something wrong with the current system. Everyone has one or more nightmare stories about certain papers. Once, a paper of ours that after many months' worth of hard work and two rounds of revision eventually got the explicit approval of all three referees was eventually rejected on the astonishing grounds that the editor did not find it sexy enough (sic). Since then, I anxiously search for the sexy side of every paper I read. Still I have not found any — that is aside from those on courtship behaviour and mating in *Drosophila*. Then, there are the cases in which referees do not do their job properly. It happens now and then, and is infuriating. The solution is not trivial, but something must be done. I fully agree with Conly Rieder who, in this same column proposed first, that referees should be paid, and second, that they should be proud enough of their work to be happy to see their signed reports published side-by-side with the article. This solution is not a panacea, but I believe that it would ameliorate the problem.

If you knew what you know earlier on, would you still pursue the same career? If I had the impossible chance of starting up a new carrier again, I would certainly try something else. There are so many worlds to be explored — architecture, nanotechnology, many more — that it would seem silly to waste the opportunity. If the question is more along the line of whether I regret having pursued a career in biology, then the answer is positively not. It has not come without tough moments, but the rewards are priceless. Anyone who has had the pleasure of discovering a new molecule, a new function, a new process, will agree. I actually think that we scientists running our own independent research are, in many regards, privileged people. To prospective new colleagues I would strongly advise (I actually do every time I have the opportunity to do so) that a Ph.D. is not what comes naturally after graduation, or the kind of job you embark on for lack of anything better. This career requires lots of dedication. If you do not long for it and feel passionate about it, you will be much better off doing something else.

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Essay

British roots of Italian neurophysiology in the early 20th century

Giovanni Berlucchi

The recent Congress of the Italian Society of Neuroscience in Verona attracted several hundred participants, attesting to the vitality of a scientific enterprise that was started 23 years ago with the Society's first meeting in Rome. During the first Congress in Rome, four eminent Italian scientists were appointed honorary members of the Society in recognition of their outstanding contributions to neuroscience: the neurobiologist Rita Levi-Montalcini, the neuropharmacologists Daniele Bovet and Vittorio Erspamer, and the neurophysiologist Giuseppe Moruzzi. Their world-famous work inspired and provided the climate that encouraged the development of the neurosciences in Italy, and inspires Italian neuroscientists to this day. I have benefited from Moruzzi's teaching throughout my scientific career, and my purpose here is to tell how Moruzzi's teacher Mario Camis, and Moruzzi himself, benefited in turn from the teachings of the British founders of modern neurophysiology, Charles Scott Sherrington and Edgar Douglas Adrian.

Origins

In the early years of the past century, Italian science could pride itself on having produced some of the best students of the nervous system in the world. In histology, Camillo Golgi from the University of Pavia was awarded the 1906 Nobel prize in Physiology or Medicine for his discoveries concerning the fine morphology of the nervous tissue [1]. In physiology, Angelo Mosso from the University of Turin was the first to show regional changes in the blood flow through the brain during responses to sensory stimuli, mental work and emotional experiences [2], providing the basic rationale for the functional neuroimaging of the present day [3]. Important discoveries were also made by Luigi Luciani, who taught Physiology in Siena, Florence and Rome, and pioneered the localization of functions in the cerebral cortex and cerebellum [4]. Surprisingly, the scientific interactions between Golgi and the two great neurophysiologists of his time were very limited, and practically irrelevant for the development of their respective fields of research. Like Cajal, Golgi paid little attention to the findings of the physiologists, because he felt that the conclusions drawn from such findings were too indirect and far-fetched, and that only the

