Rise of neurone sciences in the 20th century First part: Neurone physiology (1900–1940): from nervous physiology to neurophysiology

Jean-Gaël Barbara

Psychiatr. Sci. Hum. Neurosci.
DOI 10.1007/s11836-011-0163-1

ÉDITORIAL / *EDITORIAL*

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

The rise of neuron sciences in the 20th C.

Part I. Neuron physiology (1900-1940): from nervous physiology to neurophysiology

Jean-Gaël BARBARA, CNRS, Université Pierre et Marie Curie,
laboratoire de neurobiologie des processus adaptatifs, CNRS UMR 7102,
université Denis Diderot, laboratoire sciences, philosophie, histoire,
SPHERE, CNRS UMR7219.

ABSTRACT: In the late 19th century, the introduction of the neurone concept led to vivid oppositions in many fields of enquiry, especially in the physiology of the nervous system. In Great Britain, novel research programs (Sherrington and Adrian) supplanted the general common hostility to conceive of the neurone as a general and fundamental physiological element. These new paths of research lead to a unique neuronal physiology rewarded by the Nobel prize for physiology or medicine in 1932. This first form of neuro-physiology expands abroad and is under the attack of American physiologists concerning the functional role of the neurone soma *vs* the more fundamental and hypothetical function of the axon. During the 1930s and the 1940s, a series of polemics progressively die out with the establishment of the fundamental bases of a new and international neuronal physiology which will lead to the rise of neuroscience after the Second World War.

Key words: *neurone, neurophysiology, neuroscience, electroencephalography, oscillography.*

INTRODUCTION

The study of the constitution of the neuron as a scientific object is based on an investigation of the ways in which the concept of the neuron and its associated anatomical concepts have been objectified by different scientific disciplines [1, 5, 6]. Enunciated in 1891 by Heinrich Wilhelm Waldeyer (1836-1921), the neuron concept represents the beginning of neuronal theory. This theory states – in line with the cellular theory of the early 19th^{e} century (Matthias Jakob Schleiden and Theodor Schwann) – that the entire nervous system is made up of *cells.* With the neuron theory, "nerve cells", as they were previously called, were no longer seen as distinct from the surrounding nerve fibers, which had been visible under light microscopy since the work of, for example, Felice Fontana (1730-1805). Each cell stained using Golgi's new technique (1873) appears to be made up of extensions of finite dimensions, of two types: dendrites, and the finer, single axon previously discovered (Otto Deiters, 1865).

The neuron represents the ensemble of a cell body (a "cell") and large extensions, but with "free ends", i.e. contiguous rather than continuous with neighboring nerve fibers. The concept of the neuron is, in short, a stoichiometry and topology of the neuron's constituent elements, objectified by pure microscopic investigation.

Psychiatr. Sci. Hum. Neurosci.
DOI 10.1007/s11836-011-0163-1

ÉDITORIAL / *EDITORIAL*

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

By the end of the 19th century, the neuron theory had become widely accepted, due to the discovery of other staining techniques – such as Erlich's methylene blue staining – which led to the same general results. On the other hand, certain embryological arguments demonstrated that neurons progressively differentiate during development from globular cells, emitting short extensions, elongating and differentiating into dendrites and axons in defined territories.

The concept of the neuron thus emerges from the context of cell theory, microscopy and histology, and from a new science that takes advantage of the dyes created by the then-expanding chemical industry. However, these scientific contexts were ultimately highly specialized, and the resulting works revealed only the general structure of the neuron, its outer envelope, with nothing to say about its internal constituents, or its modes of function, particularly electrical and chemical.

Studied in isolation by histology, the concept of the neuron is essentially a form, a "black silhouette", but not really a unique representation associating this histological knowledge with intracellular mechanics. Neither its action potential, nor its synaptic activities, nor are known its ion and protein migrations according to transmembrane and intracellular flows respectively. The concept of the neuron as a scientific object bringing together all this new knowledge from the new biological sub-disciplines of the 20th century does not exist.

