THE SPATIAL DISTRIBUTION OF ELECTRICAL ACTIVITY IN THE CEREBRAL CORTEX OF MAN AND ANIMALS

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The study of the bioelectrical activity of the cerebral cortex, which has attracted the attention of many investigators, has mainly followed the lines of study of parameters of frequency, amplitude, and so on in the electroencephalogram of individual points on the cortex. More general processes, encompassing the cerebral cortex as a whole, have received less attention, as has the spatial distribution of cortical activity.

In recent years there have been efforts to build instruments, called "toposcopes," that would give a spatial and topographic representation of the electrical activity of the cortex (Goldman, et al., 1948, 1949; Walter, et al., 1951; Shipton, 1952; Remond and Offner, 1952; Petsche and Marko, 1954, 1955; and Litty and Cherry, 1955).*

But the designs proposed have found only limited application in experimental work, and no practical application in the clinic. It is only through the invention of the electroencephaloscope and the appropriate methods [6] that it has become possible to employ toposcopy widely for the investigation of the bioelectric mosaic of the cortex and subcortical formations in clinical and experimental situations. This method permits us to study not only changes in the cortex as a whole, but also more localized and short-term processes. By drawing together the study of general and local processes in a single investigation, it gives more information about the regular features of the spatial distribution of the brain's electrical activity. This is especially important since the reflex mechanism, "which is the foundation of the central nervous system, comes down to a matter of spatial relationships" (I. P. Pavlov [9]).

The very first investigations involving the use of this new method disclosed a number of hitherto unknown regular patterns. These are concerned primarily with the appearance of foci of elevated activity during the establishment of a conditioned reflex, and with a particular form of synchronous electrical activity known as an "overflow," or spreading wave of activity [2,5,6,7], the study of which is the subject of this paper.

METHODS

Examinations were carried out on persons whose cortical functional states were altered by the application of various influences: maximal deprivation of external stimuli, the development of sleep inhibition and return to the waking state, the influence of external stimuli, the production of a delayed conditioned reflex, performing an association experiment, etc. We also examined rabbits in states of waking and of sleep induced by amobarbital sodium. In this work we used an ÉÉS-50 electroencephaloscope (in an Anan'ev–Livanov system, 1955) and an electroencephalograph. The method of recording human cortical potentials, and the electrodes used, are described in an earlier paper of ours [8]. Here we will mention only that we distributed the electrodes evenly over the entire surface of the head, in five rows with 10 electrodes in each row. The cortical potential at each point was recorded in relation to the mean level of activity of the whole cortex.

RESULTS

Our investigation showed that under certain conditions a distinctive change in electrical activity occurs in the cortical mosaic of healthy individuals and patients. That is, in one region of the cortex a synchronous elevation of electronegativity (from 30 to 200μv) develops for a brief period (1/20-3/20 second), being displayed as an increase in the brightness of points on the electroencephaloscope screen. The next moment this electronegativity moves to a different region (lying either next to the first or some distance away from it) and thus, so to speak, executes motion, creating a spreading wave in a definite direction, leaving behind it a state of electropositivity. This motion may then occur in the opposite direction, or take a new direction (Fig. 1).

To obtain a clearer idea of the character of a spreading wave, we made a photometric analysis of a

* Cited by M. N. Livanov, V. M. Anan'ev, and N. P. Bekhtereva [7].

motion picture record containing a spreading wave, and described the activity of each point in numerical fashion. This numerical diagram shows how and within what range the activity changes during the passage of a spreading wave. From the figure presented herewith (Fig. 2) it can be seen that the electronegativity maximum in the parieto-occipital region moves to the frontal region (second frame). At this time electropositivity develops in the other parts of the cortex, with a maximum of its own and its own changes of position. The distinctive picture on the electroencephaloscope screen gives an idea of the form and the motion of the spreading wave.

The most obvious form of spreading wave that we have recorded was an elevation of electronegativity (positivity) in the frontal divisions corresponding to an electropositivity (negativity) in the occipital divisions. At the next instant this relationship was reversed. The accompanying figure (Fig. 2) shows a motion picture record in which the spreading waves described above are clearly seen. We call these "reciprocal" waves, since the relationship between the activity of the anterior and posterior portions of the brain at any given moment is a reciprocal one.