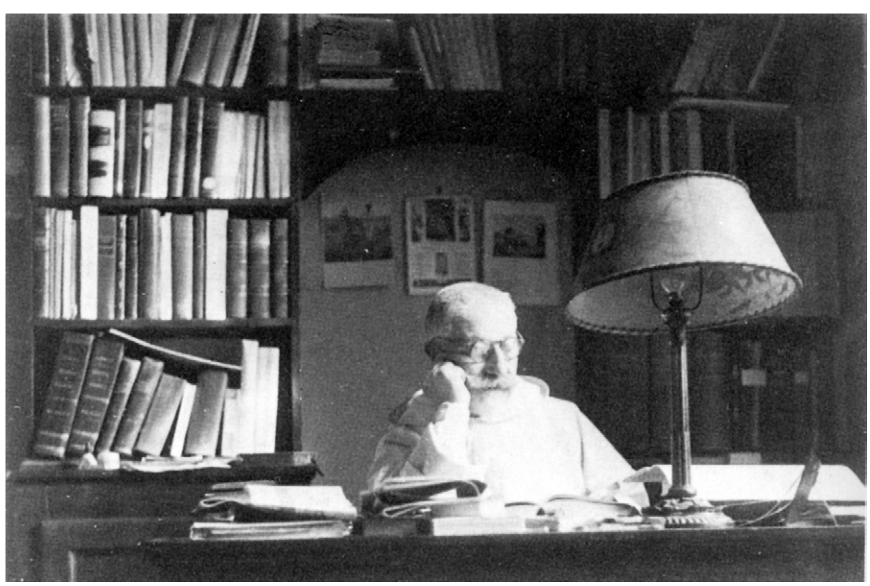
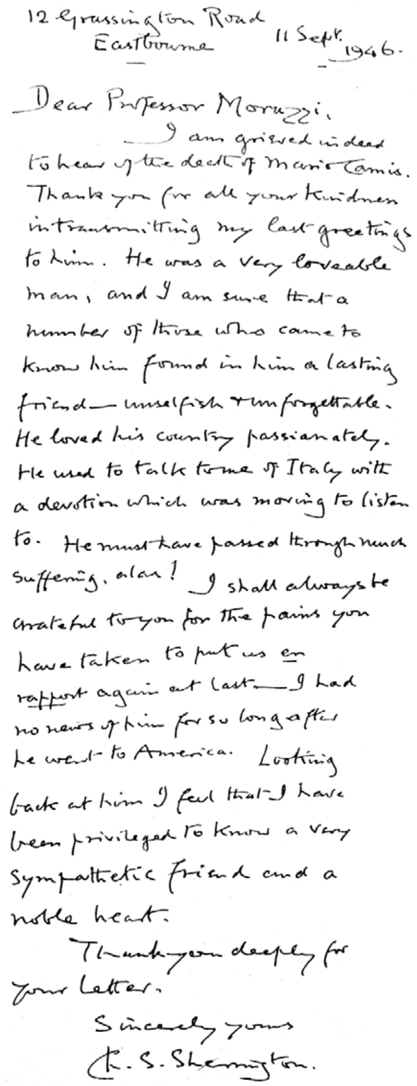


Figure 1. Mario Camis in his monastic cell at the St. Dominic convent in Bologna.



12 Grassington Road
Eastbourne
11 Sept. 1946.

Dear Professor Moruzzi,

I am grieved indeed to hear of the death of Mario Camis. Thank you for all your kindness in transmitting my last greetings to him. He was a very loveable man, and I am sure that a number of those who came to know him found in him a lasting friend — unselfish & unforgettable. He loved his country passionately. He used to talk to me of Italy with a devotion which was moving to listen to. He must have passed through much suffering, alas! I shall always be grateful to you for the pains you have taken to put us en rapport again at last — I had no news of him for so long after he went to America. Looking back at him I feel that I have been privileged to know a very sympathetic friend and a noble heart.

Thank you deeply for your letter.

Sincerely yours
C. S. Sherrington.

Current Biology

Figure 2. Letter of Sir Charles Sherrington to Giuseppe Moruzzi about Camis'death (courtesy of Professor Paolo Moruzzi).

microscope could provide cogent and definitive answers to functional as well as to structural questions [5].

Archives Italiennes de Biologie, the journal founded and edited by Mosso, published some of Golgi's studies in French, making the work known to the international scientific community. Yet curiously the most important scientific exchange between the two had nothing to do with the nervous system. Mosso had done some extravagant experiments which he felt supported a bacterial origin for malaria, in contrast with Golgi, who had provided decisive evidence that the disease is caused by a plasmodium [6]. The controversy threatened to end a friendship, but after Mosso admitted his error there was a reconciliation, and later Mosso nominated Golgi for the Nobel prize [7].

