STRUCTURAL CHANGES IN DENDRITES OF THE CORTICAL PLEXIFORM LAYER: AN EEG STUDY

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The electroencephalogram (EEG) is a widely used indicator of the state of brain function. It can reflect gross, and frequently irreversible, brain lesions, and is widely used for this purpose in neurology [4]. However, virtually no information is so far available on correlation between the EEG and reversible microstructural changes in single brain cells and, in particular, in the cerebral cortex. The question of the contribution of individual components of the nerve cell to its electrical activity is still debated.

The writers showed previously that the loci of the cerebral cortical nerve cells most sensitive to the action of extremal factors and, in particular, to deep anesthesia, are the distal segments of the dendrites in the plexiform layer. The structural manifestation of this reaction is selective and local swelling. It has been suggested that this morphological modification of the dendrites may lead to their functional "blocking" [3].

Is there any correlation between selective damage to dendritic structure in the plexiform layer and the ability of the cortex to respond ability connected with restoration of the structure of the dendrites? To test this hypothesis, a structural and functional analysis was undertaken of changes taking place during recovery from deep anesthesia, for it is only due to the inertia of this process that it is possible to monitor the connection between changes in cortical structure and changes in the EEG. As the electrophysiological indicator we used the EEG, and tested the EEG activation reaction in response to weak anodal polarization of the cortex.

During analysis on the EEG attention was concentrated on the theta-rhythm, for it is connected with function of the nonspecific system, and we know that the greater part of the nonspecific afferentation from subcortical centers travels to the plexiform layer [7]. Polarization of the cerebral cortex by a weak direct current has been shown to create a local focus of increased excitability [5] and to potentiate the theta rhythm of intact animals [1]. Potentiation of the theta-rhythm in turn indicates activation of the nonspecific brain zones [2], to whose system the plexiform layer of the cortex belongs.

EXPERIMENTAL METHOD

The investigation was conducted on ten albino rats in acute experiments under pentobarbital anesthesia. The stimulating electrode (the anodal pole) consisted of a previously chlorided silver plate 1 mm thick and 25 mm^2 in area, implanted into the cranial bones above the sensomotor cortex. The cathodal pole consisted of silver wire 0.3 mm in diameter and 30 mm long, inserted into the auricular muscle.

The EEG was recorded by means of silver ball electrodes made from wire 0.3 mm in diameter, and inserted as far as the inner table of the skull. The recording electrode was located beneath the polarizing plate electrode and the reference electrode was secured in the nasal bone.

Pentobarbital was injected into the rats in a dose of 40 mg/kg body weight. After recording of the control EEG and respiration rate, the anesthesia was deepened to give a sharp reduction in respiration rate and amplitude of the EEG. Next, during deep anesthesia and recovery from it, the sensomotor cortex was polarized by the anode of a weak direct current (10 μA) and the EEG response to polarization was analyzed and material taken for light and electron microscopy.

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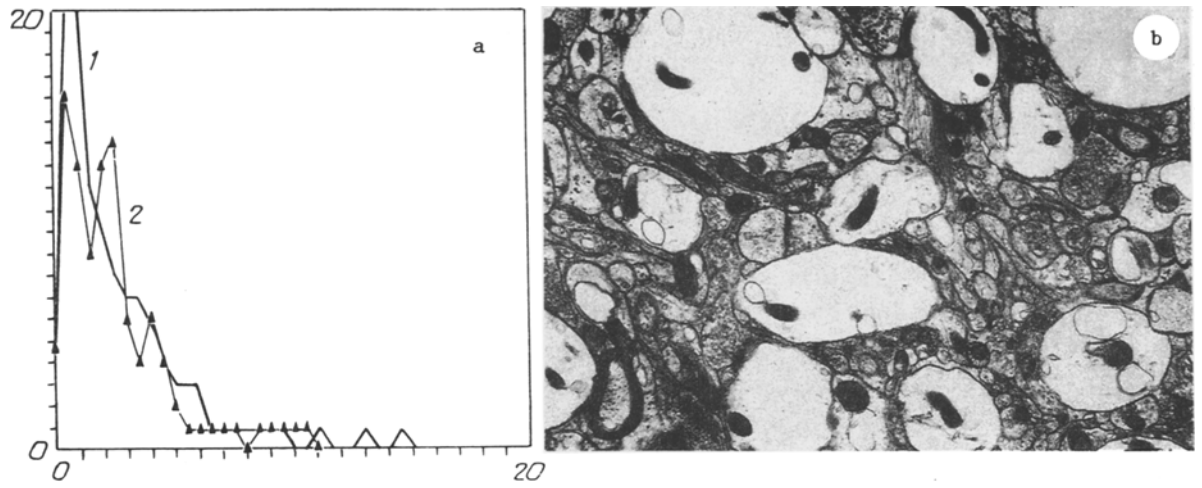

Fig. 1. Power spectrum of EEG response to weak anodal polarization (a) and structure of plexiform layer of rat cortex (b) in early stage of recovery from deep anesthesia. Massive varicose expansions of dendrites are visible. Here and in Fig. 2: 1) Power spectrum before polarization; 2) power spectrum of EEG immediately after polarization. Abscissa, frequency of waves (in Hz) from 0 to 20 sec with step of 1 Hz; ordinate, power (conventional units). Magnification: 11,500.

