ELECTRICAL CHANGES IN THE DOG CORTEX DURING THE DEVELOPMENT OF DEFENSIVE CONDITIONED REFLEXES

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Recently, many electrophysiological studies of conditioned reflexes in man and in animals have been made.

Consistent potential changes in different parts of the brain have been found to occur during their formation. [1, 4 - 10, 12 - 18]. Attention has been frequently directed to changes in reactivity (in the magnitude of the electrical response) during the formation of conditioned reflexes. By using rhythmical stimulation, regular synchronized oscillations close to the stimulus rhythm or to multiples of it were observed [2, 6 - 10]. When the stimuli were presented irregularly, desynchronization usually occurred [5, 13]. However, insufficient attention has been paid to the distribution of electrical activity in the different parts of the cortex or to its changes during the development of conditioned reflexes.

It has been shown in rabbits [3, 9, 10] that during the formation of temporary connections in the sensory cortex there is a similarity in the electrical potentials corresponding to the associated stimuli. Subsequently, as the conditioned reflex becomes more accurately defined, the similarity becomes less marked.

In our experiments on dogs we associated two unrhythmical stimuli (light and passive lifting of the foot), and it was shown that first there was a similarity in the form of the electrical potentials of the cortical motor areas of the front and hind limbs, and that later the potentials in the visual cortex came to resemble those of the motor cortical centers.

The object of the present investigation was to study the relationships between the electrical activity in the different parts of the cortex in dogs in which a defensive conditioned reflex was established. We were particularly interested in those parts of the cortex which received no direct stimulus.

METHOD

The experiments were carried out on two dogs in a sound-proof room.

Both carried electrodes held by implants fixed to the skull bone by the method described by L. G. Trofimov and R. N. Lur'e [11].

The electrodes were arranged as follows: eight were implanted in the bone over the right hemisphere, four over the motor cortex (the third and fourth over the hindlimb area, and the fifth and sixth over the forelimb area, the eigth and ninth were placed over the auditory cortex, the seventh and tenth over the postcentral gyrus, and two electrodes were implanted in the bone over the left hemisphere over the visual cortex. The first was the indifferent electrode. However in most cases, bipolar recordings were made with an interelectrode distance of 3 mm.

The potentials were fed to amplifiers with symmetrical condenser resistance couplings, and recorded on a string oscillograph.

In dog No. 1 a set (stereotype) of defensive conditioned reflexes was developed as follows: Bell (+) 1,000 cps sound generator (+), 300 cps sound generator (-), 12 w electric lamp (+). In dog No. 2 the left foot was also used and separate conditioned defensive reflexes to sound and to light were elaborated. In all cases rhythmical stimuli were used. Reinforcement was given by electrical stimulation of the skin of the foot by an induction coil and at a voltage of 1 - 2 cm above threshold on the scale of the instrument, and the rhythm of the voltage applied was the same as that of the conditioned stimulus. The duration of the unconditioned (electrical) stimulus was one second.

The experiments were carried out every second day. In each experiment, four to five combined stimuli were applied.

RESULTS

In both dogs, before the elaboration of the conditioned reflexes, no resemblance was observed between the waves of the visual auditory, cutaneous, and motor cortex nor between the cortical areas corresponding to the front and hindlimbs (Fig. 1 a and b). These cortical areas responded very little to adequate stimuli. However, when a pattern of conditioned reflexes (stereotype) was developed in dog No. 1, even by the second experiment there was a marked response in the relevant cortical areas to the combined stimuli. At this time a change was first noticed in the relationships between the waves of the different cortical areas: there was some synchronization of these waves in the auditory cortex and hind limb