For his part, Luciani cited extensively Golgi's findings and ideas in various editions of his *Textbook of Physiology*. After an initial lukewarm expression of support for Golgi's diffuse nerve net theory, Luciani became convinced that Cajal's neuron theory provided a much better approach to understanding how the nervous system functions. He also rightly criticized the neglect of the physiological discoveries on the nervous system by the great histologists of his time, and made it clear that such discoveries had been made without help from current neurohistology [8].

Luciani and Mosso called themselves physiologists rather than neurophysiologists for two good reasons: first, they had been trained in first-rate German laboratories to investigate the functions of various organs other than the nervous system, and they maintained their eclectic scientific interests throughout their life; and second, although Oskar Vogt had named one of the sections of the Berlin Hirnforschung Institut "Neurophysiologie" as early as 1901, the term became popular only after Dusser de Barenne, Fulton and Gerard founded the *Journal of Neurophysiology* in 1938 [9]. The first physiologist to concentrate his research interest exclusively on the nervous system was Charles Scott Sherrington, who taught Physiology at Liverpool and Oxford and can be regarded as a foremost founder of neurophysiology, along with Edgar Douglas Adrian in Cambridge. They were jointly awarded the Nobel prize in 1932 for their discoveries regarding the functions of neurons.

By always approaching physiology through anatomy, and by consistently adhering to the neuron theory, Sherrington's "*The Integrative Action of the Nervous System*" [10] crystallized the elementary mechanisms of nervous functioning in an elaboration of the concept of reflex action, which was defined as the greatest single contribution of the physiologist to clinical neurology [11]. Sherrington's great merit was his choice of the neuron and its interconnections as his analytical unit, a choice which has been at the root of the conceptual and experimental advances of neuroscience up to this day. To Sherrington we owe the crucial concept of the synapse, an 'antiregurgitation' valve which determines the unidirectional march of impulses along neural pathways. His relatively simple behavioral observations following accurate peripheral and central nervous lesions allowed him to categorize many types of reflex activities and to infer from them that the output mechanisms of the nervous system are aimed at serving but one action and one purpose at a time. He understood that such adaptive functional integration requires inhibition as much as facilitation, and devoted his Nobel lecture to inhibition as a crucial component of the normal working of the central nervous system [12].

Like Sherrington, Adrian's greatness in neurophysiology comes from his decision to make the neuron his analytical unit, though by a different means. By recording the electrical activity of single nerve fibers, Adrian proved that the messages conveyed to the brain in each fiber from all sensory organs are trains of electrical impulses varying in frequency, but not in amplitude, with the intensity of the stimulus. Whether a sensation is tactile, auditory, visual or some other modality depends on the sensory organ and the cortical area receiving the signals, not on the nature of the signals, which are unvarying across sensory systems. Similarly, the commands sent by each motoneuron to the muscle fibers under its control are based on all-or-none action potentials coursing along individual nerve fibers [13].

As mentioned, Sherrington and Adrian exerted strong influences on Italian neurophysiology through two interrelated Italian scientists who played a major role in the development of the discipline in their country: Mario Camis and Giuseppe Moruzzi.

Mario Camis

The scientific pedigree of Mario Camis can be linked to both Luciani and Mosso, because he did his M.D. thesis in Physiology in Rome under Luciani and then worked as an assistant in the Physiological Institute of the University of Pisa headed by Vittorio Aducco, the most successful pupil of Mosso. A born physiologist, Camis spent a few years in England at the beginning of the last century working first on blood and respiration with Langley and Barcroft in Cambridge. Then he moved to Sherrington's laboratory in Liverpool, where he fell permanently in love with neurophysiology [14].

In Liverpool, Camis studied the spinal reflexes of the muscle semitendinosus of cats, reaching the conclusion that, though a spinal motor center can be regarded as functionally divided into several independent groups, such independence is not absolute. More specifically, when two or three afferents to the center are simultaneously stimulated with maximal intensity, the resulting muscle contraction is less than the sum of the component contractions observed separately [15]. Neglected for several years, this interference effect was resurrected by Cooper, Denny-Brown and Sherrington [16] who recognized the importance of Camis' observation, confirmed it and distinguished the effect from reflex inhibition by naming it 'occlusion'.

