THE ORIGIN OF THE "SPONTANEOUS" ELECTRICAL ACTIVITY OF THE FROG BRAIN

L. N. Smolin

Laboratory of Experimental Pathology of the Nervous System
(Head–Professor S. I. Frankshtein) Institute of Normal
and Pathological Physiology (Director, Active Member AMN
SSSR V. V. Parin) AMN SSSR, Moscow
(Presented by Active Member AMN SSSR V. V. Parin)

Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 52, No. 12,
pp. 17-22, December, 1961
Original article submitted December 30, 1960

There are two opposite views concerning the origin of "spontaneous" neuronal activity in the brain. According to one which the work of Berger [13] has made especially popular, there are neurones in the brain which are capable by themselves of producing a true spontaneous activity, i. e. an activity which is not associated with external stimulation.

The opposite view was formulated in the last century by I. M. Sechenov. According to him, the rhythmical potential oscillations which he found in the medulla oblongata were, strictly speaking, not spontaneous, but were elicited by stimuli involved in making the preparation [9]. He thought that in general "the nervous system cannot operate otherwise than through external forces" and that, in particular "centers work only under action from without" [10].

The problem of the origin of the "spontaneous" electrical activity of the brain has been studied in experiments with neurologically isolated brains, or isolated parts thereof. However, these experiments gave ambiguous results. Burns [15], and later Lissák and his co-workers [29] found that electrical activity disappeared completely from an isolated strip of cerebral cortex. They concluded that the "spontaneous" electrical activity of the cortex is due to afferent impulses. The opposite result was found by Gerard and Young [23], who were the first to record continuous electrical activity in a strip of olfactory cortex from the frog brain. From experiments of this kind, Libet and Gerard [28] conclude that "such facts represent a fundamental proof that these rhythms are truly spontaneous in the sense that no nervous impulses are required to elicit them". I. S. Beritov and L. Tskipuridze also observed continuous electrical activity in a small piece of olfactory cortex and came to a similar conclusion that "spontaneous electrical activity of the different portions of the brain is due to rhythmical self-excitation of the intra-cerebral internuncial brain cells" [3]. Many other authors have observed continuous electrical activity in nervous tissue which has been completely separated from the remainder of the nervous system [12, 18, 19, 20, 24, 25, 27].

Burns [16] explains these contradictory results by supposing that the surgical interference involved in complete neurological isolation of a particular portion of the brain inevitably causes damage: "Some accidental trauma may be the cause of an increased or a reduced excitability of isolated cells."

We encountered the problem of the origin of the so-called spontaneous electrical activity of the brain when studying the frog EEGs. Until now, all studies of the frog EEG had been made in acute experiments–either on the brain after removal from the skull [3, 6, 7, 9, 23, 28], or on one which had been separated from the spinal cord [1, 2, 4, 14, 26, 30 and 33], or in frogs which had been rendered immobile either by destruction of the spinal cord [1, 8, 21, 33] or by anesthetizing or curarizing and leading off potentials from the exposed brain [2, 4, 8, 11, 17, 22, 23, 32, 34 and 35]. Under these conditions, continuous electrical activity was recorded from different parts of the brain. As a departure from the researches described above, in our present experiments we have recorded the electrical activity of the brain by electrodes implanted into intact unanesthetized frogs which had not been immobilized. Normally they sat in a small jar containing water with the feet and ventral surface of the body covered by it. The jar was placed in a screened and darkened room. Thus, in our experiments, external stimulation was reduced to a minimum. Under these conditions we were able to record periods during which there was no electrical activity in the brain.

METHOD

The experiments were carried out on 30 spring-summer and autumn-winter frogs (Rana ridibunda). The potentials were led off from bipolar electrodes separated by 1-2 mm; the electrodes were needles implanted through the thin layer of the bone in the skull covering the mid-brain, fore-brain, and rhinencephalon. The potentials were amplified in a 4-channel amplifier having a frequency characteristic which was flat from 0.2 to 1,500 cycles. Recordings were made with an ink-writer having a frequency response flat from 0.2 to 70 cycles, and on a string oscillograph type MPO-2, covering frequencies from 0 to 1,500 cycles.

