THE RELATIONSHIP BETWEEN THE BACKGROUND IMPULSE ACTIVITY OF CORTICAL NEURONS AND THE ELECTROCORTICOGRAM PHASES

(UDC 612.825 : 612.822.3)

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Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 59, No. 6
pp. 3-7, June, 1965
Original article submitted February 11, 1964

For analysis of the functional structure of the cerebral cortex at the neuronal level it is of interest to study the relation between the activity of individual neurons and the cumulative electrical processes (EEG, ECoG, etc.). The investigations of Jasper and co-workers [14-16] demonstrated the virtual absence of direct relationships between the electrocorticogram (ECoG) waves and the peak activity of individual neurons. The results of these studies elicited the complex mechanisms of the formation of cumulative electrical processes in the cerebral cortex and indicated the need to search for a relation between the impulse activity of the neurons and those properties of the ECoG or EEG which are most informative with respect to the functional state of individual neurons and of the brain as a whole. It was recently noted that the phase structure of the EEG can be such an index [4, 5, 8].

We attempted to determine the relation between the background peak activity of individual cortical neurons and the ECoG phases by A. A. Genkin's method [4, 5].

METHOD

The experiments were carried out on mature cats immobilized by procuran. The monopolar surface ECoG was led off by an annular platinum electrode (1.5 mm in diameter) from the exposed somatosensory cortex (S_I and S_{II}). Glass microelectrodes filled with 0.6 M solution of K_2SO_4 and having an input resistance from 0.5 to 5 megohms were embedded in the cortex through the opening of the electrocorticographic electrode by means of a hydraulic manipulator. The peak activity of the neurons was led off extracellularly. The spontaneous ECoG and background peak potentials of individual neurons were recorded on film from the screen of a double oscillograph.

Each second segment of the ECoG was divided into 60 intervals, during the course of which the ascending and descending phases were distinguished by A. A. Genkin's method [4, 5, 8]. For each neuron we separately counted the total number of peaks for the ascending and descending phases for 5 sec or more. The ratio of the larger of these number to the smaller was taken as the coefficient of asymmetry of the phase distribution of the peaks.

Values of the asymmetry coefficient close to one indicate a uniform and random distribution of the peaks by phases.

RESULTS

Only in 10% of 130 neurons were we able to observe an evident relation between the appearance of peak potentials and certain ECoG waves and their phases. Such relationships were primarily encountered during the period of high-amplitude and infrequent waves of the ECoG at frequencies of 1-8 per sec. Sometimes the background activity in the form of high-frequency groups of peak potentials appeared at the summit of a negative wave or on its slope (Fig. 1, a). In other cases the background activity arose only during the change of infrequent ECoG waves to a more frequent rhythm (Fig. 1, b). In this case during the period of high-amplitude and slower waves the background activity of the neurons was generally inhibited.

