ROLE OF CORTICOFUGAL INFLUENCES IN MECHANISMS OF FORMATION OF CORTICAL BIOELECTRICAL ACTIVITY

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In experiments on cats anesthetized with a mixture of chloralose and pentobarbital, reversible cooling of the 1st sensomotor area (SM-I) unilaterally to between 25 and 23°C was accompanied by a simultaneous and generalized change in the activity of other parts of the cortex. These changes were expressed either as the appearance of slow high-amplitude activity or, on the other hand, by a marked decrease in amplitude of the EEG. Warming the cooled region of the cortex was followed by restoration of the normal EEG of the other parts of the cortex. These changes in electroencephalographic activity of the cortical areas are discussed in connection with the existence of synchronizing and desynchronizing subcortical brain structures.

KEY WORDS: brain – cortical electrical activity; cooling; corticofugal effects.

The reverberation character of excitation affecting certain subcortical and cortical structures has been demonstrated by electrophysiological methods [12, 14]. More recent observations have extended ideas of reverberation circles, including the cerebral cortex [9, 16] or only subcortical formations [15]. The study of the neurophysiological mechanisms of formation of behavioral responses has shown that the degree of involvement of the subcortical structures and the character of reverberation of excitation are both determined by the biological quality of the response itself [1, 10].

After these discoveries the artificial character of the distinctions between corticopetal or corticofugal effects became evident, for under conditions of function of the whole brain cortico-subcortical relations with a reverberating character of excitation exist.

One way of analyzing cortical-subcortical relations is by the reversible blocking of one or more cortical projection areas by cooling. Not only functional connections of various parts of the cortex with subcortical structures in acute experiments but also disturbances of the integrative activity of the whole brain under free behavioral conditions have been studied by this method [2, 6].

The object of the present investigation was to examine the role of the 1st sensomotor area of the cortex (SM-I) and its functional state in its relations with other parts of the brain as reflected in the electrical activity of cortical structures.

EXPERIMENTAL METHOD

Adult cats were anesthetized with chloralose (60 mg/kg) and pentobarbital (10 mg/kg), injected intraperitoneally. The animals were fixed in a stereotaxic apparatus, the skin and muscles of the scalp removed in layers, and the skull trephined in the region of area SM-I on the left and above the level of the midbrain. Area SM-I was cooled to a temperature of between 25 and 23°C by application of ice. The temperature of the surface of the cooled area of cortex was monitored by a type TSM-2 electrothermometer. The EEG was recorded with needle electrodes from symmetrical points of the left and right hemispheres on a Racia polygraph. Unit activity of the mesencephalic reticular formation was recorded extracellularly by means of glass microelectrodes. For this purpose UBP-01 preamplifiers with external cathode follower and a Disa

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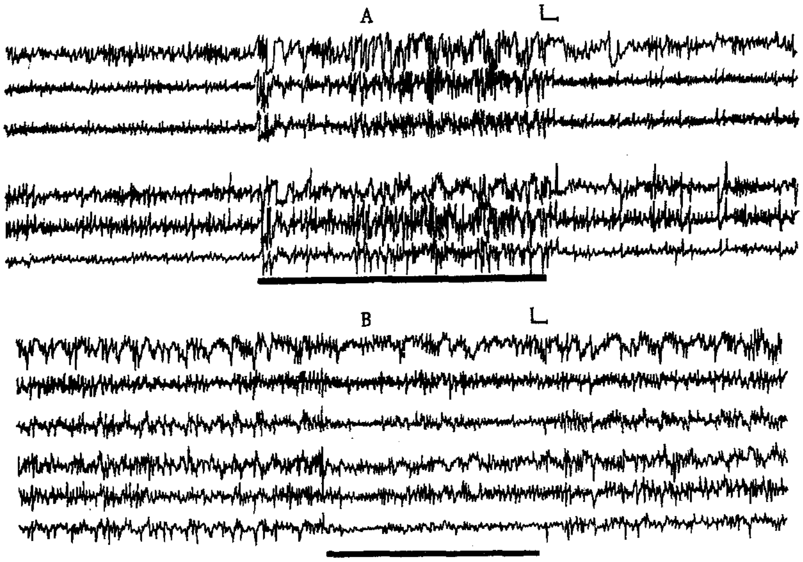

Fig. 1. Two types (A and B) of change in EEG of various cortical areas in response to cooling of area SM-I on the left. From top to bottom: left frontal, parietal, occipital regions; right frontal, temporal, occipital regions. Black band denotes period of cooling of area SM-I. Calibration: 100 μV, 1 sec.

Electronic recórder were used. The projection of the microelectrode was determined in histological sections frozen with CO_2 and with a thickness of 50 μ.