We present this adventure in two parts. The first will illustrate the initial physiological research devoted to the neuron, and the emergence of neuronal physiologies that eventually converged on the unified discipline of *neurophysiology*. The second part will focus on post-World War II neurophysiological research and the rise of a new interdisciplinary movement, *neuroscience*.

This first part therefore begins at the time when the theory of the neuron was being formulated, and during the years when was being disseminated the already impressive work of the Spanish histologist Santiago Ramón y Cajal (1852-1934), devoted almost exclusively to the neuron and which earned him the 1906 Nobel Prize for Physiology or Medicine, in association with Golgi (1906) [3]. However, we will take a brief foray into the 1860s to outline the limitations of the old Bernardian physiology on the question of communications between nerve cells and muscle, in order to show the character of the new and expanding physiological disciplines that would lead to new cellular interpretations and initiate the renewal of physiology.

A NEW PHYSIOLOGY AT THE TURN OF THE 20TH CENTURY

Between the 1860s and the turn of the 20th century, the rise of the neuron theory gave rise to a complex set of reactions in all fields, not only scientific, but also in philosophical circles and in the Catholic press. The adoption of cellular theory for nervous tissue, and the refutation of diffuse nervous networks in the brain, contributed to the revival of a materialistic vision of the mind. Imagination, dreaming, sleep and memory were interpreted by some scientists as the direct result of labile physical contacts between neurons, which were thought to be made and unmade according to physiological conditions. The considerable authority of the new neuron doctrine led many scientists to admit that they had finally understood the workings of the mind by studying the density of contact points between neurons (synaptic buttons).

This new interpretative approach (histophysiology), analyzing purely anatomical data, was based on the renewed credo – though opposed by Claude Bernard – of strict "anatomical determinism", admitting that the simple inspection of structures provided the key to the physiological functioning and functions of organs and anatomical elements.

Obviously, this physiology was wrong, and that's why we need to retrace the steps taken by the various currents of physiological research into nerve cells to understand how this emerging path will create a genuine *neuronal physiology* which foundations are those of current neuroscience.

Claude Bernard and its critics: the controversy over curare's mode of action

Experimental physiology is an ancient approach, dating back to the IIIrd century BC, with, for example, Herophilus' work on the distinction between sensory and motor nerves. But the development of this field of research, as a progressively institutionalized medical discipline, accelerated in the first decades of the 20th century with the emblematic figure of François Magendie (1783-1855), Claude Bernard's teacher at the Collège de France.

Physiology owes much to medicine and the work of French physician Xavier Bichat (1771-1802). In his studies, he achieved the first form of synthesis between anatomy and physiology, defining the

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

essential constituents of organs such as mucous membranes or muscles – the *tissues* – by combining anatomical, physiological and pathological properties. To achieve such an approach, Bichat studied tissue reactions to stings, acids or infections, and attempted to correlate the distribution of tissue reaction properties with the topography of their anatomical features. For example, the mucous membranes of the respiratory tract were considered a single tissue, not only because there is a continuity of texture between them, but also because an infection can spread from the nose to the bronchi and vice versa via the pharynx and larynx.

Bernard's study of the effects of poisons on nerve tissue is a field of experimental physiology directly inspired by similar work from Bichat and Magendie. In particular, Claude Bernard studied the mode of action of curare on nerves, the lethal substance found on the poisoned arrows of certain Amazonian Indians. According to Bernard, curare "kills" the nerve, since stimulation of a poisoned nerve no longer determines movement in the innervated muscle. On the other hand, this muscle can still contract through direct electrical stimulation of its muscle fibers. However, all Bernard's ingenious experimentation did not bring him to a definitive conclusion. Throughout his life, Bernard hesitated as to the exact site of action of curare, which he most often – and erroneously – located at the root of the motor nerve, at its junction with the spinal cord. On this question, Bernardian physiology became bogged down and inconclusive, while his young colleague Alfred Vulpian admitted – correctly – that curare acts by breaking the communication between nerve and muscle. In today's terminology, curare blocks synaptic transmission from nerve to muscle.