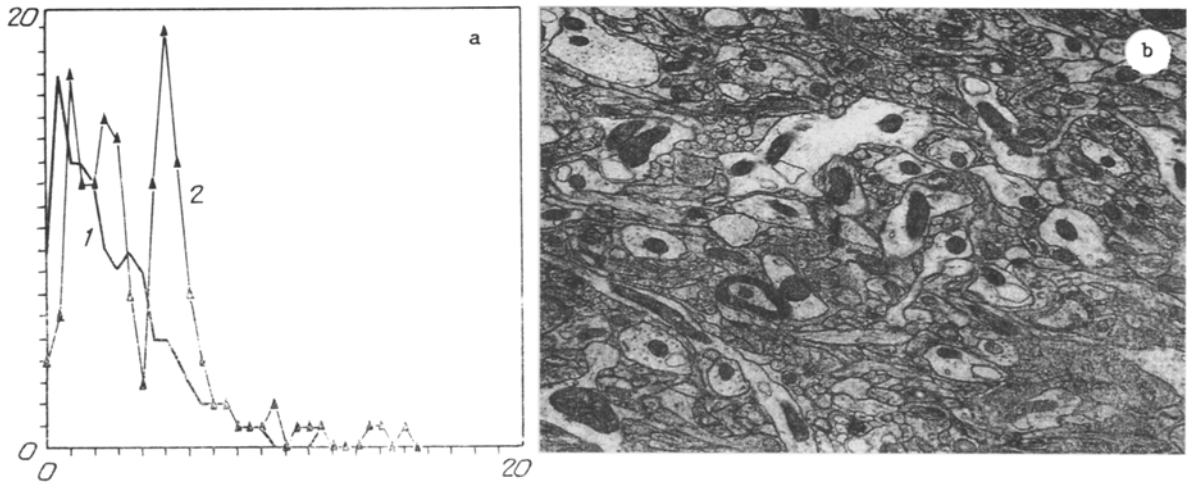

Fig. 2. Appearance of peak in theta-band at frequency of 5 Hz in EEG power spectrum in response to weak anodal polarization (a), and connected with recovery of structure of dendrites in plexiform layer of rat cortex (b) in late stage of recovery from deep anesthesia.

In the experiments of series I (5 animals) polarization followed by removal of material was carried out immediately after restoration of the amplitude–frequency characteristics of the EEG to values typical of the control level of anesthesia (40 mg/kg body weight). In the experiments of series II (5 animals) polarization followed by removal of material for morphological investigation was carried out 30-40 min after restoration of the amplitude–frequency characteristic of the EEG to the control values.

The method of taking material for morphological analysis, and of processing the EEG and the morphological data, was described previously [3].

EXPERIMENTAL RESULTS

Early Stage of Recovery. In the experiments of series I polarization was carried out immediately after recovery of the amplitude–frequency characteristics of the EEG to values typical of the control level of anesthesia (40 mg/kg body weight). It will be clear from Fig. 1a that immediately before polarization the maximum of the EEG spectrum was in the delta-band at a

frequency of 0.5-1 Hz. Immediately after testing polarization, besides the peak at a frequency of 1 Hz a second peak appeared in the delta-band at a frequency of 2.5 Hz. The structure of the plexiform layer at this time was virtually indistinguishable from that during very deep anesthesia and depression of the EEG (Fig. 1b). In the distal parts of the dendrites in the plexiform layer, the spines had disappeared and beadlike varicose expansions appeared, indicating swelling of these loci in the dendrites of the nerve cell. The diameter of some varicose expansions often exceeded the diameter of the intact dendritic trunk by 5-10 times. Microtubules characteristic of the normal state were not present in the cytoplasm of the varicose regions of the dendrites, but the structure of the mitochondria was virtually unchanged. In the region of varicose expansions endocytosis of dendrites was frequently observed in neighboring structures. Synaptic endings, astroglia, and myelin sheaths of axons did not differ from those in the control animals.

Calculations showed that in the experimental animals at this particular stage of recovery from deep anesthesia the total areas of the varicose expansions of the dendrites amounted to 28.4 ± 1.0% of the total constant area of section in the plexiform layer of the cortex (n = 150), which did not differ from the corresponding values during deep anesthesia, but was about twice as great as in the control animals [3].

