CHANGES IN THE BIOELECTRICAL ACTIVITY IN VARIOUS AREAS OF THE CEREBRAL CORTEX IN DOGS, DURING THE FORMATION OF A TEMPORARY CONNECTION

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In the extensive literature on electroencephalography there is comparatively little data on the interrelationships between individual cortical areas. Certain authors [1, 2, 10, 11] have reported the synchronous flow of α-waves in different areas, and have explained this by irradiation of activity. Having noted the synchronism of the waves of action potentials, however, these authors have failed to give an adequate explanation of the physiological meaning of the phenomenon.

We investigated this problem [3] in M. N. Livanov's laboratory [4, 6, 7], when we showed that during the formation of a temporary connection in a rabbit, there is an evident similarity in the fluctuations of the action potentials in the cortex of the corresponding analyzers.

It was felt to be of considerable interest to examine the changes in the interrelationships between the waves of action potentials in various areas of the cortex during the formation of a temporary connection in dogs.

METHOD

Experiments were carried out on three dogs in a soundproof, screened room, and were of long duration.

Using the method described by L. G. Trofimov and R. N. Lur'e [7, 8], 11 electrodes were inserted into the cranial bones of each animal. When unipolar leads were used to tap the potentials, the indifferent electrode was applied to the nasal bones of the animal, and when bipolar leads were used the distance between the electrodes did not exceed 3-4 mm.

The potentials were fed into amplifiers, assembled by a symmetrical resistance-capacitance coupling scheme, and recorded on a loop oscillograph.

RESULTS

When the bioelectrical activity was simultaneously recorded from two points of the cortex situated within the bounds of the visual or auditory analyzers, it could be seen that waves of action potentials develop at nearly identical times. Differences were observed in the amplitude and also in the magnitude and duration of the reaction to adequate stimulation (especially in the cortex of the auditory analyzer, but the background activity was synchronous (Fig. 1, a, 1).

On the other hand, when action potentials were recorded simultaneously from two points of the cortex, one of which was situated in the visual analyzer and the other in the auditory, hardly any resemblance was shown in the timing of the bioelectrical activity.

In the same way, waves of action potentials were asynchronous when taken from two points of the cortex of the motor analyzer (or two areas when bipolar leads were used) corresponding to the representation of the fore and hind limbs*, even when the distance between them was 5 mm. No resemblance could then be observed between the flow of action potentials, whether with unipolar or bipolar leads (Fig. 1, b).

In dog No. 1, for instance, a very clear rhythm (about 25 waves per second) was recorded in the area of representation of the forelimb, which disappeared on passive elevation of the left fore limb (see Fig. 1, b). An analogy may evidently be drawn between this rhythm and the Rolandic rhythm in man.

It is apparent from the same figure that in the area of representation of the hind limb the amplitude of the action potentials was increased in response to passive elevation of the paw. At the same time a clear synchronism was observed between the waves of potentials in two points situated either within the area of representation of the forelimb or that of the hind limb (Fig. 1, a, 2).

These observations, which were evidence of the fine differentiation of the nucleus of the motor analyzer, demonstrated the necessity for accurate designation of the areas from which leads are taken for recording the EEG from the motor area.

*The correct positioning of the electrodes was verified by electrical stimulation of areas of the cortex situated beneath the inserted electrodes.

