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# Sir John C. Eccles: from synapses to consciousness

**M.L. García de la Rocha**
Department of Neurology Hospital Nuestra Señora del Prado. Talavera de la Reina. Madrid.
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**ABSTRACT**

The fascinating life of Sir John Eccles of Australia, Nobel Laureate in Medicine in 1963, spanned nearly all of the 20th century. Eccles finished his postgraduate work in Oxford in the late 1920s and early 1930s. His advisor Sherrington was a strong influence, as Eccles himself recognised. Upon his return to Australia, he managed to lead important projects, despite receiving little to no financial support. At a later date, in New Zealand, he put together the best-equipped laboratory of its time. In addition, his capacity for designing experiments and leading and unifying work groups delivered numerous first-rate publications. On this basis, he was named director of the Canberra laboratory. The 13 years he spent there prior to his retirement were extraordinary: he directed the most important neurophysiology facility of its time, which trained a generation of distinguished scientists. In later years, he continued working in the United States. When at last he gave up laboratory activity, 50 years after having begun, he remained abreast of new developments in the field and continued publishing articles. Sherrington awakened his interest in the higher cerebral functions, an interest that would remain with Eccles for life. It was strengthened by his meeting with Popper, and then evolved to become the main focus of his intellectual activities after his retirement from experimental science.

**KEYWORDS**

John C. Eccles, Nobel, neurophysiology, synapse, Karl Popper, mind-brain relationship

## Introduction

Sir John Eccles' life spanned nearly all of the 20th century, from 1903 to 1997. He began conducting laboratory experiments in 1925 and retired from laboratory work in 1975. In these 50 years of professional activity, he produced no fewer than 500 articles and more than 15 books, whether as a solo author or a contributor. He won multiple prizes and awards, including the 1963 Nobel Prize for Medicine together with Hodgkin and Huxley. He continued publishing articles throughout his retirement and almost up to his death at the age of 94. His tireless activity focused on the physiology of the nervous system, from the iconic phenomena in the synapse to the 'wiring' in the cerebellum. And yet, his focus consistently reflected the doctor's interest in using knowledge to reveal the basis of consciousness; he himself said that he was drawn to physiology by the mind-brain enigma.

1. The early years

Eccles was born in Melbourne, Australia, on 27 January 1903.[1] his parents, both schoolteachers, were Catholics of English and Irish descent. He studied in that city until earning his medical degree in 1925, at the age of 23. In addition to being a talented student, Eccles organised and participated in meetings, social events, and dances, activities which he always enjoyed; he was also an outstanding athlete. He already displayed boundless curiosity and was an avid reader. During his university years, he read Sherrington's book *The Integrative Action of the Nervous System*, published in 1906, and decided to become a researcher under Sherrington. With this goal in mind, he applied for, and was awarded, a Rhodes scholarship for the State of Victoria, allowing him to begin his studies at Oxford in October 1925.

Corresponding author:
Dr María Luisa García de la Rocha
C/ Bocangel 18 2D 28028. Madrid

E-mail: delarocha@hotmail.es

2. Oxford

After two years of reading natural sciences, that is, physiology and biochemistry, he earned his BA degree. Eccles always recalled Oxford's 'multidisciplinary' environment in which students representing the most diverse branches of knowledge came together and talked of all things human and divine (his close friends professed their passion for English philology, chemistry, the Classics, philosophy, and theology).[2]

Later, he achieved his goal and worked under the tutelage of Sir Charles Sherrington, describing him as "the one man in the world whom I wished to have as a master".[2]

Oxford in Sherrington's time was a magnificent place for research. The techniques employed in the physiology lab were the most advanced of that epoch. Its prestige attracted the very best researchers, and the university was visited by top scholars from Europe and North America.

The end of the 19th and the beginning of the 20th centuries witnessed a whirlwind of activity in the field of the neurosciences. Once Cajal's neuron theory had been widely recognised, scientists began exploring the connections between individual neurons. Sherrington was one of the first scientists to embrace neuron theory. It was also Sherrington who coined the term 'synapse' to designate the points of contact between neurons.[3]

In autumn of 1927, in Exeter, Eccles began his first research project on the cerebellum. The project was supervised by Sherrington and directed by Denny-Brown and Liddell.[3]

Shortly thereafter, he began experiments on inhibition in the spinal cord in partnership with R.S. Creed. In 1928, he began research into the crossed extensor reflex with Granit.[4] He soon revealed his powers of observation when he discovered that muscle contraction recordings (the means used to measure the reflex response) were distorted by friction in the bearing of the myograph making the recordings. He designed another type of myograph that eliminated this artefact.[5] In December 1929, he presented this device before the Physiological Society, which had just accepted him as a member. In the same year, he was also awarded his MA and PhD.