Late Stage of Recovery. In the experiments of series II in the late stages of recovery from deep anesthesia and immediately after polarization with a weak current, we observed the appearance of a peak in the theta-band of the EEG spectrum, which frequently had greater power than the maximal peak in the delta-band. For instance, it will be clear from Fig. 2a that in this case the maximum of the power spectrum lay in the theta frequency-band (5 Hz). The structure of the plexiform layer in this case was restored (Fig. 2b). As the calculation showed, during recovery from deep anesthesia the mean value of the ratio between the total areas of the varicose expansions of the dendrites and the total constant area of section in the plexiform layer of the cortex was 14.4 ± 0.7% (n = 150), only half of that found in the early stages of recovery, and similar to the control values [3].

The EEG theta-rhythm is known to be an indicator of general activation of the brain. This activation is closely connected with the action of the nonspecific system of the brain. The initial structures which may be responsible for the appearance of the theta-rhythm are the nonspecific structures of the brain stem, involved in the general activation reaction [2].

Most of the nonspecific afferents entering the cortex terminate on dendrites in the plexiform layer, and mainly in its upper third [6], where, according to our data, the most important morphological changes take place in the dendrites. The increase in the degree of swelling of the distal segments of dendrites of the plexiform layer in the stage of deep anesthesia may be the cause of blocking of incoming impulsation from the nonspecific activating system of the brain and the insusceptibility of the cortex to the testing effect of the applied polarization, as shown by disappearance of the activation reaction to stimulation by a weak direct current.

These findings suggest that distal segments of apical dendrites, constituting the greater part of the plexiform layer, may play an important role in interaction between the nonspecific system of the brain and the cerebral cortex. Spectral analysis of the background EEG did not give an unambiguous answer to the problem of the state of the dendrites in the plexiform layer. The only objective electrophysiological indicator of recovery of the structure of the dendrites in the plexiform layer is the EEG reaction to direct cortical stimulation, which takes the form of the appearance of a peak in the power spectrum of the EEG in the theta band.

Varices in dendrites, which are often found under the influence of extremal factors and in several kinds of CNS pathology, besides other changes in them (loss of microtubules, disappearance of spines), may be the structural basis of functional "blocking" of these loci in the nerve cell, which is responsible for absence of the EEG activation reaction to cortical polarization. Ability of the cortex to respond by an EEG activation reaction is linked with the intact state of the dendrites in the plexiform layer.

Consequently, depending on absence or appearance of an EEG theta rhythm in the cortex in response to its direct stimulation can be used to judge the morphological state of the dendrites of the plexiform layer.

This combined structural and functional approach provides a means of judging concrete structural changes in the cerebral cortex under experimental and some pathological conditions.

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SEX DIFFERENCES IN RESERVE CAPACITY OF THE RAT PITUITARY-ADRENOCORTICAL SYSTEM

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The writers showed previously that sensitivity and mobility of adaptive systems is higher in females than in males in situations of short emotional stresses [1]. An important property of adaptive mechanisms is their reserve capacity, on which not only the intensity of responses to stress but also the velocity of recovery processes [3, 9] and, consequently, the readiness of the individual to respond adequately to new and unforeseen stress [13], depends. This quality, because of the abundance of stress situations in present-day human life, assumes particular significance.

The aim of the investigation was to study the dynamics of responses in female and male albino rats to complex emotional stress and sensitivity to additional stress at different times of the stress and poststress periods.

EXPERIMENTAL METHOD

Experiments were carried out on 370 animals. Complex emotional stress consisted of a combination of immobilization for 60 min in a constriction cage, vibration on a shaker, loud dissonant music, and a flashing light. The corticosterone levels in the adrenals and blood plasma, collected at decapitation of the rats 10 and 60 min after the beginning of stress, and again 20, 40, 120, 180, and 240 min after its end, were determined fluorometrically. Additional stress consisted of strict immobilization for 10 min, applied 60 min after the beginning of the basic stress, and again 40, 120, 180, and 240 min after its end. Analysis of the results included calculation of the coefficient of variation and Student's test [7]. Vaginal smears taken after decapitation were studied in the females.

EXPERIMENTAL RESULTS

Calculations of the coefficients of variation revealed homogeneity of the groups of animals relative to reactivity to stress, in groups both of males and females, irrespective of their stage of the sex cycle. Just as in our previous experiments [1], sensitivity of the females to stress was higher than that of the males. The corticosterone concentration in the adrenals (Fig. 1a) and plasma (Fig. 1b) in females 10 min after the beginning of stress showed an increase of 3.3 and 4.7 times respectively, and it was maintained at about the same level until the end of stress. In the males, 10 min after the beginning of stress, the concentration of the hormone in the adrenals (Fig. 2a) and plasma (Fig. 2b) was increased by 2.5 and 2.9 times, but by the 60th minute of stress, although the corticosterone level in the plasma remained high, in the adrenals it fell to basic values and was 3.5 times less

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