The study of Vulpian's rationalism shows why Bernard was wrong, and clarifies the limits of the old Bernardian physiology. For Vulpian, curare doesn't affect intrinsic nerve function either, as the drug doesn't prevent the propagation of negative variation (of the nerve current) along the nerve, a new finding of German electrophysiologists. But for Bernard, a nerve killed by curare can still be the site of a negative variation. It's as if Bernard couldn't accept that the nerve's entire function layed in the propagation of an electrical nerve impulse. Vulpian's own training in electrophysiology surely explains his adherence to this idea. For him, the reason curare blocked neither muscle nor nerve function was that it blocked transmission from one to the other. For him, this transmission involved a non-nervous, non-muscular element, which he identified with a new structure discovered in microscopy, the "motor plate" between nerve and muscle (the synaptic element). Vulpian showed himself to be sensitive to the new results of electrophysiology and histology, which he practiced, even though Bernard had not trained himself in these new disciplines, which he nevertheless defended by supporting his students Arsène d'Arsonval and Louis Ranvier.

Vulpian thus proposed a first model of nerve transmission, identifying the motor plate as a transmission element between nerve and muscle, blocked by curare. This is all well and good, but Vulpian was wrong on one point. This element is not non-nervous or non-muscular, but *both* nervous and muscular (the synapse). Because the property of blocking function by a drug is not homogeneous in an anatomical element; this property can be localized. This was the result of the new pharmacology of the nervous system at the beginning of the 20th century.

Poisons and the new pharmacology of nerves

This pharmacology, mainly British at the time, studied the mode of action of other drugs, such as nicotine, and enabled the first distinction to be made between sympathetic and parasympathetic nerves regulating organ function. On the other hand, work on nerve ganglion poisoning with nicotine suggested that the propagation of nerve impulses from one nerve fiber to another in a ganglion involved a nerve relay blocked by drugs. For Henry Dale (1875-1968), synapses could be blocked pharmacologically, and their functioning relied on a chemical mechanism that a molecule could prevent.

This chemical theory of neurotransmission was in direct agreement with Vulpian's hypothesis on the mode of action of curare on the motor nerve. It was also in line with Nobel Prize winner Otto Loewi's (1873-1961) famous experiment on the isolated frog heart, whose rhythm was slowed by infusion of a solution punctured from another isolated heart whose sympathetic nerve had been stimulated. Loewi's hypothesis was that this stimulation triggered the release of a chemical substance from the nerve, which was recovered from the heart and could act on another heart. This substance would be identified by Loewi himself, in collaboration with Dale, as acetylcholine.

Confronting neuronal anatomy and physiology: Sherrington's synapse

At the time of Vulpian's work, the concept of the synapse did not exist, whereas the work of Dale and Loewi concerned synaptic transmission. The concept of "synapse" was coined in 1897 between these two

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

bodies of work by British physiologist Charles Sherrington (1857-1952), winner of the Nobel Prize in Physiology or Medicine (1932).

There's a remarkable conceptual continuity between these scientists, which leads us to try to better understand how Sherrington came to forge this concept.

The context of this work is very different from the highly speculative histophysiology. Yet Sherrington's thinking begins with a critique of Cajal's physiological speculations. For Cajal, neurons are ordered in chains from the periphery to the nerve centers and vice versa. But always, the axon points in the direction of influx propagation, from the cell body to other neurons. The axon seems to be the element that transmits nerve impulses from one neuron to the next. Cajal deduced that the functioning of a single neuron is polarized, and that nerve impulses can only propagate in one direction within a neuron, particularly in an axon. But now Sherrington admits that the function of a nerve fiber, or axon, is to be a simple excitable element, a simple conductor. This belief in a fundamental and general property was in line with Vulpian's intuition. What's more, Sherrington himself demonstrated, on the spinal cord of a dog, that conduction (known as *antidrome*) can occur experimentally in the opposite direction to the physiological one. For Sherrington, the propagation of a nerve impulse in a neuron cannot therefore be polarized. But Sherrington did not entirely abandon Cajal's idea, as the orientation of neuron chains indicated a real anatomical polarization of neuronal circuits. Somewhat in the manner of Vulpian, Sherrington then imagined that polarization wass the property of the communication element between two neurons, which he believed functioned like a diode. The neurons are therefore contiguous, and their contacts enable polarized communication. It was to defend this idea that Sherrington coined the term "synapse", to define a polarized conduction standard for interneuronal communication. Sherrington went on to use this term to define the anatomical element of communication that was then called "neuronal articulations" in French-language literature. The synapse was born.