After returning to Italy, Camis applied the Sherringtonian approach to the vestibular system in order to understand the actions of the labyrinth on the reciprocal innervation of limb muscles and on vegetative functions such as vasomotor regulation and the control of glycemia. He also used the cord galvanometer for obtaining the first recordings of cerebellar electrical responses to vestibular stimulation. His expertise on the vestibular system allowed him to produce a monograph [17] that was translated into English by Richard S. Creed [18], a pupil of Sherrington, and was plauded as excellent in the classical *Textbook of Physiology* of John F. Fulton [19] and in the biography of Sherrington by Granit [20]. But by far the most important contribution of Camis to neurophysiology was his training of young researchers, including Giuseppe Moruzzi who, as we shall see, stands out as the most eminent Italian neurophysiologist.

The last years of Camis' life were tragic because of his Jewish origin and the abominable racial laws of Mussolini which, in 1938, deprived Camis of his University position and ousted him from the Accademia dei Lincei. Many years before he had become converted to the Catholic religion and had entered the Dominican order, and the Dominicans saved his life during the Nazi occupation of Italy by offering him shelter in Rome (Figure 1). After the war he was entitled to be reinstated in his academic positions, but the process was delayed by questionable accusations of support to the Fascist regime, which he had no opportunity to counter because of his death from a heart disease in 1946 [14]. When Camis died, several eminent scientists, among whom were Sherrington and Adrian, expressed their sorrow to his pupil Moruzzi. Sherrington wrote that Camis was a lasting, unselfish and unforgettable friend (Figure 2), and Creed defined Camis an excellent ambassador of Italian science abroad. In his obituary of Camis [21], Creed also mentioned his 'admirable' monograph on the mechanisms of emotions [22], in which Camis had sided with Sherrington against the Lange–James peripheral theory of emotion.

