BIOGRAPHICAL MEMOIRS

Ragnar Granit, 30 October 1900 - 11 March 1991

S. Grillner


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30 October 1900 — 11 March 1991

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Elected For. Mem. R.S. 1960

BY S. GRILLNER

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RAGNAR GRANIT was born in Finland in 1900, during the period when Finland was still a Grand Duchy within the Russian Empire. He was the son of an affluent forester, and the grandson of a sea-captain. His father’s family came from the small island of Korpo in the Åboland archipelago, which reaches from Finland to Sweden. His family had Swedish as their native tongue, as most Finns living in the coastal areas around the Baltic have had for centuries. Granit grew up in Helsinki and started school early. He received a classical training in the ‘Swedish Normal Lyceum’ with latin and to some degree greek – a schooling which, according to his own account, fostered logical reasoning. His schooling was interrupted in the spring of 1918, when civil war arose as Finland succeeded in breaking loose from Russia, as a consequence of the Bolshevik revolution. The young man from the lyceum joined the forces trying to make Finland independent, fighting against the socialist forces which strived to instead make Finland into a ‘Soviet republic’. A very bitter civil war followed. For several months Granit was actively engaged as a soldier at the front and was decorated with the Cross of Freedom (Cl. IV, with sword). He mentioned this period not without pride. He then returned to school to complete his training in 1919.

STUDENT IN HELSINKI

In 1919 he started at Helsinki University and soon became interested in experimental psychology, stimulated by Eino Kaila, then docent in psychology. In 1923 he received what corresponds to a bachelor’s degree, comprising philosophy, psychology, aesthetics and chemistry. During this period he became interested in research and particularly in the understanding of vision and sensory processing. The young student decided, however, that in order to understand these processes, a knowledge of the structure and function of the retina and the brain was needed, and furthermore that psychology in itself did not provide a
sufficient framework for studies of this nature. Apparently Granit was not satisfied with the ‘black box’ description of the visual systems that psychology could provide. As a young student, he also explored, however, ‘gestalt psychology’ and even visited Gelb’s laboratory in Frankfurt, and studied critically Freud’s ‘Traumdeutung’ and ‘Vorlesungen über Psycholanalyse’. He also attempted to relate visual perceptions to modern art. To obtain an appropriate biomedical training he took up medicine in 1923, while he conducted exploratory research work in the physiology department. He became an assistant in the physiology department in 1926, and an M.D. in 1927. During this period he was also very actively engaged in a variety of roles among students and in university life. For instance, he was for three years (1923–26) editor of a student journal, which appears to have had very high ambitions in terms of poetry, essays and aesthetics. Throughout his life he managed to combine a deep interest in the humanities with science.

**DOCTORAL STUDENT**

As an assistant in the physiology department he continued to explore vision, although the head of the department, Carl Tigerstedt, had very different interests, as did the remainder of the staff. Granit reported on his research in the first Nordic conference on physiology in Copenhagen (1925), where he met several Scandinavian colleagues. Of major importance for his research development was his decision to visit Sherrington’s laboratory in Oxford for half a year in 1928. At the time Sherrington, then 70 years old, had Denny Brown, Sybil Cooper, Creed, Eccles and Liddell as collaborators, all of whom were to have a major impact in their respective fields. This intellectual environment no doubt affected Granit’s attitude to science – and his conception of how to pursue science. Sherrington apparently was very supportive of the young student from Finland and interested in his intention to study vision – despite the fact that Sherrington himself was then engaged in studies of the basic mechanisms of coordination in the brainstem–spinal cord. Granit also completed with John Eccles a study on the crossed extensor reflex (1929). He interacted with Stephen Creed, with whom he experimented with visual afterimages in different parts of the visual field.

During these few months he became a close friend of John Eccles, a friendship which led to a lifelong interaction and a correspondence between the two young researchers, both of whom were to become Nobel laureates (1963, J.E.; 1967, R.G.). I have had the great pleasure of reading a part of their correspondence which John Eccles has been kind enough to place at my disposal. These letters deal with the problems of their time, in science as well as in everyday life, from 1928 throughout the 1930s and later.