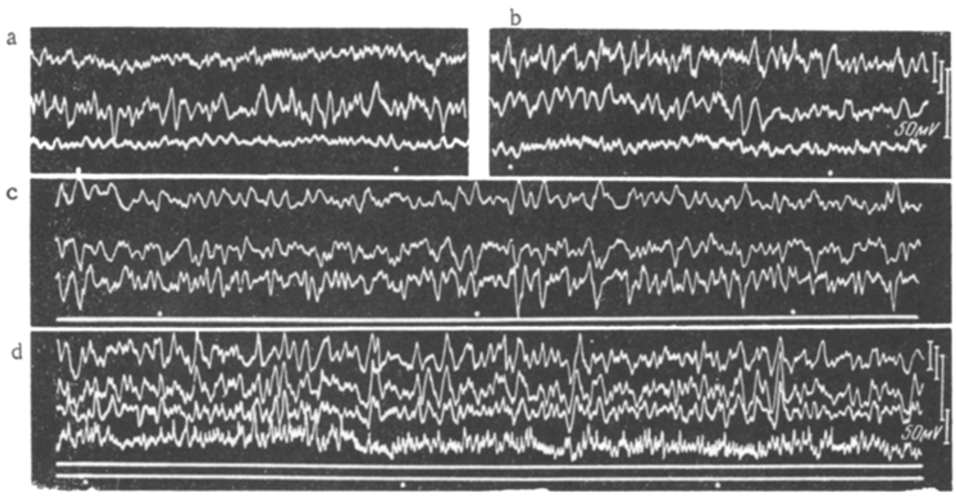

Fig. 1. Electroencephalogram of dog No. 1. Spontaneous activity. (Bipolar recording; time marker, 500 msec; calibration, 50μv). a − Before developing the conditioned reflex. Curves, from above downwards; EEG of the hind limb cortical area; b − after developing the conditioned reflex. Curves, from above downwards: EEG of the cutaneous area, EEG of the forelimb area, EEG of the hind limb area; c − development of a conditioned reflex pattern (stereotype). Curves, from above downwards: EEG of cutaneous area, EEG of auditory area, EEG of hind limb area; d — development of stereotype. Curves, from above downwards: EEG of cutaneous area, EEG of auditory cortex, EEG of hind limb area, EEG of forelimb area.

areas (Fig. 1c lower trace), but from the electroencephalogram traces it appeared that the cutaneous area (Fig. 1c) was not yet influenced.

In the next experiment, in addition to the auditory cortex and hind-limb area, the general sensory area also became synchronized. However, the change was temporary and disappeared three to four minutes after the combined signals had been given. Not until the seventh experiment was there a definite synchronization which was maintained until the end of the experiment in both the auditory and hind-limb motor cortex (Figs. 1, 2).

The last change was that of the visual cortex. At the same time, the fore-limb area as before showed no synchronization (Fig. 1d and Fig. 2b). It should be noted that the involvement of the visual cortex is very short-lived, and is not maintained as well from one experiment to another as the activity in the hind limb, cutaneous, and auditory areas (Figs. 1d and 2b). Possibly the effect is due to the instability of the conditioned reflex to light as well as to the placement of the electrodes (they were implanted in the bone over the right visual cortex, while all the other electrodes were on the left side).

It was important that the conditioned stimulus abolished the synchronization. This occurred chiefly through reducing the response in the hind limb cutaneous area, and also through the appearance of rapid waves characteristic of the visual cortex (Fig. 2e).

When the stereotype became firmly established, the synchronization of the waves in the cutaneous and auditory cortex was maintained even during the action of the conditioned stimulus. When the regular combination of signals were no longer given, the time for the recovery of synchronization in the above mentioned cortical areas was from 20 to 90 sec. After recovery, synchronization was mantained until after the end of the experiment, i.e. for one − two hours.

At the same time as the disturbances in the relationship of the activity of the different parts of the cortex occurred there were also changes in their reactivity: At first the effect of the conditioned stimuli was to cause the appearance of electrical waves having a rhythm either equal to the stimulation frequency or to a multiple of it (Fig. 2c); subsequently, these same rhythms were found in the areas corresponding to the unconditioned stimulus (Fig. 2d), and finally occurred in the latter area only (Fig. 2e). At this time there was a fall in the reactivity in the forelimb cortical area.

In dog No. 2, defensive conditioned reflexes to both sound and light were elaborated.

In Fig. 2f it can be seen that there is a marked similarity in the waves of the visual cortex and motor areas (the electrodes were implanted only over the hind limb area). In response to the conditioned stimulus, in addition to the conditioned limb movement there were also synchronized potentials developed which had a frequency equal to that of the stimulus.

The synchronization of the waves of the different parts of the cortex occurred only after all preparations had been completed and the door of the room closed (see Fig. 2b).