Along with the electroencephaloscopic study of this type of activity, we were interested in recording a spreading wave in electroencephalographic form. For this purpose we recorded cortical potentials from the same individuals under the same conditions by these two means.

Using bipolar recording with the electrodes located near the midline, about 2.5-3 cm apart (in the fronto-occipital direction), we recorded similar slow waves in all four leads. Examination of the phase of these variations disclosed that a shift occurred which amounted to a phase difference of 180° between the anterior and posterior regions of the brain. A calculation of the magnitude and direction of the phase shift coincided with the duration and direction of the spreading wave (Fig. 3, a).

Somewhat different relationships were observed with monopolar recording of the potentials. The four "active" electrodes were placed as in the preceding case; the "indifferent" electrode was placed on the ear lobe. As shown in Fig. 3, b and c, a difference in the amplitude of similar variations appears clearly in all four leads. A calculation of the magnitudes gave us an idea of the movement of the maximum amplitude over the cerebral cortex within the region where the electrodes were placed. On comparing the results with the electroencephaloscope

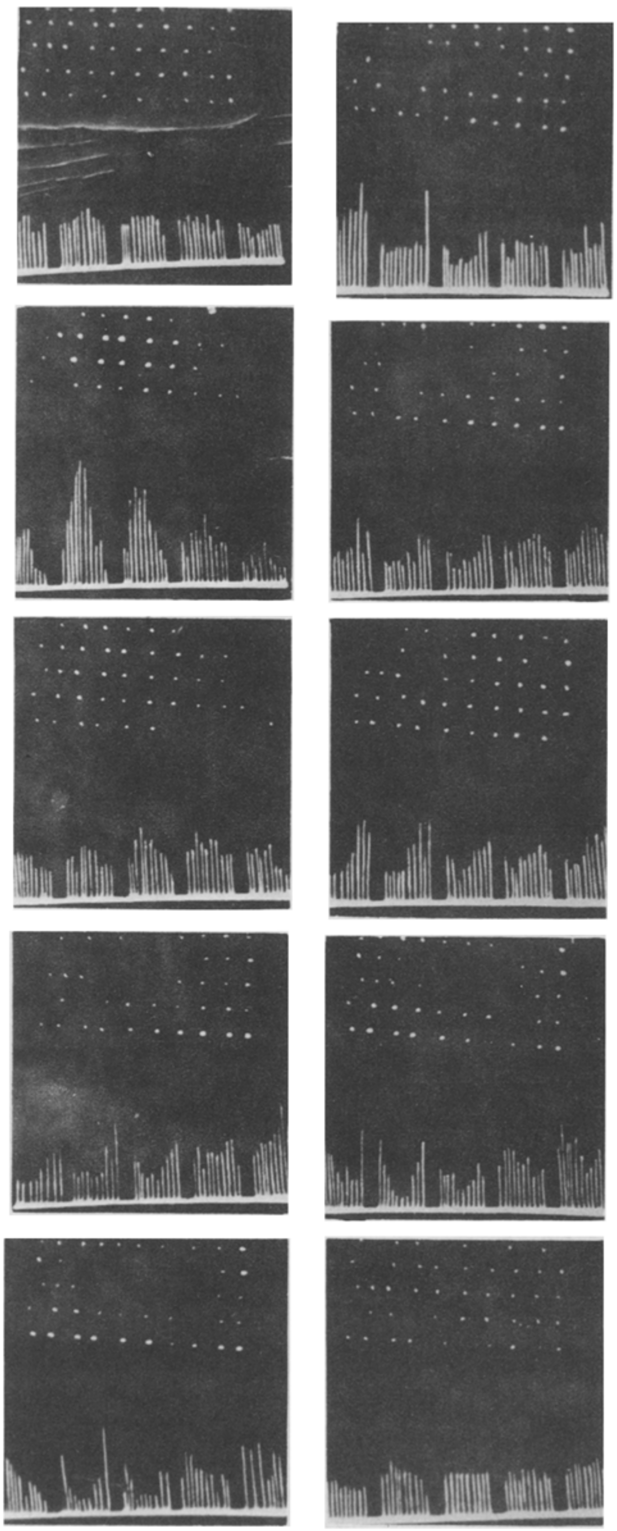

Fig. 1. A slow spreading wave with a complex "circular" motion, encompassing both hemispheres of the cerebral cortex (Successive frames of a motion picture record lasting 0.4 seconds. Each frame was exposed for 20 msec.). Explanation: in the upper part of the frame are 50 points, corresponding to 50 electrodes placed on the subject's head. The first row corresponds to the frontal electrodes, followed by fronto-parietal, parietal, and parieto-occipital; the last and lowest row corresponds to the occipital electrodes. The points on the extreme left and right correspond to temporal electrodes. In the bottom part of each frame the frequency-amplitude spectrum of all 50 points is recorded.

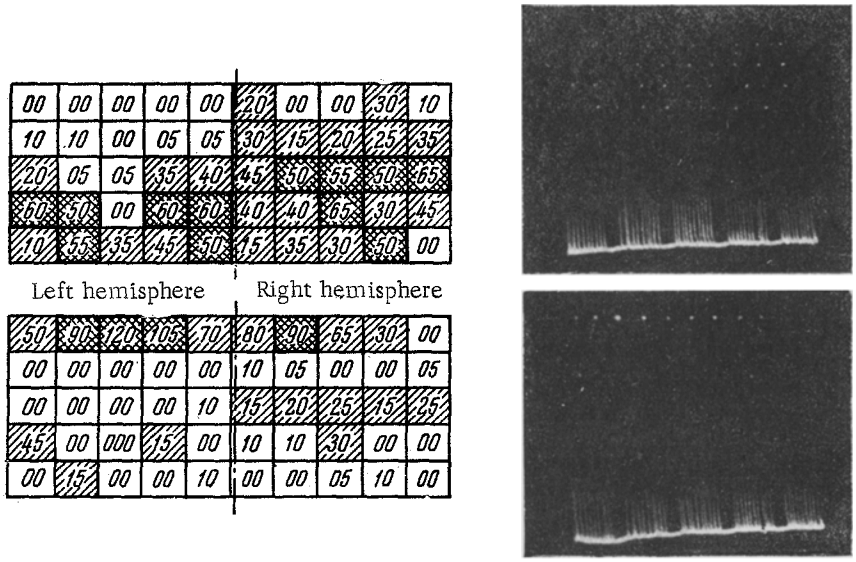

Fig. 2. Photometric analysis of a spreading wave (at the left is a numerical diagram of the wave represented in the photographs on the right). The explanation of the motion picture records is the same as in Fig. 1.