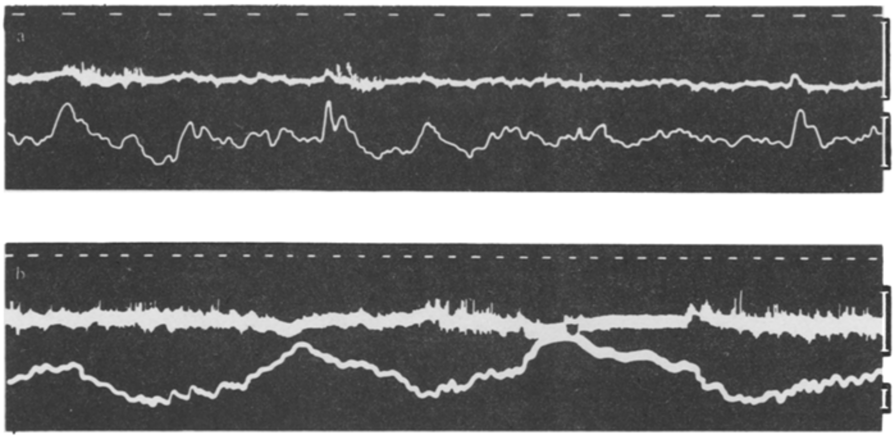

Fig. 1. Simultaneous recording of the background peak activity of individual neurons (upper curve) and surface ECoG (lower curve). a) Neuron at depth of 0.43 mm from surface of cortex; b) at depth of 1.53 mm. The upward deflection of the tracings corresponds to the appearance of a negative potential under the cortical electrode and microelectrode. Time marker, 1/20 sec. Calibration of the microelectrode channel 3 mV, for the ECoG 200 μV.

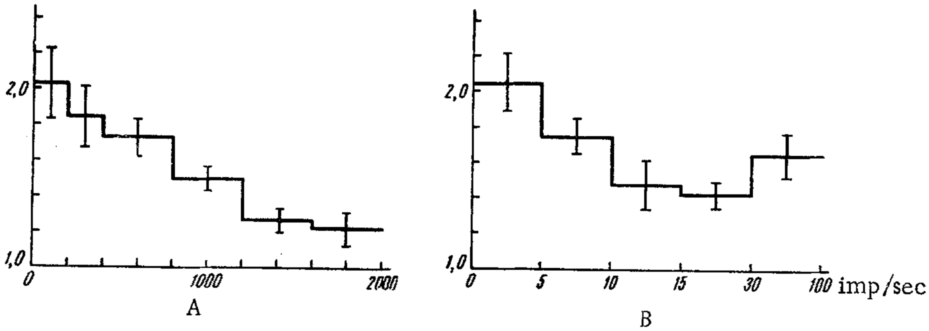

Fig. 2. Dependence of the asymmetry coefficient on depth of neurons in cortex (A) and on the frequency of the background impulse activity of the cortical neurons (B). A) Along axis of abscissa, depth of embedding microelectrode in cortex (in microns); along axis of ordinate, magnitude of asymmetry coefficient. The magnitude of standard deflections is shown by vertical segments. B) Along axis of abscissa, frequency ranges of background rhythm (in impulses/sec). Other designations are the same as in Fig. A).

When the ECoG is dominated by waves with a frequency of 11-14 per sec and more frequent ones (20-30 per sec) it is not possible to find visually any relation between the arising peak potentials of individual neurons and the rhythmical waves of the surface ECoG. Similar observations were made earlier by Jasper and co-workers [14-16].

Studying the statistical distribution of peak potentials with respect to the ECoG phases, we could find the presence of asymmetry of this distribution in most of the investigated cells. On the average the asymmetry coefficient was equal to 1.66 ± 0.06 (at extreme values of from 1 to 4). In some neurons (41%) the peak potentials occurred primarily during the ascending phases of the ECoG, and in others (59%), conversely, during the descending phases. In this respect the cortical neurons resemble the nerve cells of most nuclei of the thalamus where a correlation between the peaks of individual neurons and certain phases of the cumulative electrical activity in the nucleus has also been detected [19].

A further analysis showed that the average values of the asymmetry coefficient depend on the depth of the neurons in the cortex and the frequency of their background impulse activity. The larges values of the asymmetry coefficient were detected in the superficial layers of the cortex (to 800μ) and at infrequent frequencies (to 10 impulses/sec) of the background rhythm (Fig. 2). The deeper the neurons, the smaller the asymmetry of the

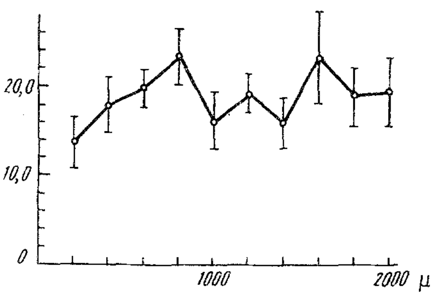

Fig. 3. Average frequency of the background rhythm of cortical neurons at different depths from the surface of the cortex. Along axis of abscissa, thickness of cortex (in microns); along axis of ordinate, frequency of background rhythm (in impulses/sec). The vertical segments indicate the standard deflection.

distribution of the peak potentials. At a frequency from 10 to 30 impulses/sec we also observed the lowest values of the asymmetry coefficient, and at a frequency of 30 to 100 impulses/sec we noted a certain increase of this coefficient.