NEURAL PHYSIOLOGIES IN THE UK

All the preceding work concerns physiological experiments on nerves and nerve fibres. Although physiology is interested in the concept of the neuron, and defines the synapse as a neuronic element, it does not yet have the technical means to directly measure the physiological properties of individual neurons.

Nevertheless, after the First World War, two neuronal physiologies emerged in initially opposed theoretical contexts, one of which depended on real technological innovation.

Sherrington's interdisciplinary approach to anatomy and nerve physiology

Sherrington's research focused on the study of reflexes in dogs, using classical physiological instruments as developed and used by Étienne-Jules Marey (1830-1904). Sherrington's work makes extensive use of the concept of "integration" developed by philosophers Herbert Spencer (1820-1903) and Alexander Bain (1818-1903) in their reflex studies [7]. Sherrington demonstrated that the spinal cord is a nervous organ for integrating sensory information during reflex mechanisms. But Sherrington's originality lies in providing a neural model of this integration and justifying it with precise experiments and measurements, as well as with new physiological concepts developed at the neural level.

To understand this model, which will lead to a neuronal physiology, we need to imagine, for example, the dog's scratching reflex. When an animal's flank is scratched, it makes an oscillatory scratching movement with its hind leg on the corresponding side. The intensity of the motor response is proportional not only to the strength and spatial extension of the stimulation, but also to its frequency. All this sensory information adds up in the medulla to determine the strength of the reflex. Several sensory nerves are involved in this phenomenon. Sherrington wanted to understand how stimulation of an area more anterior than the previously stimulated area determined a stronger reflex. How does the sensory nerve of the anterior region could affect the reflex elicited by stimulation of the nerve of the posterior region? Sherrington developed the concept of "facilitation" of the stimulation of one sensory nerve on the response of another. Previous stimulation of one nerve sensitizes the second, resulting in a more intense response than that obtained from the second alone.

Sherrington imagined that the mechanism of this facilitation was *neuronal*, involving the installation of a state of sub-liminal excitation of the motor neurons, which were thus rendered more excitable, but not excited, so as to understand why a greater number of motor neurons were excited on

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

stimulation of the second nerve. This mechanism explained the increase in reflex strength.

This complex model may seem speculative and peculiar, but if we dwell on it a little, it was the founder of a neuronal physiology that served as a heuristic basis for subsequent research well into the 1930s and 1940s. What's more, the concepts forged by Sherrington were objectified by electrophysiological measurements, such as the resting potential of neurons, during these same years. As a result, this model was largely validated with regard to the general functioning of neuron electrogenesis, i.e. its capacity to emit action potentials as studied in neuroscience today.

Edgar Adrian's reductionist approach to technological innovation

Adrian's approach is apparently opposed to Sherrington's, since it is based on the idea that the fundamental properties of nerve fibers are sufficient to explain the functioning of nerve centers. For Adrian, Sherrington's neuronal model is superfluous, and facilitation is a process of nerve fibers, not of the cell bodies of neurons.

To study the elementary properties of nerve fibers, Adrian develops original new instruments for measuring the action potentials of a single nerve fiber. He exploited the new possibilities for amplifying electrical signals with diode lamps used in wireless telephony. He perfected microcinematographic procedures for recording capillary electrometer measurements. He demonstrated that nerve action potentials are *all-or-nothing* (elementary constant amplitude) and that their frequency carries the information transmitted by fibers and neurons (such as the intensity of a sensation).