recording one is readily persuaded that this movement corresponds to a spreading wave. Simultaneous electroencephalographic and electroencephaloscopic recording established that there is complete correspondence between the spreading waves, with their recorded phase shifts, and the movement of the maximum amplitude of variations over the cortex.

The features described above can be understood on the basis of the concept that impulses which periodically reach the cerebral cortex and determine the state of local excitation within it strike different regions of the cortex at different times and with different intensities. For this reason the maximum electronegativity that develops at any given moment may move about over its surface.

The spreading wave as a form of bioelectrical activity can be characterized in at least four ways: first, with respect to the magnitude of the maximum of electronegativity (positivity); second, as to the time occupied by the passage of the spreading wave; third, with respect to the cortical area involved in the spreading wave – its "massiveness"; and finally, with respect to the direction of its movement and its tendency to recur.

In our investigations we succeeded in recording spreading waves lasting 1/10-1/12 sec, as well as longer ones lasting 1/3-1 sec. Two motion picture records can be cited as an example of the differences in duration (see Fig. 1 and Fig. 2). The first shows a wave lasting 400 msec, and the second shows a wave that occupied only 60 msec. Ordinarily the duration of the wave is related to the dominant rhythm in the electrical activity of the brain. The higher the frequency of potential variations, the faster the wave spreads, and vice versa. Figure 3 shows a spreading wave against a background of dominant alpha activity (b) and of slower delta activity (c). In the first case the amplitude maximum moves faster than in the second case. If the spreading wave repeats in sterotypic fashion, we may speak of its frequency, and the duration of the spreading wave can then be compared with the period of the dominant rhythm. It may equal the period of the dominant frequency or exceed it. With respect to the "massiveness" of the spreading waves one can say that this depends on the particular functional state. In our investigations the more extensive waves developed during the more profound states of sleep. During extensive spreading the extent to which the waves were directed was greater, and their pattern was repeated in a more stereotyped manner.