If the frequency of the background activity of the neurons were to depend on their depth in the cortex, then we could assume an interrelationship between the noted regularities. However, it turned out that the frequency of the background rhythm of individual neurons is practically the same in different layers of the cortex since the observed differences are not statistically reliable (Fig. 3). Only a certain tendency toward a drop in frequency in the superficial layers of the cortex was noted. Moreover, it is necessary to take into account the fact that the neurons with an infrequent frequency of background impulses (up to 10 per sec) are encountered at the most diverse distances from the surface of the cortex. Consequently, the dependence of the asymmetry coefficient on depth and frequency has some other causes.

As is known the slow cumulative electrical processes in the cortex are diverse and complex temporary structures of spike and primarily postsynaptic potentials of enormous statistical aggregates of neurons [1, 9, 10, 13]. Only in the superficial layers are the intracortical cumulative electrical potentials synchronized with the spontaneous activity on the surface of the cortex [9, 15]. Starting with a depth of about 1 mm we observe a tendency toward distortion of their phases, or complete disappearance of any regular correspondences between the surface and deep ECoG.

Therefore, even in spite of the complex mechanisms of the formation of the cumulative electrical potentials we should expect for the surface neurons a more intimate relationship with the phases of the surface ECoG. Hence it is understandable why for such neurons we noted an evident and statistically stable asymmetry of the phase distribution of the peaks, whereas for the deeper neurons this distribution approached a random on (the asymmetry coefficient tended toward unity). Thus we can consider that the dependence of the asymmetry coefficient on depth is mainly determined by the characteristics of the formation of the cumulative electrical processes in the cortex and their reflection in the surface ECoG.

Li, Chou, and Howard [17] showed that the spike activity of the cortical neurons is regulated mainly by two mechanisms: fluctuations of the membrane potential and the postsynaptic potentials whose intracellular current participates in the formation of the cumulative electrical processes [1, 9, 10, 13]. We discussed earlier certain mechanisms of neuronal instability [2]. If the level of the membrane potential is quite far from the critical at which, as is known, the peak potential is generated [10], then for the occurrence of cell discharge comparatively large synaptic effects and fluctuations of the membrane potential are needed. In such cases both a more infrequent rhythm of impulses and a more intimate relation with the cumulative intracellular potentials will be observed.

Evidently at a high rhythm of impulse activity the membrane potential is quite close to critical, its fluctuations are smaller, and the negligible exciting postsynaptic potentials, which probably are slightly reflected in the cumulative electrical activity, will be accompanied by generation of peak potentials. Under these conditions, of course, the relation between the appearance of peaks and certain waves of the cumulative electrical processes is weakened: the neuron works practically independent of the phases of bioelectrical activity.

If we assume that the level of the background activity of the neuron reflects the state of its excitability, as was assumed by N. E. Wedensky [3], then the relationship with the phases of the electrical processes is more expressed for neurons with a low level of excitability and less evidenced for highly excitable neurons. Actually, Li, Cullen, and Jasper [16] were able to observe how the probability of a relation between peak activity and certain waves of the ECoG increases with a decrease of the functional state of the brain (for example, in anoxia).

The results of our observations also indicate that between the spontaneous rhythm of a neuron and the cumulative indexes of brain activity (ECoG, EEG, etc.) there are primarily statistical relationships which generally reflect the statistical character of organization of the nervous system as a whole [6, 7, 12].

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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.
