

THE IMPORTANCE OF I. M. SECHENOV'S ELECTROPHYSIOLOGICAL RESEARCH

(On the 150th anniversary of his birth)

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Abstract. In his electrophysiological studies I. M. Sechenov described for the first time the spontaneous electrical activity of the isolated brain, the physical electrotonus in the CNS, the amplifying action of anodic polarization on spontaneous and induced electrical activity, phenomena of inhibition of spontaneous and induced electrical oscillations of the brain upon tetanization of sensory nerves and negative shifts in the potential of the brain. Thus Sechenov discovered some basic electrical manifestations of the activity of the CNS and initiated fundamental electrophysiological studies of the brain.

In 1856 Sechenov attended in Berlin a course of Du Bois-Reymond's lectures on electrophysiology of muscles and nerves and mastered the methods of working with the galvanometer (multiplier). He brought all the necessary apparatus from Germany to Petersburg and began to deliver at the Medical Academy lectures with demonstrations on electrophysiology; in 1862 he published these lectures under the title *On animal electricity* (20). He also published a study on nerve excitability in connection with transverse sections made on the nerve; a good deal of attention was devoted in this study to methods of electrical stimulation. It is interesting to note that the homogeneity and absence of polarization of the stimulating electrodes were controlled by means of a multiplier (19). But only many years later did Sechenov carry out his first and only study in the field of "animal electricity", one of the most brilliant, as I take it, in the history of electrophysiology.

In 1879 Sechenov began at the Petersburg University experiments

in electrophysiology of the central nervous system (CNS) to which he devoted 2.5 years. The circumstances under which he did that are not quite clear (39); the results of his studies are not always correctly interpreted; some of his important propositions have failed to attract attention and have not received their due appraisal.

The reason that prompted Sechenov to start his electrophysiological studies can, I think, be traced several years back, to the time when he had been forced to defend again his concept of central inhibition by proving to his opponents — first to Cyon (24) and then to Brücke (25) — the correctness of his arguments based on a logical comparison of results of his experiments carried out in the 1860s (21, 23). Sechenov could not fail to see that those arguments lacked direct proof.

In his galvanic studies (26, 27) Sechenov made a preparation of isolated CNS in connection with which there remained dissected sciatic nerves and a bone residue with small muscles; the preparation was placed in a moist chamber. It was actually the first electrophysiological study of the CNS *in vitro*. That excluded the nervous influences from the periphery and the humoral factors, to say nothing of the movements and pulsation of the brain. In this case the possibility to excite the CNS by electrical stimulation of the nerves was retained, while the muscles could serve to indicate the spread of excitation from the brain to the spinal cord and then to the periphery. Wedensky subsequently wrote (38) that the procedure required enormous caution and skill.

The bioelectrical potentials were led off through nonpolarizable electrodes to a new model of multiplier (Wiedemann's) to which Sechenov imparted maximal sensitivity. He was well aware of the shortcomings of the apparatus, i.e. its inability to react to rapidly occurring changes in the current and noted with regret that he had no capillary electrometer. In typical experiments one of the recording electrodes was placed on the cross section of the medulla oblongata (M. obl.) transected along its superior border, the second electrode being placed on its ventral surface.

Samoilov, who worked with Sechenov for 10 years, wrote that "Sechenov was a specialist who had mastered every trifle, every detail of the corresponding experimental techniques, and a virtuoso and past master in his experimental endeavours" (18). I think that this appraisal applies mainly to his study entitled *Galvanic phenomena on the medulla oblongata of the frog*. A few unessential additions and the use of a cathode-ray oscillograph with a DC amplifier would have made this Sechenov's study a masterpiece even today.

Spontaneous discharges. Some time after application of the recording electrodes to the M. obl. jerky negative oscillations began to arise

“without any determinable external cause, as though by themselves; I shall therefore call them arbitrary oscillations, as well as arbitrary discharges”, writes Sechenov (28). In the German text (27) he uses the term “spontanne Entladungen” (“spontaneous discharges”); this term was used in 1884 by Wedensky (37) and later by Sechenov himself in his papers in Russian (30, 32). Thus Sechenov for the first time discovered on a preparation of isolated CNS that the brain is able to generate electrical oscillations without any visible cause and for the first time used the term “spontaneous” pertaining to the electrical activity of the brain. More than 50 years later, already in the oscillographic era, Gerard and Young recorded from the frog brain in vitro “spontaneous” electrical activity, designating by this term the activity that takes place without any nerve impulses entering the CNS. In his study of 1882 (27) Sechenov very cautiously speaks of stimulation of the cross section as the possible cause of the spontaneous discharges and points out that neither the nature of the stimuli acting on the cross section nor any methods of eliminating them are known. He is more categorical, however, in the *Physiology of nerve centers*, where he holds that the existence of direct tonic excitation from the surface of the cut cannot be doubted (29). He conducted clever control experiments which showed that shaking and drying the preparation, as well as contact with the electrodes and passing compensation current are not the cause of the spontaneous discharges for they do not arise in the spinal cord isolated from the brain; on the other hand, they are observed upon recording the currents from the spinal cord which is connected with the M. obl. Thus it was shown that spontaneous oscillations of current are not inherent in the isolated spinal cord and are a prerogative of the brain. The experiments he conducted with sections of the M. obl. enabled him to ascribe these oscillations to the activity of the superior part of the M. obl. It should be noted that in recording from the spinal cord isolated from the brain Sechenov observed a negative oscillation of current upon stimulation of the sciatic nerve, i.e., saw a bioelectrical reaction of the spinal cord to peripheral stimulation (26).