The waves from these cortical areas recorded during the preparatory period show no similarity (Fig. 2a).

• This result shows that the potential waves really do represent changes in the relationships of the different

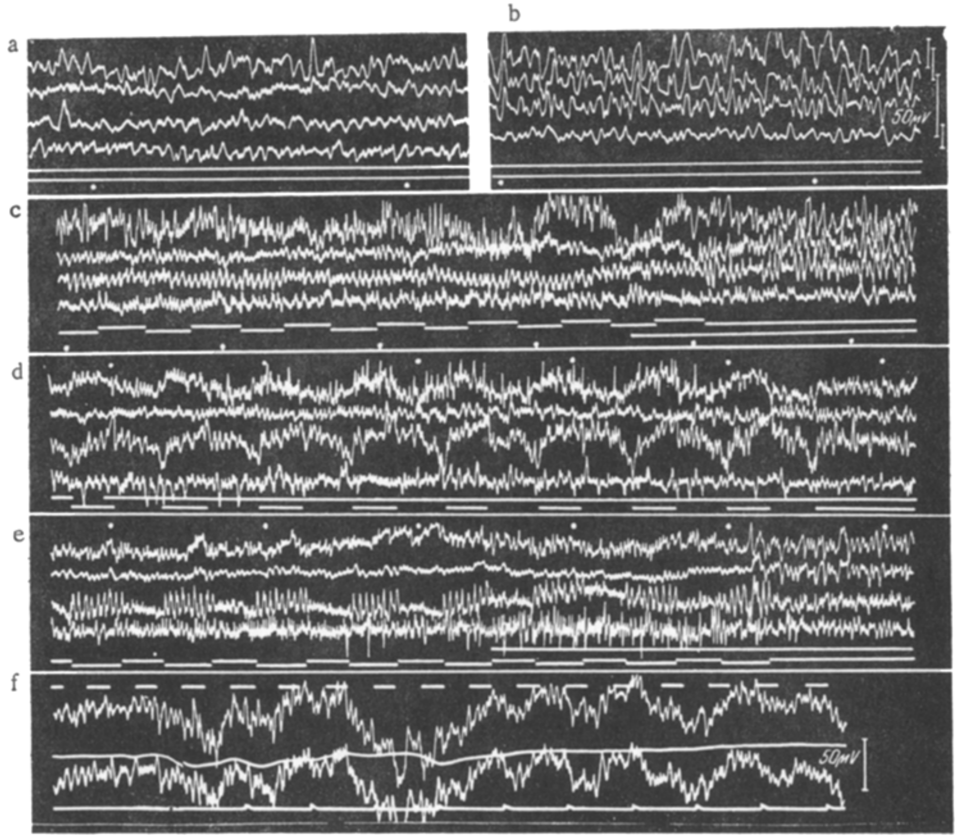

Fig. 2. Electroencephalograms of dog No. 1 (a – e) and dog No. 2 (f). Bipolar recording; time marker, 500 msec; calibration, 50μv). a Room open; b – two min after door was closed. The curves, from above downwards show EEGs of: auditory area, cutaneous representation, hind limb area, forelimb area, stimulus marker, record of limb movement; c – response to conditioned sound stimulus (indications as in Fig. 2 a,b); d – response to conditioned light stimulus. Curves, from above downwards show EEGs of: visual cortex, cutaneous representation, hind limb area, forelimb area, trace of limb movements, stimulus marker; e – response to sound conditioned stimulus. Curves, from above downwards show EEGs of: auditory cortex, cutaneous representation, hind limb area, visual cortex; record of limb movements, stimulus marker; c, d, and e are to be read from right to left; f – response to sound stimulation (monopolar recording). Curves, from above downwards: Time marker, 170 msec, EEG of hind limb area, trace of limb movements, EEG of auditory cortex, stimulus marker.

cortical areas and are of functional significance. Further evidence is that in a dog which in one experiment received the standard set of rhythmical stimulations, but at half the normal frequency, there was no disturbance of the electrical potentials. The reactivity of the cortial areas concerned and the magnitude of the conditioned reflexes were both greatly reduced. Subsequently, when the stimuli were once more given at the normal frequency, normal relationships were restored. Synchronization failure was also observed in another experiment when when the stereotype was altered by omitting the electrical reinforcement to the skin.