Consequently, on the basis of everything we have said it may be concluded that the spreading wave is a particular form of dynamic distribution of synchronous electrical activity in the cerebral cortex, in which the peak of electronegativity (positivity) moves from some cortical regions to others. In some instances the new regions are immediately adjacent to the first, while in others they are considerably removed. In this case a distinctive dynamic pattern appears on the electroencephaloscope screen, either one that is constantly changing or one that repeats itself in stereotypic fashion. The spreading wave is not connected with any one frequency of potential variations, but appears in its most obvious form when generalized slow rhythms are predominant in the cortex.

Some conditions favor the appearance or the enhancement of spreading waves. They may be recorded with particular clarity while the subject is asleep, when they are characterized by relatively slow movement in

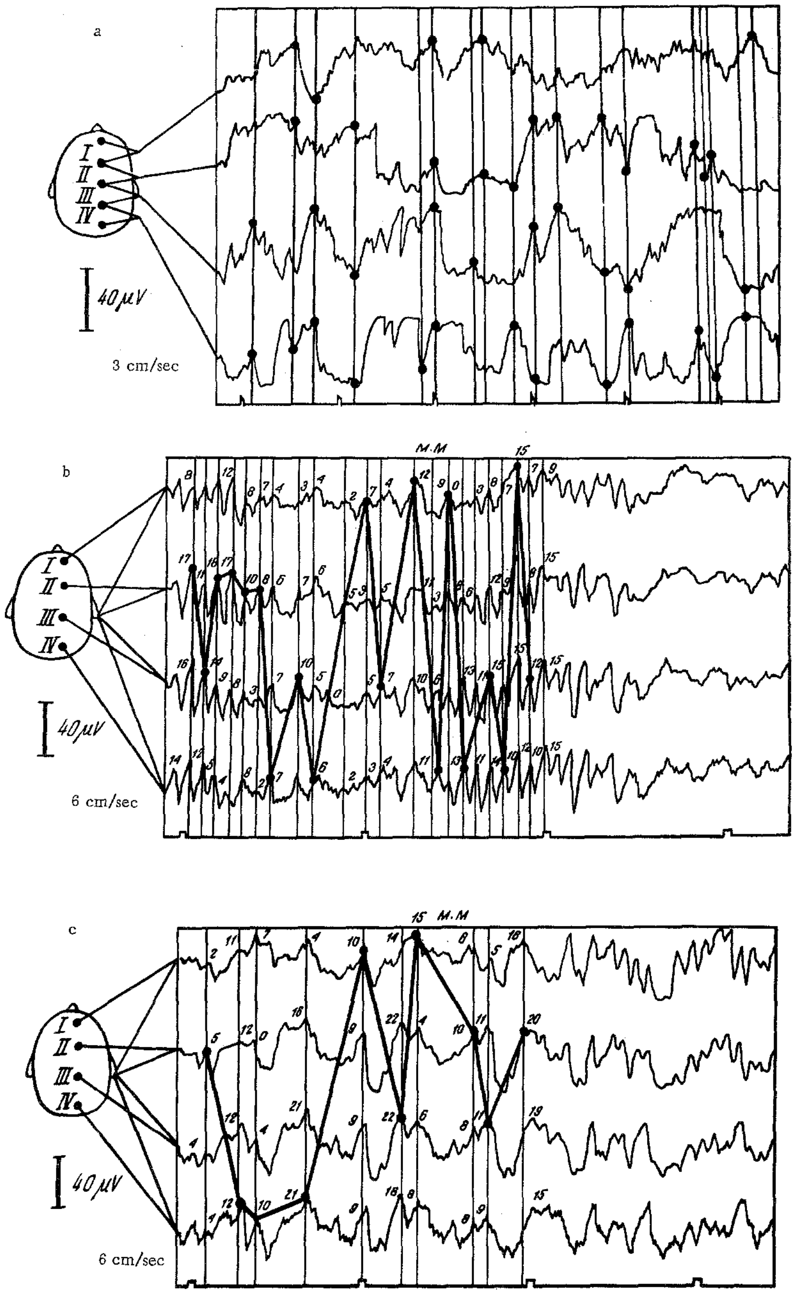

Fig. 3. Electroencephalographic form of a spreading wave recorded with bipolar (a) and monopolar (b and c) electrodes.

the fronto-occipital direction and, to a lesser extent, across the hemispheres. As a comparison with an electroencephalogram during sleep snowed, these slow spreading waves correspond to the delta wave stage. They usually disappear on arousal. But we have made some observations in which spreading waves were not present in the cortical mosaic during sleep, but reappeared shortly after awakening. Spreading waves can be recorded in the resting-waking state in the absence of external stimuli. In contrast to the spreading waves seen during sleep, these have a greater rate of movement and no definite directional tendencies, i.e., they move in various directions. The effects of external stimuli on spreading waves are different, depending on the initial functional state. Most often, application of an external stimulus (light, sound) against a background of spreading waves causes them to stop. On the other hand, when the same stimuli are applied during the waking state with no spreading waves present, they may appear in a pronounced degree. Apparently we must look for the cause of this phenomenon in the physiological intensity of the stimulus that evokes this reaction. A number of other conditions may also elicit the appearance of spreading waves. Thus, for example, the development of a conditioned delayed motor reflex in man, and so-called conflict words in an association experiment, result in the appearance of this form of electrical activity. Marked spreading waves can be recorded in certain pathological brain conditions. N. P. Bekhtereva [1] has observed spreading waves in subcortical tumors of the brain. F. A. Leibovich [4] mentions stable transhemispheric spreading waves in epilepsy. We have observed spreading waves at the site of localization of arachnoiditis.

