THE RELATION BETWEEN IMPULSE AND TONIC COMPONENTS IN THE ELECTROENCEPHALOGRAM

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The electroencephalographic method is widely used in both neurophysiological and clinical investigations. But in electroencephalographic theory there is so far no unanimous opinion as to the nature of the bioelectric processes that are recorded with the electroencephalograph (i.e., those variations in electrical potential of the brain whose frequency spectrum lies between 0.3 and 100 cps).

The idea, first put forth by E. Adrian and B. Matthews in 1934 [6], and supported by subsequent investigations of E. Adrian and G. Moruzzi in 1939 [7], that the electroencephalogram is the summed effect of the activity of a large number of nerve cells, continues to hold sway at the present time. On the basis of this hypothesis, electroencephalographic phenomena began to be interpreted as manifestations of synchronous or asynchronous activity of neurons. It was on the basis of this idea that such concepts as "synchronization," "hypersynchronization," and "desynchronization" came into the practice of electroencephalography. Whereas synchronization and hypersynchronization reflect (in the opinion of the proponents of this view) different degrees of synchronousness in the activity of a large number of nerve cells, desynchronization is supposed to reflect asynchronous electrical activity of nerve elements.

The spontaneous rhythmic activity that can be recorded from a nerve cell with a microelectrode would seem to be confirmation of this hypothesis. But it is necessary to explain how the extremely delicate coordination of the activity of a large number of neurons is accomplished in order to create, as a result of algebraic summation of single cell discharges (the duration of a cell discharge is equal to 1 msec), the quite prolonged electroencephalographic wave (for example, the alpha wave, which lasts about 100 msec).

In order to explain the mechanisms of synchronization of neuron activity, a number of theories have been proposed which make it possible to understand this process to one degree or another: the chemical theory of H. Hoagland [14], the neuron theory of J. Eccles [11], the electrical theory of R. Gerard and B. Libet [13], and A. Fessard's theory [12] of the presence of a special pacemaker.

Alongside this viewpoint, there exists another view of the nature of electroencephalographic variations, whose adherents believe that these variations are an independent process, and not the summed effect of the impulse activity of nerve cells. Thus, V. S. Rusinov suggests that the principal forms of bioelectric phenomena in the cortex—delta, theta, alpha, beta, and gamma waves — represent an independent process and reflect local excitation of neurons or groups of neurons [3].

In support of the idea that electroencephalographic variations are not the summed effect of the impulse activity of nerve cells, a number of investigations carried out with the utilization of microelectrode techniques could be cited. The authors who made these investigations were unable to find a clear-cut relation between changes in the electroencephalogram and changes in the impulse activity of single neurons at the same site in the brain [8, 9, 10, 15].

But an analysis of the activity of a single neuron and of the over-all electroencephalogram recorded from the same point on the cortex still does not give us the right to reject the view that the electroencephalogram is the summed effect of the impulse activity of a large number of neurons, since it is always possible to assume that the very neuron being studied is for some reason not synchronized in activity with the other neurons, and consequently, has no substantial effect on the production of the electroencephalographic wave.

Our task, therefore, was to characterize the impulse activity of as many neurons as possible at the site from which the gross electroencephalogram was being recorded, and to show what sort of correlation there is between the gross electroencephalogram and the im-

pulse activity of neural elements situated at the point of recording of the electroencephalogram.

METHODS AND RESULTS

The microelectrode technique, which permits us to study successfully the electrical activity of a single neuron, becomes inconvenient when it is necessary to determine the electrical activity of many nerve elements (tens or hundreds) in a small volume of tissue. It is difficult to introduce more than 2-3 microelectrodes into a small region of the brain, but more important, a large number of amplifiers, as well as of recording channels, are required; this complicates the investigation and sometimes makes it impossible In looking for an alternative procedure, we began with the following considerations:

1. The nerve cell discharge has the form of an impulse lasting 0.8-2 msec [3, 16]. Consequently, to record cell discharges, it is necessary and sufficient to use an amplifier with a transmission band of roughly 500-3000 cps.

