A MECHANISM OF THE DIFFUSE COMPONENT OF THE CONDITIONED-REFLEX REACTION

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Electrophysiological investigations [1-4, 7] have shown that the formation of conditioned reflexes always begins with diffuse generalized changes in the electrical activity of both the cerebral cortex and the structures of the brain stem. Although as the conditioned reflex becomes established the changes in the electrical activity of the cortical and subcortical (including brain stem) structures of the linked analyzers become more clearly defined, the diffuse component constantly accompanies the conditioned-reflex reaction. One of the mechanisms of development of the diffuse brain changes is by the wide irradiation of excitation through collaterals of the principal afferent pathways and through the reticular formation of the brain. The present communication gives evidence that an additional source of the diffuse changes in the nervous system may be the feedback of afferent impulses to the brain.

We describe the results of an investigation of the electrical activity of various structures of the medulla and cerebral cortex of dogs during the formation of defensive and food conditioned reactions to light and sound stimulation.

EXPERIMENTAL METHOD

The electrical activity of the dogs' brain was recorded by bipolar electrodes (interelectrode distance 1.5-1.8 mm in tracings from the brain stem, 4-5 mm in tracings from the cortex) and a six- and 16-channel ink-recording electroencephalograph. The electrodes were inserted by a method described elsewhere [5, 6].

EXPERIMENTAL RESULTS

We noted that in 4 dogs, in response to the action of the unconditioned (defensive and food) stimulus or the conditioned sound stimulus, changes in the electrical activity of the visual region of the cortex were observed (high-amplitude waves), similar in appearance to the waves appearing during the action of flashes of light (Fig. 1, A).

It will be seen in Fig. 1, B that the action of the electrical stimulus on the skin of the right forelimb was accompanied by a very slight increase in the electrical activity of the structures in the medulla from which recordings were made, by signs of desynchronization (increased rate and decreased amplitude of the electrical waves) in the motor (gr. cruciatus) and auditory (gyr. sylvius, gyr. ectosylvius) zones of the cerebral cortex and the appearance of high-amplitude (150 μV) in the visual cortex (gyr. marginalis), with a duration of 200 millisec and very similar in amplitude and shape to the potentials evoked by light stimuli (see Fig. 1, A). As Fig. 1, B shows, these potentials sometimes appeared in the absence of stimulation.

In Fig. 1, C we show the recording of the electrical activity of different structures of the medulla and cortex during a conditioned defensive reflex to sound, producing a decrease in the electrical activity of the brain-stem structures before formation of the reflex. The action of this conditioned sound stimulus (10 distinct clicks per sec, each 10 millisec in duration, 56 dB) caused desynchronization of the activity in the structures of the medulla and of the cortical ends of the linked analyzers (auditory and motor). The defensive reaction coincided with a decreased activity in the medullary structures. The decrease in activity was most marked in the nuclei of the fasciculi gracilis et cuneatus and of the reticular formation of the brain stem, and less marked in recordings made from the cochlear nucleus. Repeated elevation of the limb and electrical stimulation of the skin were accompanied by restoration of the initial electrical activity. Throughout the period of action and after-effect of the sound stimulus, high-amplitude waves were observed in the visual zone, similar to those observed during the action of the sound stimulus.