**VISITING SCIENTIST IN PHILADELPHIA AND OXFORD**

Upon returning to Helsinki, Granit finished his dissertation and subsequently became a ‘docent’ in physiology in 1929. He married Marguerite (Daisy) Bruun (born 1902), a Finnish–Swedish baroness brought up in St Petersburg, and on a country estate in Finland – a lifelong marriage lasting for more than 60 years. They had already known each other for a decade. In 1930 they had a son, Michael, who was to become professor of architecture in Stockholm. Directly after the marriage the young couple went to Philadelphia. Granit had been offered a position as researcher at a new research institution, the Johnson Foundation, headed by Detlev Bronk, on the recommendation of Sherrington and the head of the
Rockefeller foundation. Ragnar Granit, Keffer Hartline and William Rushton had been hired – Granit and Hartline, who were already interested in vision, were later to share the Nobel Prize (1967), and Rushton was later to take up vision in interaction with Granit. The working conditions in the laboratory were very good in that the young researchers were given complete independence. The laboratory facilities and the workshop were excellent. They had the possibility of interacting and critically evaluating each others’ progress. These were most likely years of critical importance. Granit conducted his psychophysical experiments on humans in which he tried to correlate his findings with the novel physiological experiments conducted by Adrian, who had recorded from the ophthalmic nerve in the eel and shown a form of spatial summation from different parts of the retina with neurophysiological methods. Granit obtained corresponding findings in man, and in a series of studies he dealt with excitatory and inhibitory interactions. He interpreted his findings in terms of a processing at the level of the retina, rather than within the central nervous system.

PROFESSOR IN HELSINKI

Upon returning to Helsinki he decided to develop electrophysiological methods of recording from the retina. After building a suitable electronic amplifier, he returned to Oxford (1932) on a Rockefeller fellowship for 18 months to focus on studies of the electroretinogram (ERG) – that is the mass electrical activity, which can be recorded on the surface of the eye, as the eye is exposed to light. This analysis was performed in Oxford and continued in Helsinki on his return in 1933. Throughout the 1930s he worked on the ERG and defined different components thought to correspond to the activation of rods and cones, and obtained evidence for excitation as well as inhibition at the retinal level. This work provided new and important insights, and established Granit as a leading researcher, in what was then a small but developing field of neurophysiology and ophthalmology. After a long and seemingly bitter struggle he was appointed Professor of Physiology in 1937 at the Medical Faculty in Helsinki (see below).

THE MOVE TO STOCKHOLM IN 1940

During this period he was close to abandoning Helsinki and returning to Oxford on a five-year fellowship. During his earlier stays in Oxford he had developed a lifelong affection for the town and England in general. Granit was offered a new prestigious position in 1940 at the Harvard Medical School as Director for the laboratory of ophthalmology in the Massachusetts Eye and Ear Infirmary. The laboratory would have had a focus on fundamental research. He initially decided to take this position – when a second offer came up from the Karolinska Institute. Carl Gustaf Bernhard, a young researcher from the Karolinska, who had spent some time in Granit’s laboratory in 1939, had been able to initiate an action which resulted in an offer to create a neurophysiological laboratory at the Karolinska financed by the Wallenberg and the Rockefeller Foundations for an initial five-year period. Granit accepted this offer at short notice and sailed his own yacht across the Baltic to Stockholm through the minefields in August 1940. He immediately started to build up the new institute – which in 1945 was to become the Nobel Institute for Neurophysiology at the Karolinska Institute and in 1948 a new building was inaugurated at the new campus of the Karolinska Institute. Granit became the first Professor of Neurophysiology in 1946.
Research on Colour Vision

The actual work that led to Granit's Nobel prize together with Hartline and Wald 'for their discoveries concerning the primary physiological and chemical visual processes in the eye' had already started in 1939, when Granit and Svaetichin, with a type of microelectrode developed by Svaetichin, succeeded in recording from single units of different types in the retina. They discovered that one 'dominator' type of unit had a broad frequency range corresponding to that of cones, but that three other types of units had a separate and more narrow frequency spectrum corresponding to the colours of blue, green and red (figure 1). These units were called modulator units. This preliminary work was expanded upon by utilizing eyes from a variety of vertebrate species having preferentially cones or rods, etc. Different fish, amphibians, reptiles, birds and mammals were studied in Stockholm, mainly in studies conducted by Granit alone (1940–45). This work established beyond all reasonable doubt that colour vision in vertebrates depends on three separate afferent channels mediating the intensity of light in wavelengths roughly corresponding to blue, green and red. This work was summarized in several reviews and in two influential monographs 'Sensory mechanisms of the retina' (1947, reprinted 1963) and 'Receptors and sensory perception' (1955). The conclusions were amply confirmed by other investigators recording from the receptor elements in the eye and from other neural elements in the retina.