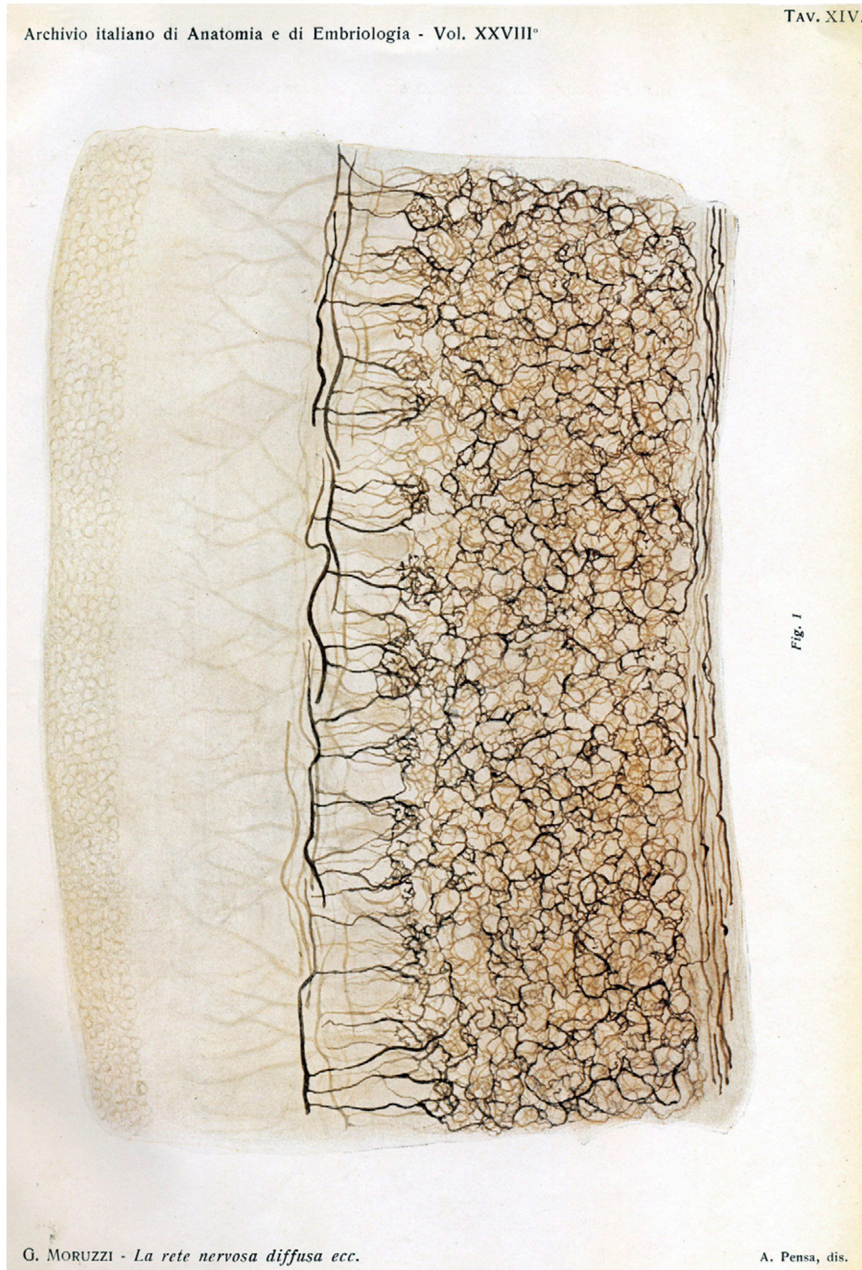


Figure 3. Drawing by Pensa reproducing an histological preparation in the first paper of Moruzzi [23].

The figure is supposed to show that the baskets around the bodies of Purkinje cells (left) send fibrils to the neuropile in the granular layer on the right.

Giuseppe Moruzzi

Moruzzi was initiated into scientific research as a medical student by Antonio Pensa, a pupil of Golgi who headed the Institute of Anatomy of the University of Parma and was eminently

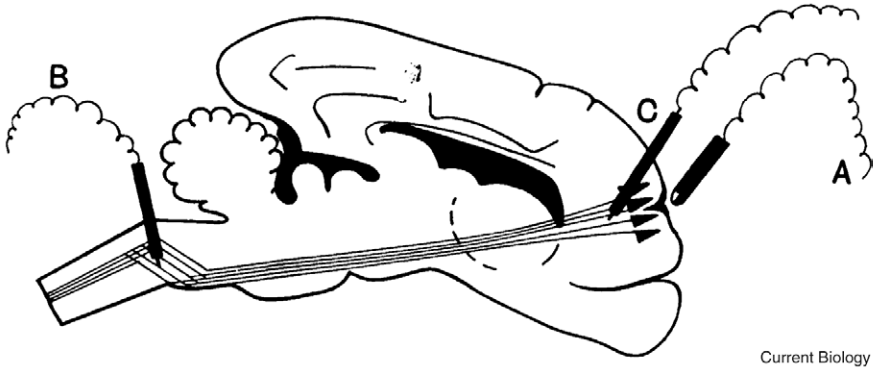


Figure 4. Electrode arrangement in the cat brain in the experiment by Adrian and Moruzzi [28]. Electrode A is for stimulating the motor cortex, electrode B is for recording from pyramidal tract fibers, and electrode C is for recording from the white matter under the cortex.

skilled in the neurohistological techniques. Pensa felt an obligation to defend Golgi's theory of the diffuse nerve net, but he also recognized the existence and importance of synaptic contacts between neurons and entertained a view of the nervous system that tried to conciliate those of Golgi and Cajal. From Pensa, Moruzzi learned to apply Golgi's black reaction to the cerebellar cortex with a view to contribute to an old debate between Cajal and Golgi that had been in the limelight at the time of their Nobel award. Cajal thought that the 'baskets' around the bodies of the Purkinje cells were terminal structures, while Golgi claimed that they were not because they contributed fibrils to the diffuse nerve net in the granular layer. As a result of his research, the 20 year old Moruzzi published as a sole author a paper supporting Golgi's position [23], in which Pensa reproduced one of Moruzzi's histological preparations in a masterful watercolor drawing. As shown in Figure 3, the drawing documented several fibrils connecting the baskets to the neuropile in the granular layer.