RESULTS

In all parts of the frog brain which we studied, we observed periods which lasted sometimes as long as two minutes, when the ink-writer drew what was almost a straight line (Fig. 1, A). It might be expected that such a straight line would result from a high degree of desynchronization of the electrical activity of the brain, and that the ink-writer does not reproduce these high-frequency, low-voltage oscillations. We therefore recorded potentials by means of a string oscillograph which was capable of responding to potential changes up to 1,500 cycles, and had a sensitivity of 5-6 μv. However, during these periods, also the oscillograph recorded a straight line (Fig. 1, B). These facts indicate that in an unanesthetized frog, sitting quietly and isolated from external stimuli, there really are periods during which there is no cerebral electrical activity.

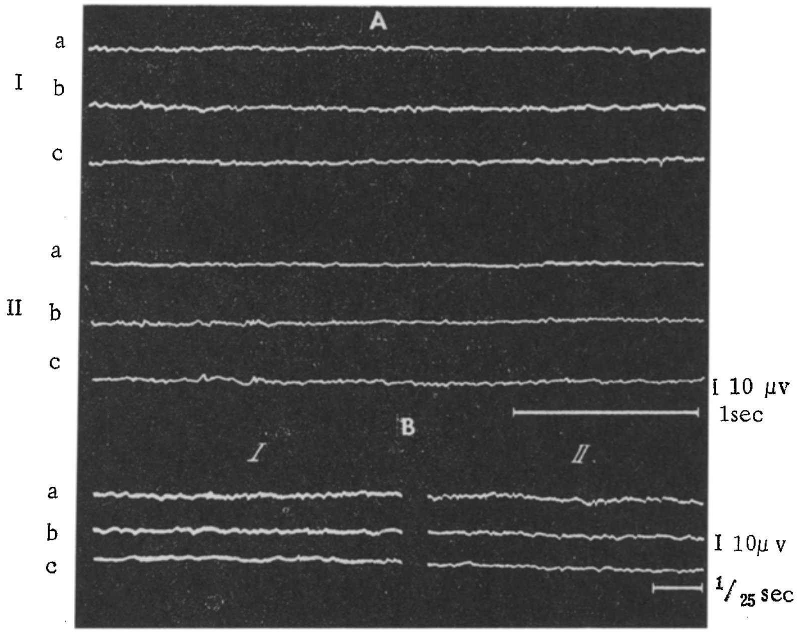

Fig. 1. A period during which there was no electrical activity in the brain of an intact unconstrained frog, seated naturally. A) Ink-writer recording; B) string oscillograph recording; indications, in both cases: I) bipolar lead: a) from the rhinencephalon; b) from the fore-brain; c) from the right side of the mid-brain; II) preparation removed, record of the amplifier noise.

At this time, various stimuli—flickering light, tactile stimulation, section of the skin and muscles, section of the spinal cord and brain—were found to induce electrical activity. In the EEG of all the leads, instead of a straight line, there appeared slow rounded respiratory waves having a frequency of 0.75 - 2.25 per second, and very rapid, well-marked synchronized oscillations (Fig. 2). During the first second, the ink-writer showed a burst of high-frequency pointed waves having a frequency of 30 - 40 cycles and an amplitude of 8-12 μv, which were superimposed on a wave of amplitude 20-30μv and frequency of 15-20 cycles. After 3-4 seconds, these waves disappeared, and were replaced by very well-marked synchronized waves having a frequency of 8-16 cycles and an amplitude of 8-20 μv. In the first few seconds after these waves had appeared, the rhythm was usually more rapid (13-16 cycles) with an amplitude 10-20μv. Then gradually the rate was slowed to 8-11 cycles, and the amplitude reduced to 8-15μv (Fig. 2, A). This activity could be observed for several minutes. If the frog was left quietly, the waves gradually became less distinct and were reduced in amplitude, and the clear regular 8-11 cycle rhythm was replaced by irregular waves at a frequency of 4-6 cycles. After 3-20 minutes, these waves also disappeared, and once more, either a straight line, or one showing only respiratory waves, was recorded (Fig. 2, B).