However, in the course of these studies, Adrian observed that the maximum frequency of a nerve fiber's action potentials was limited by what he believed to be a "refractory" period. This concept was first defined by Marey for cardiac contraction. It is a period of brief non-excitability that follows contraction (of the heart) or action potential (of a nerve fiber). Adrian conceives that a refractory period exists in the axons of central neurons as well as in the sensory axons of the skin, leading him to believe that this property is in fact determined not by the axon, but by the cell body of the neuron. In reality, this is pure speculation, but it brings Adrian closer to Sherrington's ideas. According to them, the neuronal soma possesses intrinsic properties that determine nervous phenomena measured in axons.

Adrian's physiology is an elementary physiology of the neuron, which for the first time objectifies the spatio-temporal propagation of nerve impulses in a single fiber, and interprets the conditions of this phenomenon using both nervous and neuronal parameters.

The rise of British neurophysiology

For their work as a whole, Sherrington and Adrian were awarded the 1932 Nobel Prize in Physiology or Medicine. Their results were the starting point for British neurophysiology, whose research program from then on focused on understanding neuronal electrogenesis. A model was developed in the 1930s, and became the fundamental theory of neurophysiology. It's interesting to note that it's more or less the same model as that of French physiologist Louis Lapicque (1866-1952), set out as early as 1907, but on entirely speculative grounds: a neuron has a fixed base potential, and its excitation determines a time-varying drop in this potential that triggers a brief action potential if a certain threshold is reached. Every action potential has a refractory period, which determines the neuron's maximum discharge frequency. This model integrates different approaches to nerve physiology and the physiology of nerve centers by taking account of neuron theory. With this new theoretical basis, neurophysiology takes off on an international scale, adopting a major new tool – the cathode-ray oscillograph.

EXPANSION OF NEUROPHYSIOLOGY ON AN INTERNATIONAL SCALE

Alfred Fessard's school in Paris

While Lapicque's model is still much admired for its early conception, his physiological work, which was refuted by the Cambridge school in the 1930s, is a different story. In reality, Lapicque, then a professor at the Sorbonne, exercised a veritable authoritarian mandarinate, defending erroneous theoretical conceptions with no real regard for either his students or his detractors. His school gradually became isolated, and Parisian neurophysiology – which for a time had been the bearer of a new way of understanding the brain – sank into mediocrity.

However, Henri Piéron (1881-1964), Professor of Sensation Physiology at the Collège de France, created a new school of neurophysiology that became prosperous and international after the Second World War. His pupil, Alfred Fessard, carried out both elementary physiology experiments using the

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

new oscillography and psychophysiology, work physiology and electroencephalography experiments on humans [2].

In 1934 and 1936, Fessard was awarded two Rockefeller Foundation fellowships to work in the UK at the Plymouth Biological Station, then at the Adrian Physiology Department. During these stays, Fessard acquired the research style of the new British neurophysiology [4]. In particular, he and Adrian's collaborator Brian Matthews recorded elementary synaptic potentials in the frog spinal cord for the first time.

Back in France, Fessard's favorite field of research was the electrophysiology of electric fish, in particular the torpedo from the Arcachon biological station. This research theme led to international collaborations not only at Arcachon, but also with the Brazilian laboratory of Carlos Chagas, who had defended his thesis in Paris.

These oscillographic studies of the torpedo's electrical apparatus enabled Fessard to integrate himself and his school into the international boom in neurophysiology from the 1930s to the 1950s.

The American "axonologists" group

The adoption of oscillography as a common tool multiplied exchanges between neurophysiologists. The instrument gave rise to much discussion about its specific operating procedures and how to obtain reliable, comparable measurements. As a result, much more than before, scientists were able to compare their results and establish competitive relationships, not only with regard to the theoretical consequences of their often not directly comparable results, but on the measurements themselves and the technical means used to obtain them.

The group of researchers who pioneered the development of these new measurements included American physiologists Herbert Spencer Gasser (1888-1963) and Joseph Erlanger (1874-1965), winner of the 1944 Nobel Prize in Physiology or Medicine, and their students.