2. A nerve cell discharge can be recorded not only by introducing an electrode into the cell, but also in the case where the recording electrode is some distance away from it. But in this case, the amplitude of the electrical discharge drops markedly as the distance from the cell increases [17]. Thus, if we selectively amplify the impulse component, it will be possible to record it, using conventional electrocorticographic electrodes.

As a result, we used an electrocorticographic electrode with a recording surface of 1-2 mm^2, and a biological-current amplifier with a transmission band of 300 to 10,000 cps; but, since we employed an ordinary standard ac amplifier with a transmission band of from 2 to 10,000 cps for this purpose, the lower end of the band was raised with a capacitative filter. For recording the electroencephalogram, on the other hand, the signal was taken from a different output of the wide-band amplifier

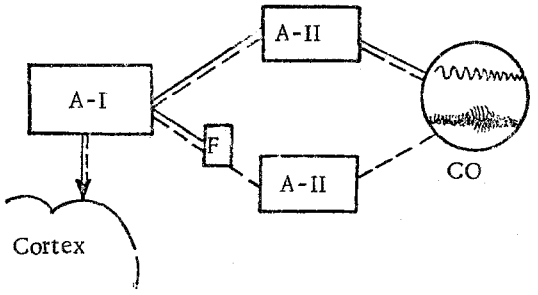

Fig. 1. Over-all diagram of apparatus. A-I – Wide-band amplifier; F – capacitative filter; A-II – amplifiers in cathode-ray oscillograph; CO – recording part of cathode-ray oscillograph (solid line shows path of low-frequency electroencephalographic signal, broken line shows path of high-frequency impulse signal).

(i.e., without restricting the range). Thus, two signals were taken from the wide-band amplifier: one containing frequencies between 2 and 10,000 cps (electroencephalographic) and the other containing frequencies between 300 and 10,000 cps (impulse). These two signals were fed into different inputs of a double-beam cathode-ray oscillograph and recorded on photographic film. Utilization of the cathode-ray oscillograph was necessitated by the high frequency of the impulse process being studied.

It must be noted that there was a considerable difference between the amplitudes of the electroencephalographic and impulse signals: the magnitude of the former was 200-500 μv, while the magnitude of the latter, with this method of recording, was 10-20-50 μv. Therefore, the two signals were finally amplified to different extents by means of the amplifiers in the cathode-ray oscillograph. Figure 1 shows the over-all plan of the method described.

The essence of the method, therefore, is that, out of the whole gamut of frequencies of the incoming signal, we selectively amplified the high-frequency signal, which is smallest in magnitude and represents the total impulse activity of the nerve cells lying near the recording surface of the electrode, and we recorded this high-frequency signal. The low-frequency (electroencephalographic) signal was recorded from the same point with the same electrode; but the low-frequency component has a greater amplitude, so that at this amplification it was clearly displayed, while the impulse component, having a voltage only one-tenth to one-fifteenth as great, was practically indetectible It is true, however, that in individual instances it was possible to observe some superposition of the impulse signal on the low-frequency component.

This method does not permit us to estimate the activity of individual neurons. It does allow us to characterize the impulse activity, and the degree of synchronization of the impulse activity, of a group of neurons in the vicinity of the recording electrode.

The experiments were performed on unanesthetized rabbits with chronically implanted electrodes, and in acute experiments on rabbits under urethan anesthesia. In all, 37 experiments were carried out.

When the hindleg of the rabbit was stimulated, the following changes in electroencephalographic and impulse activity were observed: in the sensorimotor cortex, more or less "synchronized" electroencephalographic activity gave way to "desynchronization." Against the background of desynchronization, 1-2 seconds after it appears, intense impulse activity developed, continuing for from one to five seconds and generally ending before the desynchronized electroencephalogram returned to its initial state (Fig. 2a). It is readily seen from the oscillogram shown here that the appearance of high-frequency activity is reflected in the electroence-

phalogram in the form of small-amplitude, high-frequency variations; if the electroencephalogram is recorded on an ink-writing electroencephalograph, these variations may be scarcely noticeable, or take the form of high-frequency variations (with a mean period of 0.01-0.02 sec) of insignificant amplitude, superimposed on the electroencephalogram.