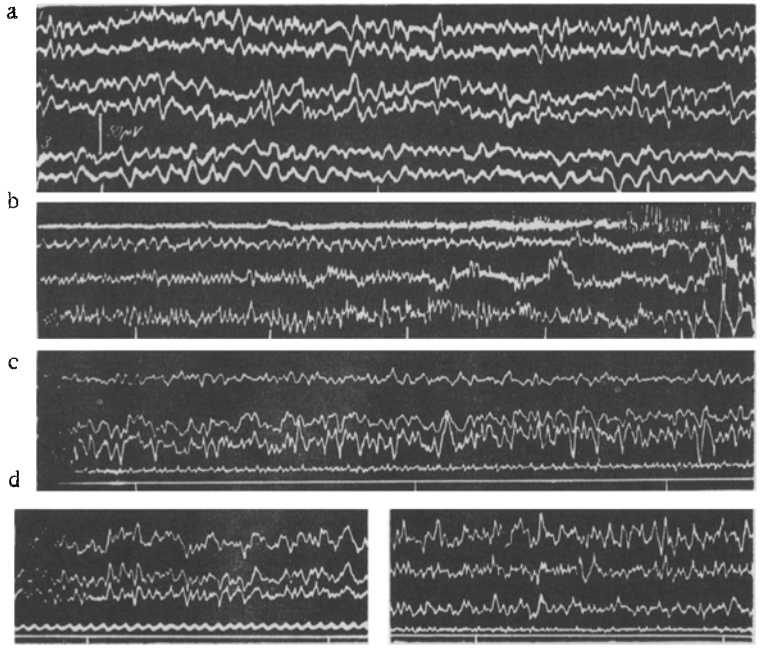

Fig. 1. Character of the interrelationships between the action potentials in the cortical ends of various analysors. a) Before formation of a conditioned connection (unipolar lead). From above down: 1) EEG from two points of the cortex in the area of the visual analysor; 2) the same, from the area of representaiton of the fore-limb; time marker (0.5 second); b) the same as in a (bipolar lead). From above down: Electromyogram (EMG) of the flexors of the fore limb; EEG of the cortex of the visual analysor; EEG from the area of representation of the hind limb; time marker (0.5 second). The arrow indicates the beginning of passive elevation of the limb; c) in response to a combination of a light and passive flexion of the forelimb (unipolar lead). From above down: EEG of the cortex of the visual analyzer; EEG taken from the area of representation of the hind limb; EEG from the area of representation of the fore limb; EMG; stimulation marker; time marker (0.5 second); d) the same as in c. From above down: EEG from one point in the area of representation of the forelimb; EEG from another point in the same area; EEG taken from the area of representation of the hind limb; EMG; stimulation marker; time marker (0.5 second); e) the same as in c and d. From above down: EEG from one point in the area of representation of the hind limb; EEG from another point in the same area; EEG of the visual analysor; EMG; stimulation marker; time marker (0.5 second).

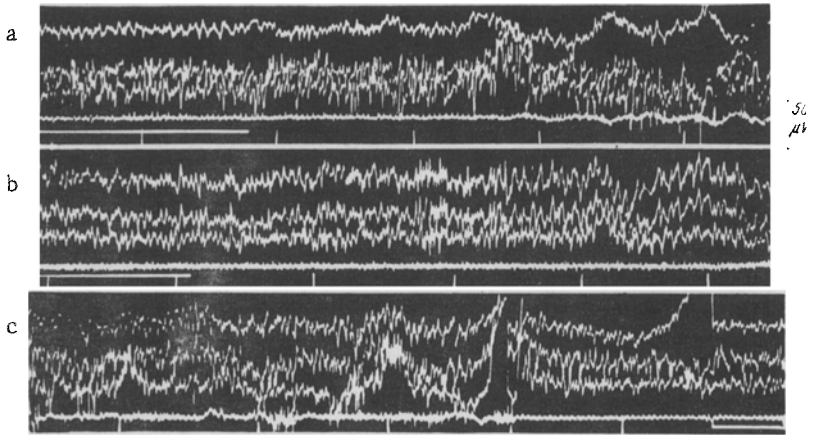

Fig. 2. Electrical activity of the nuclei of different analyzers during the time of action of a conditioned stimulus (unipolar lead). From above down: a) EEG from the area of the visual analyzer; EEG from one of the points of a "synchronous pair" in the area of representation of the hind limb (beneath the 8th electrode); the same, in the area of representation of the fore limb (beneath the 10th electrode); EMG stimulation marker; time marker (0.5 second); b and c) EEG from one point in the area of representation of the hind limb (beneath the 8th electrode); the same, in the area of representation of the fore limb (beneath the 10th electrode); EEG taken from the cortex of the visual analysor; EMG; stimulation marker; time marker (0.5 second) (c — to be read from right to left).

No regular rhythm was observed in two other dogs (Nos. 2 and 3), although the relationship between the electrical activity in the various areas of the cerebral cortex was the same as in the previous dog.

It was considered of interest to examine the changes in these relationships during the period of formation of a temporary connection. For this purpose a conditioned reflex was formed in dog No. 1 in response to a combination of the light of an electric lamp (5 seconds) and passive elevation of the left fore limb. Into the cranial bones of this dog were inserted 11 electrodes: 5 electrodes over the nucleus of the motor analyzer (the 8th and 9th – over the area of representation of the hind limb; the 10th and 11th – over that of the fore limb; the 7th over the area of representation of the hind limb in the opposite hemisphere); 2 electrodes (5th and 6th) – over the cortex of the auditory analyzer; 2 electrodes (3rd and 4th) – over the cortex of the visual analyzer; and 2 electrodes (1st and 2nd) were used as indifferent electrodes.

After the first [1-3] combinations, an evident change in the magnitude of the electrical reaction in the cortex of both the visual and the auditory analyzers was observed in response to the action of the light. No appreciable changes were observed in the interrelationships between the waves of action potentials in the nuclei of the different analyzers.

