemistry, but to some extent also in physiology as well. The place of this subject must be established if we are to approach the patient with a humane understanding of his mind, as well as an undoubtably important knowledge of his physics and chemistry.

Quite apart from this, I may add that as in the study of the physical side, in which the normal is always studied before the diseased, we must be taught normal mental function before we attempt to understand abnormal mental function.

………

………(five subsequent chapter headings on other matters followed the above two)

SUMMARY

(1) Some physiology and biochemistry taught is superfluous.

(2) Psychology should be taught, **and** *by a psychologist.*

(3) Etc.

Hygeia

Such a direct public accusation against Eccles and the teaching of biochemistry and physiology could not remain unanswered. Letters were published by both Drs Brooks and Eccles in the local Dunedin Otago Daily Times (O.D.T.) newspaper, where the unfortunate introduction of the word "fool" tended to divert attention away from the main issues raised by Hygeia.

The first to jump into the fray was Chandler Brooks in an address reported on August 1st 1947:

SHARP REPROOF

OTAGO STUDENTS TAKEN TO TASK - PRAISE FOR DR ECCLES!

High praise for Dr J. C. Eccles, head of the Physiology Department at the Otago Medical School; was expressed by Dr C. Mc. Brookes, associate professor of physiology at Johns Hopkins University, United States, when addressing the, Otago University Graduates' Association last night. Dr Brookes has been engaged in neuro-physiological research at the Otago Medical School for about a year. Producing a copy of Critic, the official organ of student opinion at Otago University, Dr Brookes indicated an article written on the work of the Physiology Department at the Medical School. *"I am going to accuse the student body of having low aims,"* he said. He considered that criticism had been directed against the head of the department, Professor J. C. Eccles. *"This is my personal opinion."* Dr Brookes' declared. *"There is one great man at the Otago University and quite a number of good men. Professor Eccles is probably one of the greatest men you have had in your university, if not the greatest. The requirements of the medical profession will be higher in the future, and men will need to be ahead of the game, not behind it. Professor Eccles is one who is ahead. "I have come a long way to study with this man, and I am not going to let the students call him a fool,"* he asserted. Dr Brookes said that Professor Eccles was known by medical research people all over the world, yet a group of students said he did not know how to teach physiology. *"We are going to have the best neurophysiological unit in the world at Johns Hopkins, and I am taking something back,"* he said. The president of the association, Miss L. S. Morton, was in the chair, and a vote of thanks was moved by Dr W. E Adams.

More comments from Hygeia appeared in the O.D.T. on August 2nd in a column entitled:

Reference to Professor - No Reflection on Ability Intended:

"I do not represent the student body as a whole, nor did I refer to Dr Eccles as a fool," was the comment by a senior medical student, the author of an article in the student journal Critic, which was criticized by Dr C. Mc. Brookes in an address to the Otago University Graduates Association on Thursday night. Dr Brookes is associate professor of physiology at Johns Hopkins University, United States, and has been engaged in neurophysiological research with Professor Eccles at the Otago Medical School for about a year.

"The opinion expressed in the articles were my own, although they are also held by other students," said the student. *"Criticism was directed at the curriculum and not the personal ability of Dr Eccles.*

"Medical students receive about 2700 hours' instruction in physics and chemistry and their application to animals and men," he continued, "and then receive a paltry three lectures on psychology to tell them that, strangely enough, man can be approached from another direction. Surely here is the reason why so many doctors scarcely seem to realise that their duty is to treat men and women with disordered minds and bodies, rather than to regard them purely as a vehicle for the disease with which the doctor is at war. It is obvious that since these three lectures are one of the duties of the professor of physiology, they may theoretically be given by a person who knows less of the subject than the students whom he is teaching. Psychology should be taught and by a psychologist."

Eccles replied publicly in the O.D.T. on August 4th 1947 to Hygeia's criticisms; eagerly referring to the Catholic Church's Saint Francis of Assisi (known in the literature as "God's fool") as part of his response. Some confusing typesetting misplacements occurring in the newsprint column, have been corrected here [as insertions within brackets]:

Otago Medical Course - Physiology and Psychology

"Now that criticisms of my department have entered the public press, I should like to clear up some misunderstandings," said Dr J. C. Eccles, professor of physiology at the Otago Medical School, when asked for comment on the statement made by a medical student in Saturday's Daily Times following a report of an address by Dr C. McC. Brooks, professor of physiology at John(s) Hopkins University, on the subject of medical teaching.

"*In the first place,"* Dr Eccles said, *"Dr. Brooks was misreported in the Daily Times on Friday last as saying: 'I have come a long way to study with this man, and I am not going to let students call him a fool.' He actually stated that he did not want students to think him a fool for travelling half round the world to work in the physiology Department.*

Psychology Lectures

"No doubt through courtesy to a distinguished visitor, the reporter transferred the implied foolishness to me – I am not complaining, merely explaining – but unfortunately the anonymous student critic in his statement on Saturday refuses to concur in this transfer; so the implication of foolishness must return to Dr Brooks.

"In the same article." Dr Eccles continues, *"the anonymous student (A. S.) is reported as stating that: 'It is obvious that, since these three lectures (on psychology) are one of the duties of the professor of physiology …' Which goes to show that perhaps I am the fool after all, because I was quite unaware that it was one of my duties. In view of A. S.'s handsome repudiation of my alleged foolishness, it may appear churlish if I suggest that A. S. might have assumed naively that, because* [*I*] [*out*] *of the kindness of my heart, gave three lectures in psychology* [*it was*] *'one of my duties'. I hope no reader is unkind enough to suggest the addition of another 'S.' for really A. S. means very well in asking that doctors should treat their patients as human persons. One however does hope that Dr A. S. will be more careful than A. S. in turning assumptions into facts.*

Part in Medical Education

"So now we have three claimants for the title of fool," Dr Eccles said, *"and it seems that no more than one can qualify. Wouldn't St. Francis of Assisi have enjoyed the situation?*

"But more seriously, I hope A. S. is not suggesting that a more humane medical profession can be created by some 30 lectures in psychology, which in many guises is just as mechanistic as physiology and far more insidious in its influence. If our doctors are to grow in compassion and human understanding, then I would suggest that it is religion they need rather than psychology, though, of course, my attempt to give spontaneously 'a paltry three lectures on psychology' (I hope paltry knows where it belongs) should indicate that I regard normal psychology as necessary in medical education."

Footnote; [The initials "A.S." were appended to the original article in the student journal, "Critic."]

On August 4th 1947 Hygeia concluded the argument with the following letter to O.D.T:

Sir, - I do not wish to prolong further the controversy which has recently been prominent in your columns on the subject of my article in Critic of July 10 on "Medical Education in Otago". The bringing of this matter to the attention of the general public was not of my choosing, nor do I consider that any useful purpose has arisen from it. I would like, however, to correct your statement in the Daily Times of August 4 that "the initials A. S. were appended to the original article in the student journal Critic" The article in question was signed "Hygeia," and the initials A. S. were used by Dr Eccles for the first time.

__ I am, etc., ***Hygeia***

Footnote: [The initials "A. S." were wrongly interpreted as having been appended to an article in the student newspaper. Professor Eccles used them merely as an abbreviation of the term "Anonymous Student," It is desirable also to point out that Dr Brooks in his address to the Graduates Association did not accuse students of using the word "fool" as applied to Professor Eccles, and comment on such a basis without substance. We regret that this error occurred. -- Ed. O.D.T.]

BD. [E] Eccles' student, (later Sir) John Scott[453], reminisced:

This was a golden age for the Otago Medical School. Probably a majority of undergraduates did not appreciate the environment, but those who did, benefited enormously. The presence of Eccles and his team in Dunedin attracted a steady stream of prestigious visitors from Europe, United States and Australia. Some such as Wilfrid Rall spent considerable time at Otago, such was their regard for the environment and its leader. Eccles was proud of the fact that "the majority of the senior faculty of the newly founded Medical School at Auckland University" had been his students. In retrospect, he valued the breadth of the teaching he was compelled to undertake. (Scott, 1999; Scott, 2006) Teaching commenced in 1968 at the new Auckland Medical School (the second Medical School to be established in New Zealand).

BD. [F] Indeed, several of Eccles' students in Dunedin subsequently played leading roles in the 1968 founding and development of New Zealand's second medical school at the University of Auckland. They are listed here in alphabetical order, using data combined from two sources. (Stuart & Pierce, 2006; Page, 2008, p. 318).

453 Scott, Philip John (26.06.1931 – 20.10.2015) NZ heart disease clinician, medical criminality investigator.

<u>Table 1</u>: Notable students of Eccles at Dunedin

Name	Discipline, year Otago MB ChB gained	Began Auckland
DS Cole	Surgery, graduated 1948	1966
GL Glasgow	Neurology, graduated 1948	1976
AW Liley	Obstetrics & gynecology, graduated 1953	1959
JDK North	Medicine, graduated 1950	1968
PJ Scott	Medicine & pediatrics, graduated 1955	1973
JD Sinclair[454]	Physiology, graduated 1950	1968
JS Werry[455]	Psychiatry, graduated 1955	1970

BD. [G] Details of Graham Liggins' illustrious career can be found in the obituary by Gluckman & T. Buklijas, (2013).

BD. [H] The future professor of neurophysiology at Otago, John Hubbard came as a student and particularly enjoyed the Friday 9 am lectures on the nervous system, when Eccles eagerly told of the events in the previous all-night experimental session. Hubbard's successor, Pat Cragg, wrote of him:

John began his MBChB degree in 1948 at the University of Otago Medical School. In 1951, intrigued by the field of neurophysiology, John undertook a year of research for a Bachelor of Medical Science in the Department of Physiology, under the guidance of Professor A. K. McIntyre and Sir John Eccles. John Hubbard became the first new Zealander to win an Oxford University clinical scholarship completing a BA with first class honours in Physiology in 1954 and an MA, Bachelor of Medicine and Surgery in 1957. Still fascinated by neurophysiology, John returned to the southern hemisphere in 1958 as a PhD student supervised by Sir John Eccles in Canberra… After achieving his PhD in 1961, he received the top academic appointment as Professor of Biological Sciences and Engineering Sciences at the Northwestern University, Chicago USA… In 1972 John Hubbard was attracted back to the University of Otago's Department of Physiology to a new position as the first professor of Neurophysiology, a position he held until his untimely death (Cragg, 1996, p. 10).

BD. [I] The book (Fillenz, 1990) examines the mechanisms that regulate the release and synthesis of the neurotransmitter noradrenaline.

BD. [J] Although not specifically mentioned by Eccles, the students North[456], Scott, Sinclair and Werry later became leaders in their respective fields.

Philip John Scott became Associate Professor of Medicine at the Auckland Medical School, later headed the Medicine department at Middlemore Hospital in south

454 Sinclair, John Desmond "Jack" (1927-2018): NZ Prof. Physiology Auckland Med. School 1968-93.

455 Werry, John Scott (1931 –): NZ Prof. Psychiatry Auckland Med. School 1970-91.

456 North, John Derek Kingsley (1927-2016) NZ Prof. of Medicine at Auckland Medical School 1969-1979.

Auckland and achieved fame in successfully hunting down a notorious "quack" doctor. (Buchanan, 2016).

BE. [A] Eccles yearned to continue his animal experimentation following the enforced war-time interruption and, in addition to his teaching duties, soon returned to his preferred subject, the cat, as depicted in (Fig. X14) and (Fig. X15). Fillenz wrote in her contribution to the Eccles memorial book:

At the same time as he was preparing this enormous teaching program, Eccles was setting up his research facilities. He had brought with him from Sydney the research equipment he originally had assembled in Oxford. His first task was to have a shielded room built, which was always known as the "tin room". (Fillenz, 2000, p. 13).

Kuffler wrote about his war-time work in the Sydney area, which was mainly staffed by people from Johns Hopkins University Medical School:

There I functioned as a consulting neurologist working on nerve injuries that were quite plentiful in the Pacific war. These activities, however, were not full-time and I continued research work in Eccles's laboratory, even after Eccles had left for New Zealand in 1943. Eccles's laboratory was not reconstituted after the war Katz, 1982, p. 254-5).

The unrecovered equipment that Eccles left behind in the Kanematsu building in 1943 might have been used previously for a while by Archie McIntyre, who published two papers; (McIntyre, 1939) where equipment typical of the Sherrington/Eccles era was employed (Matthews oscillograph, thermionic valve amplification, Faraday cage with fine wire-netting shielding and a light-optics version of the torsion myograph). Further justification for this supposition comes from an interview of cancer geneticist Sir Henry Harris[457] with Sir Peter Stanley Harper[458] (as immigrant Russian Jew, Harris, had in 1944 embarked on a medical degree at Sydney University inspired, he claimed, by the works of literary doctors, in an attempt to become a latter-day Chekhov.[459] Harris began to dabble in experiments during his medical training, and this developed into an obsession with basic biomedical research that captivated him for the rest of his life). An excerpt from this interview follows:

PSH. Do you think in terms of factors making you come into medicine, apart from the literature, do you think there was any other clear factor, which took you towards science and medicine, or was it just the interest of it?

HH. Well, there was a theory at the time that positive and negative afterimages, visual after-images, were all due to effects taking place at the retina and I thought well, why only the retina. It could be the lateral geniculate body or visual cortex or what not, and I thought I should be able to sort this out if we put electrodes in the right place and shine lights into cats' eyes, we would be able to find something out. Well, there was

457 Harris, Henry (18.01.1925 – 31.10.2014) RU(J) Oxford professor of medicine, cancer geneticist.

458 Harper, Peter Stanley (28.04.1939 – 23.01.2021) UK geneticist; myotonic dystrophy & Huntington's.

459 Chekhov, Anton Pavlovich (29.01.1860 – 15.07.1904) RU physician and prolific writer/playwright.

some equipment that Eccles, Katz and Kuffler [Stephen] who had worked at the Kanematsu Institute at Sydney Hospital, had left and ended up in the University and there was a bloke who thought he could use it. I asked him whether I could have a go at this experiment and so we got a cat, and we anaesthetized it as I can remember. The first, really, we got from what we thought was the optical cortex was a biphasic wave going boomp boomp boomp. We'd got an electrocardiograph from the optic nerve! It turned out this fellow thought he knew how to use the equipment, didn't know how to use it and I was mucking about with it, when Archie McIntyre, who was a good neurophysiologist (I think he became Professor in Adelaide and stayed there for many years), blew through the place and he asked me, he was told there was a crazy kid down there mucking about. And he asked me why we chose the cat for these things and shone various coloured lights, green lights, red lights into the cat's eyes. I said physiologists always work on cats. He said "yes, but cats are almost colour blind". Anyhow, that piece of information finished my career as a neurophysiologist (Harper, 2007).

BE. [B] Eccles' shielded research setups followed the design used previously by him at his Oxford and Sydney labs.

I have left around the world a trail of elaborately designed shielded research rooms stripped of equipment! (Eccles, 1977, p. 1).

Extraneous electrical disturbances are eliminated by housing the preparation and all the apparatus (entirely battery operated) in an electrically shielded room constructed of galvanized iron sheets soldered together (Eccles & O'Connor (1939 [1A-058]).

Son, Peter James Eccles (1931-2005) reminisced about this "tin" room years later: See section FA in the family reminiscences (from Mennis, 2000, p. 204).

The "*equipment*" retained by Eccles included rheotomes. In particular, his research colleague in Dunedin, Ainsley Iggo, noted:

He had also cornered the world's stock of Lucas pendulums; (pre-electronic electro-mechanical instruments designed about 1910) and with these high-precision mechanical devices, could deliver electrical stimuli to peripheral nerves at intervals less than 1 millisecond, which was necessary to cope with the speed at which events occur in the central nervous system (Iggo, 1997).

BE. [C] We read that:

Enthusiastic cooperation and expertise came from colleagues John Coombs, Lawrence Brock and also electronics technician Arnold Annand (Gibb, 2011).

Eccles asked John ("Jack") Coombs, a physicist, to find help with the electronics for doing the microelectrode work. Coombs decided it was interesting and would do it himself, constructing the needed cathode follower amplifier with high input impedance to reduce input capacitance and neutralize pipette capacitance by negative feedback (Shepherd, 2010, p. 92).

Brock developed techniques for making and filling glass microelectrodes, and Coombs, a physicist, aptly described by Eccles as a 'shy genius', designed a versatile and readily operated electronic stimulating and recording unit, later widely known as *the 'ESRU', together with amplifiers and a cathode follower input stage, essential for recording with high resistance electrodes* (Curtis & Anderson, 2001a).

BE. [D] Eccles used Pentobarbital (trade name: Nembutal) a short-acting barbiturate drug which acts as a central nervous system depressant, as the anaesthetic for his Dunedin experiments. For details concerning the isolation of the cat's spinal cord experimental region in a moist atmosphere and the preparation of thin metal electrodes see Eccles, (1946) [1A-075] p. 88.

BF. [A] An unexpected bonus for Eccles was meeting and befriending in 1944 the brilliant Austrian philosopher, Karl Raimund Popper, who was then lecturing at Christchurch University – a journey by steam train taking just over seven hours from Dunedin (Fig. X16). Carmody has outlined the early life of Popper, and how he influenced Eccles (Carmody, 2002).

The enormous success of Popper's talks prompted Eccles to have his own (and Fillenz's) detailed notes from the lectures edited, duplicated and given out to his students. The main tenet of Popper's philosophy, which so fascinated Eccles probably lay in the following statements in Popper's second lecture - relating to the testing of theories:

Scientific objectivity is fortunately something that does not depend on the objectivity of a scientist, but rather on the character of scientific method, that is, on the public nature both of the publication of a theory and of its attempted falsification...

In order then that the testing of theories can occur, we have to have a theory that has some new implications, i.e., the scientist has to take risks, to say more than he knows, not as an assertion, but as a hypothesis. This is a direct contradiction of the inductive, rationalistic attitude, which only believes the evidence of the senses and what can be proved from this. This is contrary to the adventurous spirit of true science: It leads to the saying of nothing because it won't take any risks. The true outlook of the scientist is to take risks and make the widest possible theory, then test it where there is believed to be its weakest point, where there is the greatest likelihood that it will break down. (Penny, 2012, p. 18).

Further information concerning Popper's influence on Eccles is provided in Eccles' "Odyssey" memoirs (Eccles, 1975, p. 162 [1A-417]); (Eccles, 1977, p. 6 [1A-436]), the reprinted "Research and the University" (Allan et al., 1991) and the annotated obituary of Eccles (Curtis & Anderson, 2001a). In addition, Marianne Fillenz published memoirs of both Popper and Eccles in New Zealand during her time as schoolgirl in Christchurch and later as medical student at Dunedin during the 1940s (Fillenz, 2000; Fillenz, 2012).

BF. [B] Popper's original paper in German is Popper, (1934).

BF. [C] Relevant to Popper's philosophy is the quotation from Rushton:

"A theory which cannot be mortally endangered cannot be alive". (Personal communication quoted by Platt,[460] 1964, p. 349).

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460 Platt, John Rader (29.06.1918 – 17.06.1992) US physicist/biophysicist "strong inference".

The British physicist Sir Hermann Bondi[461] said that "*there is no more to science than its method, and there is no more to its method than Popper has said.*", Magee, 1973, p. 2.

<u>BF.</u> [D] Before he departed from New Zealand, Popper, together with Eccles and several other university colleagues in the sciences, published an important pamphlet which was to lead to major changes in New Zealand university teaching of science. Entitled "Research and the University" (Allan et al., 1945) their thesis was essentially:

*A manifesto setting out the requirements of the University if it were to become a research institution. Of its six authors, four were from Canterbury College, one from the University of Otago and one from Auckland University College. The initiative was driven by the Viennese philosopher Karl Popper who was a lecturer at Canterbury College for nine years. Popper and his colleagues went on to assert: "we regard research and teaching not as separate functions of a university teacher but as complementary parts of a single entity" (*Allan et al. 1945, p. 2*). The commonly held view that the University is primarily a teaching institution should be abandoned. Rather the University should be looked upon as an institution in which "the spirit of free enquiry is preserved and cultivated" (p. 2).* (Robertson & Bond, 2005, p. 517-520)

In their pamphlet, Popper and his colleagues proposed that:

In order to remedy the situation as it exists in New Zealand a complete change of attitude is required. It must be recognised that a specialist might achieve much greater educational result by teaching his speciality than by spreading his teaching over what is traditionally considered the balanced content of his subject. The view that it is the task of the University to hand to the students a definite body of examinable knowledge must be discarded (Allan et al. 1945, p. 3).

<u>BG.</u> [A] The electrical characteristics of naturally occurring ephapses in unmyelinated crab nerves were described by Angélique Arvanitaki (Arvanitaki, 1942).

<u>BH.</u> [A] Eccles' American visit in 1946 involved several epic journeys:
The Sword Knot trip from Wellington to Honolulu, Hawaii;
The China Clipper trip from Hawaii to San Francisco;
The delivery flight from Los Angeles to Melbourne.

"China Clipper" was the name generally applied to all Pan American World Airways series of 4-engined luxury flying boats (Fig. F14). Eccles probably flew in the last Pan Am 314 flight before it was retired -- the *California Clipper* NC18602, which in 1946, had accumulated more than a million flight miles. Pan Am's "Clippers" were built for "one-class" luxury air travel. The seats could be converted into 36 bunk-beds for overnight accommodation; with a cruising speed of 188 miles per hour (303 km/h), but typically, flights at maximum gross weight were flown at 155 miles per hour (249 km/h). In 1940, Pan Am's schedule for *San Francisco* to *Honolulu* was 19 hours. The 314 series had a lounge and dining area, and the galleys were crewed by chefs from

[461] Bondi, Hermann (01.11.1919–10.09.2005) AT/J Mathematician and cosmologist. "Gravitational waves".

four-star hotels. Men and women were provided with separate dressing rooms, and white-coated stewards served five and six-course meals with gleaming silver service (Klaás, 1998).

BH. [B] The International Congress contribution was Eccles (1946) [1A-077].

BH. [C] Eccles obviously enjoyed humorous escapades when at conferences. During a recorded interview, the pharmacologist Alex Karczmar (AK) spoke of Eccles' involvement at a later conference (Eccles, 1961, [1A-198]; Chagas & Paes-de-Carvalho, 1961) in a practical joke on Nachmansohn, who held stubborn adherence to his own private concept of the role of the cholinergic system:

AK: *He was very stubborn. Let me tell you an anecdote which is pertinent. Nachmansohn participated in a 1959 Symposium in Rio de Janeiro and during a break, he went to the beach where he fell asleep in his chair. So, Eccles and others started pushing Nachmansohn in his chair into the sea. Nachmansohn wakes up in the middle of this activity, sees himself deep in the water, and says: "You can kill me but you cannot kill the theory"* (Costa, 2007).

BH. [D] Dante's "Divine Comedy", a long Italian epic poem completed in 1321, described (allegorically) the spiritual journey of the human soul towards God. It was divided into 3 major sections; Inferno, Purgatorio and Paradiso, each consisting of 33 cantos. Dante's Inferno (Hell) comprised 9 concentric circles, the first (Limbo) being resided by "virtuous non-Christians and unbaptized pagans" whereas the innermost circle (Treachery) was reserved for the worst category of sinners. Several English translations of this famous literary work have been published; e.g., Cary, (1892), Sinclair, (1939).

BH. [E] Some memoirs of the pioneering aeroplane delivery journey, Los Angeles to Melbourne, include a 1942 National Geographic map of the Pacific Ocean, (Fig. F17) and a photo made of the plane with crew and passengers standing beneath it. John Eccles can be recognised (tall with hat, 7th from left) standing beside the captain (Fig. F17upper).

BI. [A] More improvements in experimental extracellular potential measurement technique are described, (Brooks & Eccles 1947 [1A-080], p. 252); in particular the use of a paraffin bath covering the exposed nerves of the cat spinal cord and the use of 50μ diameter enamel-insulated steel or tungsten needles, ground down even further to sharp chisel points.

BI. [B] Of his time with Eccles, Chandler Brooks wrote:

In 1945 I was granted a John Simo Guggenheim fellowship… I had intended to study with Dr. Houssay but Peron put him in prison and he wrote advising me not to come to Argentina… My other opportunity was to join J. C. Eccles in New Zealand and learn the techniques of action potential recording. This I did, arriving in Dunedin during the summer of 1946. Eccles quickly informed me it would be impractical to record from fibre of the pituitary stalk or nuclei of the hypothalamus; I should join him in his research. This I did and I found him to be a kind and patient instructor and a very stimulating scholar and I have continued to work in neurophysiology throughout the *years since that time. I was with him when he began his analysis of central inhibitory processes for which he eventually received a Nobel Prize.* (Brooks, 1975, p. 72).

BI. [C] See: Brooks and Eccles (1948), p. 372, fig. 6, [1A-084].

BJ. [A] In a letter to Popper dated March 16th 1947, Eccles described his enlightenment and excitement concerning a new theory involving Renshaw cells:

We had had several good experiments and I kept on telling Chandler [Brooks] that we might expect to develop a satisfactory theory in a few months – there was at least an air of expectancy. Then we had our best experiment on December 18th and worked on till 1.15 the next morning. As I was about to go to sleep, I started thinking over some remarks Chandler had made on the way home, when suddenly the theory hit me. I knew at once that it provided the clue for which so many of us have been searching for years. It made sense of so many hitherto un-relatable observations. I remember now that I was tired and over-wrought and feared I would forget it all in the morning. However, I woke up some hours later and went over it in detail in my head. It fitted precisely into everything that I could think of and shed light on a wide field of neurology. You will see for yourself how simple it is – it looks absurd that it could have been missed for so long, and yet nowhere in the literature is there the slightest suggestion of such a theory. Well, Chandler and I discussed it for several days and I read the literature to gather up what I had forgotten and then we had the thrill to receive from America two papers published by Lloyd in November, which gave precisely the results which would be predicted by the theory – in fact I had made the predictions and we were planning the experiments. Lloyd had completely missed the theoretical significance of his results, but had pointed out that they could not be explained by any current theory of inhibition. Of course, now we have to test predictions and that is going to be a long job. However, this theory, together with the excitatory theory, now mark a stage in the journey I set out on nearly twenty years ago. In 1927 I started work for my D. Phil. on the subject of Excitation and Inhibition – it was my first love in research and has remained so ever since – a pretty good example of constancy! And now after nearly twenty years there are the two theories sufficiently good to challenge (and invite) falsification. I have given you a full account of the origin of the inhibition theory, because it provides such a good illustration of your ideas on the subject (Labisch, 2011, p. 113).

BK. [A] see Graham & Gerard, (1946): Membrane potentials and excitation of impaled single muscle fibres. For a detailed history of the glass micropipette see Bretag, (2017).

After marriage, Judith Graham Pool worked toward her Ph.D. in physiology. Her dissertation was on the electrophysiology of muscle fibres. She worked in the laboratory of neurophysiologist Ralph Waldo Gerard[462] at Hobart College. In 1942, Pool, Gerard, and Carlson published a paper in which they described the use of a microelectrode to record electromagnetic impulses in frog muscle fibres. Gerard

462 Gerard, Ralph Waldo (07.10.1900 – 17.02.1974) US neurophysiologist. Psychopharmacology, schizophrenia.

furthered the research and was nominated for a Nobel Prize in 1950 for his work. Pool's contribution was largely overlooked, according to the book *Women of Science: Righting the Record.*

See: [*https://biography.yourdictionary.com/judith-graham-pool*](https://biography.yourdictionary.com/judith-graham-pool)

BL. [A] Victor Macfarlane, initially trained as parasitologist, decided to undertake a medical course at the University of Otago to remedy his lack of training in physiology and biochemistry. In Curtis' obituary of Macfarlane, we read:

In his final examinations he topped his year and won numerous academic awards. As a resident medical officer at the Dunedin Hospital, he assisted the neurosurgeon Murray Falconer and attended neurophysiological seminars in the university's department of physiology, of which Professor (Sir) John Eccles was head. Developing an interest in the mechanisms underlying nerve and brain function, in 1947 he was appointed senior lecturer in physiology. In addition to teaching, he collaborated in research with Eccles, acquiring expertise in electrophysiological techniques. Moving to Australia, in February 1949 Macfarlane became professor of physiology at the University of Queensland. (...) Early in 1959, wishing to have more time for his multiple interests and research activities, Macfarlane took up a post as professorial fellow in the department of physiology, John Curtin School of Medical Research, Australian National University, Canberra, again under Eccles (Curtis, 2012).