After having accomplished this major piece of work on the neurophysiological bases of vision – Granit appeared gradually to lose interest. During his time in Helsinki and later in Stockholm he trained a number of doctoral and postdoctoral students, many of whom were to assume leading positions in ophthalmology or vision research in Finland, Sweden or the rest of the world. Suffice it to mention researchers like Karpe, Dodt, Donner, Arden, Ingvar and Enroth-Cugel. Granit's own interest in the eye laboratory declined gradually with the thesis of Christina Enroth in 1954. In parallel with the studies of vision, Granit initiated and stimulated research within several different areas. During the first years Carl Gustaf
Bernhard and Carl Rudolf Skoglund served as assistants and helped build up the new laboratory. In 1947 they both moved over to the newly formed physiology II department at the Karolinska Institute in which Bernhard was to become the first professor and C.R. Skoglund, reader in physiology. For a certain period there was to become a very strict dividing line between the two laboratories.

**DISCOVERY OF THE CONTROL OF MUSCLE SPINDLES**

During this early period (1945) Lars Leksell completed his well-known thesis in which it was shown that the γ-efferents do not produce any detectable contraction of the extrafusal muscle fibres but a mass discharge of afferent nerve fibres. This important work demonstrated that muscle spindles are subject to an independent control by a separate group of motoneurones conducting at a slower ‘γ-rate’. This work was corroborated by Kuffler, Hunt and Quilliam (1951), and opened up a new important research area. In this field Granit came to assume a very central role, in relation to the demonstration that γ-motoneurons and thereby the sensitivity of muscle spindles can be controlled by different structures in the central nervous system – and furthermore that the tonic activity in afferent muscle spindles could contribute to the overall excitability of α-motoneurons ‘controlling’ the muscle contraction. Many influential papers co-authored by several postdoctoral students, such as Kaada, Merton and others, had a central role in this field.

Granit and colleagues had observed that motoneurons projecting to α- and γ- motoneurons of the same muscle were often co-activated during the course of a movement or as the consequence of the stimulation of a central structure or a sensory nerve. They coined the expression α–γ linkage for this condition (it is still used today), with the implication that muscle spindles even during a muscle shortening should be able to provide a signal from the muscle to the CNS. This turned out to be a very common occurrence. This area was further developed at the Nobel Institute by Curt von Euler, who took up the neural mechanisms of respiration. He showed in very influential studies that α and γ motoneurons become co-activated during each contraction of the respiratory intercostal muscles – and later explored the central neural mechanisms for respiratory control.

**MOTOR CONTROL**

Granit strived to reach an understanding of the basic general control principles underlying movement, and referred to this area as ‘motor control’. In addition to the control of muscle spindles, he studied the activity of other muscle receptors, the role of recurrent inhibition from motoneuron collaterals, tonic and phasic α–motoneurons, the activity pattern of cerebellar Purkinje cells and their climbing fibre input (with Charles Phillips). He provided a systematic study of the different basic components of the motor system.

The essence of good science is to formulate testable working hypotheses of relevance at the current stage of development of a given area, and to be able to design and carry out the appropriate experiments to be able to reject or support the hypotheses. Granit was very able in this respect. The last novel question he addressed experimentally was simple but very relevant. How does a nerve cell transduce synaptic current (excitatory and/or inhibitory) to discharge frequency, which is all that matters on the output side? In the early 1960s, together with Kernell and Lamarre, he addressed this question by impaling spinal motoneurons...
with microelectrodes intracellularly. He then injected current in long pulses (1s or more) so as to mimic a continuous synaptic excitatory barrage. He could then observe the relation between synaptic current and frequency of discharge, and even was able to test which functions are of importance for the spike frequency adaptation. Superimposed on the current plateau, he could provide tonic synaptic excitatory and inhibitory inputs to test if the effects were summed. This was a very efficient and new approach, 35 years ago, and started the still continuing search for the integrative properties of the somadendritic membrane of nerve cells – which is central to our understanding of the central nervous system.