In the middle months of 1928, he began working directly with Sherrington. These researchers discovered two populations of peripheral motor nerve fibres differentiated by their diameters.[6] In 1945, Lesksell proved that these fibres were the axons of alpha and gamma motor neurons.

Eccles also worked with Sherrington in a series of experiments on flexor reflexes that were documented in several articles published in volume 107 of the Proceedings of the Royal Society of London in March 1931. These were the last experiments that Sherrington, then 74, was to conduct personally.

In those years, the mechanism behind signal transmission in CNS synapses was a controversial subject. Studies by Loewi and Sir Henry Dale provided robust evidence that signal transmission in peripheral NS synapses (either excitatory or inhibitory) involved a chemical mechanism. Others (including Eccles) believed that signal transmission in the CNS resembled the electrical propagation of impulses occurring in nerve fibres. The debates that followed every presentation in the Physiological Society were certainly lively, but in the very English spirit of good sportsmanship, criticism was neither offered nor interpreted as a personal affront. Guests who knew about members' very different opinions were surprised by Eccles' cordial relations with Dale, Feldberg, Gaddum, and Brown, all of whom supported the chemical signal transmission theory. In fact, Dale and Eccles remained lifelong friends, even throughout the long debate that remained unresolved until 1952.[7]

Another indication of his skill and thoroughness is that Eccles, who had just earned his doctorate and was not yet 30 years old, was invited to collaborate with Sherrington, Denny-Brown, Creed, and Liddell in writing *The reflex activity of the spinal cord*,[8] published in 1932. Sherrington won the Nobel prize the same year.

Eccles was granted a permanent position in Oxford in 1934. He continued his experiments on synaptic transmission, focusing at that time on the superior cervical ganglion of the sympathetic trunk (a simpler system than the spinal cord). He stayed at Oxford until 1937. In those years, Europe was becoming an uncomfortable place to live, and Eccles found Oxford a changed place without Sherrington.

So he left Oxford, taking with him lessons that would mark him for life: his experimental techniques and systematic working style, plus the emphasis on interdisciplinary communication and the dualist/interactionist view of the mind-brain relationship which he had inherited from Sherrington.

3. Kanematsu Institute, Sydney

In 1937, Eccles was invited by Kellaway to return to Australia. In those times, there was only one oasis of research to be found in the Australian desert: the Hall Institute associated with Melbourne Hospital. Here, the expansive Kellaway spearheaded research in close cooperation with both hospital and university activities.[9] Kellaway asked Eccles to join the Kanematsu Institute in Sydney for the purpose of developing its potential and making it comparable to the Hall Institute. The challenge was a tempting one, but Eccles' new setting left much to be desired. Physically and spiritually, the Institute was separated from both the hospital and the university; in fact, there had never been a formal association with the latter. As a city, Sydney lacked intellectual pursuits, and Eccles found himself with no assistants and no authority. In fact, he mentioned that the building in which he was put to work was promptly shut up and locked every day at 5 pm.[2]

Hospital personnel were distrustful of his activities 'lacking in practical utility'. Eccles conducted studies on atrophy due to disuse of striate muscle in order to satisfy the requirement that experiments have 'clinical relevance'. For someone who lacked Eccles' tenacity, motivation, and talent, this could well have spelled the end of his research career.

His only breath of fresh air was the arrival in 1938 of Stephan Kuffler who had fled Austria, and being awarded a grant in 1939 to add Bernard Katz to the team. While investigating neuromuscular junctions, these three scholars discovered the end plate potential, its pharmacological basis, and the part it plays in generating impulse discharges along muscle fibres. Katz would go on to be awarded the Nobel Prize in 1970, specifically for his studies of the action mechanism of acetylcholine, the discovery of miniature potentials, and the role of calcium in neuromuscular synapses.

In 1941, World War II reached the Pacific. Eccles, who had been elected a Fellow of the Royal Society in March of that year, was included in a number of committees and research projects addressing vision, hearing, and noise problems on board aircraft and tanks. Conducting research was becoming increasingly difficult.