In investigations on rabbits it has also been observed that certain conditions favor the appearance of spreading waves. In particular, they appear in drug-induced sleep, and are the more pronounced the greater the dosage of amobarbital sodium. According to the data of I. N. Knipst, T. A. Korol'kova, and M. N. Livanov [3] spreading waves are also intensified in the stage of synchronization during the extinction of a conditioned reflex, and disappear when the conditioned reflex is reestablished. The effect of external stimuli on spreading waves in rabbits is similar to that in man.

Thus, the spreading wave is a rather widespread phenomenon in the electrical activity of the cerebral cortex of man and animals. Its mechanism is still unclear, but there have been suggestions that subcortical influences are important [1]. We also feel that the mechanism of spreading waves is connected with the activity of subcortical formations, but would like to underscore the significance of a definite functional state of the cortex for its realization. Interesting data have recently been obtained by our graduate student Yu. Izosimov, which suggest that the reticular formation of the midbrain is important for the appearance of spreading waves. Further study of this type of activity is of great interest, since a spreading wave, which usually appears against a background of intensification of inhibition in the cortex (sleep, extinction of conditioned reflexes, delayed inhibition, etc.) may be an indicator of the intensity of this process. Apparently, it may also serve as an index of the influence of the reticular formation on cortical tone.

SUMMARY

Using the electroencephaloscopic method of Livanov and Anan'ev, the author studied the spatial distribution of cortical electrical activity in man and animals. He noted that in certain physiological and pathological conditions of the central nervous system a special form of dynamic distribution of synchronous electrical activity (cortical mosaic) is recorded, called an "overflow," or spreading wave of activity, representing a movement of the peak of negativity (or positivity) from certain areas of the cortex into others, with a generalized rhythm of bioelectric activity all over the cortex. Recorded with monopolar leads, spreading waves appear as movement of the point of maximum amplitude of corresponding potential variations. With bipolar leads, it is manifested mainly as a phase shift in space.

Certain conditions for these spreading waves are described, and an attempt is made to analyze their mechanism.

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