The nature of the spontaneous activity of the bulbar centers is still an unsettled question. Thus, as regards the respiratory center, it is still incomprehensible how continuous chemical stimulation (CO_2) leads to rhythmical depolarization of the neuron membranes to the critical level (10). It is assumed that a capacity for “spontaneous” excitation may be inherent in certain neurons in virtue of a special structure of their membrane (8).

Sechenov arrived at the conclusion that the “excitations underlying the strong spontaneous oscillations should be regarded as periodic series

of pulses" (27). He arrived at this conclusion because on very excitable preparations a strong spontaneous discharge in the M. obl. was attended with a tetanic contraction of the pelvic muscles. He could have obtained direct data, as he writes, by means of a capillary electrometer (see above). The correctness of this conclusion was demonstrated in the experiments conducted by Wedensky (37) who precisely reproduced Sechenov's experiments, but recorded the currents from the M. obl. on the telephone and not on the galvanometer. He established that Sechenov's spontaneous discharges corresponded to periodically arising noises; such noises could also be heard in the beginning of stimulation of the sciatic nerves. Hence, on the basis of the telephone studies of nerves and muscles he had conducted it could be concluded that spontaneous discharges in the M. obl. gave rise to nerve impulses with a relatively low rhythm (34). Of interest to interpretation of the spontaneous discharges are the data obtained by Wedensky in experiments on nerves with simultaneous recording of the action currents on the telephone and the galvanometer (36); in the former case he heard sounds of various character, depending on the conditions of the experiment, while in the latter case he observed slow negative oscillations of the magnet of the same order of magnitude as in many of Sechenov's experiments.

Thus Sechenov's studies for the first time obtained facts evidencing that upon spontaneous excitation the nerve centres discharge a series of nerve impulses. But, as we know now, these discharges of impulses could take place against the background of slow oscillations of the electrical potential, which could not be distinguished by means of a multiplier or telephone. From Sechenov's studies, where all facts are described with extraordinary accuracy, it may be concluded that the spontaneous discharges, when they were not strong, were not accompanied by contractions of the pelvic muscles; it is quite possible that at that time slow oscillations of the potential took place without impulse activity.

Setting forth in his dissertation the results of Sechenov's preliminary communication (26), Beck (2) writes that the spontaneous electrical oscillations express the spontaneous excitations of the centers located in the superior part of the M. obl., probably the respiratory centres. But this is an obvious misunderstanding: having pointed out that periodical acting respiratory and locomotor centers are localized in this part of the M. obl., Sechenov emphasizes, after appropriate argumentation, that the spontaneous discharges reflect excitation of the centre of forced movements, i.e., the locomotor center. In our literature the opinion is still current that Sechenov discovered in the M. obl. a spontaneous electrical oscillations in the respiratory rhythm and that he was

the first to show the automatic activity of the respiratory center and to localize it in the M. obl. (1, 6); moreover, in doing this reference is made to Sechenov's study of 1882. But neither in the preceding study, which was just mentioned, nor in this one, nor yet in any of the subsequent studies did Sechenov even raise the question of a possible connection of the spontaneous discharges with the respiratory center. It is characteristic that to Wedensky, who had but recently worked with the respiratory center of the frog (35) it also never occurred to interpret the sounds he had heard from the M. obl. as an expression of activity of the respiratory center; together with Sechenov he regarded them as a manifestation of "forced movements" (37); nor did Beritashvili ever doubt that Sechenov's spontaneous discharges were connected with motor impulses (3).

Of course, this does not mean that the activity of the respiratory center of the frog is not manifested electrically; but in two communication on recording the respiratory rhythms from the M. obl. in isolated frog CNS (11, 14) the recording electrode was placed on the dorsal surface, i.e., the conditions of recording were the most unfavourable for the manifestation of Sechenov's spontaneous discharges (see below).

Sechenov established that between the condition of emergence of spontaneous discharges of the M. obl. and those of emergence of forced movements from the M. obl. there was a complete parallel.