The increased reactivity observed in the first stages of the formation of a temporary connection was preserved, however, for only a very short time, and had disappeared by the 4th-5th combination. It was evidently brought about by an orientational reaction of the animal.

It can be seen from the electroencephalograms of this subsequent period that no change had taken place in the rhythm observed previously in the area of representation of the forelimb (see Fig. 1, b) in response to light; perceptible reactions in the area of representation of the hind limb and in the cortex of the visual analyzer were also absent.

Immediately after discontinuation of the sixth combination, the appearance of an obvious similarity between the bioelectrical waves in the areas of representation of the fore and hind limbs was observed for the first time. At the 8th combination this similarity was also maintained in the background activity, and it was further preserved during the combination and the after-action.

After two more experiments, the areas in which synchronism of the waves of action potentials was observed became concentrated. Synchronism was now observed only between two separate points of the cortex (see Fig. 1, c) one of which was situated in the area of representation of the forelimb (beneath the 10th electrode) and the second in that of the hind limb.

A pair of points with synchronous activity was thus formed in the nucleus of the motor analyzer. The similarity between the potentials of these points and of their pairs within the area of representation of the same limb was disturbed (compare Fig. 1, d and e with Fig. 1, a, 3). In addition, an obvious increase in reactivity was observed in these points of the cortex and also in the area of the visual analyzer in response to the action of the conditioned stimulus (Fig. 2, a).

These changes in the interrelationships between individual areas of the cortex in the areas of representation of the fore and hind limbs were evidently due to complex coordinational relationships, established in the nucleus of the motor analyzer when the animal was standing with its limb elevated. At this time, however, the cortex of the visual analyzer, to judge by the electrograms, was not yet connected with the cortex of the motor analyzer of the corresponding side.

At this stage synchronism was observed in the activity of the visual area and that of the area of representation of the hind limb on the opposite side. At the time of appearance of the conditioned reflex elevation of the limb, an obvious synchronism was found between the potentials in the nucleus of the visual analyzer and the "synchronous pair" of the nucleus of the motor analyzer (Fig. 2, b).

It is perfectly clear that in this case there are no grounds for speaking of manifestations of desynchronization. This is especially interesting because the combined stimuli were nonrhythmic and, as many authors have observed [5, 9], during the formation of conditioned reflexes to nonrhythmic stimuli changes of a desynchronizational character are found.

After the formation of a conditioned reflex to light, a defensive conditioned reflex to sound was formed.

A few combinations of a sound with electrical stimulation of the skin led to the disappearance of the selective synchronism, described above, in the activity of the two points in the cortex of the motor analyzer, and to the restoration of the original relationships (synchronism within the bounds of the area of representation of the fore and hind limbs).

Subsequently, during repetition of the combinations of the sound and the electrical stimulation of the skin, the synchronism between the action potentials within the area of representation of the fore limb became considerably weakened, and was preserved only in the area of representation of the hind limb in which the conditioned reflex was formed. At this time the cortex of the auditory analyzer gradually became involved in activity which was synchronous with the activity of the area of representation of the hind limb.

On reapplication of the combination of the light and elevation of the forelimb (after $1^1/_2$ months), the corresponding conditioned reflex appeared at the first trial; synchronism of the action potentials in the nuclei of the visual and motor analyzers was also restored (Fig. 2, c).

It must be emphasized that the synchronism of the bioelectrical activity, described above, was observed when the waves of potentials in each of the areas under comparison were polyrhythmic in character. Synchronization of rhythms could frequently arise without special preliminary procedures (especially by the use of rhyth-

mic stimulation). Similarity between action potentials in the form of irregular waves (especially if the areas of the cortex to be compared belonged to different analyzers) appeared only in response to the action of combinations.

These phenomena are of great interest, for they are evidence of selective connections between particular areas of the cortex.

It may evidently be suggested that the appearance of synchronism between waves of action potentials in particular areas of the cerebral cortex, which is found at a certain stage in the formation of a conditioned reflex, is one of the signs of the establishment of a temporary connection.

SUMMARY

Under the combined effect of two stimuli (nonrhythmic light and passive raising of the forelimb), a considerable change occurred in the character of the bioelectric activity in various cortical areas.

At first, these changes were limited to the nucleus of the motor analyzer (synchronic course of the waves of action potentials at two points of the cortex located in the areas of representation of the fore and hind limbs). Later, there appeared synchronous waves of action potentials between these two points and the nucleus of the visual analyzer. It may be suggested that the similarity in the waves of action potentials of various cortical portions points to the presence of selective connections between them and is one of the signs indicating establishment of a temporary connection.

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