Granit’s laboratory, in the 1950s and 1960s, was a major centre for studies of motor control and it can be said that in this area he continued to work on problems developed by Sherrington, in a more fundamental way than any other of his pupils did, and with a focus on the understanding of basic principles of operation of the neural networks that control movement. Granit retired in 1967 and did not maintain an experimental laboratory of his own, only an office for writing at the Nobel Institute. He spent time in Oxford and at NIH in Bethesda, doing some studies in collaboration with for example Ed Evarts. However his main occupation was to write different types of overviews and several books including a biography of C.S. Sherrington (1967), *Basis of Motor Control* (1972), the *Purposive Brain* (1977) and an autobiography in Swedish *Hur det kom sig* (1983).

Scientifically Granit became one of the leaders in two distinctly separate areas of research, vision and motor control. His position in both areas was such that when he was awarded the Nobel prize in 1967, John Eccles (1968), when commenting on the prize, mentioned that he himself had nominated Granit in 1967 but for his work in motor control rather than vision. The discovery of the afferent channels for colour vision was obviously, however, a very well defined and prizeworthy contribution. The combination of Granit (colour vision), Hartline for the discoveries of the activity pattern of single visual receptors-afferents (intensity-transduction and lateral inhibition) and Wald for the biochemical definition of the visual pigment was clearly a very attractive one. Their complementary findings provide new significant insights, and therefore, very well deserved the prize.

**THE NOBEL INSTITUTE FOR NEUROPHYSIOLOGY**

The Stockholm laboratory of Ragnar Granit had a major impact both from a Swedish and an international perspective. During the quarter century it was headed by him, he trained an overwhelming number of scientists in both clinical and basic neuroscience, a large number of whom were to hold professorships in leading institutions. When he arrived in Stockholm he asked the clinical professors in neurosurgery, neurology, psychiatry and ophthalmology if they would like to send some of their young residents for research training in his department, and they did so. That is why a number of the leading clinicians in the fifties and the sixties had received their research training with Granit. He was broad enough to realize the importance of having a variety of techniques and expertise represented in the laboratory. He invited Bror Rexed, then associate professor in histology to have a laboratory at the Nobel Institute, and it was then he did the classic work, on the spinal cord with the classification of the ‘Rexed laminae’, which still today is used by all spinal cord neuroscientists.

Let me mention some of the Nordic scientists trained by Granit, divided into basic neuroscience: C.G. Bernhard, K-O. Donner, Christina Enroth-Cugel, C. von Euler, B. Frankenhauser, B. Kaada, J.O. Kellerth, D. Kernell, A. Lundberg, B. Rexed, C.R. Skoglund,
S. Skoglund, U. Söderberg, S. Therleff, Å. Vallbo; and clinical neuroscience: K.E. Hagbarth, D. Ingvar, G. Karpe, E. Kugelberg, L. Leksell, G. Steg. For a period it appears that Granit almost monopolized the research training in neuroscience in Sweden. At present many of his pupils have already retired, but his influence is still to be perceived in many areas.

How is it that Granit could achieve this remarkable result? Clearly, he was very respected when he arrived in Stockholm, and highly motivated. He appears to have had a knack for breaking up interesting problems into precisely formulated studies and to have been a very stimulating and thoughtful mentor for his collaborators. His deep concern for both Nordic and foreign collaborators is well documented with regard to both science and other aspects of life.

It should also be noted that the post-war period during which he was building up his laboratory, was that of a rapid expansion and with a development of new disciplines. The Swedish government was very supportive of research, and in addition Granit received continuous support from the Wallenberg and the Rockefeller Foundations, which provided the necessary flexibility and allowed the development of new equipment and staff. It is interesting to follow the rapid development of the Nobel Institute for Neurophysiology during Granit’s era in the annual reports which he submitted each year to the Nobel committee. The basic staff was always comparatively small but it could focus on research since it did not have any teaching obligation to the undergraduates.