4. University of Otago, Dunedin, New Zealand

Eccles left the Institute in 1943, following a change in directorship. He was hired as a physiology professor by the only faculty of medicine in New Zealand, pertaining to the University of Otago in Dunedin. As he himself remarked, this was "the closest university to the South Pole".[2] He arrived there in January 1944.

In the following two years, he dedicated his time to teaching university students and reshaping his teaching style in an attempt to reproduce his ideal model: that of Oxford. His official title was Professor of Physiology and Biochemistry, and he recalled having to devote nearly all of his time to brushing up on the material that he would be presenting in class.

A key moment in Eccles' life was his meeting with Karl Popper in May 1945; Popper, a Viennese philosopher, had fled to New Zealand because of his Jewish roots. He had been affiliated with Canterbury University College in Christchurch since 1937, and taught philosophy of science in that institution. He accepted Eccles' invitation to spend a week in Dunedin participating in seminars and debates.

Popper's ideas, which were first published in German in 1934, influenced the way Eccles framed his experiments and interpreted their findings. For Popper, a theory is scientific when it is clearly stated in such a way that it may be tested by experiment.[11]

The typical way of doing science, which follows the inductive method, can never produce a 'law' or a truth. This is because no matter how many times we observe that A is followed by B, we can never state that this is always so. If the event occurs frequently, this supports our belief, but does not guarantee it. The scientific method is essentially deductive. The scientist (an active, creative party) proposes theory T, from which certain consequences can be deduced (c1, c2, c3, ...). These consequences must testable by empirical methods, understanding this to mean that it must be possible to refute T if empirical data do not coincide with predictions $c_i$. The strength of a hypothesis lies in the number of times attempts to falsify it have failed, and not in the evidence which appears to support it. As a result, a scientific theory is always provisional and understood to be true until it is proved otherwise. This is an evolutionist point of view: the best theories are the ones that survive. All these ideas took root in Eccles' thought processes, since his experiments were designed to establish the basis for a loftier theory, a theory of consciousness.

Eccles' ability to locate and recruit valuable collaborators served him well once again in Dunedin, where he teamed up with John Coombs. Coombs, a physicist who had studied electronics while working with radars during the war, renovated and modernised Eccles' laboratory equipment. He also created the amplifiers that would be used with Brock's micropipettes (serving as microelectrodes) to deliver the first intracellular recordings from the spinal cord of a cat in 1951 (this had already been performed in the axon of a giant squid).

Using these means, Eccles was able to investigate electrical transmission at the synapse. In line with what he had learned from Popper, he redefined his theory so that it could be tested by a key experiment. He proposed that presynaptic action potentials were the ones that initiated local depolarisation responses in specialised areas of the postsynaptic membrane. The synaptic delay and the time course of the action potential would be due to the progression of presynaptic currents and the electrical properties of the postsynaptic membrane. His hypothesis pointed to the presence of a short-axon interneuron (Golgi cell) forming a synapse with motor neurons, but which does not discharge an action potential when it is excited by inhibitory afferent impulses. Such impulses originate currents that flow through the axon terminals of the Golgi cell and passively decrease motor neuron excitability. Intracellular recordings showed that inhibition was produced by active hyperpolarisation of the motor neuron membrane. The recorded change in potential was the opposite of what Eccles' hypothesis had predicted. In his own words, "since the experimental evidence has falsified the Golgi-cell hypothesis of inhibition and left the chemical transmitter hypothesis as the only likely explanation, it suggests further that excitatory synaptic action is also mediated by a chemical transmitter".[12]

He then recognised Dale's position as correct in a public letter. True to his character, he expressed himself in such clear and uncertain terms that Dale compared the letter to Saint Paul's conversion on the road to Damascus.

5. Canberra: the summit of success (1951-1966).

In 1951, Eccles accepted a position as professor of physiology at Australian National University in Canberra. It took him 15 months to ready his new laboratory and begin experiments (he had brought with him from Dunedin four electrical stimulating and recording devices designed by John Coombs, and according to Eccles, "the best general research instruments for electrophysiology in the world".[2] He also spent some of this time travelling

**Figure 1.** Photograph of Eccles in his laboratory in November 1963. Image courtesy of John Curtin School of Medical Research, Australian National University.

to England and the United States. During his stay in Oxford, he taught eight master classes (the Waynflete Lectures) on the neurophysiology of the membrane and the synapse, neural plasticity, memory, conditioned reflexes, the cerebral cortex, and the mind-brain relationship. These were published in 1953 under the title *The Neurophysiological Basis of Mind: Principles of Neurophysiology*. His dualist perspective on the mind-brain relationship,[13] already published at this time, was a topic of intense debate. He visited Sherrington in February 1952, and upon his mentor's death on 4 March, Eccles returned to Dunedin by way of the United States, where he participated in the Cold Spring Harbor Symposium on the neuron.