The spontaneous discharges were expressed best upon attachment of the recording electrode to the ventral surface of the M. obl. (second electrode on the cross section); they were poorly expressed when recorded from the dorsal surface of the M. obl., and were clearly recorded when both recording electrodes were placed on the lateral surface of the M. obl. or on the lateral surfaces of the spinal cord connected with it.

As early as 1865 Sechenov established by the method of transactions that the motor pathways of spontaneous movements in the frog run in the ventral part of the spinal cord, beginning in the superior part of the M. obl. (22). This corresponds to the modern morphologic data, according to which the superior part of the M. obl. in the reticular formation of the frog contain large neurons that give rise to fibres of the bulbospinal tract, the main descending tract of amphibians; this tract runs in the ventral and lateral fasciculi of the M. obl. and the spinal cord (40). This morphologic information completely corresponds to the above electrophysiological data on the recording conditions of spontaneous discharges. Thus the spontaneous discharges of the M. obl. reflect excitation of the locomotor centre which is periodically excited (after separation of the M. obl. from the superior parts of the brain)

and generates motor impulses that spread along the ventral and lateral parts of the M. obl. and the spinal cord.

Electrical responses of the M. obl. to stimuli. In these experiments Sechenov ordinarily used preparations with infrequent spontaneous discharges. In response to a single stimulation of nerves or the spinal cord, negative oscillations were recorded from the M. obl. Weak stimuli evoked weak responses and, if a stimulus preceded a spontaneous discharge, the weak negative deflection passed directly into the discharge. An increase of the induction shock had little effect on the character of the response, but turning on a strong DC could cause a considerable negative deflection that even exceeded the spontaneous oscillation. Sechenov interpreted these phenomena as an expression of reflex excitation of the locomotor center of the M. obl., which, as he was well aware, could become excited in response to a single stimulation of a nerve that led to coordinated movement, after which its excitability declined until it was recharged with energy. From this point of view it is significant that especially strong oscillations were followed by long pauses in the spontaneous discharges. Thus Sechenov for the first time studied the electrical responses of the brain to single stimulations of a nerve, i.e., he was the first to conduct experiments in the way that in our time is most commonly done in oscillographic studies of the CNS.

Electrotonus. In these experiments the nonpolarizable electrodes for passing current were placed on the ventral fasciculi of the spinal cord, and the recording electrodes — as usual, on M. obl. Turning on the current of the descending direction (anode closer to the M. obl.) caused a shift of the magnet in the direction of the resting current; turning on the ascending current (cathode closer to the M. obl.) shifted the resting current in the opposite direction. These experiments were complicated by excitation of the M. obl., the evoked negative deflections were superposed, but nevertheless it was possible to see the aforesaid phenomenon clearly. Thus was discovered a lateral spread of the current from the spinal cord to the M. obl., the phenomenon of physical electrotonus in the brain.

I think that, in these experiments, the current spread electrotonically, mainly along the axons of the bulbo-spinal tract, in a, so to speak, antidromic direction; from this point of view it will be possible to explain one important fact discovered by Sechenov in experiments which were conducted by him to find out whether electrotonic changes in the excitability of the M. obl. occur. When the cathode was closer to the M. obl., the effect of turning the current on was vague; when the anode was closer to the M. obl., the spontaneous discharges were amplified during the passage of the current, the effect was observed

as long as the current was turned on, and this usually lasted for minutes. The negative deflection arising in response to the turning on the current of the descending direction, was of greater amplitude than that arising in response to turning on the current of the ascending direction.

Thus Sechenov for the first times studied the action of DC on the spontaneous electrical activity of the brain and established that the anode can amplify the electrical manifestations of activity of the CNS. Similar studies are now being conducted in many laboratories, but the mechanism of DC action on the CNS is not quite clear as yet (17).

Evidently the amplification of negative deflections recorded from the M. obl. upon polarization of the spinal cord was based on hyperpolarization of axons of the bulbo-spinal tract and an increase in the amplitude of electrical potentials spreading along them in connection with spontaneous or reflex excitation of the corresponding center of the M. obl.

Inhibition of spontaneous discharges. A tetanization of the sciatic nerves resulted depending on the strength of stimuli, in a decrease in the frequency or a complete cessation of the spontaneous discharges of the M. obl.; the depression of spontaneous discharges lasted as long as the tetanization. The same thing occurred upon chemical stimulation of these nerves. Thus Sechenov for the first time showed the phenomena of depression of the spontaneous electrical activity of the brain as an effect of peripheral stimulation.

During the period of depression of the spontaneous discharges a single electrical stimulation of the spinal cord, i.e., its direct stimulation, ceased to evoke negative deflection in M. obl. The possibility of suppressing the evoked potentials of the brain by peripheral stimulation was thus demonstrated. Sechenov attached a considerable importance to this fact; he considered this a direct proof that during a strong tetanization of the sensory nerves the entire cerebrospinal axis is in a state of diminished excitability, i.e., in an inhibited state.

