ELECTROGRAPHIC MANIFESTATION OF DROWSINESS IN THE ISOLATED CAT CORTEX

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Electrical activity of the neuronally isolated cortex during waking and the onset of sleep was investigated in experiments on freely behaving cats. The transition from wakefulness to sleep is accompanied in the isolated cortex by the appearance of a stage of drowsiness, accompanied by corresponding changes in the electrocorticogram of the isolated hemisphere. The electrographic manifestation of the stage of drowsiness in the isolated cortex depends on the time elapsing after the operation and it is most marked in the late period after isolation of the cortex.

KEY WORDS: sleep in animals; isolated cortex; EEG of sleep.

The process of going to sleep, normally taking place rapidly, is noteworthy not only because it has received little study but also because its elucidation could provide the key to the understanding of several problems connected with the mechanisms of onset of normal and pathological sleep. One such problem is that of the primary component in the system of brain structures involved in "sleep" activation, i.e., those structures that are the first to manifest activity usually regarded as the reflection of sleep processes.

A number of investigations of this problem have already been made, including some based on recording brain electrical activity [1-5, 7], but in those investigations potentials of different structures were recorded with all conducting systems of the brain intact, i.e., under conditions that did not permit unreserved conclusions to be drawn regarding the primacy of the brain structures involved in the process of sleeping. This criticism applies completely also to results obtained by the investigation of cortical electrical activity. Nevertheless, the study of this problem in the neuronally isolated cortex provides additional opportunities for removing the uncertainties mentioned above.

The object of this investigation was to study electrical activity of the cortex, isolated from subcortical nervous influences, in the process of sleep in animals.

EXPERIMENTAL METHOD

Sixteen cats of both sexes weighing 3-4.2 kg, with the cortex isolated, were used. Four intact cats weighing 3.2-3.9 kg acted as the control. The operation of cortical isolation was performed in one hemisphere by Khananashvili's method [7]. Simultaneously with the operation mentioned above, bipolar Nichrome electrodes 100 μ in diameter, in glass insulation, were implanted. In some cases (5 cats) stainless steel screws, inserted into the animal's skull, were used as electrodes. Both types of electrodes were located above the motor area, parietal region, and visual area of the isolated cortex and intact hemisphere. The reference electrode was secured into bones above the frontal sinus. The electro-oculogram was recorded by means of steel needle electrodes inserted into the animals' orbits. Activity of the neck muscles was recorded by electrodes consisting of Nichrome wires, 30 mm long and 100 μ in diameter.

The experiments started on the first day after isolation of the cortex and continued until 10 months after the operation. The electrocorticogram (ECoG) of the sleeping animals was recorded continuously for

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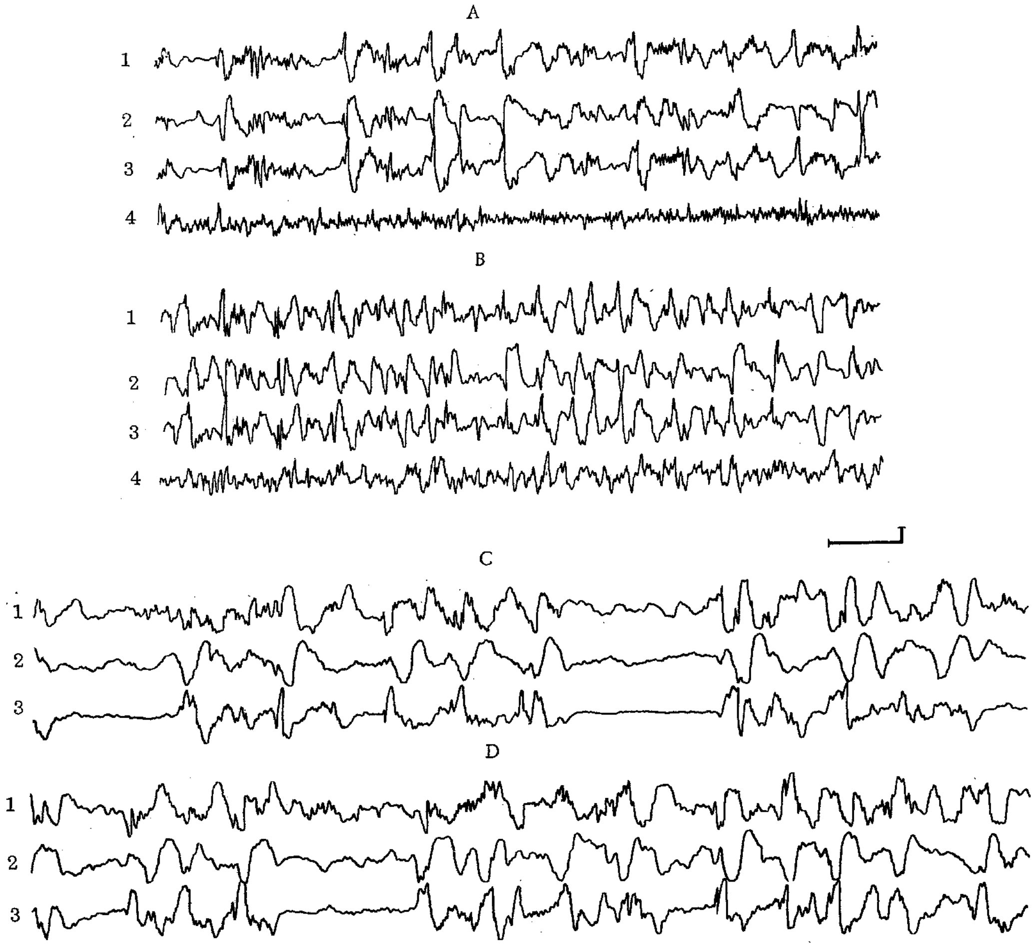