In McIntyre's detailed and sympathetic obituary of Macfarlane, one can read in detail his collaboration and friendship with Eccles. An excerpt is given here:

He and Eccles must often have discussed philosophy as well as neurophysiology, both being greatly interested in the unorthodox views about scientific method of Karl Popper, who had come to Canterbury University College in 1937 and who lectured on his views in Dunedin in 1945 shortly before returning to Europe.

In the department of physiology, Victor was soon busy. As well as a heavy teaching load, he was actively engaged in research, and so began to acquire Eccles' electrophysiological expertise. During that year, the department was host to a Guggenheim Fellow from Johns Hopkins University, Chandler Brooks, who came to learn basic neurophysiological techniques to use in his studies of hypothalamic function. As those who have worked with Eccles well know, his experiments often last well into the early hours of the morning. Sandwiched between a busy teaching day and a 9 a.m. lecture the following morning, their conduct required considerable powers of endurance, no new thing for Victor. He wrote: 'Spinal cord neurones and neuromuscular junctions filled days, nights and weekends. The old sub-culture of neurophysiology, which was just entering its exponential phase, opened up a tremendously lively intellectual ground base. Chandler Brooks came from Johns Hopkins to try to learn to record from hypothalamic neurones. He learned a good deal about spinal cord neurones instead'.

Victor's principal research was on the basic mechanism of neuromuscular transmission, involving electrical recording of the endplate potential under various controlled conditions including the presence of pharmacological agents. The results *provided further confirmation that release of acetylcholine from the nerve terminal is responsible for the transmission* (McIntyre, 1985).

BL. [B] In 1948 Eccles was joined by Archie McIntyre, who he appointed as senior lecturer in his department. Otago historian, Dorothy Page, wrote:

His [Eccles'] successor, Archibald McIntyre, believed that his teaching was unbalanced, with too much time spent on controversial neurophysiological topics and not enough on the more clinically applicable aspects of physiology, but that it also had 'the great merit of keeping the students in touch with at least part of the growing frontier of knowledge (Page, 2008, p. 131).

BL. [C] Ainsley Iggo, one of the first workers with Eccles in Dunedin, later wrote:

Professor Ian Coop, my M.Agr.Sc. Supervisor, suggested that I go to Otago, where there was an internationally recognised physiology department. My way home by train from Christchurch to Invercargill took me through Dunedin. During a 20-minute refreshment break at Dunedin (there were no restaurant facilities on New Zealand trains) I made a telephone call from the railway station that was to change my life. I phoned Professor J. C. Eccles. More than 50 years later on the occasion of my retirement, he wrote to remind me of this, our first contact. He did not at the time seem unduly impressed with my suggestion that he hire me as a research assistant. Instead, he suggested that it would be not just better, but necessary, for me to learn some physiology first. I was penniless, having used my last penny on the telephone call. My cousin, Edward Iggo, a pharmacist, rescued me with a generous loan to cover an undergraduate year at Otago. There I spent a rakish year exposed to the brilliant teaching of 'Synaptic Jack' Eccles and, among others, neurophysiologist Archie McIntyre, biochemist Norman Edson, and neurologist Victor McFarlane. The next year I became an assistant lecturer, giving a course of lectures to Home Science and Diploma of Physical Education students while I was doing honours physiology. Under the powerful influence of Eccles, I began, with his daughter Rose, an investigation of synaptic transmission in autonomic ganglia.

Eccles was still promoting the electrical hypothesis of synaptic transmission, although this was challenged by the Dale School in England and former colleagues of his Sydney era, Bernard Katz and Stephen Kuffler. It was clear that peripheral synapses were influenced by acetylcholine. Rose and I excised superior cervical ganglia to record extracellularly in vitro to test ganglion blocking drugs. Eccles suggested that the ciliary ganglia [parasympathetic ganglia located behind the eye] offered a particularly interesting model since both pre- and postganglionic transmissions were cholinergic. Attempts to isolate viable ciliary ganglia from experimental cats were unsuccessful. End of story.

The seduction of overseas study and the new experiences it offered nullified J. C.'s blandishments to stay and enrol for a postgraduate degree (Iggo, 2001, p. 287).

Iggo's choice of isolated ciliary ganglia as experimental material puzzled a later colleague, John S. Kelly, who wrote in his obituary of Iggo:

With the financial help of a cousin and later an assistant lectureship he was able to study physiology under Eccles, Archie McIntyre and others and take part in a research *project recording extracellular potentials from excised superior cervical and the ciliary ganglia with Eccles' daughter, Rose Eccles. The project was a flop and Ainsley turned down the opportunity to work for a PhD in Otago. It is not clear why J.C. Eccles suggested isolating the ganglia. In his 1935 papers* (e.g., Eccles 1935 [1A-033], p. 181) *describing his work in Oxford, Eccles emphasized the need to preserve the blood supply to the ganglion, 'care being taken not to endanger its blood supply'* (Kelly, 2012, p. 26).

Ainsley Iggo moved to Scotland to become a pioneer in the neurophysiology of cutaneous nerve cells.

BL. [D] The Gifford lectures were later published as a book, *The human mystery* in 1979 [1B-a17].

BL. [E] Wilfrid Rall joined Eccles' group in 1949 after completing his requirements for a master's degree and stimulated by Eccles' electrical theory of synaptic inhibition. He decided to work in New Zealand as physiology lecturer, mainly with the goal of completing his PhD thesis under him on *"The field of biophysics"*:

He soon became engaged in an in-depth study of the synchronous responses of a pool of motoneurons to a synchronous activation of the sensory fibres to them. This required careful dissections of the spinal roots of the cat (Fig. X17) *and long sessions recording the input-output relations. Nevertheless, Rall was later left abandoned with his subject when the main research direction of Eccles' Department suddenly changed. During this time, news of the advent of intracellular recording techniques was brought to Dunedin, and Eccles threw himself into the experiments which led to his breakthrough in 1951-52. Rall, however, continued with his independent project under Archibald McIntyre.* (Shepherd, 2010, p. 107).

Rall described his time at Eccles' department in Dunedin as follows:

The physiology department had a very busy schedule, which included lectures and labs for 2 years of medical school, plus a general physiology course, as well as special courses for dental, nursing, and home science students. Nevertheless, Eccles aimed to keep up his basic research momentum with at least one experiment a week; this involved an all-day/night experiment on cat spinal cord. I gave lectures in general physiology and helped run the student lab courses, but my major responsibility was to be fully involved in the research. This included dissections, assembling the set-up, and sharing with Eccles the planning and conduct of the experiments and the subsequent analysis of the data (recorded on glass photographic plates). When the experiment went well, it continued far into the night. Fortunately, I had the needed stamina and interest to keep up with Eccles during this rigorous routine (Rall, 2006).

During Rall's time in Dunedin, he noted that:

At that time, most of our recording was from ventral roots; some was also done with steel electrodes inserted into the spinal cord. This was 2 years before the beginning of micropipette recording from individual motoneurons. In Dunedin, we first learned about micropipette recording from Dexter Easton, who came as a Fulbright Fellow from the University of Washington (in 1950)…

Eccles decided promptly that he must not fall behind in the application of micropipettes to motoneurons of cat spinal cord. Brock was asked to focus on learning to make micropipettes, and Coombs was recruited from the physics department to take charge of modernizing stimulating and recording electronics. They produced early results in time for the Cold Spring Harbor Symposium on Quantitative Biology held in June 1952. (Rall, 2006, p. 560)

Rall wrote later:

Although I had done extracellular recording with Brock and Eccles in Dunedin (1949-51), I did not participate in their sharp electrode experiments; my focus then was on completing my PhD research, aimed at matching experiment and theory for a reflex input/output relation, using monosynaptic responses in spinal cord motoneuron populations (Rall, 2008, p. 310).

BL. [F] A biography of Walter Griesbach, a Jewish immigrant professor from Nazi Hamburg, is the subject of a prize-winning thesis by Viola Schwarz in 1999 entitled "Walter Edwin Griesbach (1888-1968) Leben und Werk", later translated into English as "Walter Edwin Griesbach (1888-1968) Life and Work", published by the Griesbach-Hallenstein Foundation in Switzerland.

BL. [G] Administrative details of the Physiology Department administration under Eccles have been investigated in the course of a thesis study:

In 1944, Professor John Eccles replaced John Malcolm in the Physiology Department. ... By 1945, he was chairman of the Neurophysiology and Neuropathy Committee of the Medical Research Council (MRC). He was to stay in Dunedin only until 1950 before returning to Australia, but he made a big impact on research at the School and in the MRC. Eccles brought a great research impulse into the School and into his Department. [He] published a stream of publications in [neurophysiology], which enhanced his own reputation and that of the Medical School. ... This work was only made possible by the financial help of the Medical Research Council. The committee's aims were 'to promote the study of the way in which the brain and other parts of the nervous system control the limbs and organs of the body.' The research focused initially on investigating cases of sciatica admitted to the Dunedin Hospital, but moved on to the exploration of acetylcholine and neuromuscular transmission, along with studies of the spinal cord. The members of the committee in 1946 represented a cross-section of the Departments of the School: William Adams from Anatomy, Murray Falconer from Surgery, Smirk from Medicine and Eccles from Physiology. Having the MRC within the School had an influence on the teaching of students, the researchers sharing their latest findings in lectures – a habit not universally popular with the students. A former student of the early 1950's commented on Eccles as a lecturer: 'We as medical students knew more about neuromuscular transmission and neurophysiology, but we knew bugger-all about the physiology of the kidney, because the emphasis was on this ground-breaking research that was being done' (Le Couteur, 2013, p. 323).

BM. [A] Published as Eccles & McIntyre (1953), [1A-113].

BN. [A] Eccles' nagging fear was that by remaining in Dunedin he could become "out of touch" and fall behind his research competitors in the increasingly desperate race to publish and student Fillenz provided the reason compelling Eccles to move: *Teaching occupied too much of Eccles' time in Dunedin* (Fillenz, 2012).

There were many other factors which could have also influenced Eccles decision to leave New Zealand. In the early 1950s Dunedin would have been the remotest place in the world to receive news updates of European and American research. Mail and printed research journals could take many weeks to arrive; other relevant publications could not be afforded from the limited funding available at Otago University. Telegrams and overseas telephone conversations via cable were expensive and the luxury of attending overseas research conferences was seldom possible, especially if week-long return sea voyages were involved.

Otago neuroanatomist, Ted Jones[463] commented on New Zealand's severe isolation, persisting even into the late 1960s:

It is hard to imagine now a scientific environment where journals arrived by surface mail 3 months after their publication and where many routine laboratory supplies, mostly obtained from Britain, took a similarly protracted time course before delivery. Commonly, chemicals obtained in this way arrived in poor condition. Glutaraldehyde, [An essential cytological fixative used at pH of 7 for TEM research], *for example, arrived with a pH of close to 3, much of it having been oxidized to glutaric acid and requiring lengthy passage through activated charcoal for purification* (Jones, 2011, p. 254).

After Eccles' departure Ted Jones, Associate Professor in the neighbouring Department of Anatomy, made the following comments:

There was some excellent neurophysiological research going on in the Department of Physiology under the leadership of Archie McIntyre. Archie had succeeded John Eccles in the chair which Eccles has held from 1944 to 1951 when he left to take up his position as founding Professor of Physiology at the new John Curtin School of Medical Research at Canberra in Australia. The first intracellular recordings from spinal neurons, the work for which Eccles in 1963 was awarded the Nobel Prize, were obtained in Dunedin. Eccles was remembered more for his irascibility than for his scientific achievements. Many years later, at a meeting at the Vatican, in introducing me to an audience, he described himself and me as being the only two neuroscientists who had been to Purgatory and back because we had both been on the faculty of the University of Otago. It was an unkind remark, but it reflected the difficulty that we both had in setting up and maintaining a productive laboratory in one of the remotest medical schools in the world (Jones, 2011, p. 237).

BO. [A] Although Cardinal Newman's book was first written in 1852; many editions exist, e.g., Newman (1905).

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463 Jones, Edward George (26.03.1939 – 06.06.2011) NZ anatomist/author "Cajal on the Cerebral Cortex:".

BO. [B] In pages 15/16 of his book, "The concept of mind", Gilbert Ryle introduces for the first time (with deliberate abusiveness) the concept of "*the dogma of the Ghost in the Machine*"; claiming in page 22 that *the dogma maintains that there exist both bodies and minds; that there occur physical processes and mental processes; that there are mechanical causes of corporeal movements and mental causes of corporeal movements*. Ryle argued that "*these and other analogous conjunctions are absurd"* (Ryle, 1949).

BO. [C] The publication based on his "Passmore lecture" is (Eccles, 1951) [1A-097].

BO. [D] For a critical review of "The Self and its Brain", see (Dennett,[464] 1979). The influence of Popper on scientific research and the speculative writings of Eccles have both been examined in a science history dissertation by Brian Casey, (Casey, 2009).

BO. [E] Élu associé (Classe des Sciences), le 14 décembre 1968. Status: Académie / Académicien décédé.

BO. [F] Dream researcher, J. Allan Hobson[465], commented on Eccles' 1951 hypotheses as follows:

Eccles hypothesized that the liaison of brain and mind occurred only in the cerebral cortex, when that part of the brain was activated. In particular, he ascribed dreaming to "bursts of activity in the electroencephalogram," as if he believed (as I do) that dreaming was a kind of consciousness. Eccles also held that every perceptual experience was a function of a specific pattern of neuronal activation and that memory was caused by an increase in synaptic efficacy. Given these reasonable assumptions, it is difficult now to see why Eccles felt that experience and memory were "unassimilable into the matter-energy system." Because of this conclusion, he felt it useful—and even necessary—to postulate that the activated cortex had "a sensitivity of a different kind from any physical instrument" and that "mind achieves liaison with the brain by exerting spatio-temporal fields of influence that become effective through this unique...function of the active cerebral cortex." But to the monist, a simpler and more elegant explanation is that subjective awareness is an intrinsic, emergent aspect of brain activation (Hobson, 2004).

BP. [A] The cathode follower, first employed with valve amplification (later as "common collector" or "emitter follower" in transistor amplifiers) is an impedance-matching device with a very high input impedance and very low output impedance. Although the voltage gain is less than 1, the power gain may be appreciable. Circuit performance is stable and relatively independent of changes in component values and gain depends only on the amplification factor, which is the most stable of the small-signal parameters.

464 Dennett, Daniel Clement (28.03.1942 –) US philosopher, writer, and cognitive scientist.

465 Hobson, John Allan (03.06.1933 – 07.07.2021) US psychiatrist. "Rapid Eye Movement in sleep".

BQ. [A] Until 1950, Eccles had only been able to record voltage potentials extracellularly by using insulated fine metal electrodes placed near spinal motoneurons; but then the ability to be able to record within these cells became increasingly important. In this respect the influence of his newly arrived colleague, Archie McIntyre, on Eccles' research was crucial. This is clearly detailed in the following selected passages from the obituary of McIntyre by Australian physiologists, Robert Porter, Uwe Proske and Richard Freeman Mark:

*He [McIntyre] worked during 1946–1948 in the company of major figures in neuroscience including Herbert Gasser, Lorente de Nó, Birdsey Renshaw and David Lloyd. His work with David Lloyd, who had been a Rhodes Scholar in Charles Sherrington's laboratory in Oxford, provided McIntyre with the foundations for his future work in experimental neurophysiology. Lloyd had one of the most modern laboratories, equipped with the latest valve-operated electronics. Together, Lloyd and McIntyre studied long-spinal reflexes, the origin of dorsal root potentials and the central projection pathway for Group **I** afferents in peripheral nerves. Lloyd himself was a shy, sensitive person who prided himself on his dissection skills and on the care he took in assembling data before coming to any firm conclusion... Towards the end of his time in New York, McIntyre was awarded a Nuffield Scholarship to work in Cambridge, England, with Bryan Matthews…*

While in Cambridge, Archie made frequent visits to London to see his friend Bernard Katz, whom he had met in Australia when Katz was working at the Kanematsu Institute with Eccles and Kuffler on neuromuscular transmission. Katz returned to London in 1946 where he began a series of experiments that laid the basis for our present-day understanding of synaptic transmission and which brought him the Nobel Prize in 1970. An important and revolutionary feature of Katz's work in the post-war period was his use of microelectrodes to analyse details of the trans-membrane events in neuromuscular transmission. McIntyre was deeply impressed with this technique and developed the idea that a similar approach could be used to analyse synaptic events within the central nervous system. Here he was combining his experience of whole-nerve recordings of reflex events acquired at the Rockefeller Institute under David Lloyd with Katz's novel approach at the single-cell level… While in Cambridge, McIntyre received an offer from Eccles to take up a senior lectureship in Eccles' department in Dunedin, New Zealand, which he accepted after some hesitation...

The vacancy arose because of the departure from Dunedin of Victor Macfarlane who had left to take up the Chair of Physiology at the University of Queensland. McIntyre had met Eccles some years previously while Eccles was still at the Kanematsu Institute. Eccles was interested in McIntyre because he knew Archie had worked with Lloyd, one of Eccles' main competitors in the field of central synaptic action… When McIntyre arrived in Dunedin, he assembled an electrophysiology recording set-up of the kind he had used in New York and began to explore the technique of pushing microelectrodes into the spinal cord of anaesthetised animals as a means of recording activity in central neurons, at the single-cell level...

Initially Eccles did not show much interest in what McIntyre was trying to do. He soon recognised the importance of this approach, however, and began to use McIntyre's equipment in experiments on motoneurons with Jack Coombs and Lawrence Brock that would eventually bring him the Nobel Prize". During their time in Dunedin, Eccles and McIntyre published papers together on plasticity of the central nervous system and chromatolysis in motoneurons. In these experiments Archie did most of the dissections because of the skill he had acquired under Lloyd. In writing up the experiments, Archie recalls, it was characteristic of Eccles to want to speculate further than the evidence allowed, and the speculation was often declared as a firm conclusion (Porter, Proske & Mark, 2004).

Shepherd described the scene and tenseness underlying Eccles' research explicitly:

Lawrence Brock had just completed his medical course; he was good with his hands and pulled the micropipettes. This was done on a microforge, requiring (...) extreme concentration to pull the pipettes to a fine tip and luck to get them fully filled with the electrode solution. Rall had started earlier work with Eccles but decided he would do his own project under Archibald McIntyre for his PhD thesis. McIntyre was a mild-mannered person at an early stage in his career. Eccles at the time was using the classical mechanoelectric Lucas pendulum breaks for stimulators, recording the data on glass negatives [probably produced using the falling plate camera shown in (Fig. X18)] *that were developed as they went along. When he realised he needed McIntyre's state-of-the-art equipment, he simply took it over. The experiments in McIntyre's laboratory were done behind closed doors. All efforts were bent on beating the Americans.*

I once asked McIntyre if he would write a brief account of those times, but it was too difficult for him to countenance (Shepherd, 2010, p. 92).

An unpleasant memory of Eccles' overriding dominance in the preceding years has been mentioned by the neurologist Patrick Wall[466] who interpreted his own work on afferent modulation as reflecting presynaptic inhibition, a radical concept that was roundly scorned by the academic deities of the time, including Eccles:

I was asked to visit the office of Penfield and was there confronted by Penfield, Adrian, Eccles, and Jasper. They asked me to summarize what I had said and I showed them the first source-sink analysis of spinal cord activity from which we had concluded that there was a presynaptic control of impulse transmission. They then assured me that this heresy was undoubtedly an artifact caused by dorsal root stimulation. Furthermore, they said I was the right type with my Oxford and Yale background but that I should realise that I had fallen on bad company and that there was still time to mend my ways. Their fatherly advice was a declaration of war for me. There was a little solace when Eccles adopted the main idea as his own 5 years later. (Wall, 2001, p. 482; see also Rosenberg & McMahon, 2015, pp. 9-11).

BQ. [B] Some colleagues later regretted publication of this preliminary report in the little-known "Proceedings":

466 Wall, Patrick David (05.04.1925 – 08.08.2001): UK neurologist and pain researcher. "The textbook of Pain".

...probably the most important single advance in physiology made in New Zealand was the first ever recording of trans-membrane (intracellular) potentials carried out by Professor J. C. Eccles and associates in Dunedin. This study was first reported in a local forum although it has been noted that the authors felt that publication in this medium possibly restricted the international exposure of the work [Hubbard, 1984] (cited by Pack & Cragg, 1997).

The Medical School physiologist, James Roper Robinson wrote:

Sir John Eccles, Nobel Laureate-to-be, was well established with a small but extremely active school when the Research Society was founded, and the first issue of the new Proceedings in 1951 contained a classical report by Brock, Coombs and Eccles on intracellular recordings from motor nerve cells in the cat's spinal cord. Action spike potentials of 60 to 70 millivolts and duration about 1 millisecond were recorded and shown at this meeting. A year or two before this, workers in England and America had reported potential changes with microelectrodes inserted into frog's muscle fibres. This extension to mammalian cells opened the way to much more detailed studies of single nerve cells in the central nervous system of mammals… The authors were disappointed that their communication was hardly noticed abroad. (Robinson, 1998, p. 61)

BQ. [C] Later, Eccles wrote:

There is a strange sequel. It turned out that I had been too precipitate in my complete rejection of the electrical hypotheses of synaptic transmission. The many types of synapses I had worked on are certainly chemical, but now many electrical synapses are known, and in my book on the synapse The Physiology of Synapses (Eccles, 1964) [1B-a04]) *there are two chapters on electrical transmission, both excitatory and inhibitory.* From "Facing Reality", (Eccles, 1970, p. 106); and Bennett, (1985).

BQ. [D] Student, John Scott commented on this occasion:

Eccles chose to enunciate and explore the hypothesis that central synaptic transmission was electrical, and he tested that idea until convinced that it was not so. Late one night, in 1951, he concluded from his own experiment that the central processes must also be chemical. He said calmly, "Lorente is right", and then immediately began to plan a new series of experiments. Such was the nature of the man. Scott (2006) p.676.

[This is, however, in contradiction to Eccles' description in section [BQ], where he states clearly that electrical synaptic transmission was generally accepted by many leading neuroscientists at that time for example by Lorente de Nó, so the uttered name might have been misremembered – and more likely "Dale".]

BQ. [E] The Australian neurologist, Don Todman, regarded Eccles' demonstration by intracellular recording of chemically-mediated synaptic transmission as one of the most important experiments in neurophysiology in the twentieth century and has analysed it in detail (Todman, 2008a). For an overview of the evolution of the neurotransmission concept see López-Muñoz & Alamo (2009).

BQ. [F] See also the detailed comparison (Stuart & Brownstone, 2011) of the US group (Woodbury and Patton, 1952) with the NZ group (Eccles, Brock and Coombs) in the pioneering development of intracellular recording of action potentials in neurons of the vertebrate central nervous system.

BR. [A] A table of some notable persons who worked with Eccles during his Dunedin years follows:

Table 2: Notable collaborators with Eccles in Dunedin

Name	Lifespan	Worked	Activity
Arnold Ernest Annand	1922-2011	1948-1951	electronics technician
Lawrence Brock	1923-1996	1944-1950+	glass microelectrode pioneer
Arthur Chapman	?-?	1943-1950+	Eccles' long serving technician
John Saxon Coombs	1917-1993	1950-1951+	physicist/electronics expert
Dexter M. Easton	1922-2010	1950-1951	Fulbright Research Scholar
Rosamond Eccles	1929-2024	1945-1951+	daughter, student, researcher
Norman Lowther Edson	1904-1970	1944-1951	biochemist lecturer/professor
Marianne Fillenz	1924-2013	1943-1950	student, later lecturer
John Ingram Hubbard	1930-1995	1948-1950+	student, later professor
Ainsley Iggo	1924-2012	1948-1950	student, later lecturer
John Laurence Malcolm	1913-2001	1944-1949	"Johnnie's" son; senior lecturer
Walter Victor Macfarlane	1913-1982	1947-1949	student, later lecturer
Archibald Keverall McIntyre	1913-2002	1957-1961	physiology lecturer/prof.
Karl Raimund Popper	1902-1994	1945-1950+	philosopher (based in Christchurch)
Wilfrid Rall	1922-2018	1949-1956+	student, lecturer/co-worker

Some of Eccles' associates (Fig. X19 and his best students (Fig. X20) are pictured in group photographs made shortly before he moved to Canberra.

For further information, see Douglas Stuart's complete detailed lists of Eccles' colleagues, collaborators and research students in Otago, as well as in all the other laboratories where he worked (Stuart & Pierce, 2006).

Interestingly, Eccles' Department always had a dearth of female graduates on his research staff - the result of a pact between John and Irene; as later communicated by student Marianne Fillenz:

I very much wanted to work with Eccles, but his wife did not allow him to have women collaborators. I had this confirmed by his daughter Rose Eccles who many years later told me that at Oxford, Eccles had had to ask Sherrington to permit him to stop working with Sybil Cooper. (Fillenz, 2012).

The observant fellow-student, David Cole, pithily commented:

Two other students were doing neurophysiology, Mary Hannafin and Marianne Fillenz, who idolised JCE and, in emulation, remained in research and spent her life in the heady atmosphere of Oxford (Cole, 2002).

BR. [B] The work carried out in Eccles' Department at Otago was not restricted to synaptic questions.

Another significant finding in Dunedin was that the convulsant alkaloid strychnine blocked the short latency and duration "direct" inhibition of spinal motoneurons (Curtis, 2006, p. 176-179).

Somewhat less well known is Eccles' comradely assistance (shortly before leaving Dunedin) to an enthusiastic young zoologist colleague, Elizabeth "Betty" Batham[467] during the initial stages of her almost single-handed restoration of the Portobello Marine Biological Station - situated at the tip of a hilly peninsula, jutting out from the south side of Dunedin harbour. Portobello was originally founded in 1904 as a fish hatchery, at the instigation of a local naturalist and teacher of biology at the Otago Boys' and Otago Girls' High Schools. It was managed by the Portobello Marine Fish Hatchery Board and funded by the Marine Department. During the 1930s, funding was cut and the station deteriorated until, in 1951, it was handed over to the University of Otago.

Eccles arranged use of the Portobello station for invertebrate physiological research:

Easton was a visiting faculty member on a Fulbright Research Fellowship. His NZ research focused on (1) the analysis of Lloyd's so-called "direct (primary) inhibition," using the EC ventral root recording of monosynaptic MN responses to spindle Ia sensory input in the cat, and (2) the neuromuscular system of the spiny lobster, Jasus lalandii. For the latter, Eccles arranged for Easton to work at the Portobello Marine Field Station, where he made mechanical and EC recordings in limb muscles. See Stuart & Brownstone, (2011) p. 76.

The Department of Marine Science at the University of Otago wrote in its chronology:

1950: *University of Otago negotiates to take over the fishery investigation station, having been persuaded by Professor John Eccles of the merits of having a marine station, especially for experimental neurophysiology.*

1951: *University of Otago takes over site as Portobello Marine Biological Station with Dr Elizabeth Batham as Director.*

https://www.otago.ac.nz/marinescience/about/history/otago045025.html

Here, Eccles was no doubt impressed by his English colleague JZ Young's ground-breaking experiments made on the squid giant axon and squid giant synapse in the 1930s and saw the advantage of a local marine station to facilitate research on these marine molluscs.