In March 1953, he resumed his experiments in Canberra, and would continue laboratory work for the next 13 years, now at the pinnacle of his career. Thanks to initiatives undertaken by Australian Prime Minister McKenzie, Eccles enjoyed the company of assistants from all around the world (he directed 74 visiting researchers from 20 different countries during this time), a magnificent building (although it was not finished until 1957), and a stimulating and favourable atmosphere (the institution covered visiting researchers' travel and housing expenses).

In 1963, together with Hodgkin and Huxley, he was awarded the Nobel Prize for Medicine "for their discoveries concerning the ionic mechanisms involved in excitation and inhibition in the peripheral and central portions of the nerve cell membrane".[14] At that time, he also published *The Physiology of Synapses*.[15]

After working on the spinal cord for ten years or so, he turned his attention to synaptic transmission in the cuneate nucleus, the ventrobasal nucleus of the thalamus, and the hippocampus. Here, he discovered that basket cells generate an intense, prolonged postsynaptic inhibitory potential affecting pyramidal cells, rather than the excitatory potential others had indicated. This led him to begin studying cerebellar basket cells in 1963. From that time on, almost until his retirement from experimental work 1975, he focused his efforts on the cerebellum. He worked in partnership with Janos Szentágothai, an excellent histologist from Budapest with whom he had never published before, and Masao Ito, who had worked as an intern in his laboratory.[16] In 1967, when Eccles was in the United States, the three scientists published *The Cerebellum as a Neuronal Machine*.[17] This book presented electron microscopy descriptions and results from intracellular recordings which together permitted a description of the interactions between cell types. According to one critic, "each step is the result of deductions made based on arrays of ingenious experiments that complement each other, every one of which is minutely described". Many of these experiments were published in Experimental Brain Research, a journal co-founded and co-edited by Eccles. This book is a monument to Eccles' character. He had already been awarded the Nobel Prize and had no need to build a reputation; in fact, he was officially retired when it was published.

When he was at the height of his abilities and directing the world's top neurophysiology laboratory, he turned 65 and was obliged to retire. Eccles was devastated. He kept repeating that his own mentor Sherrington had completed the most important investigations of his lifetime after the age of 60. Retirement was inconceivable. He had to find a way to stay in a laboratory.[16]

6. Chicago: Eccles' mistake (1966-1968)

In this state of mind, he accepted an invitation in 1966 from the Institute for Biomedical Research, a division of the American Medical Association (AMA) in Chicago. He would later recognise his mistake[2]: the AMA had no real interest in hiring him, and the atmosphere in his new environment was rather strained. Although he organised a laboratory and continued researching the cerebellar cortex, he left Chicago as soon as he could.

7. Buffalo

In 1968, Eccles was invited by New York State University in Buffalo, and as he remarked, "I had nowhere else to go".[2] There, he held the position of Distinguished Professor of Physiology and Biophysics (he also noted, "my age of 65 was not encouraging to universities who may have been considering me").[2] The initial agreement contemplated his retirement at 70, but he in fact stayed on until the age of 72. In these seven years, he worked with 20 collaborators from 11 countries (including Professor Rubia[18]), and published 43 articles. Among other subjects, he studied sensory afferents to the cerebellum (Purkinje cells), using a novel mechanical stimulator and early computers. He also reviewed inhibition in the hippocampus, which provided material for his last years as a laboratory researcher.[18]

8. Switzerland, the final years

After retiring from laboratory studies in 1975, he dedicated his efforts to what he defined as "the field that lured me into neurophysiology...the mind-brain problem".[2] He moved to Contra, Switzerland, but travelled frequently to the UK, Germany, Japan, and the United States to attend scientific conventions and present lectures.