Fig. 1. Electrographic manifestation of waking and drowsiness and periods of isoelectric silence in isolated cortex. A and B) Periods of waking and drowsiness respectively (third week after operation); C and D) periods of isoelectric silence at moments of waking and drowsiness respectively (first week after operation). Regions of isolated cortex: 1) motor, 2) parietal, 3) visual area of intact cortex; 4) motor area. Calibration: 50μV, 1 sec.

3-4 h on the "Orion" 8-channel electroencephalographic system. During the experiments the animals could move about freely in the experimental box, which had transparent walls and measured 60 × 50 × 40 cm. The sleep of each cat was recorded 4 to 6 times at intervals of 1-5 days. The stages of the animals' sleep were identified from their electrographic manifestation in the cortex of the intact hemisphere in accordance with the accepted classification [9].

Data relating only to those animals in which the completeness of cortical isolation was confirmed by a morphological control were used for analysis. Data obtained by a frequency integrator were subjected to statistical analysis with the use of Student's t criterion. The "Promin'-2" computer was used for all these calculations.

EXPERIMENTAL RESULTS AND DISCUSSION

Spontaneous activity of the isolated cortex in the waking animal during the first 3 weeks after isolation consisted of two main types: 1) slow-wave polymorphic activity with an amplitude of 100-200 μV and a frequency of 0.5-5 waves/sec; 2) activity consisting of periods of "bursts" (2-4 high-voltage slow waves up to 300 μV in amplitude and 50-130 msec in duration) and periods of isoelectric silence lasting about 0.8 sec.

During the transition from waking to sleep, in the stage of drowsiness the ECoG of the isolated cortex began to be dominated by regular high-amplitude slow-wave activity composed of waves with a frequency of 3/sec and an amplitude of 200-250 μV (Fig. 1). Fast low-amplitude waves superposed on the slow waves and

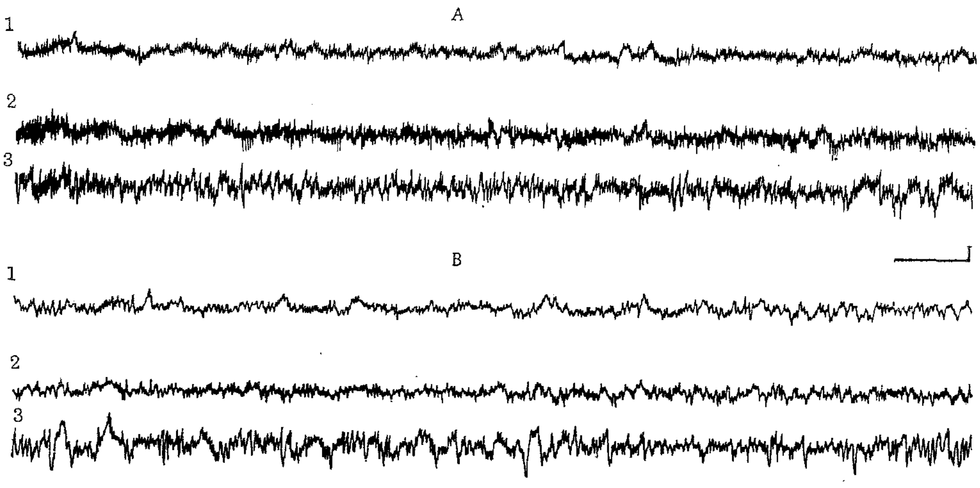

Fig. 2. Electrographic manifestation of waking (A) and drowsiness (B) in isolated cortex 10 msec after operation. Legend and calibration as in Fig. 1.