Batham's successor at Portobello, John Blackburn Jillett, wrote in his obituary of Betty following her mysterious disappearance in Wellington:

She returned to Dunedin in September 1950 to oversee the revival of the old marine station at Portobello, which was to be taken over by the university. Family ties and local marine biological opportunities made this a permanent return home, apart from subsequent study and conference leave. Batham's job was made daunting by the departure of the physiologist Professor J. C. Eccles, the champion of the marine station project. Although the medical school departments remained staunchly supportive, other internal university support evaporated as the marine station was seen as a competitor for precious resources (Jillett, 2000).

467 Batham, Elizabeth Joan (02.12.1917 – 08.07.1974) NZ marine biologist & lecturer, "Portobello".

BR. [C] Eccles' Christian faith as member of the Catholic Church underwent his critical appraisal in Dunedin after he delved with increasing intensity into the brain-mind question – later referred to by David Chalmers as the "hard problem" of consciousness (Chalmers[468], 1995, p. 201). The nearby Dunedin suburb of Mosgiel was from 1900 to 1997 the site of the Holy Cross College the national Catholic seminary for the training of priests. [see https://en.wikipedia.org/wiki/Holy_Cross_College,_New_Zealand]
The proximity to this theological "*oasis of prayer, study and seclusion"* obviously attracted Eccles.

Eccles' student, John Scott, wrote:

Intellectual life in Dunedin had been stimulated by the arrival of a number of refugees with varying scientific and academic interests and widely differing religious and philosophical beliefs. Eccles, at that stage of his life, was a devout Catholic, but he began progressively to challenge various doctrines. This was again an intellectual activity akin to that of his involvement in the great scientific debates of the time. The seminary at Mosgiel housed several notable scholars whom Eccles respected but with whom he did not agree.

Eccles, like Popper, did not believe that Descartes' concept of dualism of mind and matter had been discredited, nor that there were insuperable difficulties in interactionist views of brain-mind liaison. Eccles explored these ideas in a series of lectures in Dunedin in 1951, which became the basis for the Waynflete Lectures delivered at Magdalen College, Oxford, in 1952 and published as "The Neurophysiological Basis of Mind" (Oxford, London, 1953). (Scott, 1999 & 2006).

BS. [A] Eccles brought concrete demands for his future Australian domicile to his new employer before moving to Canberra:

The fourth medical professor appointed by Florey, John ('Jack') Eccles, Professor of Physiology, insisted that the Department of the Interior provide him with a block of land commensurate with his academic standing and family size. It was to contain a house, 'a square dance lawn, a swimming pool and a tennis court' for his wife, Irene ('Rene'), and their nine children. His demands were completely fulfilled, as confirmed by daughter Mary (Mennis, 2003, p. 31).

Eccles described the process by which he acquired a large site at 28 Monaro Crescent, Red Hill:

One had to select a suitable block of land and then have a house built on it. I had officials of the ANU helping me and eventually on October 9th I selected a very large block of land in a very good site adjacent to the Embassy area. The government owned all the land and one had to make a nominal deposit and then pay a rental of £18 a year which I did on 9th October 1950 for a 99-year lease.

The neurophysiologist did not, however, avail himself of the services of a design architect, preferring to design the house himself and engage Tom Haseler, a

468 Chalmers, David John (20.04.1966 –) AU cognitive scientist, philosopher & author.

Commonwealth Department of Works architect who had supervised University House, to complete the documentation and engage a builder (Cameron, 2012, p. 20).

Although Eccles was proud of his efforts as an amateur architect, his daughter Mary thought otherwise: '*He may have been a brilliant scientist, our dad, but he was no architect. The house, with its two long dark passages at right angles to each other, was not the best design for living.* (Mennis, 2003, p. 150).

Mary wrote of the house:

After 1967, when dad left for America, mum continued to live in the house in Monaro Crescent in Canberra for a number of years. We were able to celebrate many family gatherings with her, birthdays, Christmas etc… Towards the end of the 1970's, Mum sold the house and property to the Vatican and a large three-storied residence was built across the tree belt and tennis court. It is now the official residence of the Papal Nuncio to Australia (Mennis, 2003, p. 169).

Sophisticated Canberra people and diplomats smiled to themselves, too, when it was announced that the Vatican planned to build a residence for the Apostolic Pro Nuncio (the diplomatic representative of the Holy See) adjacent to the home of the Russian Ambassador. The Vatican was reported to have paid $150,000 for the site of about one hectare in Monaro Crescent, Red Hill, and the house it contained (Barrow, 1978, p. 11).

The Eccles House was demolished for Enrico Taglietti's 1976 Apostolic Nunciature. (See National Library of Australia, MS 9330, Folder 1, p164.).

Irene moved to Launceston in Tasmania and built a house next to the Carmelite Monastery there, where she lived a semi-contemplative life as an Oblate of the Benedictine Order.

BT. [A] Eccles' Dunedin colleague Ainsley Iggo commented:

Among later vivid recollections is a Physiological Society meeting in London in 1952. Eccles was about to present the experimental evidence that refuted his electrical hypothesis of synaptic transmission in the mammalian nervous system. His excitement was almost palpable (Iggo, 2001, p. 288).

The Waynflete lectures were given during January and February 1952) and later published in book form (Eccles, 1953), [1B-a02]. The four papers (1952a-d) that he referred to there as "still-unpublished" were published as: (Brock, Coombs & Eccles, 1952a) [1A-103], (Brock, Coombs & Eccles, 1952b) [1A-105] and (Brock, Coombs & Eccles, 1953a) [1A-110]: The "unpublished observations" paper (1952d) appeared as (Brock, Coombs & Eccles, 1953b) [1A-115].

Neuroscientist, Karl H. Pribram[469], in his reminiscences on Eccles' book, stated:

After a sufficient number of beers, I asked Eccles: "You have written such a marvellous book on neurophysiology (Eccles, 1953) – how could you end it with a really horrible chapter espousing dualism? Eccles straightened his lanky frame and we spent the remainder of the evening discussing the merits of dualism (as opposed to my monism, which Eccles wrongly interpreted to mean that I was a materialist

469 Pribram, Karl H. (25.02.1919 – 19.01 2015) AT(J) psychologist & psychiatrist; "holonomic brain model"

reductionist). I had thought that Eccles' dualism was merely that his Catholicism was showing. Although this was a correct assessment, he convinced me that he had a thoroughly thought-through sophisticated position (Pribram, 2010).

BT. [B] Fillenz described Eccles' Waynflete lectures as follows:

They were an account of his mould-breaking experiments on the elucidation of synaptic mechanisms, as well as his conversion to the theory of chemical transmission. In his last lecture, he dealt with the mind-brain problem. There was an enormous audience. (Fillenz, 2012).

Eccles' newfound belief in synaptic transmission via chemicals and his dramatic rejection of electrical transmission surprised or even amazed some of his contemporaries. Karl Popper recalled one such occasion as follows:

In about 1951 I met in Oxford a very **very** *well-known scientist and I said to him that I was a friend of Eccles and he said, "Eccles, a very good man but you know, the man must be a bit crazy; he refutes his own theories".* (Saunders, 2000).

Eccles' former opponent and long-standing friend, Dale, provided a nicely fitting allegory for Eccles' abrupt change of belief:

A remarkable conversion indeed; One is reminded almost inevitably of Saul on his way to Damascus when sudden light shone and the scales fell from his eyes. (Dale, 1954). (Here, Dale quoted from the Holy Bible; book*: The Acts of the Apostles*, 9:18.)

[The turn-about acknowledged in his Waynflete lectures enabled Eccles to escape relegation to the company of discredited scientists, such as suffered by the unfortunate bacteriologist, Adrianus Pijper[470], who was unable to retreat gracefully after defeat in a hard-contested 1950's battle in defence of his defiantly-held belief (based on sunlight dark-field LM observations) that bacterial flagella were merely artefacts; – a fight which he lost against new TEM evidence presented by Woutera van Iterson (Strick, 1996).]

GE. Stage 5 career notes (for sections CA to CH)

CA. [A] Biographer Gordon Shepherd nevertheless criticised Eccles' later treatment of Lloyd, at one time his student at the Sherrington lab:

During the 1950s Eccles engaged in several unduly harsh efforts to apply the Popper doctrine to falsifying the findings of colleagues. One was David P. C. Lloyd, a former student at Oxford, over details of synaptic connectivity in the spinal cord. (Shepherd, 2010, p. 117-118) For more details of Lloyd's life and work see his obituary (Patton, 1994).

Of interest is the congenial relationship between Eccles and an Australian athlete, Douglas Gordon Stuart:

Stuart became an associate professor of physiological sciences with tenure at UC-Davis in May 1965. At UC-Davis, Stuart had an extremely heavy teaching load with

470 Pijper, Adrianus (1886 – 1964) NL bacteriologist &pathologist in Pretoria SA.

*veterinary and graduate students. Nonetheless, he developed a sophisticated electrophysiological laboratory for spinal cord research with the assistance of a gifted young electronics/computer engineer, Robert Reinking, who remained with Stuart for 35 years before becoming a senior research engineer in the UA's Applied Mathematics Program. It was at UC-Davis that they, with the help of Sabura Homma and Koichi Ishikawa (Univ. Chiba, Japan) began to record intracellularly from mammalian spinal motoneurons. The 1963 Australian Nobel Laureate, Sir John Eccles (1903-1997), visited Stuart at UC-Davis in 1966, and subsequently incorporated Stuart and Reinking's then-unique, electromagnetic, servo-controlled muscle stretching apparatus (*see: Reinking & Stuart, 1974*) into his own new laboratory set-up at the American Medical Association's short-lived Institute for Biomedical Research in Chicago, IL. Eccles felt that Stuart had insufficient training in the nuances of spinal cord neurobiology (particularly those introduced by Sherrington and refined subsequently by his trainees, including Eccles), so he personally recommended him to Anders Lundberg at the University of Goteborg, Sweden* [where they worked together during 1970-71]. *Eccles and Stuart remained close friends thereafter, with Eccles spending many hours describing to Stuart his perception of the history and strategy of neurophysiology and, in particular, the impact of Charles Sherrington (1856-1952) on the field,* (see: Hixon, 2014 and Stuart, 2018).

CA. [B] The famous ESRU equipment is depicted in Fig. X21. Its design and use have been discussed in detail (Stuart & Brownstone, 2011).

This unit, based on the advice of Eccles and Archie McIntyre, Reader in Eccles' Department, regarding the requirements of neurophysiologists, provided facilities which were unmatched in laboratories elsewhere. (Curtis 2001b, p. 409).

Les Davies (neurochemistry researcher in Graham Johnston's neurochemistry lab. 1972-75) communicated to JPC (20.10.2020) his reminiscences about the ESRU-based electrophysiology set-ups at the JCSMR in Canberra:

I haven't seen it, but I think that the school has a 'Tardis' (aka an old electrophysiology array) from either Curtis's or Eccles's time, set up in the basement.

CA. [C] In his obituary of Paul Fatt in 2016, Jonathan Ashmore paid homage to the revolutionary advances that Paul pioneered in the difficult fabrication of special glass double-barrelled electrodes (Fig. X23) which were required for intracellular potential measurements:

Although Eccles's laboratory had just started to use intracellular microelectrodes, Paul's work in the laboratory resulted in a significant advance in understanding synaptic transmission. The first of their series of major papers established that Ia and Ib afferents to the cat spinal cord generated distinct synaptic potentials {Eccles, Fatt, Landgren & Winsbury 1954, [1A-120]}*, using the new developments in the engineering problem of making a micromanipulator stable enough for neuronal recording in vivo. The second of the papers provided the first convincing demonstration that excitatory and inhibitory synaptic potentials could be recorded intracellularly from mammalian motoneurones* {Eccles, Fatt & Koketsu 1954, [1A-121]}. *These experiments also identified the inhibitory potentials formed by a recurrent loop onto* *the motoneurones from the Renshaw cells. Their work together on motoneurones identified the ionic mechanism underlying postsynaptic inhibition as arising predominantly from an increased chloride conductance. This was deduced from the observation that microelectrodes filled with the normal KCl solution led to a progressive diminution and even reversal of the inhibitory postsynaptic potential* {Coombs, Eccles & Fatt 1955, [1A-125]}. *During this study, Paul was involved in developing the double-barrelled microelectrode technique—two glass barrels fused and twisted together by melting, and then pulled into a fine tip with a diameter of less than 1 µm. One barrel was used to record the synaptic potential changes, and the other injected current to alter the ionic composition or to pre-set the membrane potential of the motoneurone* (Ashmore, 2016, p. 174).

Curtis noted that:

Eccles had appointed an excellent and very helpful technical staff, including Arthur Chapman, who had previously been his laboratory assistant in Oxford, Sydney and Dunedin, and Gerry Winsbury, an innovative and skilled engineer. Much of the mechanical equipment, including sturdy animal frames, micromanipulators and microelectrode "pulling" machines was designed in the Department and was made in the Department, or by members of the JCSMR main workshop (Curtis, 2006, p. 177).

Some of Winsbury's work is shown (Fig. X24), also showing how his equipment would have been used for cat experiments by Eccles (Fig. X25).

Years later in the 1970s, stories of life and events in Eccles' lab were still being told in Canberra:

It was enthralling to listen to Arthur Chapman tell stories of those heady days when he worked as laboratory technician for Sir John Eccles. I often thought that it was a great pity that he never wrote his memoirs – but perhaps some of the stories told were better left unrecorded! (Davies, 2009).

CB. [A] The specialized group of inter-neurones which mediate the inhibitory path from motor axons first received the name "Renshaw cells" in Eccles, Fatt & Koketsu (1954), [1A-121], p. 533.

CB. [B] Anders Lundberg was invited to Canberra as Senior Research Fellow. Together with Rosamond Eccles he undertook systematic analysis of synaptic actions of primary afferents on spinal motoneurons and interneurons using the intracellular recording technique developed in Canberra. This work resulted in 16 major papers (1957-1961). Quoted in his obituary is Sir John Eccles' description of Lundberg's visit:

So impressed was I with the performance of Anders Lundberg that I tried ... to get him to stay in the position of a readership in my Department, which I would have had made especially for him".

Later in the obituary is Eccles' description of Lundberg as:

"... one of the leading physiological investigators in the world. In fact, I regard him as the person of his generation who is closest in neurophysiological thought to my old master, Sir Charles Sherrington" (Alstermark et al., 2010, p. 194).

CB. [C] Bob Young later wrote of his time with Eccles:

I went to the ANU in Canberra to spend a year getting an introduction to Neurophysiology from Professor J.C. Eccles who went on to become Sir John Eccles, Nobel Laureate. He was using microelectrodes to study the fine details of the behaviour of single nerve cells in the spinal cord of cats. I returned to Harvard University to spend the rest of my academic life in Neurology and Neurophysiology, using microelectrodes to record from human muscles, peripheral nerves, and eventually from cells deep within the brains of patients with Parkinson's Disease and similar disorders to permit effective treatment of their symptoms. I also became very fond of Australia. R. R. Young (Fulbright Stories September 23, 2021).
https://fulbright.org/2021/09/23/neurophysiology-robert-rice-young-australia-1956/

CB. [D] The early group of Canberra researchers is pictured in Fig. X22. Vernon Brooks later wrote: *The physiology department at the Australian National University was a small, but very exciting, place because Eccles maintained an unremitting drive to understand the mechanisms of spinal integration. The department was really his laboratory group that consisted of Jack Eccles, his daughter Rose, Jack Coombs, Paul Fatt, Bill Liley, David Curtis, and myself. I was teamed up with David Curtis, and we worked well together. Eccles spent his mornings writing, and then joined the experiment after lunch and worked with us until it was done. The John Curtin School was still a building site and we worked in army-style prefabs. The campus was unfinished and Canberra in general was in transition. The master plan for the city had not yet been implemented, and the site of the planned central lake was still sheep paddocks, but University House, just finished at the shore of the future lake, had come complete with a vice chancellor's barge that sat on the grass. Housing was scarce because the Public Service was being moved into town from Melbourne; but the university had managed to reserve housing for personnel such as us. When we arrived Landgren was just about to leave, and since Koketsu had just left, we were moved into the vacated flat. Eccles used to pick me up first thing in the morning and drop me off usually in time for a late supper or even later at night after a long run. The experiments were lengthy because we obtained as many inhibitory curves of various reflexes as possible, in addition to intracellular recordings from spinal motoneurons. The longest experiment ran for 3 days, by which time it taxed the air-conditioning* (Brooks, 2001, p. 83-84).

Eccles' daughter Rosamond contributed in many ways to the scientific success of the Eccles Department during her time here until 1968. See Carleton, (2023).

To give another impression of life in the Eccles laboratory, here is an excerpt from an interview between Jonathan Felix Ashmore (Bernard Katz Professor of Biophysics at University College London) and Paul Fatt, Eccles' research colleague in the 1950's:

JA: Did you find Eccles an easy man to work with?

PF: He was one that was just be shouting (you've met him); he's really loud and he would shout at me abuse and then I would laugh at him and he would laugh too, understand. But he had other people who were frightened of him; Coombs, who would build the electronic equipment. But no, I actually had no trouble with him; but he could be very, very difficult [...] and insistent, determined and would say "Oh yes yes yes;

that was a common thing. He was so insistent and argued with you against something. And the next day he'd come along and present your story.

JA: […] How interesting.

PF: He was not aware of it, totally unaware of it. It happened several times. That was Eccles. But his daughter [w]as also in the department. Actually, he had nine children.

JA: Goodness.

PF: Anyway, I don't go into personal things (Ashmore, 2013, p. 21).

The experimental equipment used in Canberra was impressive and of ever-increasing sophistication, thanks to local applied ingenuity. Eccles' group was also rapidly departing from electromechanical devices and entering the age of electronics. Eccles' Australian co-worker, David Curtis, wrote of the laboratory scene of 1954:

Coombs accompanied Eccles to Canberra and had also designed stable and low noise amplifiers, "cathode follower" input stages necessary for recording through high-resistance electrolyte-filled microelectrodes and many other items of equipment. All of these initially depended on thermionic "valves," and radio-B "dry" and "lead-acid" batteries. Oscilloscope traces were photographed on still or moving 35-mm film using "Grass" kymograph cameras, and averaging was performed by superimposition of many photographed traces. Many hours were spent in measuring filmed responses and in calculating results using logarithmic tables or slide rules, and later a hand-cranked [mechanical] *calculator* (Curtis, 2006, p. 176).

(The Grass Instrument Co. Kymograph Camera was designed by Albert Grass in the 1950s to photograph oscilloscope traces on photosensitive film and paper for capturing fast neurophysiological events. The original version was built and improved upon for several years e. g. the C4 model).

In late 1954, as my introduction to neuropharmacology, I joined Eccles and Vernon Brooks in a study of the effects of tetanus toxin on a number of short latency and duration inhibitions of monosynaptic spinal reflexes by single volleys in a variety of muscle and cutaneous afferent fibres. Recurrent inhibition mediated by Renshaw cells was also examined. The toxin was injected either into a peripheral muscle nerve or directly into the spinal ventral horn in order to initially localize its action so that reflexes and inhibitions on the contralateral side could initially be used as controls. These experiments usually extended for 24 hours or longer. Like strychnine, the toxin enhanced polysynaptic but not monosynaptic spinal reflexes and diminished and eventually abolished all of the inhibitions studied. Because the toxin appeared to have no effect on field potentials generated by interneurons on the "direct" and recurrent inhibitory pathways, it thus appeared to act either pre- or post-synaptically at spinal inhibitory synapses. This study resulted in my first co-authorship of a letter to Nature and a paper in the Journal of Physiology. (Curtis, 2006, p. 178).

In 1957 Eccles became aware of a newly-discovered endemic encephalitic-like transmissible brain affliction, kuru, affecting the Fore tribes of Kaintu and Okapa in

Papua New Guinea. He enthusiastically supported further its investigation (kuru was later identified as the first known human prion disease):

In late October 1957, Carleton Gajdusek[471]] *and his party set out from Okapa to traverse Papua down the Lamari River into the Gulf of Papua and to Port Moresby to get help to facilitate the clearance of all the blocks in the research programme. He arrived in Moresby on Saturday 1st November. My wife and I were hosting a party for six visiting professors and deans from Australian universities who had been invited to attend the new Port Moresby General Hospital opening on the Sunday. Carleton was invited to meet them. He arrived as he had travelled in shirt and shorts for the dinner party with only one sandshoe as the other had been lost on the trip. The professors were spellbound as they heard first hand his description of the clinical, anthropological and environmental aspects of kuru. They were like bees around a honey pot trying to understand what they saw to be a new disease being described to them for the first time. Their interest generated questions on many aspects and suggestions of how they might be able to assist with personnel and laboratory support. Profs Sydney Sunderland, a neuroanatomist from Melbourne, John Eccles, a neurophysiologist from Canberra, and Norrie Robson, a physician from Adelaide, were the most interested and proceeded in the next week to visit Kainantu and Okapa* (Scragg, 2008, p. 3663).

CE. [A] The cat, as preferred experimental animal, dominated the research lives of both Sherrington and Eccles. Eccles brought his technician, Arthur Chapman (who had remained faithfully with him from his "Sherrington days" in Oxford) to Canberra to provide assistance with feline experimental preparations. In this excerpt from the interview with Jonathan Ashmore, Paul Fatt describes Chapman's duties in Canberra (which could scarcely have differed much from those he had performed earlier in Oxford, Sydney and Dunedin):

JA: So was this the first time you had worked on whole animals, done whole animal experiments, I suppose. Is that right?

PF: Yeah.

JA: And at that stage there was no difficulty in moving to another animal?

PF: But it's still what you had to do on a frog. You have to pith it and dissect it so you were working on a whole animal in that process. You have a lobster, crayfish, you have to take the leg off and hope it doesn't hurt too much.

JA: So, were you the person, did you do all the preparatory work for that as well or was that Eccles?

PF: Arthur Chapman. He was amazing.

JA: Yeah.

PF: He was the technician. And the cats, we worked on cats; and the cats were feral animals that were caught in cages out in the bush. They were just outside of Canberra, I suppose, or in the city. They had cages with a trap door that only a cat would go in to get a piece of meat or a mouse that we had in there, and it got caught and brought

471 Gajdusek, Daniel Carleton (09.09.1923-12.12.2008) US medical researcher of kuru. (NP 1976)

in the cage into the lab. And then Chapman had to deal with it, Arthur Chapman. And he had been in Birmingham in the Salvation Army. He would still play this, it was some big instrument, a big brass instrument, and somehow, what he did depended on what he could do because of his Salvation Army duties. And yet he had time to play his big brass instrument.

JA: In the lab?

PF: No, no, he didn't play in the lab. But when he got an animal in the cage, it was delivered to him in the cage. You couldn't open the cage because these were really fierce animals. These are cats that are just wild. Actually, I'm surprised they hadn't exterminated all the other animals. Anyway, so he would poke it with a syringe while it's in the cage, so right through the cage bars, and anaesthetize it and bring it out and prepare it; but not the final dissection. I think Eccles would do that, yeah (Ashmore, 2013, p. 22).

The required steady supply of trapped feral cats (aptly termed "a destruction of cats" - the traditional English collective noun applied to wild cats) for experimental use could dwindle at times to the paradoxical situation of "a paucity of cats". Eccles' son, Peter provided reminiscences of his childhood years with the family's pet hens and cats in Dunedin which are enlightening: (See section FF).

Presumably, Chapman would have completed his part in experiment preparation by severing the cat's spinal cord at the appropriate level in the skull with the apparatus described by (Sherrington, 1915; Miller & Sherrington, 1915). The usage of this device by Eccles in Sherrington's laboratory has been described (Davenport, 1993, p. S19).

In order to comply with the British Home Office regulations on animal vivisection experimentation, which did not permit students to use anesthetized preparations (Davenport, 1993), the animals during an initial anaesthesia were either decapitated or else decerebrated by means of the Sherrington guillotine (Eccles & Gibson, 1979, p. 47).

CE. [B] See Eccles, Libet & Young, (1958).

CE. [C] Shepherd has discussed Eccles' implacable position on dendritic dominance in relation to Wilfrid Rall's research:

During the 1950s Eccles engaged in several unduly harsh efforts to apply the Popper doctrine to falsifying the findings of colleagues. One was David P. C. Lloyd, another was his former student Rall, who brought forward evidence from Eccles's own recordings for dendritic dominance of synaptic integration. Eccles would brook no opposition, claiming another explanation based on a postulated persistent current. Rall refuted this explanation, and Eccles eventually abandoned it. But as late as 1960 he was still defending the idea that dendrites had mostly nutritive roles, being too distant to affect synaptic integration, which he believed was focused at the cell body where his recordings were made. His opposition greatly impeded recognition of the significance of Rall's work and the value of theory in neuroscience, in which Rall first adapted basic cable theory followed by his new methods of compartmental analysis to show that most synaptic integration takes place in the dendrites. However, as was typical of Eccles, harkening back to his interactions with Dale, when Rall and his colleagues came *forward with evidence for novel interactions between dendrites, it was Eccles who organized and invited Rall to co-chair with him a meeting in 1968 where these new findings were presented. The reason for his harsh attacks may be traced back to his training in England, where such exchanges, as described above, could take place between colleagues within the clubby atmosphere of the Physiological Society. However, in the outside world, they were interpreted as, and had the effect of, doing unnecessary harm* (Shepherd, 2010, p. 117).

Later, Shepherd referred again to this matter:

It was early in his career, at a time when he [Wilfrid Rall] was attempting to establish the new field of computational neuroscience in the face of considerable opposition, not least by his former mentor, John Eccles. I learned at first-hand how unduly harsh criticism can bring hardship to a young investigator and deny deserved recognition (Shepherd, 2012, p. 654).

Rall also referred to this incident, which occurred at the time when he was working with the laboratory of Michelangelo Fuortes[472] and Karl Frank[473] at NIH, Bethesda. Both the Fuortes' and Eccles' groups had reported unexpectedly low values for the membrane time constant (about 1/3 the estimated values based on synaptic potential decay). Rall reminisced:

*Both groups had analysed their transient records as if they were composed of a single exponential. Although they did not say so, this meant that they had implicitly assumed a space-clamped neuron or an isopotential soma without dendrites. If one does not postulate an explicit biophysical model that includes such an essential complication as the presence of dendritic cables, then one runs the risk of using overly simple data analysis that yields an incorrect value for the membrane time constant. The error was pointed out in a brief note to Science (*Rall, 1957*) followed by a paper with a full explanation and discussion that was submitted to the Journal of General Physiology in 1958. Sadly, this paper was rejected, at the urging of a negative referee; however, it did appear in 1959 as a research report of the NMRI in Bethesda. [...] Frank and Fuortes freely acknowledged their error. Eccles did so only indirectly, by slightly revising his estimates; his postulated residual phase of synaptic current became reduced in magnitude and was later abandoned.* (Rall, 2008, p. 310)

Further discussion on this controversy can be found in (Jack[474], & Redman[475], 1995, pp. 29-31).

CE. [D] Sperry carried out experiments on transposition of muscles and nerves in the rat from 1939 onwards. See e.g.: Sperry, (1941); Sperry, (1945).

CE. [E] See Close, (1965).

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472 Fuortes, Michelangelo G. F. "Mike" (1917 – 1977) IT Physiologist. Peripheral visual system in vertebrates.

473 Frank, Karl "Kay" (1916 – 1993) DE Pioneered spine intracellular recording. "Presynaptic inhibitory action"

474 Jack, James Julian Bennett (25.03.1936 –) NZ physiologist. Student of Dr. Archie McIntyre in 1950s.

475 Redman, Stephen John (14.05.1938 –) AU Electrical engineer & physiologist.

CE. [F] Early publications on the TEM fine structure of the synapse in ultrathin sections using TEM include those of Gray, (1959), Boycott[476], Gray & Guillery[477] (1961) and Saito, (1972).