After Pensa moved back to his alma mater in Pavia, and after graduating in Medicine, Moruzzi decided to embark on a career in physiology and to join the homonymous Institute directed by Camis at the University of Parma. Camis taught him the techniques that had been the staple of Sherrington's neurophysiology, above all myography, and also made him imbibe the Sherringtonian basic concept of the nervous system as an organized aggregate of specialized and selectively interconnected neurons. By developing Camis' ideas about the relations between the vestibular system and vegetative functions, Moruzzi was able to collect the first evidence for a role of the cerebellum in the reflex regulation of circulation and respiration [24]. But because modern electrophysiological techniques were not available in Camis' laboratory, in 1937–1938 Moruzzi went to work in the laboratory of Frédéric Bremer in Brussels, where he used electroencephalogram (EEG) recordings for analysing various normal and epileptic cortical activities [25]. Bremer had worked with Sherrington at Oxford in the 1920s and had adapted some of the Sherringtonian ideas and techniques for studying spinal functions to the analysis of higher nervous activities. His conception of a generalized regulation of cortical activity, based on the EEGs of his encéphale and cerveau isolé preparations [26], had a strong influence on Moruzzi's approach to the physiology of the sleep–wake cycle, as was later proven by the epochal discovery of the arousing functions of the brainstem reticular formation by Moruzzi and Magoun [27].

But it is more important here to consider Moruzzi's relation to the other great British neurophysiologist, Adrian. Thanks to a fellowship from the Rockefeller Foundation and a presentation by Bremer, in 1939 Moruzzi moved to Cambridge to work with Adrian on the responses of single neurons in the cat medial lemniscus to somatosensory stimuli. After having accidentally found spontaneous discharges of pyramidal tract fibers in anaesthetized cats, they dropped the original project to do a thorough investigation of the relations between the EEG activity of the motor cortex and the action potentials of a single neuron of that cortical region [28]. This first successful attempt to monitor the activity of single cortical neurons by recording the action potentials from their axons in the brainstem (Figure 4) demonstrated that the frequency code discovered by Adrian in peripheral sensory and motor neurons also applied to the highest level of the brain. Like peripheral neurons, cortical neurons coded the intensity of sensory or directly applied stimuli in terms of frequency of action potentials, thus providing a principal key to the understanding of all transactions between neurons.

In short, it could be surmised that the rate and the temporal spacing of action potentials emitted by single neurons forms a unitary code for communication underlying all aspects of brain functioning, from sensation and movement to thought and action planning. Adrian's conviction that impulses in nerve fibers represent the main language in which one neuron speaks to another continues to be the basic credo of neuroscientific thought, even if other secondary means of interneuronal communication, such as paracrine chemical signals, are also known to exist. For decades up to the present, action potentials have been recorded from countless single neurons and other excitable cells in most animal species, including man, and a vast amount of current wisdom in all fields of neuroscience comes just from the use of the technique originally championed by Adrian for peripheral neurons and applied by Adrian and Moruzzi to cortical neurons [29].

It is of some historical interest that an aspect of Adrian and Moruzzi's experiment [28] can be connected to the old Italian neurophysiological tradition of Luciani. Among the direct and indirect stimulations delivered by Adrian and Moruzzi to the motor cortex was the local application of strychnine, resulting in a huge increase in the activity of pyramidal tract fibers. Such stimulation was no doubt suggested by Moruzzi who was familiar with the work of Baglioni and others on experimental epilepsy in Luciani's laboratory in Rome. Along with Magnini, Baglioni had been the first to show that strychnine applied in small doses to the motor cortex of dogs provoked a rhythmic and regular series of spontaneous