On the other hand, he recognized that the depression of spontaneous discharges was a result of inhibition due to the fact that upon the cessation of tetanization these discharges became stronger and more frequent, in accordance with the beginning of intensified movements in the frog, which followed the withdrawal of electrical or chemical stimulation of the nerves, during which the movements were suppressed. Thus Sechenov not only discovered the phenomenon of "rebound" after inhibition, but also, for the first time, observed one of its electrical manifestations in the CNS.

Sechenov interpreted the depression of spontaneous discharges in M. obl. as an expression of inhibition of the locomotor centers. According

to his hypothesis, during the "rebound" the nerve centers discharge the energy accumulated during their inhibition. The nature of "rebound" is still far from being elucidated; there are only suppositions about its possible cellular mechanisms (10).

Sustained negative shift. Sechenov encountered one more type of electrical phenomena in the CNS. Stimulation of the sciatic nerves gave rise to considerable negative deflection which later diminished, but persisted on this level more or less stably; upon the cessation of stimulation the current decayed. With intensification of tetanization the negative shift increased to a certain limit, but not linearly; up on repeated stimulation the negative deflections weakened, and in response to the 4th or 5th stimulation it could altogether fail to arise. Against the background of a negative shift the spontaneous discharges were inhibited. Chemical stimulation of the nerve was also attended with a gradual shift of the magnet to the negative side and the spontaneous discharges were depressed. As was already stated, a direct stimulation of the spinal cord at that time ceased to evoke a response in the M. obl.

In his studies Sechenov undoubtedly encountered long-lasting (DC) electrical potentials of the brain with which the inhibition of spontaneous and evoked electrical potentials was associated. The records of the changes in potentials of the M. obl. of the frog on tetanization of the sciatic nerve obtained by the use of an oscillograph (14) correspond quite well to Sechenov's descriptions.

The negative potential shifts have of late become a subject of intensive studies; these electrical reactions in the spinal cord (13) and the cerebral cortex (15) have been described in particular detail; their characteristics coincide with those of the negative shifts in the M. obl. described above. The use of microelectrode techniques for intracellular recording of electrical potentials and potassium-selective microelectrodes for measuring the concentration of these ions has made it possible to approach an understanding of this phenomenon which is associated with an increase in the concentration of potassium ions in intercellular spaces and with a depolarization of the glial cells. A depolarization of the central arborizations of afferent fibers has undoubtedly played an important role in the generation of Sechenov's inhibition (9). The interpretation of all these facts is still largely unknown for the cerebral cortex (16) as well as for the spinal cord (12). We can see that Sechenov not only observed for the first time the electrical manifestations of inhibition, but also encountered an electrical phenomenon connected with the nature of the process of central inhibition which he had discovered.

Sechenov saw the importance of his studies on the galvanic phenomena primarily in the fact that they confirmed his concept of central inhibition. He repeatedly compared the results of his three main studies in inhibition — 1863 (21), 1868 (23) and 1882 (27). He always held that the process of inhibition was a process *sui generis*.

In 1879–1882 Sechenov made numerous discoveries in electrophysiology — he discovered a treasure of new phenomena of which nobody was aware before him; moreover he encountered, as we now see, a number of basic manifestations of cerebral activity; a hundred years have elapsed, and the nature of not a single phenomenon described by him is as yet completely clear and these phenomena continue to be the object of increasingly complicated studies. On the other hand, Sechenov's study entitled "Galvanic phenomena ..." is the first fundamental study on the CNS in the history of physiology, in which the electrophysiological method is used for the analysis of the activity of the CNS; it is the first electrophysiological study of the nature of the basic nervous processes, particularly the process of central inhibition.

Wedensky (37), Verigo (33) and Beck (2) referred to Sechenov's articles in *Pflüger's Archive* (26, 27) as the first study on the electrical manifestations of cerebral activity. In 1891, after a sensational dispute on priority (4), in which, it seems, everyone but Sechenov deemed it proper to take part, it turned out that in 1875 and in 1877 Caton published in the *British Medical Journal* a report that he had observed a fluctuation of current recorded from the cerebral cortex of mammals and an emergence of a negative variation of this current in certain cortical areas in response to light and other stimuli (4); it also turned out that in 1876 Danilevsky observed essentially similar phenomena as mentioned in his dissertation (5). These studies were unknown to physiologists until the aforesaid date, i.e., 1891. Caton and Danilevsky had made use of a galvanometer for the purpose of localizing the functions in the cerebral cortex. Sechenov considered the elucidation of the nervous processes to be the main aim of using the galvanometric method.

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