CE. [G] Edward Kravitz[478], research colleague of Steve Kuffler at the Harvard Medical School, commented:

For me, it was the time [1960-1970] *of the demonstration that GABA is an inhibitory transmitter compound, a body of work carried out despite the proclamations of two international congresses (held in 1960 and 1961) that GABA was not a transmitter compound in invertebrate or vertebrate nervous systems (Ernst Florey[479] and Jack Eccles led the defense of those positions). Before I joined the laboratory, Steve, Dave Potter and other colleagues had shown that GABA was present in the central and peripheral nervous systems of lobsters. GABA also had been shown to have a high physiological specific activity, but other inhibitory compounds were present in the tissue extracts and it was not known whether any of these was uniquely associated with inhibitory neurons. Spurred on by Florey's ability to dissect single axons from crustacean nerve bundles, Steve, Dave Potter and I dissected meter lengths of single inhibitory and excitatory axons from lobster walking leg nerves, and with extracts of these nerves showed that GABA alone of the inhibitory substances was asymmetrically distributed, while glutamate, the principal excitatory compound, was present in both excitatory and inhibitory axons. Masanori Otsuka (on sabbatical from Tokyo Medical and Dental University) joined us shortly after the completion of these experiments and his studies generated the first detailed charts of the positions of identified neurons in an invertebrate central ganglion in which physiological identification, cell body location and single cell biochemistry were combined to construct the maps.* (Kravitz, 2000)

CE. [H] Co-worker, Masao Ito described Eccles' laboratory during his three years stay in Canberra:

I planned a trip to Canberra. I had been married to my wife Midori since 1956, and in February 1959, we left Yokohama Harbor on a 3000-ton ship on which we travelled for 1 month to Hong Kong, Borneo, Cairns, Brisbane, and finally Sydney, from where we flew to Canberra. Canberra was like paradise. We lived in a comfortably furnished flat, four km from the John Curtin School of Medical Research of the Australian National University; it took no more than ten minutes to drive. John Eccles' department occupied the western half of the third floor of a long brick building. At one end of the corridor was a professor's study and laboratory. At the other end was a room for technicians and a storeroom. In between were small booths for individual researchers

476 Boycott, Brian Blundell (10 12.1924 – 22 04.2000) UK zoologist and pioneering electron microscopist.

477 Guillery, Rainer Walter (28.08.1929 – 07.04.2017) DE(J)/UK anatomist/electron microscopist "EJN" founder.

478 Kravitz, Edward Arthur (19.12.1932 -) US Neurobiologist, GABA neurotransmitter, procion yellow staining.

479 Florey, Ernst (03.04.1927 – 26.09.1997) AT neurobiologist & science historian. GABA, "Neuromodulators".

on one side of the corridor, while on the other side were three laboratories used by David Curtis, John Hubbard, and graduate students, respectively. The four laboratories were air-conditioned, and fully equipped with instruments designed by Jack Coombs. If any problem occurred, several technicians rushed to fix it. In the morning, technicians distributed anesthetized animals to each laboratory, and developed films that had been exposed the day before. Data were continuously collected in these four laboratories, and numerous papers were sent out for publication. At the John Curtin School library, current and past issues of almost all journals published at that time were available. These conditions are not extraordinary today, but it seems like a miracle to me that they existed forty years ago in a university department. John Eccles' department attracted about seventy researchers from abroad. Its alumni association list includes the names of numerous eminent individuals presently considered leaders in the world of neuroscience. Among these, Per Andersen, Tatsunosuke Araki, Platon Kostyuk[480]*, Olov Oscarsson, Tomokazu Oshima, John Phillis, Tom Sears, Rod Westerman, and Bill Willis were my contemporaries. It seems to me to have been one of those rare occasions in which a single scholar attracts a large number of young talents who then became the leaders of the next generation. During the first year of my stay, I had a precious opportunity to work as part of a team with John Eccles and his daughter, Rose. We studied the ionic permeability of cat spinal motoneuron membranes by injecting two ion species in combination through double-barrelled microelectrodes, each barrel filled with a different solution. I learned the energetic and organized ways to conduct cat experiments. In addition, during the English-style tea time often held at midnight during a break from an experiment John Eccles often talked about his days in Oxford, and especially about Charles Sherrington. Apparently, John Eccles was taking Sherrington as his role model. Eccles, born in 1903, used to ask how he could stop working when Sherrington had started to fully work only after the age of sixty… The 3 years passed quickly and fruitfully and, in 1962, I decided to return home. We took with us our two children who had been born in Canberra, and a great respect for John Eccles and his department. One year later, John Eccles was awarded the 1963 Nobel Prize for Medicine and Physiology* (Ito, 1998, p. 173-174).

Jeff Watkins[481] (arriving in 1958 to work as chemist with David Curtis) retained plenty of vivid memories of life in the Eccles Department at ANU, as told during a later-published interview (Healy, 1998):

Healy[482]: What was he like, Eccles?

He had one overriding interest and that was his research. He didn't really want to talk much about anything else actually - at least, that was my impression at the time. In retrospect, I'm sure he would have talked enthusiastically about 'consciousness' and

480 Kostyuk, Platon Hryhorovych (20.08.1924 – 10.05.2010) UA neurobiologist. Calcium channels.

481 Watkins, Jeffrey Clifton (20.12.1929 –) AU organic chemist ANU 1958-65. "Neuro-excitatory amino acids".

482 Healy, David (27.04.1954 –) UK psychiatrist/psychopharmacologist/author, "antidepressants Pharmageddon".

the nature of 'mind'. I didn't get to talk to him very much because I wasn't one of his group. I virtually only saw him at seminars and in the tea room or corridor and whatnot. He obviously had a very sharp mind and dominated all the seminars - most of which he gave personally. It was nice to meet him again in 1993, after twenty-eight years, on the occasion of his 90th birthday celebration. He was still working more or less until about 4 or 5 years ago, mainly on philosophical topics and has written a number of books - none of which I've read yet, I'm afraid. I did read a very early book, The Neurophysiological Basis of Mind, based on a series of lectures he gave at Oxford in the mid-50s. The last chapter, as I recall, was on the nature of mind and I remember a neurophysiologist I was friendly with saying that the book was very good except for the last chapter. But I must say I enjoyed this chapter most of all, though I'm not sure I accepted all his assertions. Everyone in his group was well organised. His students could be there at 3 in the morning but they were nevertheless expected to be there again at 9 a.m. or before, on the next day, to process the results of the night before. The students I think also prepared the animal for each experiment and on those days Eccles himself would come into the lab about 11 a.m. to take charge of the experiment. The students took notes, I believe, while Eccles manipulated the microelectrodes. He was keen on 'wholesome' activities such as square dancing, 'social' tennis - he had a tennis court - and walking. I was invited only once for Sunday afternoon tennis. Partnering Lady Eccles in doubles I let rip one of my erratic cannon-ball services which whistled dangerously past her ear. She displayed considerable nervousness thereafter. Also, my performance seemed not to fit the description of 'social'. To make matters worse, at that time I smoked. That was definitely unwholesome. My further participation was not requested. I can tell you a story about "The Nobel Prize that wasn't". We all used to work at nights. One night a reporter on the Canberra Times rang up to say that it had just come over on the 7 p.m. BBC news, from London, that Eccles had won the Nobel Prize. She then came to see him in the lab. Aged about 18 she said "Could you tell me, Sir John, what exactly is the Nobel Prize"? Somewhat incredulously he replied: "Young lady, if you don't know that, you had better go back and send someone who does!" I went off to purchase suitable celebratory beverages, returning well stocked. Eccles - virtually a teetotaller - allowed himself half a glass of sherry, then went off home to celebrate with family and friends there. At 9 p.m. the BBC repeated the report, and the party at the lab gathered steam. By 11 p.m. most experiments had been abandoned. But in the 11 p.m. news the BBC corrected the error. Another Australian, not Eccles, but Macfarlane Burnet of Melbourne, had won the Nobel Prize, shared with Medawar. Eccles immediately came back to the lab to resurrect what he could of the experiments, staying presumably till 3 or 4 am as was customary. The next day, by chance, the real winner of the Nobel Prize turned up in Canberra while Eccles, David Curtis and I were having lunch together. Eccles leapt out of his chair, rushed over to the chap, congratulated him warmly, indeed most effusively, and showed none of the great disappointment and embarrassment he must have been suffering. Luckily, he did win the Nobel Prize two years later, which he shared with Hodgkin and Huxley. There are lots of other little anecdotes. One of the biochemists at the tea break one day said "I *am finding it difficult to keep up with the literature these days. How do you cope, Sir John?". Eccles replied that "People tend to send me reprints if they want me to know of their work. If they don't send me reprints, they don't deserve to be read!" These were unsolicited reprints of course. An Eccles tea break usually consisted of two cups of tea, swamped with cold milk, the quicker to be able to consume them. Both cups were gulped down while still standing at the counter, giving a total tea-break of approx. 15 secs plus travel time to and from his lab, one floor up. If you wanted to talk to him you had to chase after him as he left the tea room and complete your discussion, often from two paces behind, before he got back to the lab*. (Watkins, 1998, p. 355).

CE. [I] For a detailed report on Eccles' presynaptic inhibition research see Willis (2006).

CF. [A] See Eccles, (1964), [1A-261]. Published by: American Association for the Advancement of Science. This lecture (plus those of his two joint Nobel Prize awardees; Alan Hodgkin and Andrew Huxley) are downloadable from the Internet as:

https://www.nobelprize.org/uploads/2016/07/eccles-lecture.pdf
https://www.nobelprize.org/uploads/2018/06/hodgkin-lecture.pdf
https://www.nobelprize.org/uploads/2018/06/huxley-lecture.pdf

Regarding the Nobel Prize, Burton Feldman[483] commented:

Physiology won many Nobel Prizes through the 1930s, particularly in the anatomy of the nervous system, muscle, motor, and respiratory mechanism. But even as it gathered prizes, it was dissolving into the specialties it had launched. A medical historian who was also a physiologist [Karl E. Rothschuh[484]] *concluded in 1953 that physiology is "no longer a uniform and coherent field of investigation." "' Perhaps the last prize to classical physiology was the 1963 award to John Eccles, Alan Hodgkin, and Andrew Huxley for, in the Nobel citation, "elucidating the unitary electrical events in the peripheral and central nervous system."* (Feldman, 2000, p.238).

John Eccles, his personality, his research, his adoption of Popperian principles and his sudden but successful change of stance in the interpretation of synaptic transmission, which lead to award of the Nobel Prize have been analysed in detail as a case study of the requirements and politics associated with the Prize in the book: "Attributing Excellence in Medicine", edited by Hansson, Halling and Fangerau (see De Sio, Hansson & Koppitz, 2019).

CF. [B] See (Eccles 1964) [1B-a04]).

CG. [A] The research on thalamus has been reviewed by Anderson (2006).

CG. [B] The Renshaw cell was first identified by the unusual bioelectrical behaviour of certain interneurons in the ventral horn (Renshaw, 1942). More information about the Renshaw cell was presented years later (Eccles, 1985).

483 Feldman, Burton Edward (03.05.1926 – 10.01.2003) US English prof. Published history of the Nobel Prizes.

484 Rothschuh, Karl Eduard (06.07.1908 – 03.09.1984) DE coronary physiologist and medical historian.

CG. C See book: Eccles, Ito & Szentágothai (1967), [1B-a10]. Eccles also published a short biography of Szentágothai (Eccles, 1982).

CG. D See also a review article on Eccles' research into cerebellar circuitry, (Ito, 2006).

CH. A One of Eccles' colleagues, the American neuroscientist Alex Karczmar[485] commented on the rigid employment situation in Australia with an amusing story in the USA as follows:

*The Nobel Prize did not stop the Australian Civil Service from insisting on Eccles' retirement at the then mandatory retirement age of 65 (Eccles, personal communication); so, Eccles pre-empted the threat by becoming in 1966 the head of the American Medical Association's Institute for Biological Research in Chicago. A local paper announced that "**Eccles does not wash to be retired**"; this statement was quoted in the misprints column of the New Yorker with the comment: "**Dirty old man!**" The story may appear to be irreverent, but Sir John enjoyed it* (Karczmar, 2001a).

CH. B The commissioned portrait by artist Judy Cassab of Sir John (which presently hangs in the Australian National University, Canberra later appeared on the 60c Australian postage stamp in 2012. The Frith cartoon seems to have been created as a private gesture from the cartoonist and not published elsewhere. (Fig. X26). On his retirement, Eccles received a "Festschrift" entitled *Studies in Physiology*, collated by his colleagues Curtis & McIntyre, (1965).

GF. Stages 6 & 7 notes (for sections DA to FM)

DA. A The Neurobiology Unit of the Institute for Biomedical Research in Chicago was established in 1966 for brain research under the leadership of Eccles. It had four fully-equipped shielded rooms with electrophysiological equipment, and quarters for small laboratory mammalian animals (e.g. cats), bioengineering & photographic services, a small computer and an electron microscope. The Neurobiology Unit was established in order to study the cerebellum and its supposed function as a biological computer and embraced two independent lab groups. One group; involving the researchers Eccles, Provini, Strata and Táboriková, was working on pathways conveying information into the cerebellum. The second group; involving the researchers Llinás[486], Precht and Kitai, was studying the comparative biology of the cerebellum in vertebrates at various levels of evolution. Publications from Eccles' group during 1967-68 concerned patterns of "climbing fibre" and "mossy fibre" inputs to the cerebellum in relation to movement control. Nevertheless, Eccles and Táboriková departed from Chicago in 1968 to move to SUNY in Buffalo, (IBRO, 1968, p. 74).

485 Karczmar, Alexander George (09.05.1917 – 17.08.2017) PO(J)/US Chicago pharmacology prof./ book author.

486 Llinás, Rodolfo "Riascos" (16 12.1934 -) CO American neuroscientist, NYU School of Medicine.

DA. [B] Rodolfo Llinás (head of the Neurobiology Unit in Chicago from 1967 to 70) elucidated the reason for Eccles' unfortunate interlude in Chicago as follows:

Before we left for Chicago, Eccles asked me to train a colleague from Czechoslovakia. Helena Táboriková was a physician who was going to join us in Chicago as a collaborator. Helena had been trained in human electrophysiology and was not acquainted with single cell research. And so I invited her to spend some time with me in Minneapolis, and then she moved to Chicago at about the same time as my family. The time in Chicago, 1966 to 1970, was scientifically very productive but rather complicated from a human point of view. Although I was quite used to American universities and colleagues, Eccles was not, and so problems began to appear almost immediately after his arrival. Indeed, in Australia he was accustomed to a great deal of deference and respect from all who surrounded him, as befits an extraordinarily distinguished scientist who is recognised throughout the scientific world. The rather rough and ready approach of the scientific community in the United States, as well as the relation to students and technical staff, was less deferential and more confrontational than that with which he was familiar. Setting up the labs was marred by the usual delays that occur with construction efforts in a city, and so it took longer than expected to get the labs working. Meanwhile, and totally unbeknownst to all of us in the department, Eccles had decided to divorce his wife of more than 40 years and leave his family of nine children in Australia. He had decided to marry Helena, with whom he had become acquainted before coming to the United States. Not knowing about this relationship, I considered Helena a student who was starting physiology and so I did not pay her the attention or show her the deference I would have, had I known that she was not coming as a colleague but as the future Lady Eccles. This early misunderstanding generated innumerable repercussions and complications that resulted in unintended, unfortunate, and sometimes hilarious human relation problems. So, in short, what had begun as an extraordinarily cordial relation with Eccles grew into a very complex and Byzantine interaction in which people from the two labs were not allowed to talk to each other. All this engendered a dysfunctional social environment (Llinás, 2006, p. 423-4).

DB. [A] Roger Nicoll has written of Eccles' Buffalo period in great detail. Here are some snippets:

I was determined to work with the person who had so totally changed my life. So, I wrote to Sir John a third time. He expressed great interest in my coming to Buffalo, where he had recently moved.

Sir John gave me a very warm welcome into the lab and we immediately hit it off wonderfully. Having read virtually every paper that he had ever written, I encouraged him to give me all the background and gossip surrounding the papers. He was most impressed by my knowledge and was very enthusiastic about giving me everything he could remember, including his opinion of individual players in the field. This exchange was extremely important to me because I wanted to reconstruct as many of the details as possible surrounding each of his discoveries, in an attempt *to understand what went into an act of discovery. What most impressed me about these exchanges was his incredible memory and complete generosity about who came up with various ideas. Thus, when someone else in the lab had come up with a critical idea, he took delight in crediting that person with the idea and how important it was in solving the puzzle. For instance, he volunteered that it was Fatt who came up with the idea that, since the axons of motoneurons released acetylcholine at the neuromuscular junction, they might also release it from their axon collaterals onto Renshaw cells.*

The initial project that we worked on was a continuation of a series of experiments that Sir John had done for a number of years which involved studying the flow of information into and out of the cerebellum. In our study we recorded extracellularly from antidromically identified reticular spinal neurons. We were joined in these studies by Dietrich Schwarz, Joe Willie and Helena Táboriková (Lady Helena Eccles). Sir John would discuss his schedule with us so that experiments could be scheduled when he was present in the lab. Thus, he was involved in each of the experiments both in the surgery and in the recordings which typically lasted late into the night. The speed with which he did a spinal laminectomy was amazing. The experiments involved stimulating a variety of peripheral sensory nerves and constructing histograms of the effects that the stimulation had on the firing of the reticulospinal neurons. From these histograms inferences were made about the effects of the cerebellum in sculpting the firing of these neurons.

At Buffalo I was interested in using the frog spinal cord to examine the idea that the chloride gradient across neurons was not passively distributed. There had been a report by Lux[487] *(1971) that NH_4 ions could cause a depolarizing shift in the reversal potential of IPSPs in spinal motoneurons. Llinás et al. (1974) had reported a similar effect of NH_4 ions on IPSPs in trochlear motoneurons. I began to examine the effects of NH_4 ions in the isolated frog spinal cord where one could apply drugs in known concentrations. Sir John showed a keen interest in what NH_4 might be doing and suggested that we do some experiments in the hippocampus where IPSPs were very large. I reminded him of an earlier conversation when he told me that he had cut a deal with Per in which he, Sir John, would not touch the hippocampus if Per did not touch the cerebellum. With a smile Sir John assured me that the statute of limitations had long run out on this pact.*

For these studies we were joined by Gary Allen, Kasu Oshima, and Paco Rubia. We began each experiment by anesthetizing the cats with nitrous oxide and when we obtained our first stable records of IPSPs from hippocampal pyramidal cell we would inject increasing amounts of barbiturate. This would permit us to directly record the effects of barbiturates on IPSPs. These experiments went very well and we clearly established that even very small amounts of barbiturate, equivalent to a dose that would just cause drowsiness, caused a prolongation in the IPSP. Anesthetic doses caused a 5-fold increase in duration. I wrote up the first draft of a short paper for

487 Lux, Hans Dieter (15.02.1924 – 05.09.1994) DE neurophysiologist/epileptologist, "ion-selective µelectrodes".

Nature with these results and listed the authors alphabetically, as I believe he had done without fail throughout his career. Much to my surprise he put my name first, rather than his own and made a number of other suggestions (Nicoll, et al., 1975). It is hard for me to express how honored I was and still am for this generosity.

Sir John was always an extreme optimist. When something went wrong with the experiment, he would immediately think of ways of adjusting the experiment so that something, no matter how limited, could be salvaged. He really had a knack for getting the most out of an experiment. While I too would quickly adjust, I would also get extremely impatient and frustrated with the situation. His response to my impatience was a curious one. Sir John was a lover of chocolate and there was always a bar of chocolate in the lab. So, whenever, he saw my impatience mounting he would immediately state that I needed some chocolate to calm me down. In addition to chocolate, Sir John also consumed coffee throughout the day and evening. This was always made from instant coffee. The morning after one of the experiments he came in looking a total wreck. He stated that he had gotten no sleep at all, because his legs were violently twitching. We quickly came up with the diagnosis of caffeine toxicity. It turned out that someone had purchased Folger's freeze dry coffee, which is more than twice as concentrated as the instant coffee. Sir John, unaware of this difference, had consumed an extraordinary amount of caffeine…

As the two years were coming to an end it was a very poignant and bittersweet time. We were both packing our belongings and I helped him fill mail bags with his volumes of the Journal of Physiology which went back uninterrupted to the 1920's (Nicoll 2000, p. 49-58), see also Nicoll, (2018) p 471-476.

DB. [B] For details of the nationwide disturbances in US universities in 1970 see: https://en.wikipedia.org/wiki/Student_strike_of_1970

DC. [A] The "Digitimer" (**DIGI**tal **T**ime **I**nterval **M**arker and **E**vent **R**elease) was designed by H.B. (Bert) Morton at The National Hospital, London in the early 1960's. This was then manufactured and sold world-wide by Devices Limited. Digitimer Limited, Hertfordshire, UK, became an independent company specializing in electronic instruments for medical research and clinical investigations in 1972.

DC. [B] The mechanical stimulator referred to was possibly the one developed by Schmidt's group, employed for sending brief mechanical pulses ("taps" to the footpads and "air-jets" on to hairy skin) which were very effective in evoking climbing fibre responses:

The hind and fore paws of the animals were mounted, pads upwards, in a metal trough and stabilized by embedding them in high-melting point paraffin wax. Consequently, a restricted area of hairy skin on the dorsal surface of the limbs was unavailable for testing in the evaluation of receptive field areas. In two combinations, three of the four limbs were mounted in this way, the contralateral fore or hind limb being used for the insertion of arterial and venous cannulae. Two types of stimuli were applied to the foot pads: servo-controlled displacement pulses of sinusoidal shape, amplitude up to 600 µm, pulse frequency usually 100 c/s both for single (tap) or *repetitive stimuli (vibration), or constant force stimuli of 50g to 1 kg wt. applied with a cylindrical probe of 1 cm² area which was released under gravity and lifted pneumatically. Blowing of hairs tangentially to the skin with short jets of air (20 msec) was used to stimulate hair follicle receptors. The intensity of the stimulus was regulated by varying the air pressure and by changing the distance between the skin and the opening of the nozzle (for a description of the types and numbers of mechanoreceptors activated by these various mechanical stimuli.*

(See Schmidt, Senges & Zimmermann, 1967; Janig, Schmidt & Zimmermann, 1968), Eccles, Sabah, Schmidt & Tábořiková, 1972 [1A-377].

EA. [A] Eccles' huge collection of literature was donated to the University of Düsseldorf in 2008 as the Eccles Archives and is available there for study purposes.

EA. [B] Eccles' belief in the mind-body connection:

After termination of his successful scientific career in the USA, Eccles, now in quiet seclusion in the Swiss alps, concentrated on investigation of this, his lifelong interest, and contributed many articles and several books on the subject. These philosophical works have received much attention, although not universally accepted. They nevertheless remain as lasting testimony of a brilliant thinker, dedicated to resolving a troubling mind-brain paradox encountered in many human lives.

Eccles remained for his whole life a champion for his "dualist-interactionism" theory, culminating in his last contributions; the 1993 "Neuroworlds lecture" in Düsseldorf (Eccles, 1994, [1A-596]) and his book (Eccles, 1994, [1B-a29]) where he argued vehemently against other authors' attempts to define monistic interpretations of consciousness; in particular against the materialist, Daniel Dennett, whose thesis involved a union of independently evolved specialist brain circuits yoked together to constitute a "virtual machine"; which performed a sort of political miracle by creating a "virtual captain" of the crew (Dennett, 1991).

Theosophist, David Pratt, commented:

This 'virtual captain' is what we normally regard as our 'self', but according to Dennett it is really just an illusion produced by the global action of our brain circuits!... According to Eccles we have a nonmaterial mind or self which acts upon, and is influenced by, our material brains; there is a mental world in addition to the physical world, and the two interact. However, Eccles denies that the mind is a type of nonphysical substance (as it is in Cartesian dualism), and says that it merely belongs to a different world (Pratt, 1997).

For further information and discussion of Eccles' mind/brain dualist philosophy and the concept of consciousness, see Stotz-Ingenlath, (2000), Feinendegen, (2000), as well as the "Theory of Enformed Systems", (TES) proposed by Watson & Williams, (2003).

In particular, an historical survey of the conceptual foundations of cognitive neuroscience by Bennett & Hacker, (2003), critically compares the mind-body theories of Sherrington, Eccles, Dennett and other major contributors in detail.

For further information on Eccles post-retirement activities; his collaboration in the 1990s with physicist, Friedrich Beck[488], and their collaborative work at the Max-Planck-Institut für Hirnforschung in Frankfurt, Germany, see Beck, (2008). The resulting publications by Beck & Eccles, (1992) and Beck & Eccles (1998) describe possible involvement of synaptic quantum effects in consciousness.

The implications of Beck and Eccles' quantum theory have been examined in connection with energy conservation and violation of physical laws by Mohrhoff[489], (1997).

In John Horgan's book (Horgan[490], 2015, p. 173) the requirement of "quantum mechanics" by Popper and Eccles (1977) [1B-a15] in their dualistic defence of free will and rejection of physical determinism for the working of the mind is compared with the competing theories of other major writers on neuroscience - including those of Francis Crick, Gerald Edelman, Roger Penrose, Daniel Dennett and Marvin Minsky.

In his book, "The Conscious Mind", the Australian philosopher and cognitive scientist David Chalmers has criticised Eccles' quantum mechanics theory of consciousness:

Some people, persuaded by the arguments for dualism but convinced that phenomenal consciousness must play a significant causal role, may be tempted by an interactionist variety of dualism, in which experience fills causal gaps in physical processes. Giving in to this temptation raises more problems than it solves, however. For a start, it requires a hefty bet on the future of physics, one that does not currently seem at all promising; physical events seem inexorably to be explained in terms of other physical events. It also requires a large wager on the future of cognitive science, as it suggests that the usual kinds of physical/functional models will be insufficient to explain behavior. But the deepest problem is that this view may be no better at getting around the problems with epiphenomenalism than the view with causal closure, for reasons I will discuss shortly. The only form of interactionist dualism that has seemed even remotely tenable in the contemporary picture is one that exploits certain properties of quantum mechanics. There are two ways this might go. First, some have appealed to the existence of quantum indeterminacy, and have suggested that a nonphysical consciousness might be responsible for filling the resultant causal gaps, determining which values some physical magnitudes might take within an apparently "probabilistic" distribution (e.g., Eccles, 1986, [1A-561]*). Although these decisions would have only a tiny proximate effect, perhaps nonlinear dynamics could amplify these tiny fluctuations into significant macroscopic effects on behavior…*

A second way in which quantum mechanics bears on the issue of causal closure lies with the fact that in some interpretations of the quantum formalism, consciousness itself plays a vital causal role, being required to bring about the so-called "collapse of the

488 Beck, Friedrich (16.02.1927 – 20.12.2008) DE physicist & biophysicist. "Theory of Consciousness".

489 Mohrhoff, Ullrich (born 1950 –) Physicist and book author.

490 Horgan, John (born 1953 –) US science journalist.

wave-function." This collapse is supposed to occur upon any act of measurement; and in one interpretation, the only way to distinguish a measurement from a non-measurement is via the presence of consciousness… (Chalmers, 1996, p. 156-158).

Recent brain research investigations into the traditional concepts of "God, brain and thoughts" have been gathered and summarized by Kreutzberg[491] (2007) with particular emphasis on morphological and histological location of brain tissue events associated with spiritual activities. The conclusions drawn there are that the results of brain research to date provide neither evidence for, nor against God.

EA. [C] The World 3 concept of Karl Popper was first explained in his contribution entitled "Three Worlds" at the Tanner Lecture on Human Values delivered at the University of Michigan in 1978 and available as a pdf document download. See: https://tannerlectures.utah.edu/_resources/documents/a-to-z/p/popper80.pdf.

See also a review of Popper's World 3 theory by literature researcher, Brian Boyd (Boyd, 2016).