It must be emphasized that synchronization which developed through the formation of the conditioned reflexes was maintained subsequently; the electrical activity of the area representing the forelimbs never came into synchrony. This point was of special interest because the distance between the electrodes in the hind limb and forelimb areas was only 6 mm, whereas the distance between the hind limb area and the general sensory, auditory, and visual cortices had values from 16 to 45 mm. In our opinion, the results obtained agree with those which we obtained previously, and indicate that synchronization of the potentials is a sign of the formation of particular connections in the cortex during the development of coditioned reflexes.

SUMMARY

Electrodes were implanted into the skull over the different cortical sensory areas. It was found that in the development of defensive reflexes, a clear-cut synchronism in the potential waves occurred in the areas receiv-

ing the conditioned and unconditioned stimulations. This synchronism was very stable when a stereotype was elaborated. An important finding was that when training to the stimulus pattern resulted in movement of the hind limb, the electrical activity of the forelimb area never came into synchrony. These results indicate that connections developed in a dog's cerebral cortex during the elaboration of the conditioned reflex are selective even during the early stages of their formation.

LITERATURE CITED

[1] V. V. Artem'ev and N. L Bezladnova, Trudy Pavlov Inst. Fiziol 1, 228 (1952).

[2] O. V. Verzilova, Abstracts of Proceedings of the Eighth All Union Conference of Physiology, Biochemistry, and Pharmacology [in Russian] (Moscow, 1955) pp. 116 118.

[3] V. N. Dumenko, Trudy Inst. Vyssh. nervoi deyat., Ser. Fiziol. 1, 335 (1955).

[4] A. B. Kogan, Abstracts of Proceedings of the Fourteenth Congress on Problems of Higher Nervous Activity [in Russian] (Moscow, Leningrad, 1951) pp. 20-21.

[5] A. B. Kogan and N. O. Nikolaeva, Abstracts of Proceedings of the Conference on Problems of the Electrophysiology of the Central Nervous System [in Russian] (Moscow, 1958) p. 65.

[6] M. N. Livanov and K. L. Polyakov, Izv. AN SSSR 3, 286 (1945).

[7] M. N. Livanov and A. M. Ryabanovskaya, Fiziol. Zhur. SSSR 33, 5, 523 (1947).

[8] M. N. Livanov, T. A. Korol'kova, and G. M. Frenkel', Zhur. Vyssh. Nerv. Deyat. 4, 521 (1951).

[9] M. N. Livanov, Transactions of the Fifteenth Congress on Problems of Higher Nervous Activity [in Russian] (Moscow, Leningrad, 1952) p. 248.

[10] M. N. Livanov, Abstracts of Proceedings of the Conference on Problems of the Electrophysiology of the Central Nervous System [in Russian] (Leningrad 1957) p. 77.

[11] R. N. Lur'e, L. G. Trofimov, Fiziol. Zhur. SSSR 42, 4, 348 (1956).

[12] A. L. Roitbak, Abstracts of Proceedings of the Conference on Problems of the Electrophysiology of the Central Nervous System [in Russian] (Moscow, 1958) pp. 106 - 108.

[13] L. A. Novikova, V. S. Rusinov, and A. F. Semiokhina, Zhur. Vyssh. Nerv. Deyat. 6, 844 (1952).

[14] L. G. Trofimov, Abstracts of Proceedings of the Conference on Problems of the Electrophysiology of the Central Nervous System [in Russian] (Leningrad, 1957) p. 129.

[15] L. G. Trofimov, N. N. Lyubimov, and S. T. Naumova, Abstracts of Proceedings of the Conference on Problems of the Electrophysiology of the Central Nervous System [in Russian] (Moscow, 1958) p. 127.

[16] A. Gasto, F. Morrel et al., Zhur. Vyssh. Nerv. Deyat. 7, 25 (1957).

[17] F. Morrell and H. H. Jasper, Electroencephal. and Clin. Neurophysiol. 8, 201-215 (1956).

[18] N. Yoshii, P. Pruvot and H. Gastaut, Electroencephal. and Clin. Neurophysiol. 9, 4, 595-608 (1957).