Eccles and Popper strengthened their never-forgotten friendship, and in 1977 they published a three-part book titled *The Self and its Brain*[19]; the Spanish translation was published as *El yo y su cerebro*.[20] The first part, signed by Popper, puts forth his theory of the three worlds and how they interact, while criticising the materialist view and raising questions about the self and the body-mind problem. The second part, penned by Eccles, summarises his knowledge of brain organisation and function; the third part consists of dialogues between the two authors as they share their views on the possible interactions between mind and brain. In these dialogues, they attempt to present a neurophysiological view of the three worlds theory. The book clearly supports interactive dualism, but offers no in-depth explanations. It is certainly curious that, following his stellar career as an investigator in search of objective facts,[21] Eccles' position would be dualist rather than materialist. According to Popper's own postulates, the theory that Eccles proposes is by no means scientific and cannot be tested experimentally.

Eccles made good use of contributions by active researchers to update his knowledge continuously and continue publishing on neurophysiological topics[22,23] and on theories addressing the mind-brain problem.[24,25]

Nearly all his guest lectures began with a talk on neurophysiology before moving on to his theories on mind-brain interaction. These theories met with critical comments that never daunted him in the least.

He was invited to give a series of Gifford Lectures from 1977 to 1979, which were titled "Lectures on Natural Theology"; in 1979, they were published by Springer in book format as *The Human Psyche*.

Eccles was conscious of the weakness of his position, and he searched for ways of making it compatible with existing scientific knowledge. To this end, he was to spend the rest of his life proposing different approaches, from the interactions between dendrons and 'psychons' to quantum mechanics, in an attempt to explain the mind-brain relationship in a way that would not violate the laws of physics.

> It is proposed that the basic receptive units are the bundles or clusters of apical dendrites of the pyramidal cells of laminae V and III-II as described by Fleischhauer and Peters and their associates. There are up to 100 apical dendrites in these receptive units, named dendrons. Each dendron would have an input of up to 100 000 spine synapses. There are about 40 million dendrons in the human cerebral cortex. A study of the influence of mental events on the brain leads to the hypothesis that all mental events, the whole of the World 2 of Popper, are composed of mental units, each carrying its own characteristic mental experience. It is further proposed that each mental unit, named psychon, is uniquely linked to a dendron. So the mind-brain problem reduces to the interaction between a dendron and its psychon for all the 40 million linked units.[24]

Following in the footsteps of physicist Henry Magenau at Yale University, Eccles proposed that interaction could take place at microsites through quantum mechanisms, thereby not violating the laws of physics. Working with German quantum physicist Friedrich Beck, he published a hypothesis in the Proceedings of the National Academy of Sciences in December 1992. Based on the fact that exocytosis of synaptic vesicles is a quantum phenomenon ("when a bouton is activated by a nerve impulse, exocytosis occurs only with a certain probability, which is much less than 1"),[26] Eccles introduced quantum mechanical statistical concepts to calculate the probability of such events with an elaborate numerical theory. He combined this theory with known observations: first, findings for activation of the supplementary motor area during 'pure ideation', (defined as "cognitive events that are unrelated to any ongoing sensory stimulation or motor performances",[26] for example, imagining that you are moving your hand without in fact moving at all). Second, on Libet's finding that, milliseconds before a person decides to move a muscle, the cortical area corresponding to the muscle will activate (known as preparatory brain activity). Third, the finding that an intracellular reading from pyramidal neurons in the hippocampus "discloses a continuous intense activity which can be interpreted as milli-EPSPs generated by the continuous synaptic bombardment with exocytoses by the thousands of boutons on its dendrites...an impulse invading a bouton...evokes an exocytosis and a milli-EPSP with a probability of about 0.2–0.3".[26] On this three-part basis, Eccles proposed that "mental intention (the volition) becomes neurally effective by momentarily increasing the probability of exocytosis in selected cortical areas such as the SMA [supplementary motor area]...this means a selection of events".[26] When observed, this phenomenon somewhat resembles wave function collapse. This was the last article Eccles ever published, at the age of 89.

His health declined sharply in 1994, when he was 91, and he withdrew from scientific activities. He died on 2 May 1997 in Contra, Switzerland, and was buried there.

## Conclusions

Eccles' contributions to neuroscience more than justify his Nobel Prize. Not only did his published works fill volumes, but his articles were also outstanding in terms of both quality and relevance. A large part of what we know regarding the workings of the synapse is due to his research.[27] His study of the cerebellum was a masterpiece. Furthermore, instead of acting alone, he showed a knack for organising and leading research groups whose members would go on to great achievements.[28] His work ethic, talent for experimental design, and ability to conduct those experiments; his strong motivation, boundless curiosity, warm human nature, and his openness to other fields of knowledge; all of these characteristics led him to become one of those giants on whose shoulders we stand to gain a better view.

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