EA. [D] Cornelius Borck has nevertheless indicated a fading influence of Eccles during his last years:

By the sheer length of his life with further publications still pouring out, Eccles turned into a kind of dinosaur of neurosciences, isolating himself with this late activity from the neuroscientists' scientific community. However, it is exactly the coherence of the underlying framework throughout his lifelong research which provides the clue for his scientific achievements and for the nowadays more sceptical appreciation by his followers. He pursued science with an almost religious devotion and his religious faith provided the grounding for his philosophical positions (Borck, 1998).

FD. [A] Ku-ring-gai Chase is an old-established National Park (declared 1894) located 25 km north of Sydney.

FD. [B] The "Ladies of the Grail" movement was established in Sydney in March 1937. The Grail later amalgamated with The National Catholic Girls Movement.

FD. [C] Ray Triado was prime mover and leader of a Catholic pioneer-style quasi-monastic project established at inhospitable farmland, Whitlands, in North Victoria in 1941. This ambitious manual-labour project failed in 1951 as its idealism became lost.

FD. [D] One of Eccles's religious talks was reported as an article in the Catholic Freeman's Journal, Sydney, NSW: (dated 29.05.1941) Page 15. Entitled: "*Fitting Youth for Life – Education*" with publisher's subtitle: Remarkable Paper Read, at Campion Winter School.

During his talk of the previous weekend, Eccles compared the State and Catholic education systems and presented his personal views of educational deficiencies in both systems under three headings:

1 *True principles of education*.
2 *Critical examinations of existing educational conditions*.
3 *Practical suggestions for immediate application & future development towards ideal*.

491 Kreutzberg, Georg Wilhelm (02.09.1932 – 20.03.2019) DE Professor of neuromorphology & neuropathology.

This article resulted in a published reprisal (dated 5.6.1941) by the very Rev. Dr. J. C. Thompson, Director of Catholic Education in New South Wales, claiming that Eccles disparaged the good work being done by the Catholic educational workers.

Eccles replied in a subsequent letter to the editor (dated 12.06.1941) in which he greatly regretted the misinterpretation of his talk.

FF. [A] Otago can no longer claim to be the southern-most university in the world. That honour now belongs to the National University of Patagonia, San Juan Bosco, which operates a small campus in Tierra del Fuego.

FL. [A] Rose's oral contribution in Carleton's (2003) radio program.

FL. [B] Interestingly, the adjective *conscious* of the book's title only appears in the first Routledge edition [1B-a25] in 1989 and was omitted thereafter, possibly owing to confusion that could easily arise between two quite different concepts; "the conscious self" versus a negative "self-consciousness" feeling arising from company with others.

FL. [C] Rose's oral contribution in Carleton's (2003) radio program.

FM. [A] In correspondence to JPC (dated 9.4.2021) Roger Nicoll, a research co-worker during the Eccles group during the Chicago years, wrote:

I did not realize that Eccles was writing an autobiography. I do know that Per Anderson and David Curtis were very interested in writing a biography. However, Helena absolutely refused to let this happen. She wanted complete control over Eccles' image. It is not surprising to me that there would be zero interaction between her and the family. In a nutshell she was a very difficult person.

BIOGRAPHICAL NOTES/COMMENTS – Figs. X01-X26

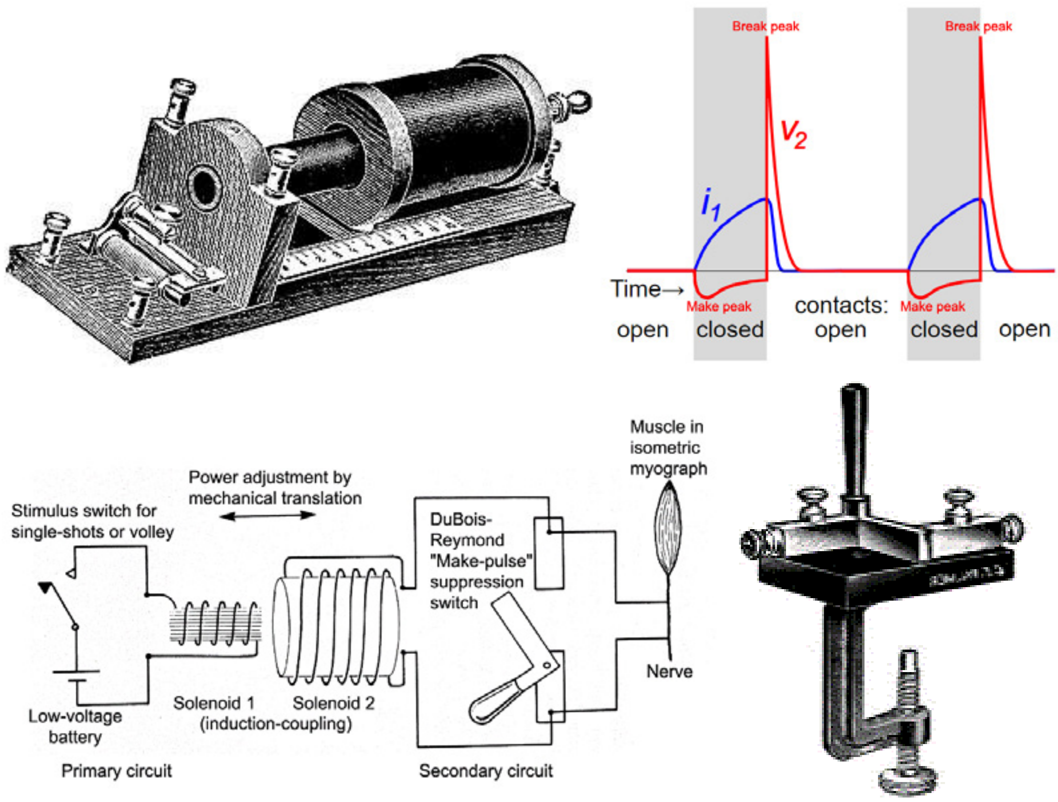


Fig. X01. du Bois-Reymond inductorium, switch and Sherrington's induction circuitry. [J]

Upper Left: Inductorium, showing narrow primary and wide secondary coils. Note sledge carrying the secondary coil and metric graduations indicating spatial relationship of the coils - for ensuring reproducibility of power settings.
From Zimmermann (1937). Wissenschaftliche Apparate, Liste 200, p. 0036, fig. 21828.

Upper right: Diagram showing large amplitude (and sign) differences between *make* and *break* pulses. (i_1 is current in primary coil, v_2 is voltage in secondary coil).
From Wikipedia. https://commons.wikimedia.org/wiki/File:Induction_coil_waveforms.svg

Lower left: Circuit (with additional labelling) of the system as employed in the Sherrington lab. The du Bois-Reymond key was used to short-circuit the secondary coil during a *make* pulse.
From Whitteridge (1982), p. 420, fig. 1.

Lower right: An example of the du Bois-Reymond key.
From Catalog C. F. Palmer 1934 (London) Ltd. England, p. 0120, fig. h1.

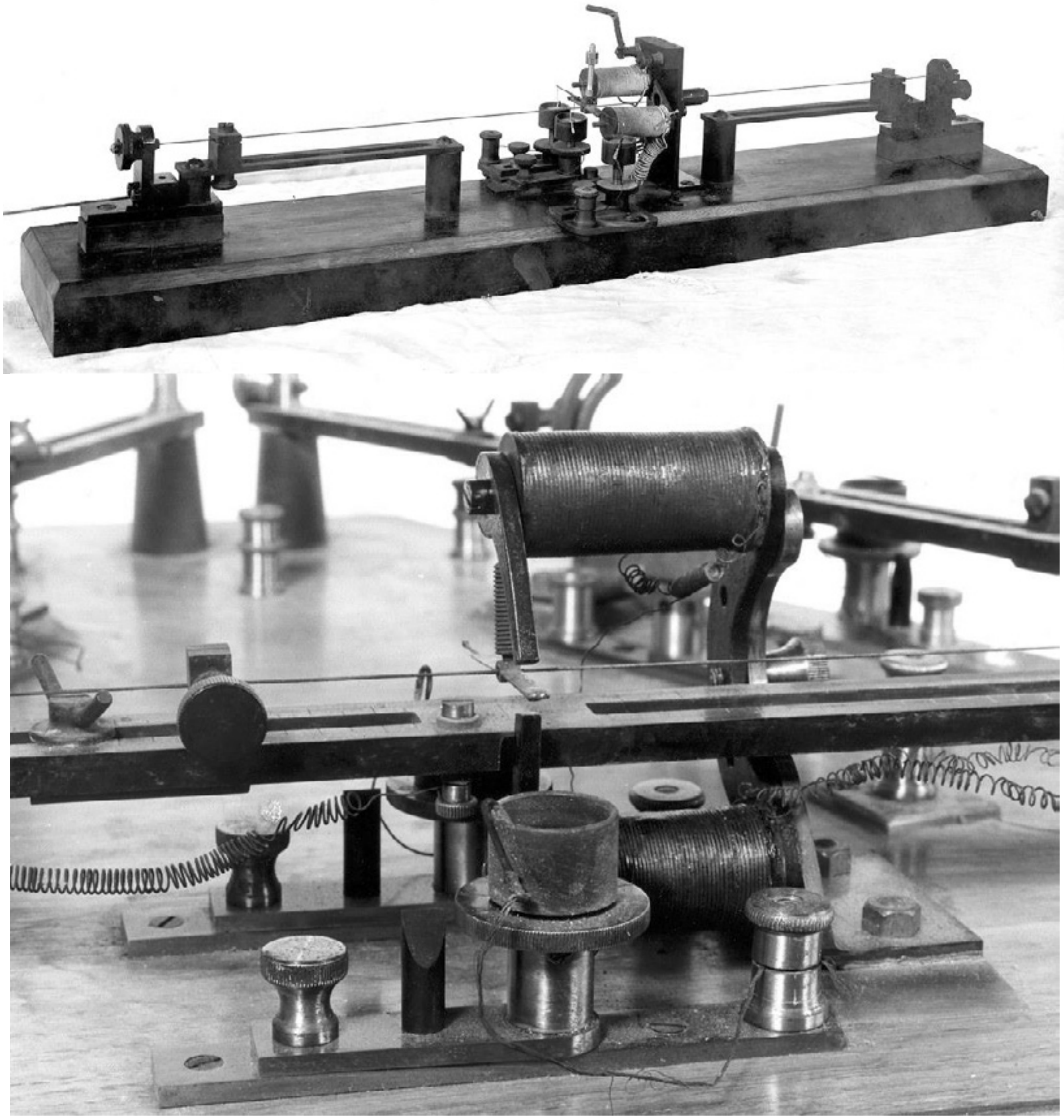


Fig. X02. Sherrington's mechanical "Separation Key" interrupter device [J]

Upper: A complete interrupter, showing torsion wire with adjustable tension to provide a range of vibration frequencies for eliciting tetanic stimulation of muscles.

Lower: The baseboard shown here (bearing three individually-tuneable interrupters) is enlarged to show one of the mercury pots situated beneath the rider, which is attached at right angles to the vibrating torsion wire. For high resolution versions of these wo images see:
Upper: https://learntech.medsci.ox.ac.uk/cslide/items/view/7260
Lower: https://learntech.medsci.ox.ac.uk/cslide/items/view/7272
From Whitteridge (1982), p. 420, fig. 1.

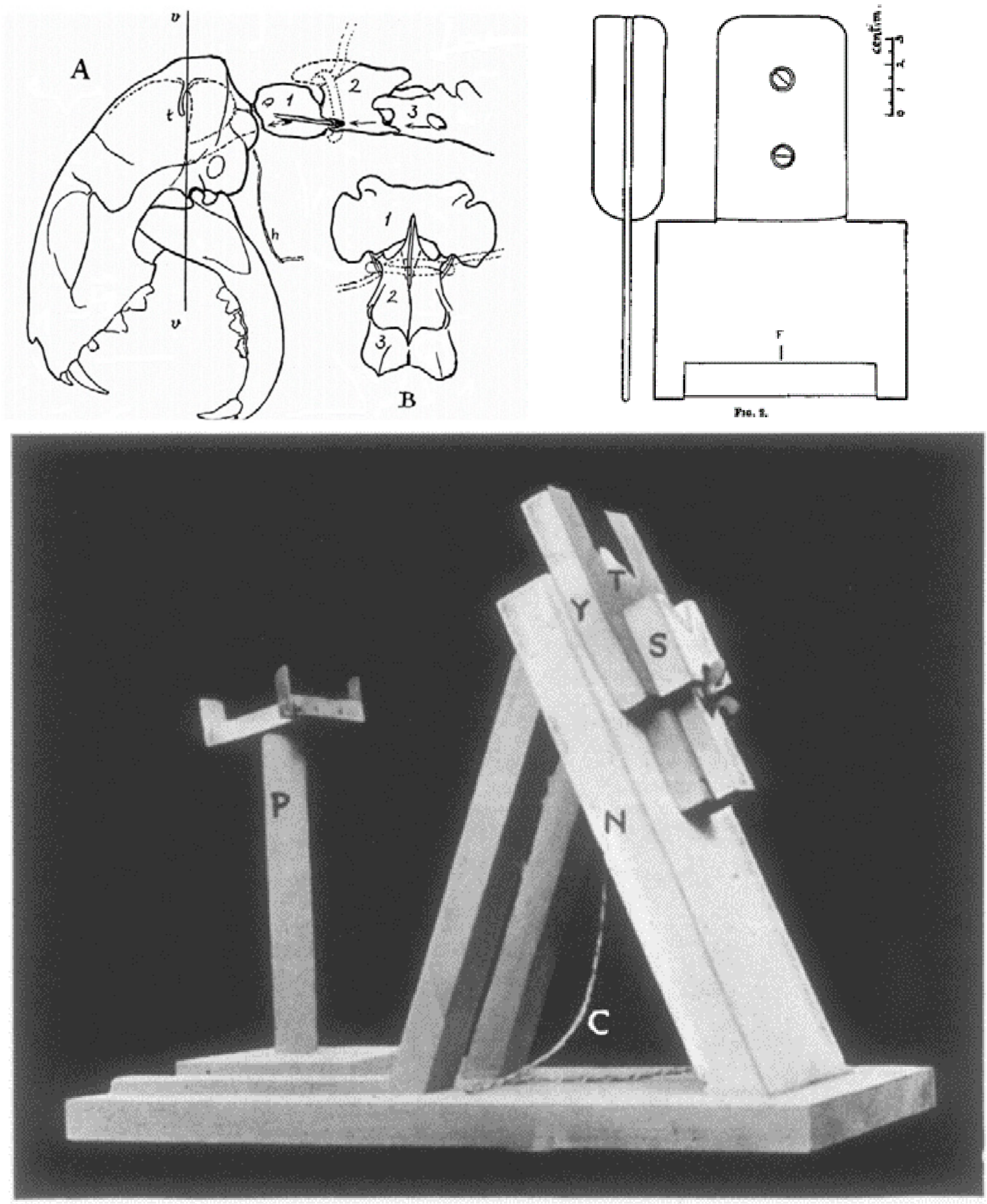


Fig. X03. The "Sherrington guillotine" for cat decerebration. [K]

Upper left: Diagram of cat head region, showing the plane of transection as a vertical line *v---v*, thus sparing the lower jaw and tongue.
From Sherrington (1915) p. LIII, fig. A.

Upper right: diagrams showing the steel guillotine blade.

Lower: the wooden guillotine apparatus designed by Sherrington for decerebrating cats;
From Miller & Sherrington (1915), p. 148, fig. 1 and p. 150, fig. 2.
[For guillotine construction details and its correct usage, see the above papers.]

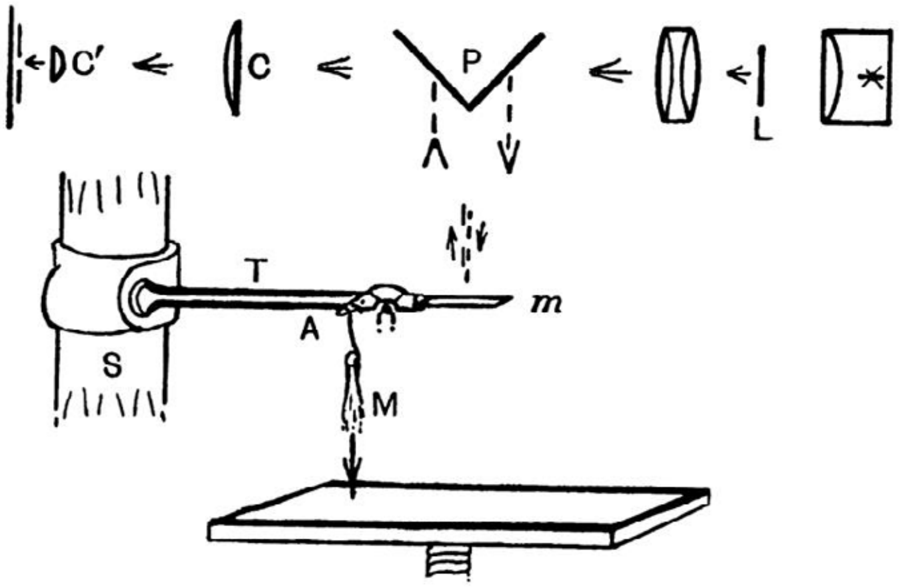


Fig. X04. Sherrington's torsion isometric mirror myograph for mammalian work. [M]

Beneath is a rigid, heavy preparation table which is adjustable in height. The bony attachments of the experimental muscle, **M**, are rigidly clamped to its upper surface. An independently-mounted steel upright, **S**, carries the rigidly-attached torsion wire (or rod), **T**, of the myograph. The free end of the muscle is attached to a torque arm, **A**, projecting laterally from the rod so that its tension results in rotational torsion of the rod. Bending of the rod under load is prevented by a special support bearing near its unclamped end. Here, a short knife-edge in the axial line of the rod near the end serves as a frictionless bearing. This knife-edge rests vertically on a polished steel surface, comprised of a slightly-grooved steel needle bedded horizontally in a rigidly-supported but vertically-adjustable hard brass plate (not depicted). The torque angle can be kept small (to avoid side-slip of the bearing edge) and magnifications exceeding 100x are easily obtained by the optical lever effect of the optical system. The natural frequency of the torque element (over 480 Hz) is determined prior to experimentation. The free end of the torsion rod carries a small horizontally-oriented plane mirror, ***m***. Above the torque arm is the wholly independent optical system which is mounted sufficiently distanced from the preparation table to allow unhindered access to the preparation. The vertically-oriented spectrometer slit, **L**, is illuminated by a light source at the right-hand side. The magnified image of the slit is deflected downwards by the rectangular prism, **P**, to be reflected upwards to the same prism by mirror, ***m***, at the end of the torsion rod and then focussed by lenses **C** and **C′** at the horizontal slit and photographic plate of the falling-plate camera, ca. 1-2 m. distant. The vertically-aligned pull from the experimentally-excited muscle is thus recorded photographically on the falling plate as horizontal displacement of the bright line-image of the slit.

From Sherrington (1930), p. 105, fig 2.

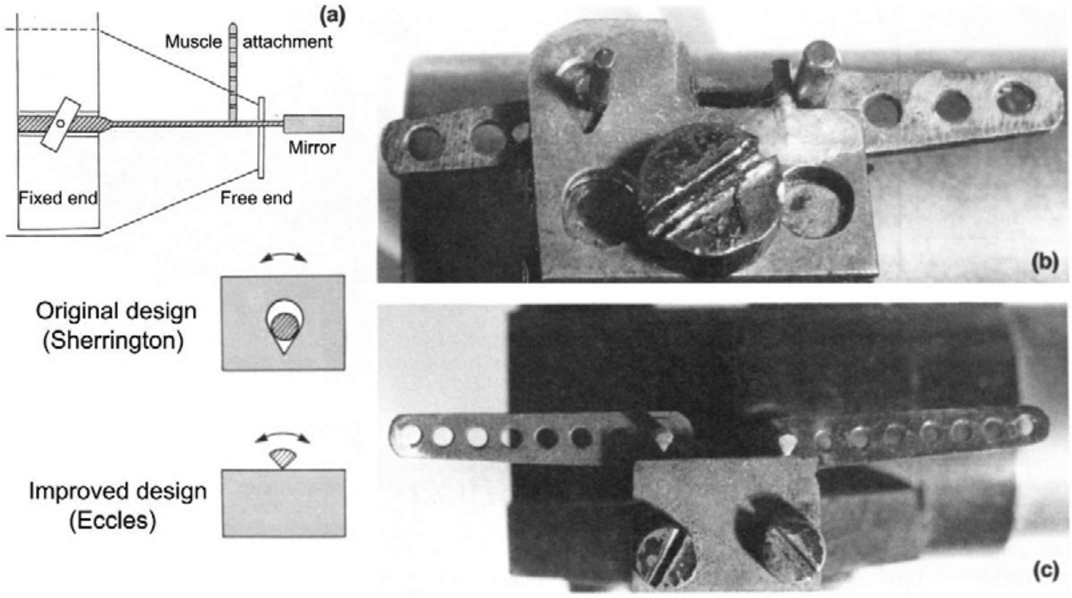


Fig. X05. Eccles' frictionless modification of the Sherrington myograph bearing. [O]

(a) plan view of the myograph.

(**b)** the original design of the torsion rod free-end support bearing allowed unrestricted rotation but suffered from friction.

(**c)** Eccles' improved frictionless knife-edge bearing at the free end, although suitable only for restricted rotation angles, is nevertheless sufficiently stable for use in the myograph. Similar to the design of analytical balances; the knife edges only make contact with the support bearing while under load during an experiment.

From Whitteridge (1982), p. 423, fig. 4.

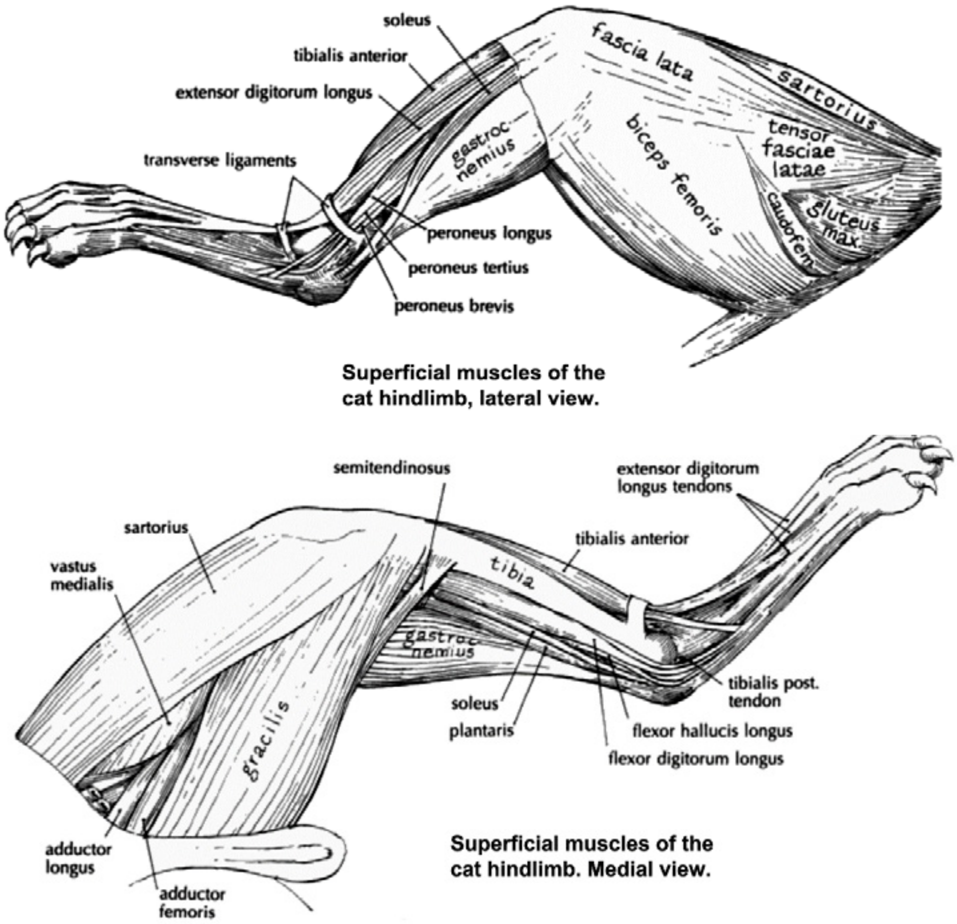


Fig. X06. Major muscles of the cat hind leg used in Eccles' experimental investigations. [M]

Upper. Muscles as seen from an external side view of the cat hind leg. From Gilbert (2000), p. 20, fig. 17.

Lower. Muscles as seen from the inner side view of the cat hind leg. From Gilbert (2000), p. 21, fig. 18.

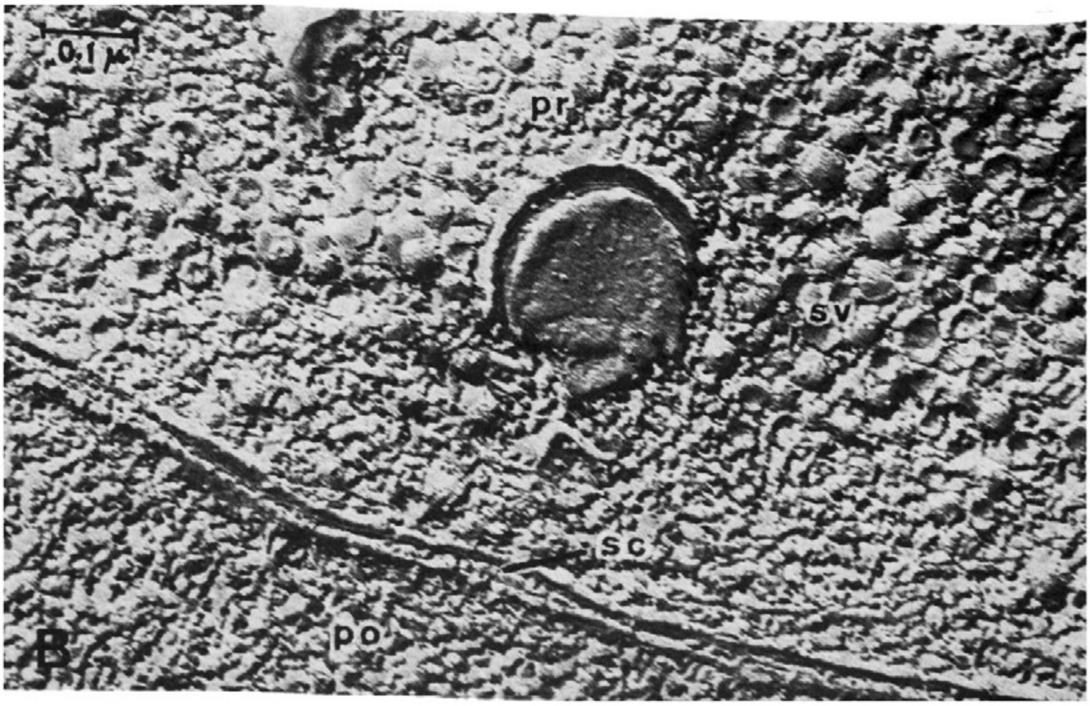


Fig. X07. A TEM image of a synaptic "cleft" replica, prepared by freeze-etching. [N, AC]

The freeze-etched axon-somatic synapse from cat brain subfornical organ. This specimen was not prefixed with aldehydes. [Image A (same area but at lower magnification) is not shown here]. Image **B** (shown here) gives details on active site, with the postsynaptic area (**po**) lying below on the left. The presynaptic area (**pr**) is less crowded with vesicles (**sv**) than the more remote areas of the end bulb. The magnification bar (labelled 0.1 μ at top left) indicates a length of 100 nm (i.e., 1000 Angstrom units, Å). The two closely-apposed membranes comprising the synaptic cleft (**sc**) can therefore be seen to be separated by about **200 Å**, or **0.02 μm**.
From Akert & Sandri (1970), p. 37, fig. 9.