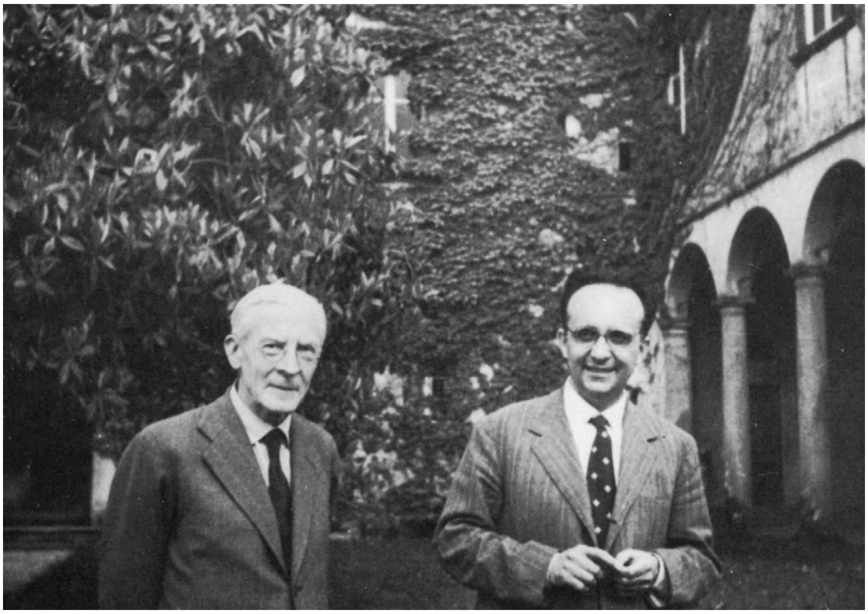


Figure 5. Adrian and Moruzzi in Tuscany in the 1950s (courtesy of Professor Paolo Moruzzi).

contractions of the corresponding muscles of the opposite side, as well as a reduction in the threshold for the motor response to local electrical stimulation. That the action of strychnine is electively localized to the cortical neurons, and not to the underlying nerve fibers, was proved by the fact that both the increase of excitability and the spontaneous rhythmic contractions disappeared completely as soon as the poisoned cortical area was removed [30].

Dusser de Barenne, who later extensively employed the strychninization of the cortex and became known as the champion of the method [31,32], tended to neglect Baglioni's priority, eliciting the following dignified response of the latter: "Finally, I shall not appear to diminish the importance and the merit of the researches of M. Dusser de Barenne by stating that he, using a method substantially identical to ours, has obtained substantially identical results [with the exception of certain theoretical deductions fully open to discussion], experimenting on the cortex of the cat, and extending the experiments to a larger number of centres" [33]. The citation of Baglioni and Magnini's study in Adrian and Moruzzi's paper rightly re-established their priority over Dusser de Barenne.

Epilogue

The collaboration between Adrian and Moruzzi (Figure 5) was remarkable, but Moruzzi's best work was yet to come. Having benefited from the teaching of Sherrington indirectly through Camis and Bremer, and from that of Adrian directly, he discovered the arousing EEG effects of the electrical stimulation of the brainstem reticular formation along with Magoun at the Nortwestern University of Chicago [27]. Even more importantly for those who have been lucky to be his students, he founded the most successful Italian neurophysiological school at the University of Pisa, where he made further pioneering studies on the physiology of the sleep–wake cycle [34,35]. Sherrington and Adrian had invented neurophysiology as a profession, that is, as a single-minded pursuit of fundamental knowledge concerning the physiology of the nervous system from it simplest components to its highest complexity. Following them, Camis and, especially, Moruzzi imported this profession in Italy by training young researchers to restrict their experimental activity to the nervous system. Yet he also taught them always to keep in mind that the other organs of the body are not inert complements to the brain, but rather specialized functional systems to be integrated by and with the brain into the unitary economy of the organism.

The emergence of a unified field of neuroscience in the last three decades of the twentieth century has strongly blurred, if not erased, the boundaries between the traditional disciplines dealing with the nervous system. The fragmentation of knowledge implicit in the terminology of the traditional disciplines may now be seen as an artifact of scholarship rather than a reflection of the real world, and the term neurophysiology may well be destined for obsolescence. Yet the young neuroscientists of the present time should know that the blessed climate of interdisciplinarity they are working in would not have come about without the achievements of those who concentrated their efforts within the confinement of a single traditional discipline. Such achievements have provided the fundamental knowledge necessary for establishing the linkages with the other disciplines. Golgi and Cajal may be criticized in retrospect because of their neglect of neurophysiological findings, and a scarce interest in clinical neurology may perhaps be blamed on Sherrington, Adrian and Moruzzi. But without the neurohistological findings of Golgi and Cajal and the neurophysiological findings of Sherrington, Adrian and Moruzzi the integrated neuroscience of today would not exist.