**ORIGIN OF SWEDISH RESEARCH COUNCIL**

In addition to running his research laboratory Granit did not usually engage himself significantly in the administrative or organizational matters in the Faculty. However, with a few colleagues he did take the initiative in the formation of the Swedish Medical Research Council in 1942, by convincing the government that a peer-review system would be a better way to support research than to let the different faculties distribute the support in a collegial manner. This action in all likelihood had a major and very favourable impact on Swedish basic research in all areas. Granit was a member of the Research Council between 1949 and 1955, and his collaborator Bror Rexed became secretary. Granit was also very active in the Royal Swedish Academy of Sciences and became its president (1963–65), he was active also in a variety of foreign institutions. For a long period he was visiting professor at the Rockefeller for a few weeks each year. At the Rockefeller he had his old colleagues Detlev Bronk (president) and Keffer Hartline.

**GRANIT – SCIENCE AND HUMANITIES**

Ragnar Granit retired in 1967, when I was still a graduate student; I succeeded him as director for the Nobel Institute 20 years later. My perspective on Granit’s active period, and on the conditions under which science was conducted from 1920 until 1965 is, therefore, limited. I find it remarkable, however, that the young Granit essentially by his own initiative decided that he was interested in vision – although there was nobody around who was competent enough to give him more than very general advice – and furthermore that he was able to get a position in a laboratory without expertise in this field of interest. Despite these difficulties he succeeded in making the right decisions and contacting the key persons. This must have required not only a strong determination but also great awareness.
In addition to his scientific determination, Granit had the clear ambition to take an active part in the humanistic activities of the Swedish speaking minority in Finland. As I mentioned above he was an editor of a student journal ‘Student Nation of Nyland’ and had a rich interaction with poets and authors belonging to this very active minority, which in the thirties felt suppressed by the very strong nationalistic elements within the large Finnish majority. This condition may have played a role in the long delay in the appointment of Granit as professor in physiology, and also in his major difficulties while setting up his laboratory in Helsinki, which probably contributed to his willingness to move to Stockholm, and even to becoming a Swedish citizen in 1942. Granit succeeded also in Stockholm continuing to bridge the gap between science and arts. He despised C.P. Snow’s *The two cultures* which appeared in 1956. He felt that this often quoted account of a perceived inherent communication gap between these two aspects of human culture was superficial and not to the point. In Stockholm he was for a long period a regular contributor to the major liberal newspaper with articles on different subjects relating to general questions.

In 1941 he published a series of essays under the title *Young man’s road to Minerva* (the goddess of arts and science). After 54 years I find it for the most part still fresh and worthwhile reading. The book is thought-provoking and filled with interesting observations and reflections. In this book and in other places he often displays his great interest and knowledge of scholars of the past, and he asks questions as to why, and what could have been the driving force for them to deal with research – rather than all other human endeavours which in most aspects can be more rewarding economically and socially.

Why for instance, did Linnaeus, the son of a poor priest in rural Sweden in the 1720s decide to study plants and animals, and be able to bring order in their classification – a system that is still in use. Against all odds he became the leading naturalist of his century.

How come that the well-to-do and rather shy Charles Darwin developed into the biologist of the next century? He found a simple but ingenious explanation as to how the animal kingdom may have evolved through a gradual transformation and a ‘survival of the fittest’ in each given environment. He spent his life searching for detailed evidence. His interpretation had a very major impact on society and even provided a challenge to the current religious beliefs.

Granit in his general writings often refers to not only Linnaeus and Darwin but also to major scientists like Berzelius, the chemist, Cajal, the neuroanatomist and very often to his teacher Sherrington, all of whom grew up under conditions which would not at first be expected to foster a first-rate scientist. Granit even edited a book *Ut ur stubbotan rot* with essays concerning Linnaeus and his pupils that explored different countries and continents to compile the first floras of a number of regions. Over a few decades they charted the plant and animal kingdoms. Granit himself wrote on Daniel Solander, a Swedish pupil of Linnaeus, who together with Banks (President of the Royal Society) explored Australia and surrounding areas on Cook’s first voyage.

One may wonder if Granit was not from very early on puzzled by the fact that he so intensely strived to become and remain an outstanding scientist. In his writings he often dwells on what could be the combined driving force and character traits that form a good scientist. At one place he quotes a list compiled by Cajal dealing with the same problem. It reads as follows: 1. independent judgement 2. perseverance 3. striving to be independent 4. passion for research 5. ambition (and vanity?).

Although most good scientists are unique, and not cast from the same mould, Ragnar
Granit himself for the most part fulfilled these criteria. He took great pride in what he did, whether in private or in science. He no doubt was thoughtful and considerate to everybody he liked, and he could also be entertaining and often became the centre of any group he was a part of. His combined interests in science and humanities guaranteed an interesting and often unexpected twist to any discussion. He smoked cigars.