Fig. X08. Two versions of the so-called "Lucas Pendulum". [O]

Left: Spring-driven horizontal "Contact Breaker" of Lucas (1907).
Dimensions (LBH): 54 x 35.6 x 10 cm, weight 7.7 kg.
From Cambridge Physiological Instruments: Booklet No. V, Cambridge Instrument Co., Ltd. (1920), p. 12, fig. 7.

Right: Vertical gravity-driven "Contact Breaker" of Lucas (1908).
Dimensions (LBH): 33 x 51 x 66 cm; (weight not stated, but heavy!).
From Cambridge Physiological Instruments: Booklet No. V, Cambridge Instrument Co., Ltd. (1920), p. 13, fig. 8.
Retrieved from
https://vlp-new.ur.de/images/img8223 and https://vlp-new.ur.de/images/img8224

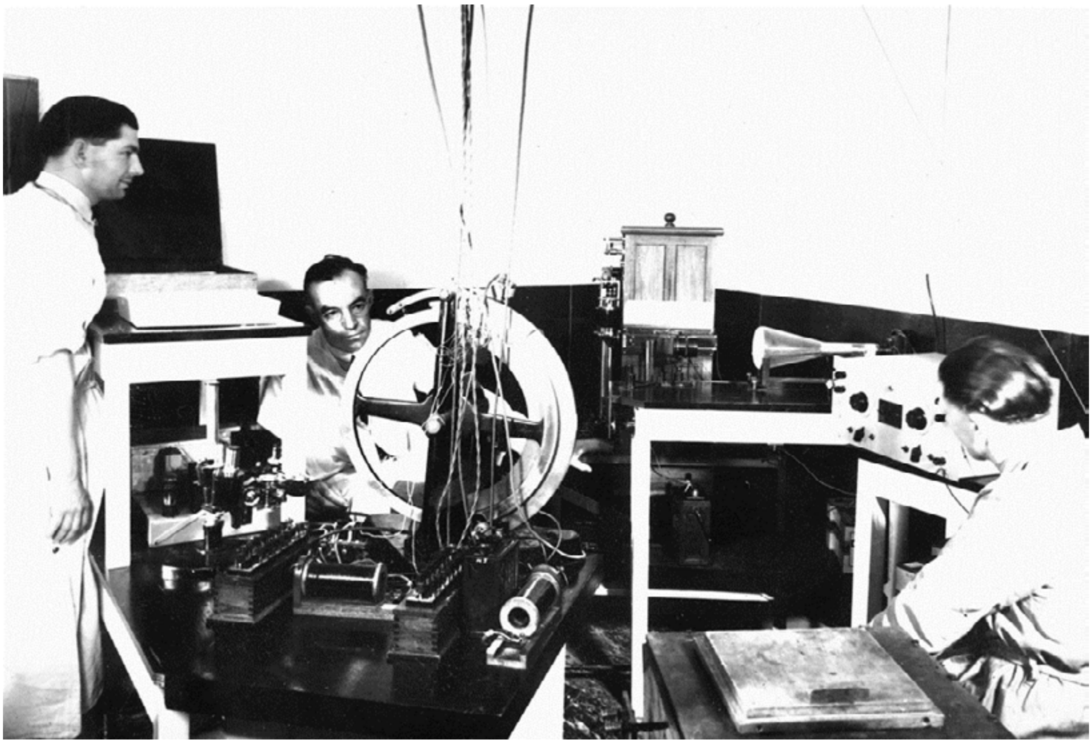


Fig. X09. Eccles with typical "Sherrington" electrophysiological laboratory equipment. [O]

John Eccles, shown operating the large upright Lucas pendulum (date of photo unknown). On his bench are batteries, resistance banks and induction coils to provide precise stimulation voltage(s). In the centre background is a Cambridge Instrument Co. falling-plate camera for recording time-varying optical signal traces. A "Cossor" cathode ray tube (with photographic camera facing it for recording electrical traces) is behind him on the viewer's right side. Standing left is technician Arthur Chapman; the other person sitting in this photograph is perhaps workshop technician Charlie Morris.
From Collis (2004) p. 59.

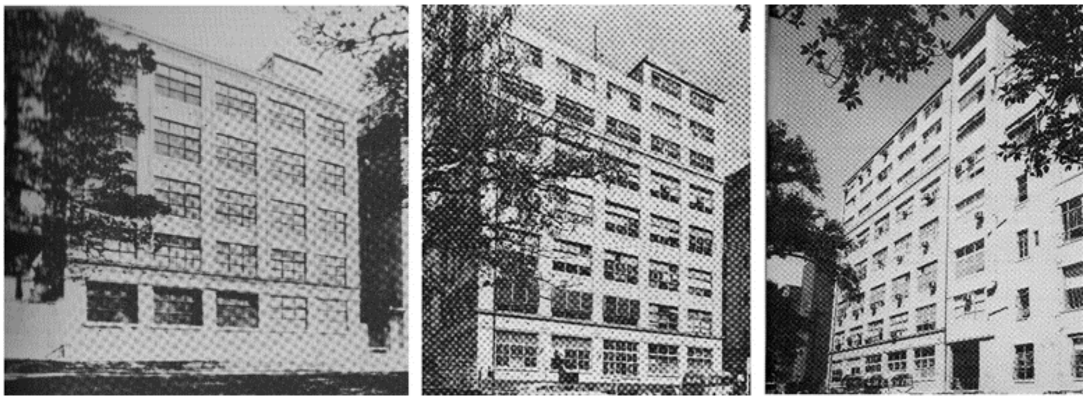


Fig. X10. The original 1930s Kanematsu building and its post-Eccles developments. [AS]
Left: Original Kanematsu Institute, as occupied by Eccles (with animal house on roof).
Middle: later development with two extra floors added in 1964.
Right: now with all three extra floors – the last one added in 1970.
Nevertheless, the building was suddenly demolished in 1982.
From Winton, (1997).

Fig. X11. Friday afternoon folk dancing at 22 Cannington Road in the early 1940s. [BC]
John Eccles with daughter Rose and two of his younger daughters, demonstrating a folk dance to several Otago Medical School spectator/participants.
From Fillenz (2012), p. 218, fig. 1.

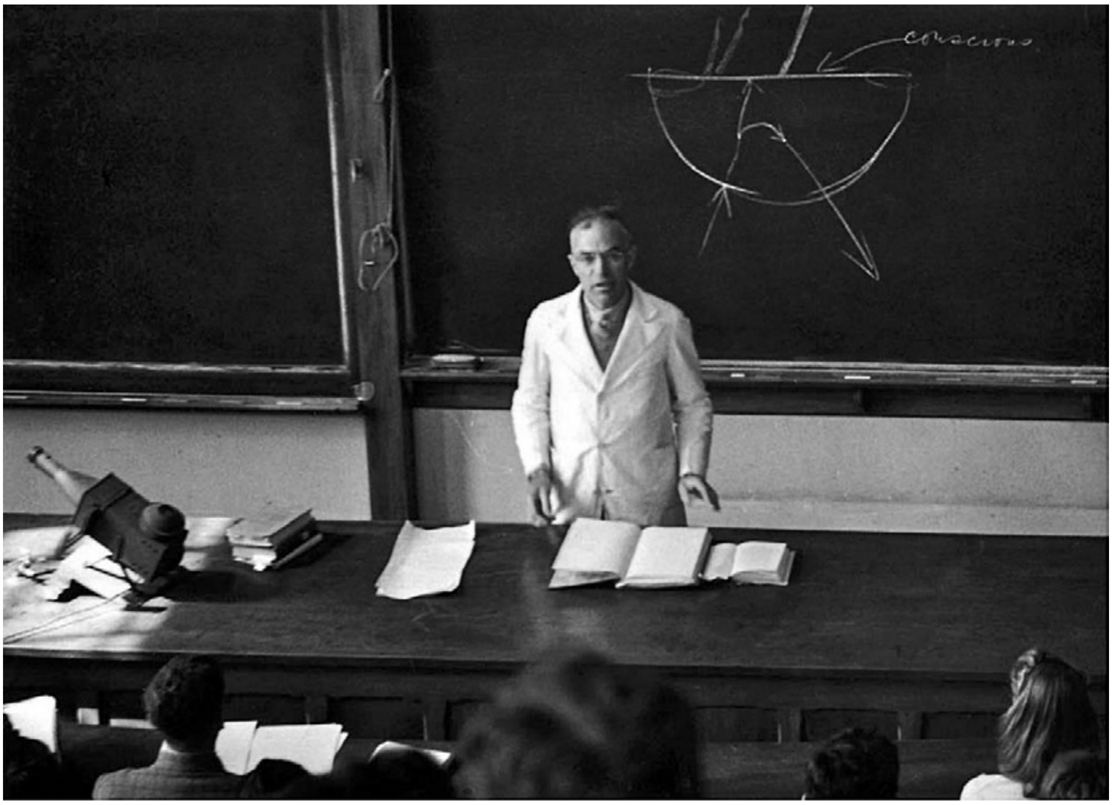


Fig. X12. Prof. John Eccles, lecturing at the Otago Medical School in the early 1940s. [BD]

Eccles wrote out and illustrated each of his lectures in a loose-leaf file so that each year additions could be made. He later calculated that he "confronted" students 20 hours a week during term time. An electric-powered projector of unknown manufacture, "magic lantern type" for large-format photography slides, can be seen at far left on the lecturer's desk.
From Fillenz (2012), p. 222, fig. 3.

Fig. X13. Bowl presented to Professor Eccles by the students, prior to his departure. [BD]

Engraved on this silver fruit bowl is: "*Presented to Prof J.C. Eccles by students of the Otago University Medical School, October 1951*". The bowl was donated in 2016 to the Medical School's Physiology Department by John Eccles' daughter, Mary Mennis.
From the Department of Physiology, University of Otago.

Fig. X14. Experimental laboratory teamwork in Dunedin. [BE]

Eccles, in 1951 photographed working with his laboratory technician, Molly Bradley. The spinal cord of a deeply anaesthetised cat is being exposed, prior to experimentation.

From the Hocken Library archives, University of Otago.

Fig. X15. Eccles, preparing a cat for an electrophysiological experiment. [BE]

These experiments required both excellent anatomical knowledge, dissection experience and manual dexterity. Eccles always performed the final preparative stages himself, as shown in this Dunedin experiment.

From The University of Otago Hocken Heritage Collection, Box-184-002.

Fig. X16. The NZ South Island Express, ran daily between Christchurch and Dunedin. [BF]

Above. Photo taken of express train *J1236* in 1969 at Shag Point, near Palmerston while underway southwards during its final run prior to decommission. Both Eccles and Popper used this means of transport for their meetings in the early 1940s.

From train-spotter collection held by Mr. Wilson Lythgoe.

Left. Postcard, dated 1878, of the *Venetian Gothic* Christchurch Railway Station (existed from 1877 until 1959, then replaced by new buildings).

From Christchurch City Library.

Right. The *Flemish Baroque* Dunedin Railway Station, circa 1925, (existing from 1906 to the date of publication).

From Alexander Turnbull Library.

Fig. X17. Wilfrid Rall, working with a feline electrophysiological preparation in 1949 [BL]

Rall is pictured here decanting a fluid (possibly warm paraffin or Ringer's solution) from a glass beaker down a thermometer on to the exposed spinal region of a cat, as preparation step for electrophysiological experimentation. The set-up seems identical with that used by John Eccles in Fig. X15, although here photographed from the opposite side.

From The University of Otago Hocken Heritage Collection, Box-184-026.

Fig. X18. Eccles posed beside his modified "falling plate" camera in Dunedin, 1949. [BQ]

This camera for recording physiological traces was manufactured by The Cambridge and Paul Instrument Company ca. 1920 (originally with maximum plate falling speed of 45 cm per second). This was modified for Eccles in Oxford to record fast-occurring events by making it a "rising plate" camera directly coupled to a heavy dashpot control, to achieve a steady maximum vertical plate translation speed of 2000 cm per second.
From The University of Otago Hocken Heritage collection, Box-184-003

Fig. X19. Eccles with Staff & Senior Students of the Physiology Department (1951). [BQ]

Back: Arnold Annand (electronics technician), Ron Stevenson, Dan Whyte (grad. student).

Middle: Arthur Chapman, Jack Coombs, Yap Tien Beng (visitor), Molly Bradley (née Andrew), Murray Ashbridge, Pearl Cousins (née Harvey, - departmental secretary).

Front: Laurence Brock, Ken Bradley, Prof. John Eccles, Eric Hook (senior technician), Charlie Morris (workshop technician), Wilfrid Rall.

From The University of Otago Hocken Library Collection, Box-011-001.

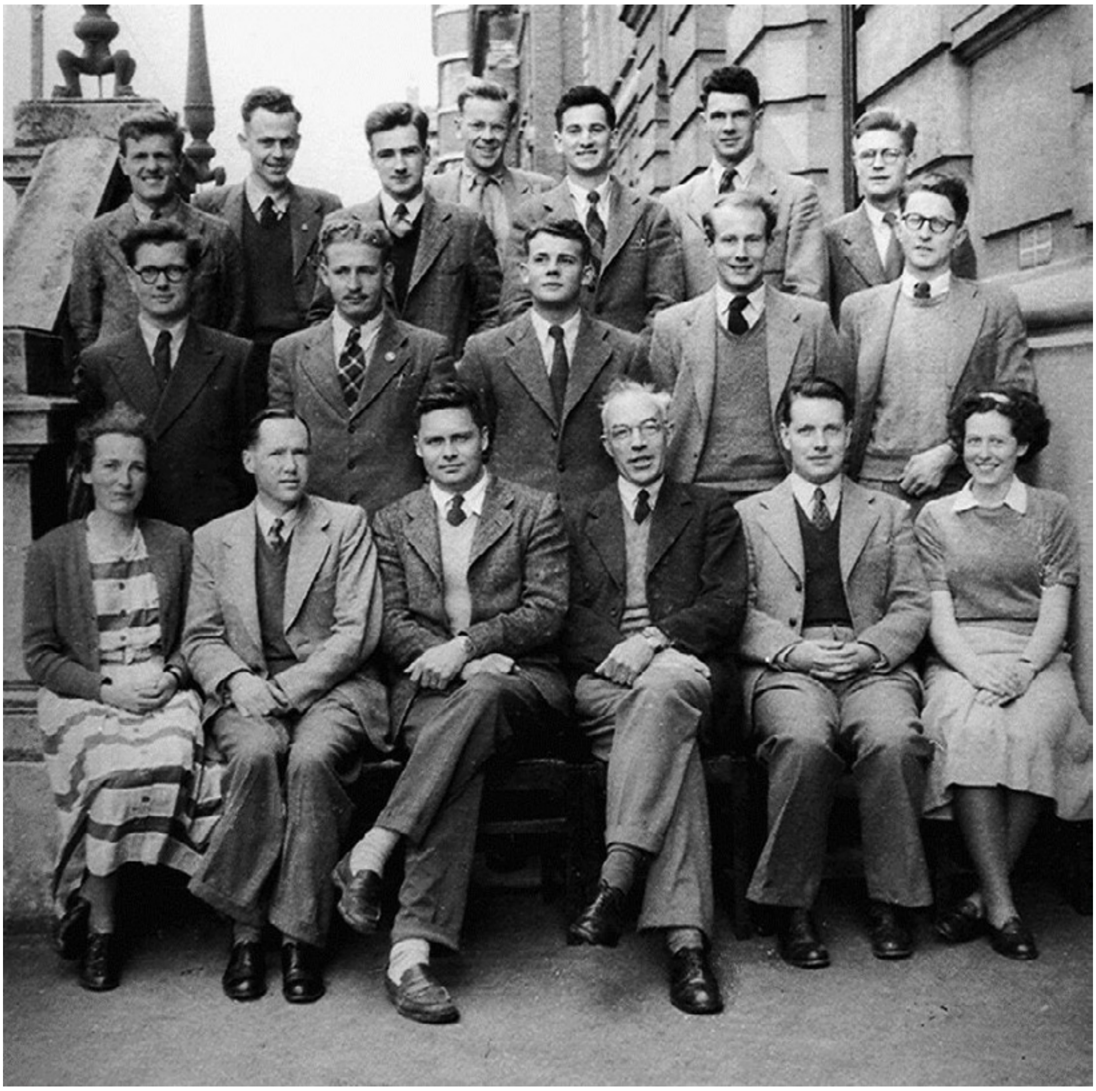


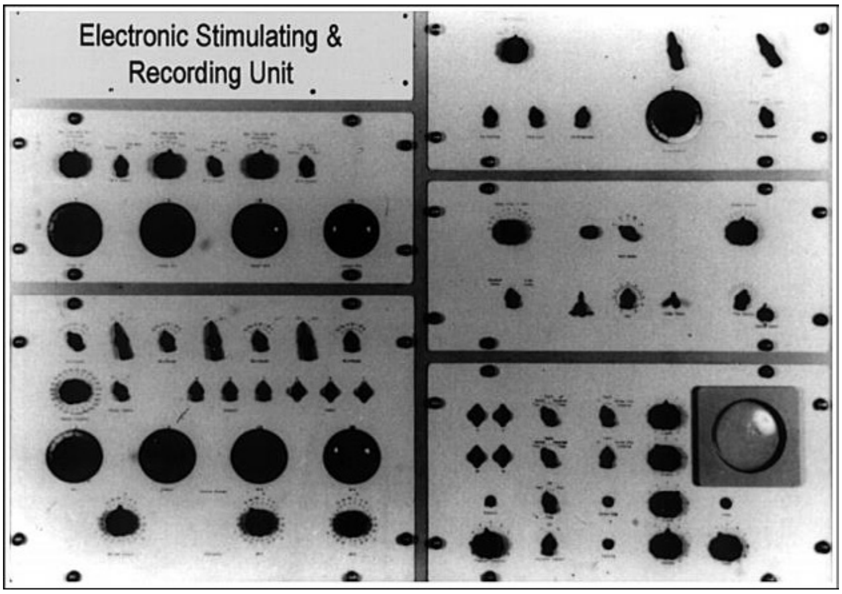
Fig. X20. Eccles with Students of the Physiology Department (October 1951). [BQ]

Back: John Werry, unidentified person, Max Webster? Murray Ashbridge, John Hubbard, Graham Jeffries, John Scott.

Middle: Ken Bradley, Bill Liley, Ken North, John Ludbrook, Dan Whyte.

Front: Rosamond Eccles, Jack Coombs, Wilfrid Rall, Prof. John Eccles, Lawrence Gordon Brock, Bronwen Bloomfield.

Students shown were identified from memory by Dr. Rosamond Mason (née Eccles) in 2017. From Todman (2008), p. 973, fig. 1.



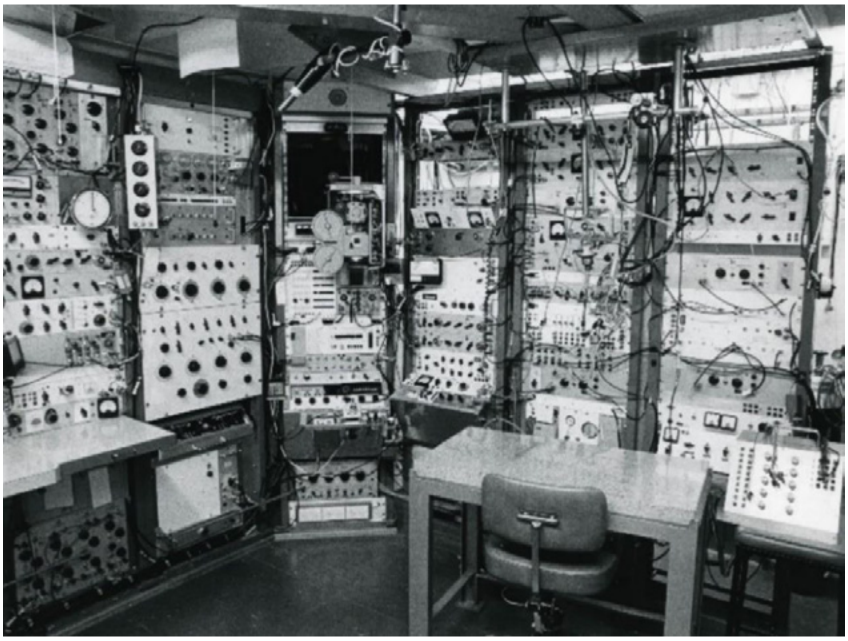


Fig. X21. Front panel of the "ESRU", constructed for Eccles by Jack Coombs in Dunedin. [CA]

Upper: The original ESRU equipment from the early 1950s was based on the use of thermionic valve technology. This was later updated by Coombs with the employment of transistorised components.

From Todman (2008), p. 975, fig. 3.

Lower: Professor David Curtis's Canberra laboratory (including his "Tardis"!) in 1977, which still contained various (here separated) constituents of Eccles' original ESRU from the 1950s.

Source: (ANUA226-639-3). Photographer: ANU Photographic Services

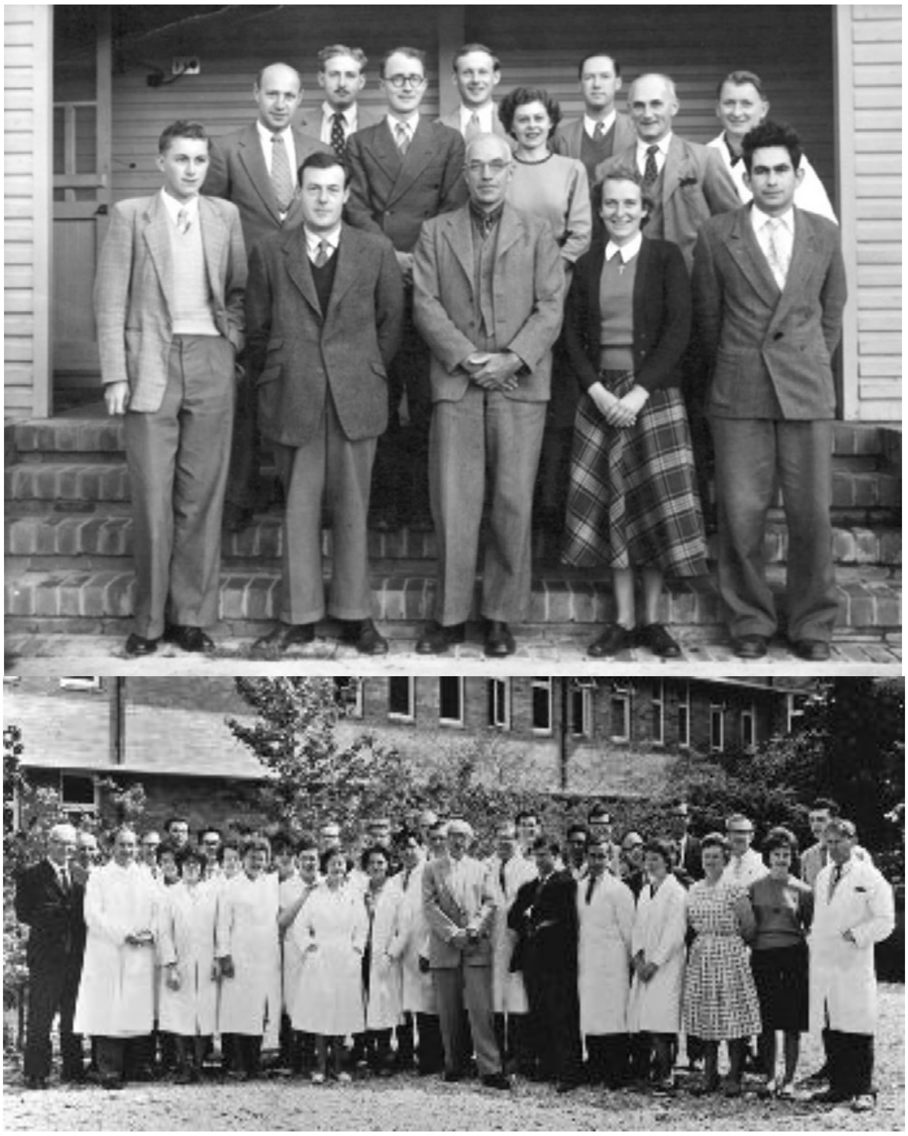


Fig. X22. Photos of the Eccles Group in Canberra. [CB]

Upper. The pioneering group pictured at the temporary building in 1954 or 1955; identified from memory by Dr. Rose Mason (née Eccles).

Back row: William "Bill" Liley, David Curtis, Jack Coombs, Vladimir "Val" Paral (photographer).

Middle row: Vernon Brooks, John Raymond Smythies (Nuffield Fellow), Ruth Burkitt (secretary), Gus Daynes (technician).

Front row: Lawrence Gordon Brock? Gerry Winsbury (head technician), John Eccles, Rosamond Eccles, Paul Fatt.

Lower. The flourishing "Eccles group", photographed several years later.

From M. Mennis, personal archives.

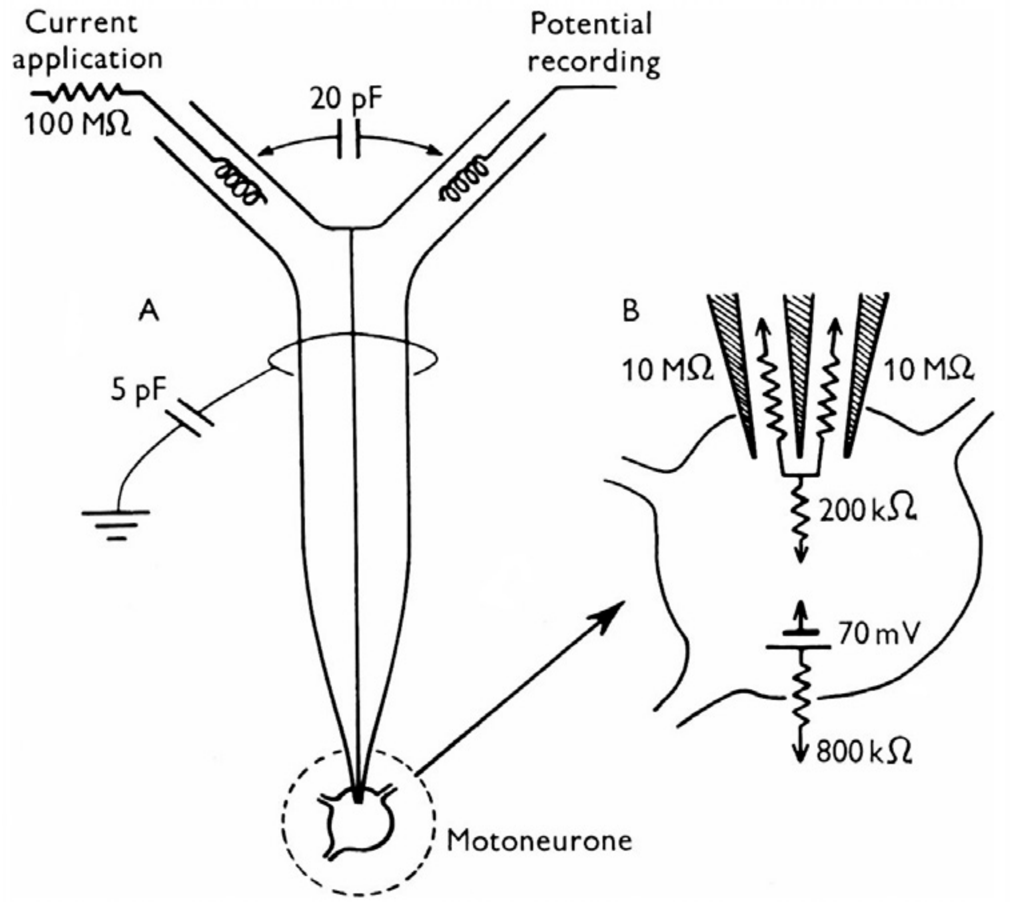


Fig. X23. Paul Fatt's double-barrelled microelectrode and its immediate connections. [CA]

A. Typical values are given of the several electrical characteristics which are significant in the use of the electrode.

B. Enlarged view of Fatt's microelectrode tip in the motoneurone. The motoneurone properties represented are the potential and resistance (ignoring the reactance) between the inside and outside of the inactive cell, as determined in this paper. For diagrammatic purposes the microelectrode tip is shown greatly magnified relative to the motoneurone.