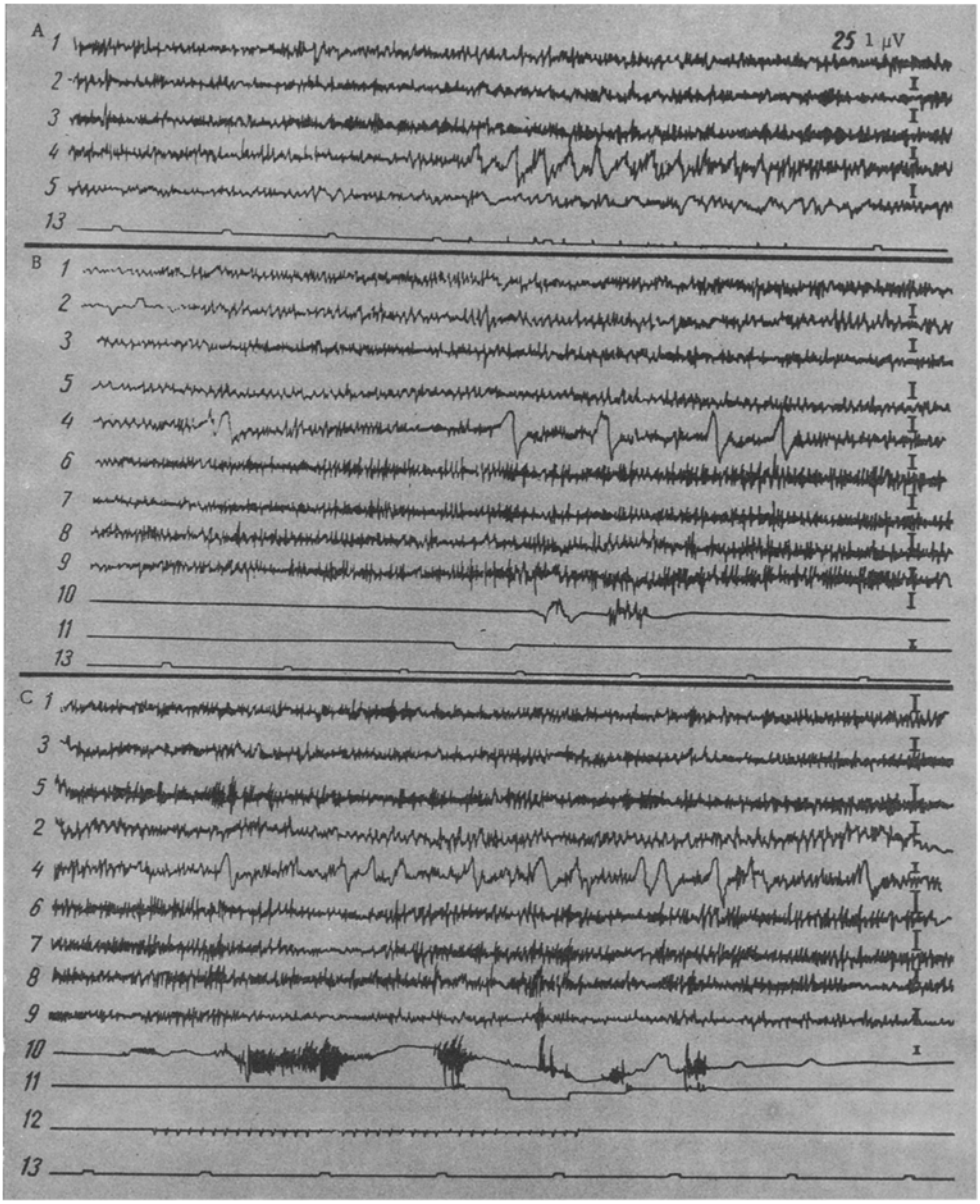

Fig. 1. Changes in the electrical activity of various structures of the brain of the dog Belyi during the action of a rhythmic (4 per sec) light stimulus of intensity 1 lx on a screen situated 1 m from the animal's eyes (A), unconditioned defensive reaction (B), and conditioned defensive reflex to a sound stimulus (C) (54th combination). 1) EEG gyr. cruciatus posterior; 2) gyr. sylvius posterior; 3) gyr. ectosylvius posterior; 4) gyr. marginalis; 5) gyr. suprasylvius; 6) gracilis; 7) nucl. cuneatus; 8) nucl. cochlearis; 9) nucl. centralis interior (form. reticularis); 10) EMG of right forelimb; 11) marker of nociceptive stimulus; 12) marker of conditioned sound stimulus; 13) time marker (1 sec) and of light stimulus (calibration 25 μV).

Analogous induced potentials in the visual cortex also appeared in response to conditioned stimuli of the defensive reaction of lower intensity (because of lack of space these are not illustrated).

A similar phenomenon could also be observed in the visual zone during the performance of food conditioned reflexes.

In Fig. 2, A we show 82 combinations of the sound stimulus (interrupted tone of 500 cps, 70 dB, 4 per sec) and the food stimulus (powdered meat and biscuit). The rhythmic sound stimulus caused well marked primary effects in the auditory zone of the cortex (gyr. ectosylvius posterior), slight increase in the activity in the gyr. orbitalis et coronaris,