As an example of another form of electroencephalographic activity, we have investigated the so-called "4-6 per second" regular rhythm. This rhythm, as is well known from the work of P. K. Anokhin [1] and N. I. Shumilina [4, 5], appears in the parietal and temporal lobes of the cortex and in the reticular formation of the brain stem and thalamus of the rabbit upon the application of conditioned defense stimuli. M. M. Bantsekina [2] has shown that this rhythm can arise in response to a single electrical stimulation of the rabbit's paw. We used this method to obtain the regular rhythm. As may be seen in Fig. 2b, in response to stimulation of the paw, the regular-rhythm reaction appeared in the reticular formation of the rabbit. 0.5-2 seconds after the electroencephalogram changes in a specific manner, a marked intensification of the impulse activity of the cells was noted, which continued for 3-12 seconds.

From these observations it follows that in response to stimulation, the electroencephalogram changes first, with a subsequent change (in our observations, an intensification) in the impulse activity of the nerve cells. The intensification of impulse activity comes to an end before the initial level is restored in the electroencephalogram. These observations show that there can be variations in the relations between the slow electrical activity – i.e., the ordinary electroencephalogram – and impulse activity.

It is clear, however, that the high activity of cellular elements in the reticular formation requires the regular slow rhythm of electrotonic variations. In desynchronization and regular rhythm we have two different forms of electroencephalographic activity, but the impulse activity is the same in the two cases. This naturally leads to the following conclusion: impulse activity cannot produce the electroencephalogram, i.e., the bioelectrical activity of the brain in the frequency range 0.3-100 cps, although it should be noted that the highest-frequency component of the electroencephalogram (with an average period of 0.01-0.02 seconds) can, to some extent, result from impulse activity of nerve cells. But the ordinary electroencephalogram, in all probability, is the reflection of electrotonic processes occurring independently, to some extent, in the brain, although they arise under the influence of the same stimuli.

SUMMARY

The author describes a method for recording both the electroencephalogram and the summed impulse activity from the same point on the cerebral cortex. As established by experiments on rabbits, a change in the EEG always precedes clear-cut changes in the summed impulse activity. Intensification of the impulse activity was observed against a background of desynchronization and against a background of "regular rhythm." This leads to the conclusion that the EEG is not the result of

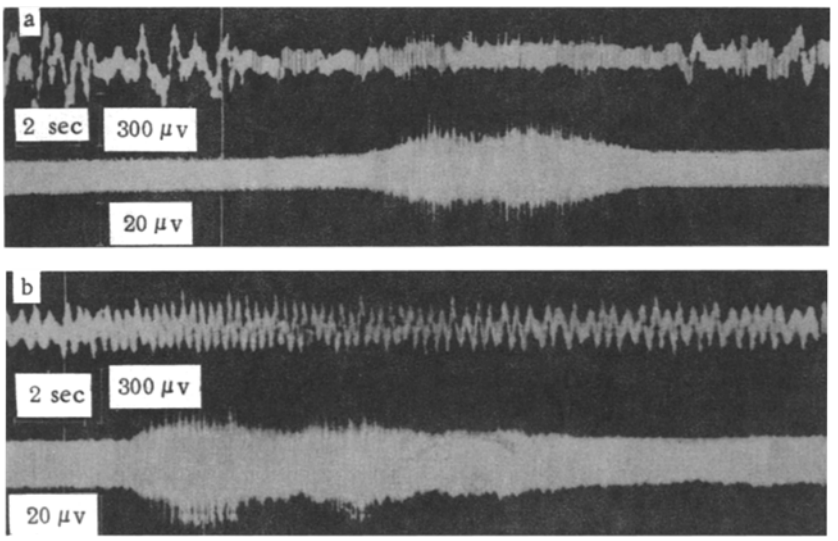

Fig. 2. Oscillogram demonstrating the correlation between the electroencephalogram (upper beam) and the impulse activity (lower beam). a) During the period of desynchronization; b) during period of "regular rhythm." Vertical line on oscillogram shows the moment when stimulus was applied.

algebraic summation of the impulse activity of a large number of nerve cells.

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