From Coombs, Eccles & Fatt (1955) [1A-125], p. 293, fig. 1.

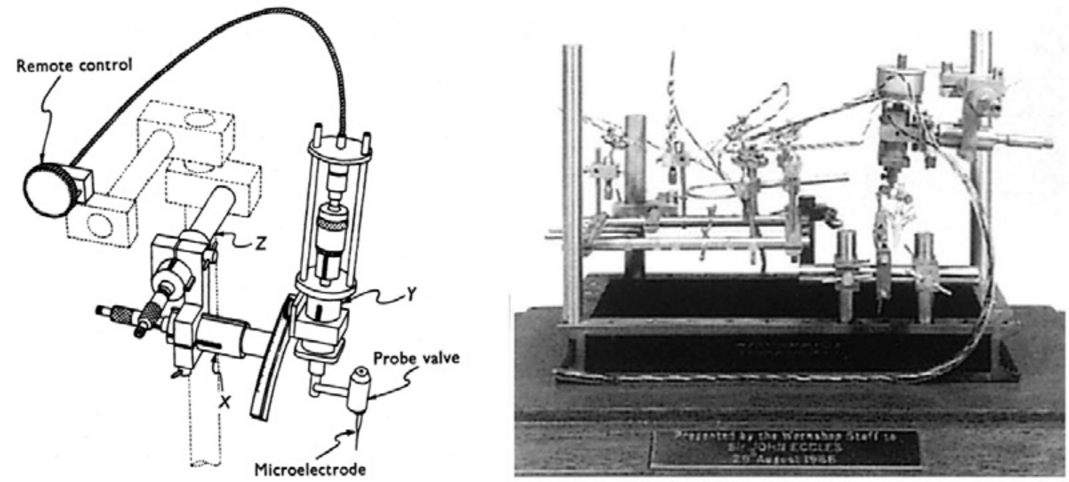


Fig. X24. Winsbury's micromanipulator probe and Eccles' animal fixation frame. [CE]

Left. Micromanipulator: The three micrometer movements used to obtain the XYZ co-ordinates of the microelectrode tip are indicated. The rigid assembly of cantilever clamps and upright post is shown in short dash outline. The X and Z movements may be clamped together in different relative positions to suit the particular experiment. An additional 50° arc adjustment enables tilting of the microelectrode entry angle. The remote control may be quickly and easily detached from the micrometer head.

From Eccles, Fatt, Landgren & Winsbury, (1954) [1A-120] p. 604, Fig. 6.

Right. The rigid frame for suspending a whole animal, offering firm support at the pelvis, lumbar and thoracic vertebrae and skull. The cerebellum was covered with a shallow pool of paraffin, care being taken that this area was not elevated above the level of the thoracic vertebrae Glass micro-electrodes, held in the micromanipulator, were attached to this animal frame. See Curtis (1959). This model of the cat fixation frame was presented to Eccles on his retirement in 1966 and is now held by the ANU.

From Foster & Varghese, (1996), p. 91.

Fig. X25. Eccles (1963), posed with animal fixation & intracellular recording equipment. [CE]

The animal fixation setup is here complemented by a conventional micrometer Z-drive and a state-of-the-art "common main objective" Carl Zeiss stereomicroscope, but with neither the "Winsbury" probe holder nor an experimental cat - whose exposed vertebrae would be located at the microscope objective's focus plane.

From ANU photographic archives.

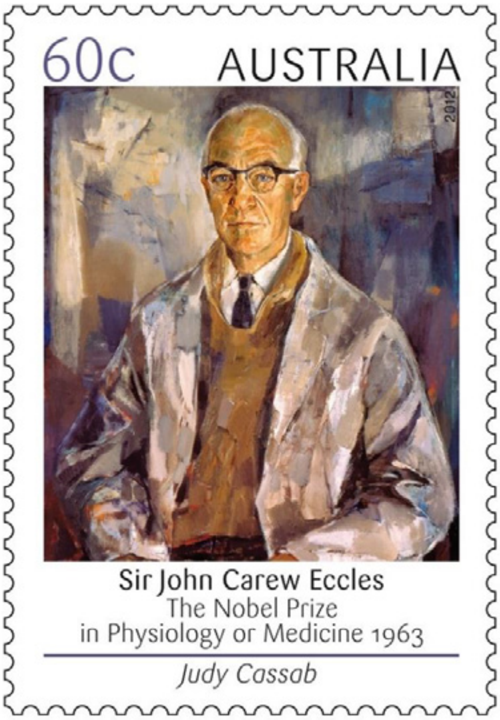


Fig. X26. Eccles' portrait, on 60c Australian stamp and Frith Cartoon. [CH]

Left. Postage Stamp series – "Australian Nobel Prize Winners". Australia SG 3828 60c Sir John Carew Eccles (physiology or medicine, 1963), Artist: Judy Cassab. Perf 14.5 x 14. Issued 28 August 2012.

Original Portrait: Sir John Eccles 1966, oil on canvas on board 104.7 x 79.8. Commissioned by the John Curtin School of Medical Research, The Australian National University, Canberra). From Pinterest https://www.pinterest.co.uk/pin/453878468677980961/

Right. Cartoon by John Frith.

The Cassab portrait and the Frith cartoon, were presented to Sir John during his farewell banquet at the ANU.

From personal property of Sir John Eccles.

Literature References

Literature References

Note: Papers authored by Eccles are also labelled [within brackets] according to the Düsseldorf classification list of his publications (Koppitz et. al, 2011) and the Catalogue Raisonné provided in Appendix 1 of this book.

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Glossaries

Glossary of Symbols, Abbreviations & Technical Words

Geographical/Nationality (2-character code, as used in the footnotes)

AT	Austrian
AU	Australian
CA	Canadian
CH	Swiss
DE	German
IE	Southern Irish (Eire)
NZ	New Zealand
RU	Russian
SE	Swedish
UA	Ukraine
UK	British (includes English, Scottish, Welsh, Cornish & Northern Irish)
US	American (USA)

Physical and Chemical Units

d.v. = tuning-fork "double vibrations", (Ellis, 1885), equivalent to frequency in Hertz.
γ = gamma, a deprecated non-SI unit of mass, equal to one microgram, μg. https://en.wikipedia.org/wiki/Microgram - cite_note-2
mm = millimetre = 10^{-3} meter
μ = micron = 10^{-3} mm = μm
nm = 10^{-6} mm = 10 Ångstrom units
Å = Ångstrom = 10^{-7} mm
sec = second
msec = 10^{-3} second
c/sec = frequency (cycles per second) = Herz
g = gram
mg = 10^{-3} gram
μg = 10^{-6} gram
mμg = 10^{-9} gram
M = mol (1 gram molecule) per litre water = 6.022141×10^{23} atoms or molecules
mM (or mmol) = 10^{-3} M/litre
μM (or μmol) = 10^{-6} M/litre
V = volt – a measure of electrical tension (named after Alessandro Giuseppe Volta)
mV = 10^{-3} volt
μV = 10^{-6} volt
Ω = ohm – a measure of electrical resistance
MΩ = 10^{6} ohm
A = amp ampere – a measure of electrical current (named after André-Marie Ampère)
mA = 10^{-3} ampere
μA = 10^{-6} ampere

mµA = 10^{-9} ampere
F = farad – a measure of electrical capacitance (named after Michael Faraday)
µF = microfarad, = 10^{-6} farad

Biochemical and Biophysical Terms

ACh: acetylcholine. An organic chemical that functions in the brain and body of many types of animals (including humans) as a neurotransmitter.
AChE: acetylcholine esterase. An enzyme which catalyses the breakdown of ACh
actin: a family of globular multifunctional proteins that form microfilaments.
afferent nerve fibres: Axons of a sensory nerve which relay sensory information (e.g. from the skin) to regions of the brain.
Group **Ia**: Sensory fibres from annulospiral endings of muscle spindles. Respond to rate of change in muscle length; rapidly adapting.
Group **Ib**: Sensory fibres from Golgi tendon organs of muscle. Respond to muscle tension changes.
Group **I**: Group **Ia** plus group **Ib**.
Group **II**: Provide position sense of a still muscle. Fire when muscle is static.
agonist: A substance that mimics the action of a transmitter at the receptor.
anion: A negatively-charged ion such as Cl^- SO_4^{2-}.
anode: Positive pole to which anions are attracted.
anoxia: Reduction of oxygen below physiological levels.
antagonist: A substance that tends to nullify the action of a neurotransmitter at the receptor.
anterior: Front part of a body (cf. posterior).
antidromic: Impulses going from axon terminals toward the neuronal soma, i.e. opposite to the usual (orthodromic) direction. An abnormal situation.
aphasia: Inability to express oneself properly through speech, or loss of verbal comprehension.
annulospiral ending (primary sensory ending): A nerve fibre type in which the fibre is wrapped around the muscle fibre near the centre of the spindle.
archicortex: The ancient part of the cerebral cortex including the hippocampus. (Also named as the archipallium).
atropine is a toxic tropane alkaloid, which can be extracted from deadly nightshade berries. Its pharmacological effects are due to binding with acetylcholine (ACh) receptors.
atrophy: The wasting-away of a body part or tissue.
axon: a long, slender projection of a nerve cell (neuron) that conducts electrical impulses (action potentials) away from the nerve cell body (soma).
cable transmission: Transmission of a potential charge along a nerve fibre in the manner of an electric cable and not as an impulse.
cathode: The negative pole to which positive ions are attracted.
cation: A positively charged ion such as Na^+, K^+, Ca^{2+} or Fe^{3+}.

Glossaries

c.e.s. (or C.E.S.) central excitatory state: The enduring neuronal process leading on to a reflex discharge.
climbing fibres: first reported by Cajal (1888) in the bird cerebellum. (For description see Palay & Chan-Palay, 1974, 242-287).
CNS (central nervous system): Refers to the brain and spinal cord combination.
cholinergic: Neurons releasing acetylcholine as the transmitter.
c.i.s. (or C.I.S.) central inhibitory state: The enduring neuronal process preventing a reflex discharge.
cortex (visual cortex): Area of the brain's cerebral cortex that processes visual information.
conditioned reflex: A reflex response which is developed in special training procedures.
conductance: measured in mhos or siemens (S). The reciprocal of electrical resistance and thus a measure of the ability of a circuit to conduct electricity; in excitable cells, a useful measure of cell membrane permeability for an ion or ions.
curare (d-tubocurarine) is a toxic alkaloid which binds readily to receptors for acetylcholine (ACh) at the neuromuscular junction, thus blocking nerve impulses to the skeletal muscles.
contralateral: Relating to the opposite side of the body.
crossed extensor reflex: a reflex in which the contralateral limb compensates for loss of support when the ipsilateral limb withdraws from painful stimulus in a withdrawal reflex.
cytoplasm: The protoplasm of a cell exclusive of the nucleus.
deafferentation: The elimination or interruption of afferent nerves.
dendrite (or dendron): a thin and branched protoplasmic extension of the nerve cell soma which carries electrochemical stimulation received from other neural cells to its own soma.
depolarization: Reduction of membrane potential from the resting value toward zero.
dorsal: Pertaining to or situated near the back (or upper) side of an animal.
EEG (Electroencephalography) is a (typically non-invasive) method to record an electrogram of the spontaneous electrical activity of the brain.
efferent nerve fibres: Axons which conduct impulses away from the named nucleus or region in the CNS.
electrochemical gradient: The value representing the voltage across a membrane for a particular charged particle, being compounded of the electrochemical potential for that particle and the voltage gradient across the membrane.
electrochemical potential: Voltage difference between two solutions insulated from each other. It is derived by the Nernst equation from the logarithmic relationship of the concentrations of the charged particles on either side of the insulating membrane.
endplate: Postsynaptic area of vertebrate skeletal muscle fibre. The specialized junction region between nerve (motoneuron) and muscle. Synonymous with "NMJ".
e.p.p. (or EPP): endplate potential (measured intracellularly).
e.p.s.p. (or EPSP): excitatory postsynaptic potential (measured intracellularly).

eserine (now known as physostigmine): a toxic alkaloid which acts by interfering with the metabolism of acetylcholine (ACh). Eserine acts as a (reversible) inhibitor of acetylcholinesterase, the enzyme responsible for breakdown of ACh at the neuromuscular junction. It can be isolated from the Calabar bean and was once used as antidote to curare poisoning.

evoked potential (or response): An electrical-potential (or movement) in a specific pattern recorded from a specific part of the nervous system (or muscle) following its irritation by a defined type of stimulus.

exocytosis: The discharge from a cell of particles that are too large to diffuse through the wall.

extensor Muscle: A muscle whose contraction straightens a joint or limb.

facilitation: Increased effectiveness of synaptic transmission by successive presynaptic impulses.

flexor Muscle: A muscle whose contraction bends a joint or limb.

ganglion: A cluster of neurons which send and receive impulses found in the peripheral nervous system, c.f. nucleus (neural).

GABA: gamma-Aminobutyric acid (or γ-aminobutyric acid) is the chief inhibitory neurotransmitter in the mammalian central nervous system (CNS). Its principal role is reducing neuronal excitability throughout the nervous system.

Golgi apparatus: A secretory organelle in the neuronal cytoplasm, easily recognised in electron microscopic studies.

Golgi type II neuron: A short-axoned neuron with an axon that arborizes in dendrite-like fashion in the neighbourhood of the cell body.

grey (gray) matter: a major component of the central nervous system, consisting of neuronal cell bodies, neuropil (dendrites and unmyelinated axons), glial cells (astrocytes and oligodendrocytes), synapses, and capillaries (cf. white matter).

hamstring: collective name for muscles in the posterior compartment of the thigh, known as the hamstrings. It consists of *biceps femoris*, *semitendinosus* and *semimembranosus*, which form prominent tendons medially and laterally at the back of the knee.

hippocampus: A special part of the cerebral cortex (see archicortex).

hydrophilic: A material that attracts water.

hypoxia: Low oxygen content or tension; deficiency of oxygen in the inspired air.

inductance: frequency-dependant resistance to a change in electrical force, much like inertia.

inhibition: Effect of one neuron upon another tending to prevent it from initiating impulses: postsynaptic inhibition is mediated through a permeability change in the postsynaptic cell, holding the membrane potential away from threshold; presynaptic inhibition is mediated by an inhibitory fibre upon an excitatory terminal, reducing the release of transmitter; electrical inhibition is mediated by currents in presynaptic fibres that hyperpolarize the postsynaptic cell and do not involve the secretion of a chemical transmitter.

initial (or non-medullated) segment of an axon: the proximal region of an axon close to the soma which is not insulated (i.e. unmyelinated).
interneurons: Short-axoned excitatory or inhibitory nerve cells in the central nervous system; see Golgi type II neurons.
ipsilateral: On the same side of the body.
i.p.s.p. (or IPSP): inhibitory postsynaptic potential (intracellular).
latency: The time between the initiation of a physiological or chemical sequence and a measurable result.
medullated: a synonym for myelinated.
medullation: Myelination, the formation of a laminated insulating wrapping (myelin) around nerve fibres.
microphotograph: Commonly-used misnomer for preferred term; photomicrograph.
mossy fibers: “fibras nudosas” first reported by Cajal (1888) in the bird cerebellum. (For description see Palay & Chan-Palay, 1974, p. 142-179).
motoneuron (motor neuron): A neuron that innervates muscle fibres.
motor unit: The axon or nerve fibre arising from a motoneuron in the spinal cord and the assemblage of muscle fibres activated by it.
muscarinic: Resembling acetylcholine or muscarine in actions at specific receptors.
muscle spindles: Encapsulated bundles of fine muscle fibres specially related to muscle stretch receptors.
myelin: Fused membranes of Schwann cells or glial cells forming a high-resistance sheath around an axon.
myosin: The contractile protein of muscle fibres, acting in association with actin and titin protein fibres.
nerve fibre: An axon (the principal branch from a nerve cell) which may extend for long distances from its soma.
neurofibrils: Fine fibres running along the interior of nerve axons.
neuromuscular junction (or NMJ): Junction of muscle and nerve; the region where neuromuscular transmissions occur. Synonymous with “endplate”.
neuron (or neurone): a nerve cell. The biological unit common to both the brain and the remainder of the nervous system.
neuron doctrine/theory: That the nervous system is composed of individual neurons biologically independent but informationally communicating by synapses.
nucleus (cytological): Large basophilic mass, usually centrally placed within the cell body. Contains the DNA which provides the genetic instruction for the cell.
nucleus (neural): A neural tissue component in the CNS (made of two substances of different aspect and colour; white matter and grey matter) first described by Cajal in 1909, representing a complex coupling or association station between the sensory conductors, that bring the neural excitation, and the motor conductors, that propagate the latter to the corresponding locomotor and glandular apparatuses. I.e. a collection of neurons that are thought to work together in performing certain functions.

orthodromic: Wave of neuronal excitation passing in the physiological direction from cell body to axonal ending. This is the normal excitation direction; (c.f. antidromic.)
phospholipids: Molecules composed of fatty acid chains and a phosphorylated polar end forming the basic structure of cell membranes.
posterior: At or toward the hind end of the body; in a tail-ward or caudal direction (in humans, behind or dorsal rather than below). C.f. "anterior".
postsynaptic membrane: The nerve cell or other receptor cell membrane immediately related to the synapse formed by presynaptic fibres ending on it.
postsynaptic potentiation: The increased synaptic action that follows intensive synaptic stimulation.
presynaptic fibres: The terminal branches of nerve fibres that end as synaptic knobs.
resistance: frequency-independent constant pushback against electrical force, an effect much like mechanical friction.
sacral: Situated near or pertaining to the sacrum (the triangular base just below the lumbar vertebrae).
soma: the thick main part (body) of a neuron cell, from where the dendrites (plus the single axon) branch off.
subliminal excitation: sensory stimulation below the threshold for effectiveness.
synaptic plasticity: The property of synapses whereby they are changed in functional efficiency, probably by virtue of changes in size.
syncytium: A multinucleate mass of protoplasm produced by the merging of cells.
tendon: a collagenous band which connects a muscle to a bone.
tetanus: here usually refers to the physiologic "motor tetanus", a sustained muscle contraction, evoked either by repetitive stimulation or when the motor nerve to a skeletal muscle emits action potentials at a very high rate. (It can also refer to "lockjaw" infection tetanus caused by the bacterial toxin of *Clostridium tetani*).
tonic: Characterized by continuous tension or producing and restoring normal tone.
trophic influences: Actions from one part of a cell to another, or from one cell to another, which are concerned with the growth, maintenance, and metabolism of the cell.
trophic transport: The postulated mechanism of transport of specific macromolecules within a cell and between cells that is concerned in exerting trophic influences.
ventral: Toward the under (or belly) side of the body.
volley: a succession (or "train") of nervous impulses at very short intervals, conducted by a nerve fibre.
white matter: Part of the central nervous system appearing white; consisting largely of myelinated fibre tracts and relatively few cell bodies (cf. grey matter).

Appendix 1: John Eccles Archives and Private Library.

An invitation by authors: De Sio, Fabio and Koppitz, Ulrich

This edition of John Eccles' unpublished autobiography also contains his catalogue raisonné. After some contemporary compilations, his disciples Curtis & Anderson had published a comprehensive article for the Australian Academy with a publication list, which was based on Eccles' own reprint collection bound in series (Curtis & Andersen, 2001a; Curtis & Andersen, 2001b). However, this most impressive list could be enhanced by over 65 additional entries and ca. 220 bibliographical specifications, mostly referring to book chapters, e. g. in conference volumes. This was not because of better online research facilities but of an ideal situation of historical sources on the basis of the original author library with voucher copies and reprints. Moreover, other researchers have graciously contributed towards completing the list.

When dealing with an author like John Eccles, prolific in both science and the humanities, books should not be underestimated. In comparison to some 5,300 pages found in the Web of Science, the *catalogue raisonné* in the following appendix counts over 14,000 pages, apart from many translations and re-editions.

Most of his library is still available on open stacks in the reading room of the Centre for the History of Neurosciences in Dusseldorf, Germany, (Sotke, Koppitz & De Sio, 2013). There, at his own desk, also the personal archive of John Eccles is available upon application. For researchers from Oceania, remote access possibilities can be envisaged as far as possible (see the central website for further practical information www.uniklinik-duesseldorf.de/eccles).

From an Oceanian perspective, the location of the archive in Düsseldorf, a place with which Eccles had only the vaguest ties, might be surprising. However, as his widow and disciples tried to find an institution willing to respect the condition of keeping the library and archive together, without dispersing the former, no offer materialised from English-speaking institutions (Freund, 2011, p. 7-8). Thus, after interim solutions in Switzerland, the archive was donated to the Department for the History, Philosophy and Ethics of Medicine in Düsseldorf, where an international opening conference was held by the Academy in 2011 (De Sio et al, 2011, 569-572). The German Research Foundation (DFG) funded the initial cataloguing via the portal Kalliope, of the Berlin Staatsbibliothek. https://kalliope-verbund.info/en/index.html

John Eccles grew up in a letter-writing culture and entertained an amazingly international scholarly network, (see Stuart & Pierce, 2006) similar to the brain researchers Cécile and Oskar Vogt, whose archive forms the other main component of the Centre.

This autobiography contains many explicit hints at correspondences, people and events, of which the archive contains valuable material. Thus, the autobiography could serve as a portal to the most important roads – in his perspective – to find one's way through John Eccles' impressive lifework preserved in the archive.

Already in the introduction to his autobiography, before his reminiscence of associates during his Odyssean stages of life, John Eccles stated that; "I am fortunate to have a clear and vivid memory and I have an immense store of letters and documents, tens of thousands". These documents survive in the Dusseldorf Centre for the History of the Neurosciences, and the interested reader may see this chapter as an invitation to study John Eccles' works and networks in detail.

An earlier, numerically-ordered list of John Eccles' publications is available for downloading at:

https://www.uniklinik-duesseldorf.de/patienten-besucher/klinikeninstitutezentren/institut-fuer-geschichte-theorie-und-ethik-der-medizin/bibliothek-sammlungen/eccles-collection/publications-by-eccles

Appendix 2: *Catalogue raisonné* of J. C. Eccles' publications.

The catalogue of publications in mere chronological order can be studied at www.uniklinik-duesseldorf.de/eccles as List of Publications by John C. Eccles.

The following thematic catalogue in addition reveals coherence and developments more clearly, although many of the 645 titles would rather fit in more than one of the 12 categories chosen.

(This list has been published already in Freund, Hans Joachim, Ulrich Koppitz, Alfons Labisch (eds.): *The Legacy of John C. Eccles: Selected Letters (1937-1963) and Guide to the Archive in Düsseldorf* (Shaker, Aachen 2011), 33-83, but was amended in 2021 by 3 titles and 8 translations marked *).

Catalogue syntax:

In square brackets firstly the label of the library is indicated [1A for articles, 1B for tetanusbooks], secondly the number [N°] of the publication in the chronological list on the website mentioned, where the search engine of the browser can be applied].

1.) **Nervous System Physiological Phenomena**
MeSH D009424 [G11.561]: titles 1-72 (published 1929-1994)

1.1) **Muscle** and **Reflex**
D009469/D012098 [A08.800.550.550.550]: titles 73-122 (1928-1963)

1.2) **Neurons**
MeSH D009474 [A08.663]: titles 123-205 (1931-1990)

1.2.1) **Synapses**
MeSH D013569 [A08.850]: titles 206-275 (1930-1986)

1.3) **Ganglia**
MeSH D005724 [A08.340]: titles 276-291 (1933-1960)

1.4) **Spinal Cord**
MeSH D013116 [A08.186.854]: titles 292-331 (1930-1982)

1.5) **Hippocampus** D00624 [A08.186.211.464.405] and **Thalamus**
MeSH D013788 [A08.186.211.730.317.826]: titles 332-345 (1963-1983)

1.6) **Cerebellum** D002531 [A08.186.211.132.810.428.200]: titles 346-424 (1929-1988)

2.) Humanities [K01] and interdisciplinary works

2.1) **Philosophy**
MeSH D010684 [K01.752]: titles 425-470 (1947-1999)

2.1.1) **Mind-Body-relationship**
MeSH D019222: titles 471-572 (1952-1998)

2.1.2) **Evolution** (Biological: MeSH D005075 [G05.355.044]; Cultural MeSH D003468 [I01.076.201.450.370]: titles 573-600 (1966-1996)

2.2) **Historiography** MeSH D006663 [K01.400.441] incl. Nuclear Warfare D009689 [I01.880.735.944.600]: titles 601-645 (1952-1992)

Nervous System Physiological Phenomena
MeSH D009424 [G11.561]

1. Eccles, John C. and Charles S. Sherrington: Improved bearing for the torsion myograph. In *Journal of Physiology* 69 (1929), i [1A-004; N° 4]
2. Eccles, John C., Ragnar Granit and John Z. Young: Impulses in the giant nerve fibres of earthworms. In *Journal of Physiology* 77 (1932), 23P [1A-020; N° 21]
3. Eccles, John C. and J. H. C. Thompson: An investigation of the visco-elastic properties of rubber. In *Proc. Roy. Soc. Lond. A* 148 (1935), 171-185 [1A-030; N° 31]
4. Eccles, John C.: Physical problems in neurology. In *Australian Journal of Science* 4 (1941), 4-8 [1A-062; N° 63]
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MeSH D005724 [A08.340]

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MeSH D013116 [A08.186.854]

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MeSH D002531 [A08.186.211.132.810.428.200]

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Appendix 3: Some Stations in the Life of John Eccles

The images in this set can be accessed from the Internet as satellite maps and street views, as provided by Google at the time of publication. The supplied https: lines can be manually entered directly into the Internet via a browser (line endings do not imply carriage returns!); alternatively, the associated QR code images are supplied to enable fast access by means of "smartphone" scanning.

Station 1: Jumbunna (birthplace and early childhood 1903-10).

The long-ago demolished school was perhaps sited to the left of building at 9 Goochs Rd. and the schoolmaster's house was probably located nearby.

S01a Approximate location of Jumbunna Primary School no 2954
https://www.google.com.au/maps/place/Jumbunna+VIC+3951,+Australia/@-38.4683336,145.7702679,113m/data=!3m1!1e3!4m5!3m4!1s0x6b2a1ea0c5596e75:0x40579a430a06ed0!8m2!3d-38.4685754!4d145.774616

S01b. Aerial view of Victorian Coast with neighbour towns; Koriot and Warrnambool.
https://www.google.com.au/maps/@-38.3250095,142.5069154,29021m/data=!3m1!1e3

S01a S01b

Station 2: Koroit (as schoolboy 1911-14).

S02a Aerial view of Koroit school and schoolmaster's house, 95 Commercial Rd.
https://www.google.com.au/maps/place/Koroit+VIC+3282,+Australia/@-38.2923124,142.3690597,454m/data=!3m1!1e3!4m5!3m4!1s0x6acd498b40df8cdb:0x40579a430a0c7c0!8m2!3d-38.2921758!4d142.3673185

S02b Street-view of Koroit school and Eccles' house (at left) on 95 Commercial Rd.

https://www.google.com.au/maps/@-38.2923124,142.3690597,3a,49y,174.98h,91.48t/data=!3m6!1e1!3m4!1staV72U4ryyZeJE2KtrFWCw!2e0!7i16384!8i8192

S02a S02b

Station 3: Warrnambool (as secondary college schoolboy 1915-18).