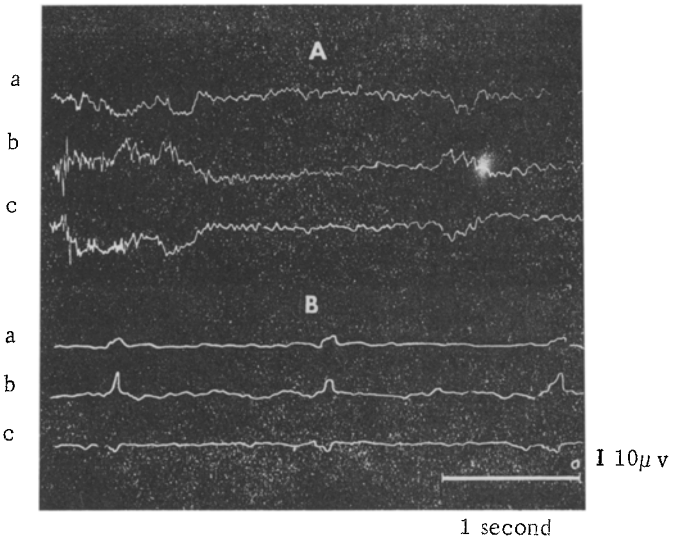

Fig. 2. Effect on the EEG of tactile stimulation applied to the intact frog, seated freely. A) First 4 seconds after tactile stimulation; B) 4 minutes after stimulation. Bipolar leads: a) from the rhinencephalon; b) from the fore-brain; c) from the left side of the mid-brain.

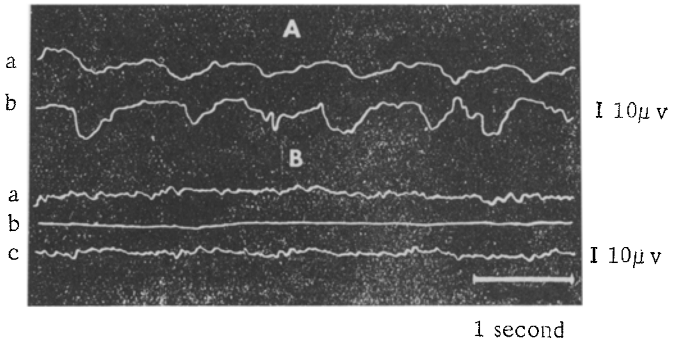

Fig. 3. A) Respiratory waves in the right optic lobe: a) intact frog, seated freely; b) same region, 15 minutes after isolation of brain; B) electrical activity of the right optic lobe of the isolated frog brain: a) before immersion in ether; b) 15 seconds after immersion in ether; c) 2 minutes after removal of the ether.

An analysis of the recorded cerebral electrical activity showed the following features. The respiratory waves are not artifacts caused by respiratory movements. In many experiments, after recording the EEG of the intact frog, we removed the head together with the implanted electrodes, as well as the eyes and the muscles from the bones of the skull, and then again recorded the EEG. In some of the preparations of the isolated brain made in this way, we were able to record slow waves in mid-brain, fore-brain, and in the rhinencephalon. In their frequency, shape, and amplitude they showed a strong resemblance to the respiratory waves observed in the EEG of the intact frog (Fig. 3, A). It may therefore be supposed that the respiratory waves recorded in the different parts of the brain result from irradiation into these regions of the activity of the respiratory center.

We never observed the bursts of impulses at 30-40 cycles in either the isolated brain, or in frogs which had been immobilized by injection into a lymph sac of 0.1-0.25 ml of 0.5% solution of the curare-like preparation diplacin. Therefore these bursts of spiked waves which arise in the first few seconds after stimulation are an artifact associated with muscular movements.

The synchronized waves at 4-16 cycles remained well-shown in the isolated brain after complete removal of the muscles from the skull. Moistening the isolated brain with ether, or inhalation of ether by the intact frog caused a great reduction in both the frequency and the amplitude of these waves, until they finally disappeared. After the ether had evaporated, the activity was resumed (Fig. 3, B). Nowadays it is generally accepted that anesthesia is brought about by blockage of interneuronal synaptic conduction [5]. We must suppose therefore, that the slow synchronized waves which we observed were due to the action of ether in blocking the synaptic transmission between cerebral neurones. Therefore, these waves having a frequency of 4-16 cycles really do represent cerebral electrical activity.

Our results therefore confirm the hypothesis of I. M. Sechenov that the electrical activity of the brain is produced either in a reflex manner, or by indirect influences acting upon it. Without such influences, there is no cerebral electrical activity in the frog.

SUMMARY

Preparations with chronically implanted electrodes showed that there are periods during which no electrical activity is present in the brain of intact, non-anesthetized frogs sitting unconstrained in water in a jar. The activity appeared immediately upon stimulation.

The results obtained confirm the suggestion of I. M. Sechenov that the electrical activity of the brain occurs either reflexly, or is due to direct effects on the brain. Without such effects, there is no electrical activity.