EXPERIMENTAL RESULTS AND DISCUSSION

The cortical electrical activity of the cat under mixed chloralose-pentobarbital anesthesia was characterized by slow-wave activity with periodic "nembutal" spindles. Application of ice to area SM-I on the left lowered the temperature of the surface of this part of the cortex to between 25 and 23°C. In turn, local cooling of area SM-I was accompanied by changes in the activity of other regions of the cortex. A marked increase in amplitude of the slow waves in all leads of the EEG can be clearly seen in Fig. 1A. Not only the extensive spread of synchronized slow-wave activity in the cortex but the simultaneous character of its onset will be noted. The low-frequency high-amplitude synchronized activity, represented by spindle-shaped waves lasting several seconds, appeared most typical under these experimental conditions. In some cases local cooling of area SM-I unilaterally was accompanied by different electroencephalographic manifestations. Instead of a marked increase in amplitude in all leads of the EEG, the level of the spontaneous cortical activity was lowered and individual low-amplitude spindles appeared (Fig. 1B). The decrease in amplitude of the spontaneous activity could not be called desynchronizing, for the EEG rhythm either was unchanged or was slightly slowed. These changes in the EEG of the cortical areas were observed during somewhat deeper local cooling of area SM-I.

Analysis of unit activity in the mesencephalic reticular formation (MRF) showed that cooling area SM-I is accompanied mainly be a decrease in the level of spontaneous activity. The study of responses of reticular neurons to stimulation showed considerable changes during reversible local cooling of the cortex. The ability of the neurons to respond to stimulation was generally reduced.

There is evidence in the literature that local cooling of the cortex is accompanied by marked changes both in the physiological properties of the cooled area [4] and in the pattern of its electrical activity. However, there is no general agreement regarding the order of the changes in the electrocorticogram (ECoG) of the cooled area. Some workers [6, 8] state that during cooling to 25-23°C the amplitude of the ECoG is first reduced, but during deeper cooling the frequency of the waves also decreases. Other workers [7] consider that the frequency changes first, in the direction of slowing, and the amplitude of the waves decreases later. Careful analysis of the electroencephalographic changes connected with cooling the brain in monkeys has demonstrated their complex character. First of all there was a gradual decrease in the amplitude of the high frequencies, then disappearance of those frequencies, followed by a decrease in amplitude of the low frequencies and, finally, by persistence of only the low-amplitude θ-rhythm on the EEG [19].

These contradictory views on the changes in brain electrical activity can be explained entirely by the experimental technique, by the presence or absence of anesthesia, and by the method and depth of cooling. The importance of anesthesia when changes in electrical activity during cooling are studied is indicated by the fact that in experiments on unanesthetized animals local cooling of one cortical area as a rule is not accompanied by any profound changes in the bioelectrical activity of other cortical areas. Admittedly, Perov [6] states that during cooling of area SM-I on the left side in unanesthetized cats slower waves predominate in the ECoG recorded in area SM-I on the right. In the present experiments, using mixed chloralose-pentobarbital anesthesia, local cooling of one area SM-I was accompanied by the appearance of high-amplitude slow activity in other parts not only of the ipsilateral, but also of the contralateral hemisphere, indicating the participation of structures with generalized effects on the cortex in this process. It is interesting to note that in patients undergoing operations under moderate hypothermia (down to 28°C), in the period of active rewarming, when the temperature reaches 31-33°C, high-amplitude synchronous potentials appear in both hemispheres [5]. The simultaneous appearance and the generalized character of the slow high-amplitude waves suggest that local cooling of area SM-I induces sharp functional changes in the structures of the mesencephalic reticular formation. Investigation of unit activity of the activating MRF under ordinary conditions, using microelectrodes, showed that an increase in the excitability of area SM-I has predominantly facilitatory effects [3, 13, 17, 21].

Local cooling of area SM-I is accompanied by marked changes in the functional properties of MRF neurons, expressed as some decrease in the level of spontaneous activity and in their ability to respond to stimulation [11].

The comparison of changes in the electrical activity of various regions of the cortex during local cooling of area SM-I and changes in unit activity of MRF suggests that the appearance of slow high-amplitude synchronized activity is connected with the considerable weakening of the generalized activating influences of MRF. Considering that the activating MRF has reciprocal relations with the synchronizing portions of the medullary reticular formation [20] and with the nonspecific thalamic nuclei [18], it must be assumed that local cooling of area SM-I to between 25 and 23°C predominantly inhibits the activity of the activating brain-stem reticular formation, thereby bringing about activation of the synchronizing subcortical structures. Deeper local cooling of area SM-I in all probability inhibits the activity of structures with synchronizing effects on cortical electrical activity, as expressed both by a general decrease in amplitude of the potentials and as a gradual change in the EEG frequency. The results of these investigations are evidence of differences in relations of area SM-I with the synchronizing and desynchronizing subcortical struc- If reverberation of excitation is present between the cortical and subcortical formations, these differences are expressed as different patterns of changes in cortical electrical activity.

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