S03a. Aerial view of Warrnambool College.
https://www.google.com.au/maps/place/Warrnambool+College/@-38.3778292,142.4995995,453m/data=!3m1!1e3!4m5!3m4!1s0x6acd4db757a4053b:0x62f43270aa6abc74!8m2!3d-38.377042!4d142.500214

S03b. Street view of Warrnambool College.
https://www.google.com.au/maps/@-38.3767661,142.5003735,3a,51.3y,215.24h,99.83t/data=!3m6!1e1!3m4!1s-O3KHUNeqDLYrwswbavMWw!2e0!7i13312!8i6656

S03a S03b

Station 4: Melbourne (as final year school student 1919-20).

S04a: Aerial view (site only) of Melbourne High School, at one time in Spring St.

https://www.google.com.au/maps/place/Royal+Australasian+College+of+Surgeons+(RACS)/@-37.8086467,144.9722941,136m/data=!3m1!1e3!4m5!3m4!1s0x6ad642c57ef11259:0x1b99f5f1d170ca5a!8m2!3d-37.8085073!4d144.9728155

S04b: Street view from the Melbourne High School Prospectus of 1910.
https://dro.deakin.edu.au/eserv/DU:30096876/melbourne1947melbournecontinuation.pdf

S04a S04b

Station 5: Melbourne University (as medical student 1921-24).

S05a: Aerial view of Melbourne University in 2022.
https://www.google.com.au/maps/@-37.7987744,144.9596929,228m/data=!3m1!1e3

S05b: Aerial view (site only) of Eccles family house at 55 Wills St., Kew, Melbourne.
https://www.google.com.au/maps/@-37.7989742,145.0253408,57m/data=!3m1!1e3

S05a S05b

Station 6: St. Vincent's Hospital, Melbourne (as medical intern 1925).

S06a: Aerial view of St. Vincent's Hospital, Regent St. Melbourne.
https://www.google.com.au/maps/@-37.8063942,144.9742289,228m/data=!3m1!1e3

S06a

Station 7: Oxford, England (as doctoral student 1925-26).

S07a: Aerial view of Magdalen College, Oxford.
https://www.google.co.nz/maps/@51.7515919,-1.2485947,179m/data=!3m1!1e3

S07b: Street view of Magdalen College, Oxford.
https://www.google.co.nz/maps/@51.751343,-1.2464502,3a,90y,358.14h,96.54t/data=!3m6!1e1!3m4!1sdPB0b2ip41VJgfIy0Of-Lg!2e0!7i16384!8i8192!5m1!1e1

https://www.google.co.nz/maps/@51.7515919,-1.2485947,179m/data=!3m1!1e3S07c: Aerial view of Rose Lane, Oxford (Eccles' first flat after arrival in Oxford).
https://www.google.co.nz/maps/@51.7515919,-1.2485947,179m/data=!3m1!1e3

S07d: Street view of Rose Lane.
https://www.google.co.nz/maps/@51.7520162,-1.2478823,3a,89.7y,241.91h,95.39t/data=!3m6!1e1!3m4!1syfI1D68THRocNM1W6iZMDA!2e0!7i16384!8i8192

S07e: Aerial view of Exeter College, Turl St. Oxford (Eccles' later Oxford accommodation).
https://www.google.co.nz/maps/@51.7538785,-1.2558913,179m/data=!3m1!1e3

S07f: Street view of Exeter College, Oxford.
https://www.google.co.nz/maps/@51.7533732,-1.2562143,3a,90y,11.52h,100.22t/data=!3m6!1e1!3m4!1srtCpvuokjEXLorpTj_i4bA!2e0!7i16384!8i8192

S07a S07b S07c

S07d S07e S07f

Station 8: Oxford, England (as married university graduate 1927-37).

S08a: Aerial view of house at1 Staverton Road, Oxford.
https://www.google.co.nz/maps/@51.7716117,-1.2635501,45m/data=!3m1!1e3

S08b: Street view of house at 1 Staverton Road, Oxford.
https://www.google.co.nz/maps/@51.7717317,-1.2637708,3a,41.3y,191.82h,94.3t/data=!3m6!1e1!3m4!1skKPj2GboSWSiavYLFvqYnA!2e0!7i16384!8i8192

S08c: Aerial view of Eccles' family annual holiday retreat at Coverack, Cornwall.
https://www.google.co.nz/maps/@50.0230284,-5.0968579,46m/data=!3m1!1e3

S08d: Street view of Coverack and beachfront, Cornwall.
https://www.google.co.nz/maps/@50.0230217,-5.0968755,3a,75y,353.94h,94.71t/data=!3m6!1e1!3m4!1sG2M-LEFv_Ggy0rp6F0a1_g!2e0!7i13312!8i6656

S08a S08b

S08c S08d

Station 9: Sydney, Australia (as research director 1937-43).

S09a: Aerial view of Eccles' house at 14 Clanalpine Street, Mosman, Sydney.
https://www.google.com.au/maps/@-33.8373475,151.238402,71m/data=!3m1!1e3

S09b: Street view of Eccles' house at 14 Clanalpine Street, Mosman, Sydney.
https://www.google.com.au/maps/@-33.8372905,151.2381501,3a,65y,105.7h,98.84t/data=!3m6!1e1!3m4!1svwxYndCZAcIT0meX0dY4Kg!2e0!7i16384!8i8192

S09c: Aerial view of presumed site of the Kanematsu Institute, Sydney University.
https://www.google.com.au/maps/@-33.8684701,151.2132236,120m/data=!3m1!1e3!5m1!1e1

S09d: Street view of replacement building at presumed site of Kanematsu Institute.
https://www.google.com.au/maps/@-33.8687084,151.2134812,3a,90y,302.58h,103.9t/data=!3m6!1e1!3m4!1sNkdphAsGST_vPYr0J0iocA!2e0!7i16384!8i8192

S09e: Aerial view of Killalea Beach, Shell Cove; venue for the Eccles' family holidays.
https://www.google.com.au/maps/@-34.6027584,150.8640087,1346m/data=!3m1!1e3

S09f: Street view of Killalea Beach, Shell Cove; venue for the Eccles' family holidays.
https://www.google.com.au/maps/@-34.607872,150.8646019,3a,75y,355.66h,76.34t/data=!3m7!1e1!3m5!1sKUvzmcskqAh42ujOpR2LSQ!2e0!6shttps:%2F%2Fstreetviewpixels-pa.googleapis.com%2Fv1%2Fthumbnail%3Fpanoid%3DKUvzmcskqAh42ujOpR2LSQ%26cb_client%3Dmaps_sv.tactile.gps%26w%3D203%26h%3D100%26yaw%3D168.41872%26pitch%3D0%26thumbfov%3D100!7i16384!8i8192

S09a S09b

S09c S09d

S09e S09f

Station 10: Dunedin, New Zealand (as university professor 1943-52).

S10a: Aerial view of Eccles' family house at 84 Cannington Road, Māori Hill, Dunedin.
https://www.google.co.nz/maps/@-45.8536719,170.5022731,71m/data=!3m1!1e3

S10b: Street view of family house at 84 Cannington Road, Māori Hill, Dunedin.
https://www.google.co.nz/maps/@-45.853811,170.5017666,3a,36y,66.42h,96.21t/data=!3m6!1e1!3m4!1sdQcofp9DYec5dQlmz7UajQ!2e0!7i16384!8i8192

S10c: Aerial view of the Lindo Ferguson Building, 270 King Street, Dunedin.
https://www.google.co.nz/maps/@-45.8691196,170.5077636,101m/data=!3m1!1e3

S10d: Street view of Lindo Ferguson Building, 270 King Street, Dunedin.
https://www.google.co.nz/maps/@-45.8692167,170.508035,3a,90y,293.2h,95.57t/data=!3m6!1e1!3m4!1su2e_vO0smfDnQJfEEBMTFw!2e0!7i16384!8i8192

S10a S10b

S10c S10d

Station 11: Canberra, ACT, Australia (as research director 1953-66).

S11a: Aerial view of Eccles' house site at 28 Monaro Crescent, Red Hill, ACT.
https://www.google.com.au/maps/@-35.3271765,149.1267039,167m/data=!3m1!1e3

S11b: Street view of redeveloped house site at 28 Monaro Crescent, Red Hill.
https://www.google.com.au/maps/@-35.3273047,149.1273663,3a,90y,238.31h,107.1t/data=!3m6!1e1!3m4!1s_wSOH4PuSFy3s2qp319Yqg!2e0!7i16384!8i8192

S11c: Aerial view of (new) John Curtin School of Medical Research, Canberra. (Original research buildings can be viewed using Google Earth with history version set at 2008)
https://www.google.com.au/maps/place/John+Curtin+School+of+Medical+Research/@-35.2820855,149.1146855,118m/data=!3m1!1e3!4m5!3m4!1s0x6b164d487b582b41:0x83b7ecdb7982e670!8m2!3d-35.2820855!4d149.1149591

S11d: Street view of (new) John Curtin School Garran Rd., Canberra.
https://www.google.com.au/maps/@-35.2818335,149.1150691,3a,84.8y,205.81h,89.53t/data=!3m7!1e1!3m5!1sH8_IhRiH0AQeK_q_k4DkGQ!2e0!6shttps:%2F%2Fstreetviewpixels-pa.googleapis.com%2Fv1%2Fthumbnail%3Fpanoid%3DH8_IhRiH0AQeK_q_k4DkGQ%26cb_client%3Dmaps_sv.tactile.gps%26w%3D203%26h%3D100%26yaw%3D72.033165%26pitch%3D0%26thumbfov%3D100!7i16384!8i8192

S11e: Aerial view of Bawley Point. (to be checked)

https://www.google.co.nz/maps/place/Bawley+Point+New+South+Wales+2539,+Australien/@-

35.5171827,150.3941691,1119m/data=!3m1!1e3!4m5!3m4!1s0x6b15b1a4f26f2c65:0x40609b490440620!8m2!3d-35.5183585!4d150.3967269

S11a S11b

S11c S11d

Station 12: Chicago, United States (as research director 1967).

S12a Aerial view (in 2022) of site formerly occupied by the Institute for Biomedical Research, American Medical Association, 535 N. Dearborn Street, 60610, Chicago, Illinois.

https://www.google.co.nz/maps/@41.8919103,-87.6294763,54m/data=!3m1!1e3

S12b Street view (in 2021) of site once occupied by the Institute for Biomedical Research.

https://www.google.co.nz/maps/@41.8915425,-87.6296813,3a,75y,58.3h,99.41t/data=!3m6!1e1!3m4!1sEM-YGOkzFNN8F3FbcFo4dw!2e0!7i16384!8i8192

S12a S12b

Station 13: Buffalo, United States (as research director 1968-75).

S13a: Aerial view of Eccles' private residence at 100 Lincoln Parkway, Buffalo.
https://www.google.com/maps/@42.9294648,-78.8744313,53m/data=!3m1!1e3

S13b: Street view of Eccles' private residence at 100 Lincoln Parkway, Buffalo.
https://www.google.com/maps/@42.929482,-78.874008,3a,66.8y,267.81h,93.96t/data=!3m7!1e1!3m5!1s5Nu7maCN5kWD9kQaKJPR0w!2e0!6shttps:%2F%2Fstreetviewpixels-pa.googleapis.com%2Fv1%2Fthumbnail%3Fpanoid%3D5Nu7maCN5kWD9kQaKJPR0w%26cb_client%3Dmaps_sv.tactile.gps%26w%3D203%26h%3D100%26yaw%3D180.59073%26pitch%3D0%26thumbfov%3D100!7i16384!8i8192

S13a S13b

S13c: Aerial view of the State University of New York at 4234 Ridge Lea Road, Buffalo, Amherst, NY 14226, USA (dated 2022)

https://www.google.co.nz/maps/place/4234+Ridge+Lea+Rd,+Amherst,+NY+14226,+USA/@42.9996172,-78.8127833,3a,75y,213.62h,88.4t/data=!3m7!1e1!3m5!1s-hk3c8wrtb3XqhgStLtKfw!2e0!6shttps:%2F%2Fstreetviewpixels-pa.googleapis.com%2Fv1%2Fthumbnail%3Fpanoid%3D-hk3c8wrtb3XqhgStLtKfw%26cb_client%3Dsearch.gws-prod.gps%26w%3D360%26h%3D120%26yaw%3D202.9%26pitch%3D0%26thumbfov%3D100!7i16384!8i8192!4m5!3m4!1s0x89d3723db2a0e645:0xe4728d1f3ebcbd36!8m2!3d42.9994903!4d-78.8128521!5m1!1e1

S13c

Stations in Jack's Life – viewed in Google Maps

Station 14: Contra, Italy (in retirement 1976-97).

S14a. Aerial view of Eccles' house site at Via Falò **122** now occupied by "Vita Silvestre". (For view of original house use program Google Earth Pro with history date set to 8/2008).
https://www.google.co.nz/maps/search/contra+Switzerland/@46.1908389,8.8374128,50m/data=!3m1!1e3

S14b. Street view of the Eccles' house at Via Falò **122** (photographed 8/2013).
https://www.google.co.nz/maps/@46.1906662,8.8376581,3a,90y,355.78h,88.1t/data=!3m6!1e1!3m4!1sdcPSBti1ShxY5ZjNtyEm-g!2e0!7i13312!8i6656

S14c. Aerial view of via Contra with: **750** municipal office, **752** church & **720** cemetery.
https://www.google.co.nz/maps/search/contra+Switzerland/@46.1881942,8.8391392,119m/data=!3m1!1e3

S14d. Street view of Contra municipal building, church and Eccles' memorial fountain.
https://www.google.co.nz/maps/@46.1886105,8.8397758,3a,90y,154.43h,90.95t/data=!3m7!1e1!3m5!1so1aYgCFyL518er-MZB2RDA!2e0!6shttps:%2F%2Fstreetviewpixels-pa.googleapis.com%2Fv1%2Fthumbnail%3Fpanoid%3Do1aYgCFyL518er-MZB2RDA%26cb_client%3Dmaps_sv.tactile.gps%26w%3D203%26h%3D100%26yaw%3D266.14493%26pitch%3D0%26thumbfov%3D100!7i13312!8i6656

S14e. Street view of the cemetery at Contra (glimpsed from road above).
https://www.google.co.nz/maps/@46.1879017,8.8385196,3a,15y,101.72h,76.43t/data=!3m6!1e1!3m4!1snzP5N6EeSibXWUv_eGUJVQ!2e0!7i13312!8i6656

S14a S14b S14c

S14d S14e

Appendix 4: Relevant audio and video media

Some Internet links to audio and video recordings relevant to John Eccles' life, are listed here. Corresponding QR codes are gathered together at the end of this section).

Audio Media

A01: "The physical basis of mind": Sir Charles Sherrington (1948):
https://soundcloud.com/wellcomelibrary/the-physical-basis-of-mind-sir?in=wellcomelibrary/sets/medical-lives&utm_source=clipboard&utm_medium=text&utm_campaign=social_sharing

A02: "I remember": Sir Henry Dale (1960:
https://soundcloud.com/wellcomelibrary/i-remember-sir-henry-dale-1960?in=wellcomelibrary/sets/medical-lives&utm_source=clipboard&utm_medium=text&utm_campaign=social_sharing

A03: Eccles Talk: "Inhibitory pathways in the spinal cord" by Sir John Eccles (probably early 1960s) from a recording found in the effects of Dr Roy Kay, Oxford. Duration: 1h:20m. Talk 58 min followed by Q&A. Location unknown, good quality.
https://learntech.medsci.ox.ac.uk/wordpress-history/seminars/eccles-talk/

A04: Sir John Eccles and other Nobel Prize recipients at the official awarding ceremony of 1963 in Sweden.
https://speakola.com/ideas/john-eccles-nobel-banquet-1963

A05: Sir John Eccles at the Lindau Nobel Laureate Meeting of 1972 (accompanied by photographs).
https://www.mediatheque.lindau-nobel.org/videos/31453/the-human-person-a-scientific-and-a-philosophical-problem-1980/laureate-eccles

A06: Sir John Eccles, as distinguished professor of physiology and biophysics at the State University of New York at Buffalo, in October 15th 1975 at the Nobel Conference XI: The Future of Science held at Gustavus Adolphus College. Eccles' speech was titled "The Brain-Mind Problem as a Frontier of Science.", (accompanied by a poor text transcription of his talk).
https://archive.mpr.org/stories/1975/10/15/nobel-conference-xi-the-future-of-science-john-eccles-the-brain-mind-problem-as-a-frontier

A07: Sir John Eccles, speaking at the Lindau Nobel Laureate Meeting of 1980.
https://www.mediatheque.lindau-nobel.org/videos/31453/the-human-person-a-scientific-and-a-philosophical-problem-1980/laureate-eccles

A08: Sir John Eccles at the Lindau Nobel Laureate Meeting of 1992 (accompanied by photographs).

https://www.mediatheque.lindau-nobel.org/videos/31454/how-subtile-chemistry-evolving-in-the-mammalian-brain-opened-it-to-the-world-of-feeling-1992/meeting-1992

A09: ABC interviewer Sharon Carleton portrays Sir John Eccles, in an Australian radio talk program. A text transcription accompanies this talk - Carleton (2003).

https://www.abc.net.au/radionational/programs/scienceshow/a-portrait-of-john-eccles---australian-nobel-laureate-who-devot/13036588

This Carleton talk of 2003 was re-issued in 2023 as:
https://www.abc.net.au/listen/programs/scienceshow/the-life-and-work-of-sir-john-eccles/102787698
or
https://www.abc.net.au/listen/programs/scienceshow/the-science-show/102725266

A10: ABC interviewer Sharon Carleton presents Sir John Eccles' dualist philosophy, also the contribution by daughter Rose to his experimental career. (a text transcription accompanies this talk), Carleton (2023).

https://www.abc.net.au/listen/programs/scienceshow/sir-john-eccles-and-the-invaluable-work-of-his-daughter-rose/102812946

Video Media

M01: A Physiological Society cinematograph presentation (monochrome& mute) with archive footage of Sherrington preparing paraffin sections of brain using a Cambridge "rocking microtome", dissecting a monkey brain and using a microscope.
https://www.youtube.com/watch?v=39rYT9YloLo&t=94s

M02: A similar film of Sherrington at work from the Wellcome collection (mute but displayed here in colour) dated about 1941.
https://wellcomecollection.org/works/c38ugb3e

M03: Sir John Eccles; interviewing Karl Popper in 1988 on the Channel 4 programme 'Uncertain Truth', No. 3/6.

https://www.upcarta.com/resources/1218-uncertain-truth-john-eccles-karl-popper

M04: Seminar: "Sherrington, Eccles and Popper". Marianne Fillenz's memories of John Eccles and Karl Popper, delivered at the Le Gros Clark Building, Dept of Physiology, Anatomy and Genetics, University of Oxford on March 3rd 2011. (Unfortunately, many of her slides were deliberately blurred - to protect copyright.)

https://history.medsci.ox.ac.uk/seminars/history-of-medical-sciences-seminar-series/dr-marianne-fillenz-sherrington-eccles-and-popper/

M05: Australian Academy of Science 2024 public speaker series. The journey of Australian science – Eccles and neuroscience; with professors Stephen Redman & Lucy Palmer. Delivered at the Shine Dome Canberra, 10 December 2024.
https://www.youtube.com/watch?v=2pRFVPDQy-k

A01 A02 A03

A04 A05 A06

A07 A08 A09

Links to historical Audio & Video Media

A10 M01 M02

M03 M04 M05

Afterword: Sir John Carew Eccles – The Person.

[How can one adequately characterise a person of Sir John's calibre? In almost every direction (especially in sport and intellect) he reigns supreme. Nevertheless, the editor (who has never met in person Sir John or indeed any members of his family) audaciously attempts to present here his perceived appraisal of the man and his life.]

Eccles' life goals and family life

Repeatedly throughout his life, Eccles seized on personal beliefs which he followed with passionate obsession, backed up by well-prepared reasoning and sometimes formidable presentation. Nevertheless, as a true sportsman, he could quickly realise defeat and respond graciously. Eccles' long-held belief in electrical (ionic) transmission of signals at the synapse was held with dogged ferocity until he proved it to be incorrect as a direct result of his own experimentation. After that epiphany he adopted and promulgated his corrected thesis of chemical transmission with renewed vigour.

It is clear that Eccles devoted most of his boundless energy towards his intellectual goals. He used women in his life to suit his requirements. Rene served as his faithful housewife for many years and she bore for him his large family of children. Nevertheless, even before he received his Nobel Prize, she was becoming somewhat of a burden to his aspirations, probably by her anticipation of a life of quiet retirement in their Canberra home. Sadly, evidence of increasing marital problems (aired during the Prize ceremony) were seized upon and headlined by the Melbourne "Truth" and New South Wales "Daily Mirror" tabloid newspapers.

Eccles, absolutely determined to continue his research at all costs, met Helena Táboriková at a Czechoslovakian conference and must have decided that she, as competent scientist and willing colleague would best fulfil his need for a future partner. He committed a grave error after his move (alone) to the USA by planning his divorce from Rene in absentia, which resulted in scorn from his family, a bitter response from the outraged Rene and the ensuing personal loss of his much-treasured lecture notes and other material still remaining in Australia.

It is difficult to escape the conclusion that Eccles' plan to escape from an increasingly boring marriage and enter a new unfettered phase of research with his new-found scientist partner did not quite lead to the happiness that he envisaged. The short time the couple first spent in Chicago his career was marred by inappropriate delusions of grandeur by his new partner. At Buffalo, the research situation improved, but it became obvious that Sir John's successful marital relationship to Helena was at the cost of complete rejection, not only of his first wife, Rene, but also of the rest of his family. Towards the end of his life, this forced rejection no doubt weighed heavily on his mind. In addition, it seems clear that Helena never wanted him to publish his autobiography with its honest revelation of research failures as well as successes, although she typewrote it out for him. The few occasions where the old man could confide with others without Helena being present were with his local Swiss physician and with his daughter, Mary, on the rare occasions when she managed to be alone with him during her visits to Switzerland.

Index of persons in autobiography & family sections

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END

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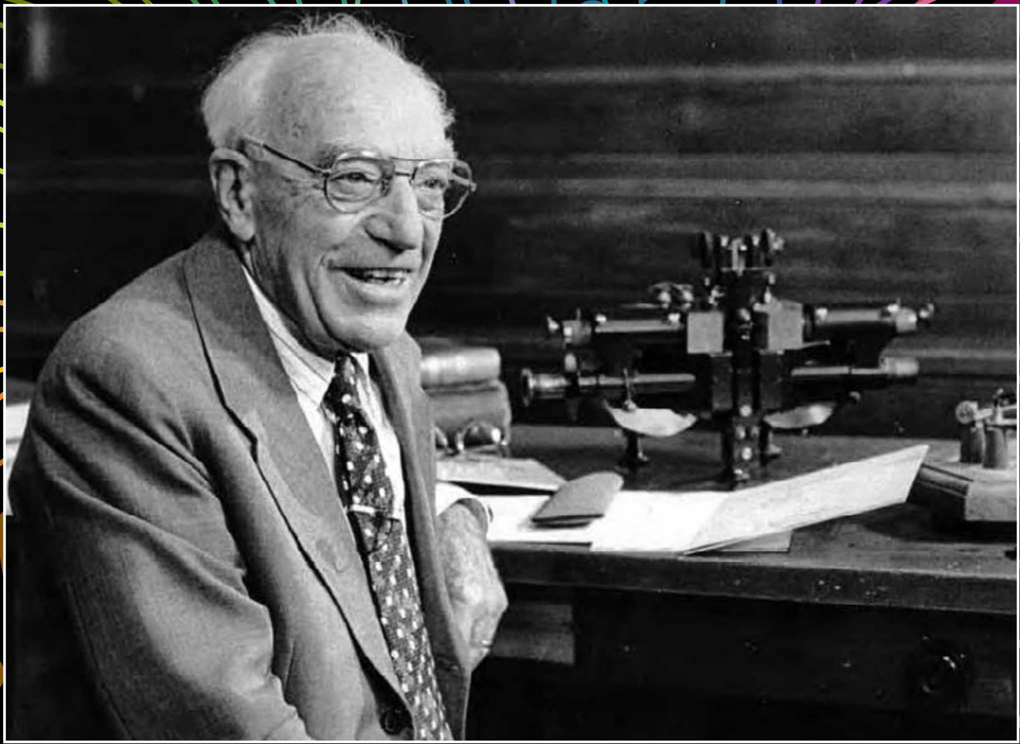
About the Authors

Mary R. Mennis is the third daughter of Sir John and Lady Rene Eccles. Born in Sydney in 1938 Mary qualified as a teacher at Syndey University and taught in Papua New Guinea arriving there in 1962. In 1964, she married Brian Mennis a surveyor and they had four children. Brian was posted to Rabaul for nine years, then Mt Hagen for six months followed by Madang for eight years. In these places Mary was an oral historian collecting history about the local Village people and studying their cultures and wrote many books. Her interest in history turned into two master's degrees in history and social science. After leaving PNG in 1982, Mary became interested in her family history, writing Hullo Eccles and Book of Eccles. She visited her father in Switzerland a few times and interviewed him. As a result, in 1991 he gave her a copy of his autobiography which is published here. Mary would like to mention her sister, Dr Rose Mason who worked as a physiologist at the Australian National University with her father for many years. However, the scientist who helped with this publication is James Chalcroft whose profile is printed below.

James Paul Chalcroft, born 07.05.1942 in Oamaru, NZ. Anglican. Secondary school education in Otahuhu, Auckland. Tertiary studies; botany (BSc), microbiology (MSc), and cell-biology (PhD) at Auckland University. Electron microscopist at Meat Industry Research Institute, Hamilton, NZ (1971-1982). Postdoctoral research in TEM tomography at Abt. Hoppe, Max Planck Inst. of Biochemistry, Martinsried, München, DE (1983-1986). Married Karin Seige in 1984. Electron microscopist at Mandelkow Group, Max Planck Inst. of Medicine, DESY, Hamburg, DE (1986-1988). OS-9 programmer at Tietz Video Image Processing Systems (TVIPS) in Gauting (1988-1994). Manager of digital darkroom & confocal microscopy facilities in Kreutzberg & Borst departments at Max Planck Inst. of Neurobiology, Martinsried, München (1995-2007). Research assistant to emeritus Prof. Georg W. Kreutzberg (2008-2017). Retirement interests; music, industrial archaeology, alpine nature walks, conservation of endangered endemic NZ flora & fauna, prevention of human despoilation of world ecosystems, ecology of extreme environments.

As a result of organizational involvement in 2008 with the 13th annual meeting of neurobiology historians (ISHN) in Berlin, Jim developed an interest in NZ neuroscience history and later became informed by Otago University physiologists of Mary Mennis and her copy of the unfinished and unpublished autobiographical notes of Sir John. After reading them with ever increasing interest, Jim decided to assist Mary by editing and expanding them for publication – the result of which is contained in this book.



Sir John Eccles – Nobel Prize winner in 1963.

Sir John Carew Eccles (1903 - 1997) – an Australian neurophysiologist was knighted by the Queen in 1958. Then in 1963 he was awarded a Nobel prize in Medicine for his work on the brain and the "self". In this he had achieved his life-long goal.

In the 1920's as a student at Melbourne university he came to realise that Darwinian evolution had no explanation for him as an experiencing self.

"So, I embarked on a study of what the great thinkers of the past had written on this, to me the very urgent problem of brain and mind. I was surprised to find that even up to recent times the brain had been almost universally ignored or misunderstood. The philosophers and psychologists that I read were very deficient in their knowledge of the brain that would have been helped them discuss the problem of the unique experiencing self. So, I decided as a medical student to devote myself especially to a study of the brain."

I first met Dr John Eccles in the 1960s and, even then I knew that I was in the presence of greatness. Will we Australians ever know his like again?

– John Carmody, December 2023

If it is true that the opinions of the wise are but knowledge in the making then Neuroscientist and Nobel Laureate Sir John Eccles profundity of the matter of what is " Self " is a read worth embarking upon.

– Professor Peter Silburn AM – Neurologist, November 2024