In the 1930s, this group began to compete with British physiologists over the actual role of the neuronal soma in neuron electrogenesis. The axonologists cultivated Adrian's first theoretical position, that of his teacher Keith Lucas (1879-1916), who regarded excitability as a fundamental property of living organisms. For the American physiologists, the excitability of the nerve fiber was a property of the fiber itself, while the excitability of the neuronal soma was merely a condition for the propagation of impulses between neurons. This controversy came to an end with the oscillographic measurement of nerve fiber and neuronal soma property parameters. In reality, these parameters did not really differ, and there was no fundamental reason to believe such rigid discontinuities in the plasma membrane of the neuron in its different regions.

Clinical and fundamental electroencephalography

It was again a question of the properties of the different parts of the neuron that set axonologists against another school of physiologists, the electroencephalographers. The technique of electroencephalography was invented by the German neurologist Hans Berger (1873-1941) in the 1920s. He had demonstrated normal low-frequency (10 Hz) rhythmic electrical activity on the human scalp in slightly drowsy but conscious subjects. British, American, then French and German physiologists reproduced this measurement, which at first seemed so strange as to be perceived as an artifact. When it was finally accepted by all, some electroencephalographers had an interpretation of this rhythm that derived from Adrian's theoretical conceptions of the change in polarity between the dendrites and the neuron body during the propagation of nerve impulses. Berger's rhythm was interpreted as an electrical polarization of the dendrites, considered as excitable elements propagating a nerve impulse in the manner of the axon. But such a conception seemed unacceptable to most other physiologists. While excitability was seen as a fundamental property of the axon membrane and the neuronal body, physiology still downplayed the functional role of dendrites as thin extensions too distant to have any influence on neuronal electrogenesis. Once again, physiologists were thinking in terms of a dichotomy that didn't really exist. These problems were only resolved by new techniques developed in the 1990s.

This controversy over the role of dendrites indicates that the neuron is emerging as a biological object very gradually, bringing together results from very different communities. What's more, a scientific result or concept from a classical line of research may contain an unexpected heuristic in a distant field (in this case, electroencephalography), which in turn benefits the body of knowledge on a certain scientific object (the neuron). This is how neurophysiology came into being on an international scale, enabling interactions between sub-disciplines to understand the general functioning of the neuron.

Psychiatr. Sci. Hum. Neurosci.
DOI 10.1007/s11836-011-0163-1

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

CONCLUSION

The gradual development of a British neuronal physiology, followed by a wider range of physiologies focusing on neuron mechanics, led to the creation of neurophysiology in the early 1930s. In fact, the opposition between nerve physiology and neuronal physiology continued until after the Second World War. But most of the polemics died down considerably by the early 1950s. By this time, consensus was emerging on the general functioning of the neuron, the chemical nature of neurotransmission, and the integration of synaptic activities. The fundamental theoretical framework of neurophysiology was thus able to benefit from the technological innovations that would enable new objectivations of neuronal mechanisms after the Second World War.

By the end of the 1940s, the neuron was already coming to life. We were beginning to glimpse its general mode of operation, but we did not yet understand how synaptic transmission was achieved, nor the intimate mechanisms of the different forms of neuronal plasticity. We were still at an intermediate stage, where the neuron was no longer the histologists' initial concept of the dead neuron, nor the scientific object that really brings it to life, but at an intermediate, speculative theoretical stage – based on precise objectivations made possible by the oscillography technique – whose heuristic richness will be revealed in the emergence of neuroscience over the next two decades.

References

1. Barbara J.G. 2006. The physiological construction of the neurone concept (1891-1952). CR Biol 329 : 437-449.
2. Barbara J.G. 2008. Alfred Fessard: a critical look at cybernetics and systems theory. In Debru C, Barbara JG, Cherici C (ed) Essor des neurosciences en France dans le contexte international (1945-1975). Paris : Hermann
3. Barbara J.G. 2009. The Cajal – Golgi controversy: Stockholm, 1906. Revue de Morphologie (no pagination).
4. Barbara J.G., Debru C. 2009. Edgar Douglas Adrian and neurophysiology in France around the Second World War. In Fox R, Joly B (ed) *Echanges entre savants français et britanniques depuis le XVII^{e} siècle*. Oxford : College Publications.
5. Barbara J.G. 2010. *La naissance du neurone*. Paris : Vrin
6. Barbara J.G. 2010. *Le paradigme neuronal*. Paris : Hermann
7. Dupont J.C. 2008. The concept of reflex: Georges Canguilhem and the history of physiology. In Fagot-Largeault A, Debru C, Han HJ, Morange M (ed) Philosophie et médecine: en hommage à Georges Canguilhem. Paris : Vrin, 91-111.