LITERATURE CITED

1. V. V. Artem'ev and E. B. Babskii, Fiziol. zhurn. SSSR, 35, No. 6 (1949) p. 623.
2. I. Beritashvili and L. Tskipuridze, Communications of the AS Georgian SSR, 3, No. 1 (1942) p. 81.
3. I. S. Beritov, Transactions of the I. Beritashvili Institute of Physiology [in Russian], No. 5 (Tbilisi, 1943) p. 193.
4. I. Beritov and L. Tskipuridze, Transactions of the I. Beritashvili Institute of Physiology [in Russian], No. 5 (Tbilisi, 1943) p. 215.
5. A. V. Val'dman, In book: Contributions to the Pharmacology of the Reticular Formation and of Synaptic Transmission [in Russian] (Leningrad, 1958) p. 13.
6. N. E. Vvedenskii, Complete Collected Works [in Russian], Vol.1 (Leningrad, 1951) p. 114.
7. B. Verigo, Vestn. klin. i sud. psikhiatr. i nevropatol., Vol. 7, No. 1 (1889) p. 82.
8. T. M. Zagorul'ko, An Electrophysiological Analysis of the Activity of the Visual Analyzer of the Frog [in Russian], Candidate's dissertation (Leningrad, 1954).
9. I. M. Sechenov, Vrach, Vol. 3, No. 42-45 (1882) p. 703.
10. I. M. Sechenov, The Physiology of the Nervous Centers [in Russian], (Moscow, 1952) pp. 23, 47.
11. N. N. Timofeev, In book: The Evolution of Physiological Functions [in Russian] (Moscow, Leningrad, 1960) p. 103.
12. A. I. Shapovalov, Abstracts of Reports of the 3rd Conference on Problems of the Electrophysiology of the Nervous System [in Russian] (Kiev, 1960) p. 402.
13. H. Berger, Arch. Psychiat. Nervenkr., Bd. 87, S. 527 (1929).
14. C. G. Bernhard, Acta physiol. scand., Vol. 1, Supp. 1 (1940).
15. B. D. Burns, J. Physiol., Vol. 110, 9 P (1949).
16. B. D. Burns, The Mammalian Cerebral Cortex (London, 1958).
17. H. Caspers and K. Winkel, Pflüg. Arch. ges. Physiol., Bd. 255, S. 391 (1952).
18. H. H. Dubner and R. W. Gerard, J. Neurophysiol., Vol. 2 (1939) p. 142.
19. F. A. Echlin, V. Arnett and J. Zoll, Electroenceph. clin. Neurophysiol. Vol. 4 (1952) p. 147.
20. F. A. Echlin, Electroenceph. clin. Neurophysiol., Vol. 11 (1959) p. 697.
21. S. Feitelberg and E. P. Pick, Proc. Soc. Exp. Biol. Vol. 49 (N. Y., 1942) p. 654.
22. W. Geets, Arch. int. Physiol., Vol. 55 (1948) p. 310.
23. R. W. Gerard and J.Z. Young, Proc. Roy. Soc., Vol. 122 (1937) p. 343.
24. C. E. Henry and W. B. Scoville, Electroenceph. clin. Neurophysiol., Vol. 4 (1952) p. 1.
25. D. H. Ingvar, Acta physiol. scand., Vol. 33 (1955) p. 151.
26. H. Klensch and E. Kuhnke, Pflüg. Arch. ges. Physiol., Bd. 256, S. 265 (1953).
27. K. Kristiansen and G. Courtois, Electroenceph. clin. Neurophysiol., Vol. 1 (1949) p. 265.
28. B. Libet and R. W. Gerard, J. Neurophysiol., Vol. 2 (1939) p. 153.
29. K. Lissák, E. Endröczi and T. Hasznos, Acta physiol. Acad. Sci. hung., Vol. 3 (1952) p. 39.
30. H. W. Müller, Z. Biol., Bd. 104, S. 244 (1951).
31. H. W. Müller-Limmroth and H. Massmann, Pflüg. Arch. ges. Physiol., Bd. 255, S. 379 (1952).
32. D. Ottoson, Acta physiol. scand., Vol. 47 (1959) p. 149.
33. E. P. Pick and M. M. Miller, J. Neurophysiol., Vol. 8 (1945) p. 47.
34. B. Rensch, Z. vergleich. Physiol., Bd. 37, S. 496 (1955).
35. A. Rivkine, Arch. intern. Physiol., Vol. 57 (1950) p. 245.

All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