ACKNOWLEDGEMENTS

I would like to thank Professor Curt von Euler for reading the memoir and providing me with information about Ragnar Granit’s time in Stockholm, and Professor John Eccles for letting me read part of the correspondence between him and Granit starting in 1928 and also for information about their time in Oxford during the late twenties and thirties. A rich source for information has been the Annual Reports from the Nobel Institute for Neurophysiology since its start.

The frontispiece photograph was taken in the late 1960s.

CAREER AND HONOURS

Education
1923 Mag. Phil., Helsingfors University
1927 M.D.

Profession
1926Assistant (demonstrator), Physiological Inst. Helsingfors
1929Docent
1929–31Fellow in Medical Physics, Eldridge R. Johnson Found., Univ of Pennsylvania
1932Fellow, Rockefeller Foundation, Oxford
1935Deputy Professor of Physiology, Helsingfors University
1937Professor of Physiology, Helsingfors University
1946Professor of Neurophysiology, Karolinska Institute

Honorary degrees
1951M.D., Oslo University
1956D.Sc., Oxford University
1958Catedártico Honorario, University of San Marco (Lima), University of Santiago de Chile and University of Bogotá
1961D.Sc., Hong Kong University
1969D.Sc., Loyola University, Chicago
1970M.D., Pisa University
1981M.D., Gustavus Adolphus, St Peter, Minnesota
1982D.Phil., Helsingfors University,
1987M.D. Göttingen University

Academies etc.
1937Societas Scientiarum Fennica, honorary member 1978
1944Royal Swedish Academy of Sciences, President 1963–65
1947Société Philomatique, Paris
1948Academia Scientiarum of Bologna
1954 The American Philosophical Society, Philadelphia
1956 Royal Danish Academy of Sciences
1958 The Biological Societies of Argentina, Uruguay and Chile, honorary member
1960 The Royal Society of London, foreign member
1961 Accademia di Medicina of Turin, honorary member
1964 Indian Academy of Sciences, honorary member
1968 National Academy of Sciences, Washington
1971 American Academy of Arts and Sciences, honorary member
1978 Accademia Nazionale dei Lincei, Rome
1978 Société de Biologie, Paris
1981 Académie Européene, Paris
1982 Accademia Mediterranea delle Scienze, Catania
1985 The Academy of Finland

**Honorary Member of Professional Societies**
The Societies of Physicians of Sweden and of Finland
The Swedish Societies of Physiology, of Neurology, of Ophthalmology, and of Clinical Neurophysiology
The Physiological and Ophthalmological Societies of Finland

The Physiological Society of Great Britain
The American Physiological Society
The German Society of Electroencephalography
The International Society of Electroretinography

**Other Memberships**
The German Society of Physiology
The Norwegian Society of Physicians

**Lectures**
1945 Thomas Young Oration of the Physical Society of London
1954 Silliman Lectures of Yale University
1967 Sherrington Memorial Lecture of the Royal Society of Medicine of London
1970 Sherrington Lecture of Liverpool University
1975 Murlin Lecture of Rochester University, New York
1975 Hughlings Jackson Lecture of McGill University, Montreal
Robert Tigerstedt Lecture of The Physiological Society of Finland
Ragnar Granit

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1935 (With P.O. Terman) Inhibition of the off-effect in the optic nerve and its Y relation to the equivalent phase of the retinal response. J. Physiol. 81, 47–48


1939 (With A. Munsterhjelm & M. Zewi) The relation between concentration of visual purple and the retinal sensitivity to light during dark adaptation. J. Physiol. 96, 31–44.


1950 The organization of the retinal elements. Ergebn. Physiol. 46, 31–70.


(With B. Holmgren & P.A. Merton) The two routes for excitation of muscle and their subservience to the cerebellum. J. Physiol. 130, 213–224.
1961 (With B. Renkin) Net depolarization and discharge rate of motoneurones, as measured by recurrent inhibition. J. Physiol. 158, 461–475.
(With D. Kernell & Y. Lamarre) Algebraical summation in synaptic activation of motoneurones firing within the 'primary range' to injected currents. J. Physiol. 187, 279–399.


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Books