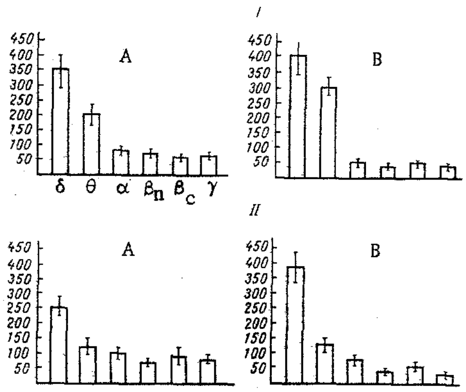

Fig. 3. Frequency distribution of electrical activity in isolated cortex 1 (I) and 10 (II) months after operation: A) waking, B) drowsiness. Abscissa, frequency bands; ordinate, electrical activity (in μV).

observed during waking disppeared. The spindles characteristic of this stage of sleep in intact animals were not found in the isolated cortex.

Periods of isoelectric silence in the isolated cortex were less marked in the animals going to sleep: The interval between groups of slow waves was shortened, the interval itself was filled with low-amplitude activity, and the number of periods of silence decreased (Fig. 2).

With an increase in the period after isolation of the cortex its spontaneous activity gradually recovered but did not reach the normal level characteristic of the intact hemisphere, and after the fifth to sixth months it remained virtually unchanged. The spontaneous ECoG of animals in a waking state at this time consisted of fast activity (10-16 waves/sec; 50-100 μV), with low-voltage potentials superposed on it (5-10 μV; 40/sec). The periods of isoelectric silence disappeared completely by the third month after isolation.

During the development of drowsiness, slow waves of increased amplitude appeared in all leads in the isolated cortex. The transition to a drowsy stage of sleep occupied 2-6 sec in different animals. The increase in amplitude during the first few seconds of drowsiness compared with the waking stage amounted to 20%, but during development of the stage of drowsiness it was 60%. The period of the ECoG dominated by slow waves was followed by a period of waves with lower amplitude, recorded at once in all three leads. This pattern was repeated several times before the next stage of sleep (slow-wave) took place. During the development of drowsiness, the fast waves became progressively smaller and the slow, high-voltage waves progressively greater.

In some animals during the 2-3 sec before the onset of drowsiness, a decrease in amplitude of the waves was observed to 10-15 μV although they retained their frequency.

Analysis of the ECoG showed that throughout the period of observation after isolation of the cortex, i.e., until the end of 10 months, the greatest activity during the development of drowsiness was recorded in the Δ and Θ bands. The histograms show that in the late stages after isolation the relative proportion of fast waves was somewhat increased (Fig. 3).

The results described above indicate that electrographic manifestations of sleeping are clearly recorded in the isolated cortex, especially in the late stages after the isolation operation. The absence of "spindles" in the ECoG of the isolated cortex during development of drowsiness can be explained by the complete isolation of the cortex from subcortical structures and, in particular, from the nuclei of the thalamic system which, as is now accepted, are responsible for their behavior [1, 4].

Since the circulation in the cat cerebral cortex is unchanged by the onset of sleep [7], it must be assumed that the nervous system of the pial vessels has no essential role to play in this stage of sleep. Allowing for this and also for the fact that the signs of sleep are manifested simultaneously in both hemispheres, the writer suggests that the development of drowsiness is determined principally by humoral influences.

The fact that "sleep" potentials appear simultaneously in the intact and isolated hemispheres seems to give greater support to the hypothesis of the cortical origin of the drowsy stage of sleep. The fact that electrical activity during drowsiness is not induced by subcortical structures but is activity of truly cortical origin, is also shown by the infilling of the intervals in the periods of silence between groups of slow waves, which is observed in the isolated cortex during the onset of sleep.

During the transition from waking to sleep in animals corresponding changes are thus observed in the isolated cortex. The electrographic manifestation of the stage of drowsiness in the isolated cortex depends on the times elapsing after the operation and is most marked in the late period after cortical isolation.

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