Acknowledgments

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Quick guide

Basal bodies

Chandra Kilburn and Mark Winey

What is a basal body? The basal body (also known as the kinetosome) is a highly conserved cellular organelle discovered over one hundred years ago. Basal bodies are barrel-like microtubular structures located near the cell surface that provide the template for the nine-fold symmetry upon which the cilium is assembled.

What is the function of a basal body? Basal bodies are thought to be involved in many aspects of cell biology, including the organization of cytoskeletal elements such as cilia. The basal body plays a role in motility, cell-cycle progression, morphogenesis and sensation, depending upon the cell type, via its function in organizing the cilium or, in some cases, organizing the architecture of the cytoskeleton.

Which cells have basal bodies? Most organisms in the animal and protist kingdoms have basal bodies. Alga, including *Chlamydomonas*, generally have basal bodies, whereas higher plants and fungi do not. In the human body, nearly all cell types contain basal bodies.

What is the difference between a basal body and a centriole? In 1898 Mihaly Lenhossek and Louis Henneguy independently published reports showing that basal bodies were identical to centrioles. This idea, known as the Henneguy–Lenhossek Theory, was not confirmed until the 1950s when electron microscopy studies showed that basal bodies and centrioles share the same fine structure. Despite these similarities, some important differences exist between basal bodies and centrioles. Specifically, basal bodies are located near the cell surface where one basal body directly nucleates one cilium. In contrast, centrioles are linked in pairs near the nucleus where they recruit the pericentriolar material required to nucleate the microtubules of the mitotic spindle. Centrioles also possess distal appendages that are lacking on basal bodies.

What is the basal body structure? The basal body cylinder, which is approximately 0.25 μm in diameter and 0.5 μm long, is composed of a symmetrical array of nine triplet microtubules with a 9(3) + 0 arrangement similar to that of the centriole (Figure 1). Basal bodies have an intricate cartwheel structure at the proximal end and a distinct structure known as the transition zone at the distal end separating the basal body from the attached cilium. The lumen of the basal body is filled with an amorphous electron-dense material. Accessory structures associated

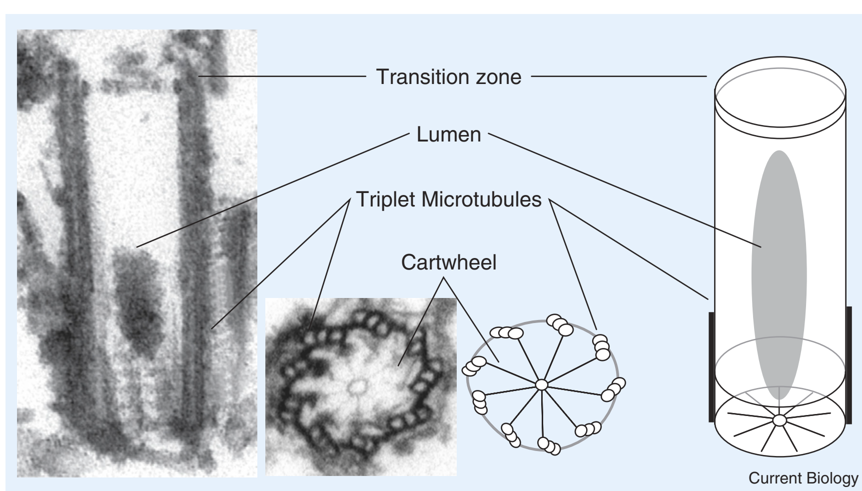

Figure 1. Electron micrographs (left) and schematic diagrams (right) of a *Tetrahymena* basal body.
Key structural features of basal bodies are indicated in both the longitudinal view (outer images) and the cross sections (inner images).