Figures

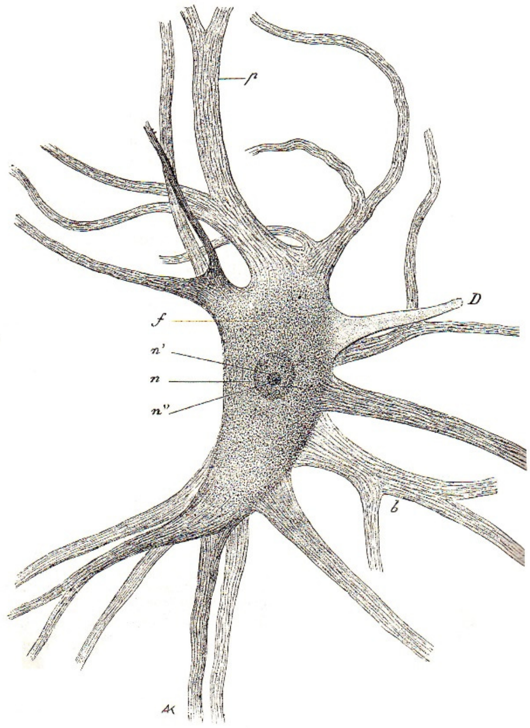

Figure 1. The nerve cell by Otto Deiters (1865), based on microscopic observations of mechanically isolated motoneurons from horse spinal cord. Ranvier, *Traité technique d'histologie*. 1875. Paris: Savy, p. 1054. *D*, Deiters' extension, is the axon, still called "cylinder-axis" in the 19th century. The other extensions (*p*) are dendrites, sometimes with bifurcations (*b*). The nucleus of the cell body (*n*) comprises the nucleolus (*n'*) and its nucleolus (*n''*). Recognition of the single axon was the first step in establishing the histological concept of the neuron.

DOI 10.1007/s11836-011-0163-1

Translated author accepted manuscript: J.G. Barbara, 2011, L'essor des sciences du neurone au XXe siècle. Part I: The physiology of the neuron (1900-1940): from nerve physiology to neurophysiology. Psychiatr. Sci. Hum. Neurosci. 9, 104-111. (PSN ed., Paris, ISSN 1639-8319)

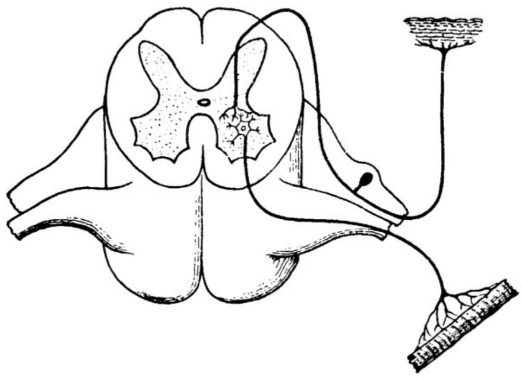

Figure 2. Diagram of the simple reflex arc. Louis Lapicque. *La machine nerveuse*. 1942. Paris: Flammarion. Top right: skin and cutaneous receptor formed by the axon of the sensory neuron whose cell body is located in the spinal ganglion. The other branch of its axon enters the spinal cord and makes contact with a motor neuron. The motor neuron axon exits the spinal cord via the ventral root and innervates a muscle fiber in a muscle (bottom right).

Figure 3. Alfred Fessard (1900-1982).
Photo credit and thanks to Jean Fessard.