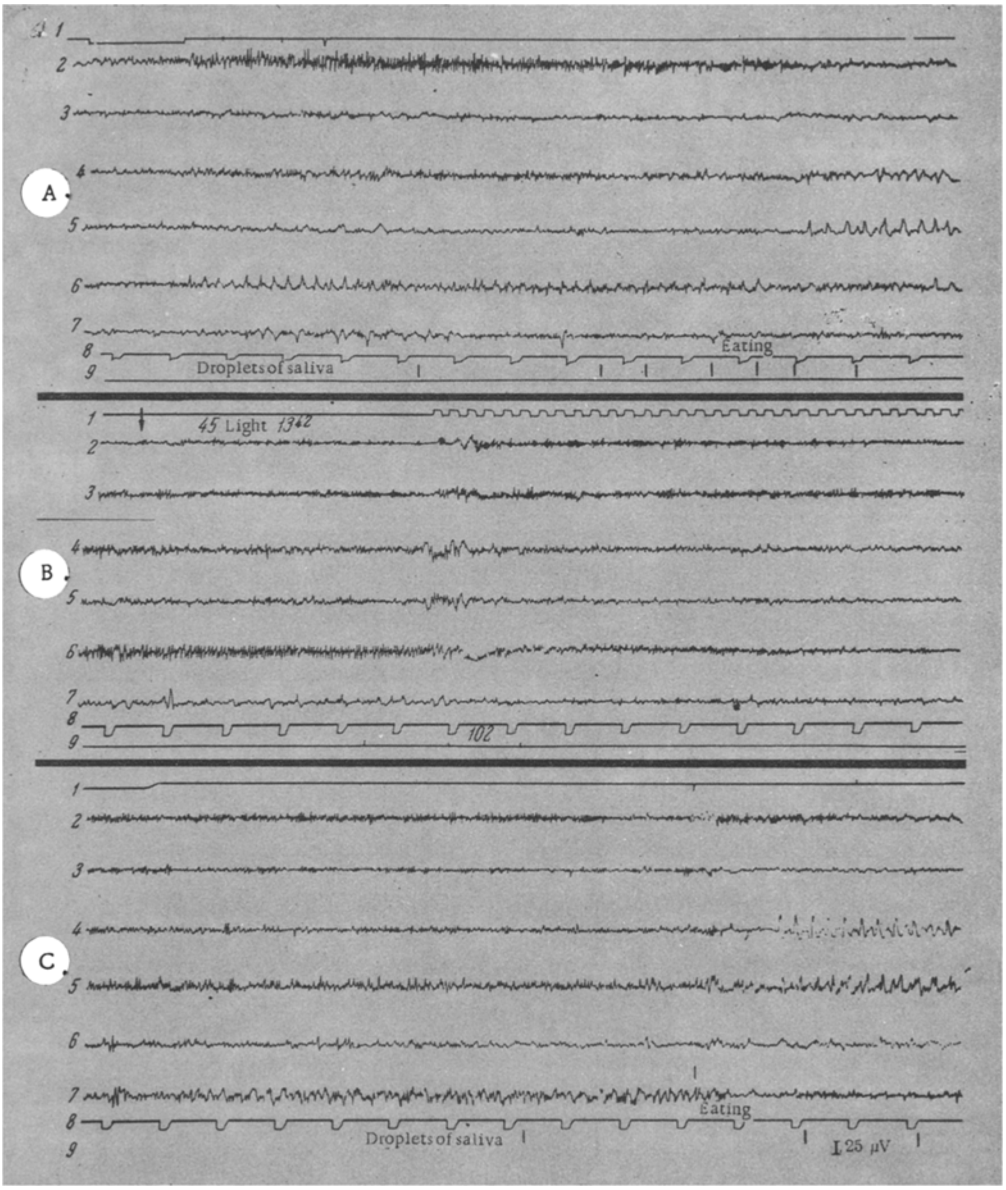

Fig. 2. Changes in the electrical activity of different structures of the cerebral cortex of the dog Kutsii during the isolated action of a rhythmic sound stimulus and during its combination with unconditioned food reinforcement (A), of conditioned inhibition and its combination with a conditioned sound stimulus (B), and of a conditioned light stimulus and its combination with unconditioned food reinforcement (C). In A: 1) marker of sound stimulus. In B: arrow) onset of action of conditioned inhibition (continuous light) from a 20 W electric lamp situated 1.5 m from the dog; marker of conditioned sound stimulus. In C: marker of conditioned light stimulus from a 20 W electric lamp situated 1.5 m from the dog. In A, B, and C; 2) EEG of gyr. cruciatus; 3) gyr. coronarius; 4) gyr. orbitalis; 5) gyr. sylvius anterior; 6) gyr. ectosylvius posterior; 7) gyr. marginalis; 8) time marker (1 sec); 9) marker of drops of saliva (calibration 50 μV).

a considerable increase in the motor cortex (gyr. cruciatus), and no visible changes in the gyr. sylvius anterior. In the marginal gyrus (visual cortex) potentials with an amplitude of 75 μV and duration of 200 millisec were observed, similar to those appearing in this region in response to the action of the rhythmic flashes of light (Fig. 2, C). During the continued action of this sound stimulus these waves in the visual cortex became less frequent, coinciding with the development of salivation and the act of eating. As we showed previously, the latter is accompanied by a rise in the level of excitation in the anterior sylvian and orbital zones of the cortex and by a simultaneous decrease in the activity in the remaining cortical zones.

An interesting feature was that if the action of the conditioned sound stimulus preceded that of the light stimulus (Fig. 2, B), i.e., conditioned inhibition was produced, the inhibitory reaction in these cases was not accompanied by the appearance of analogous induced potentials of the visual zone of the cortex, nor were induced potentials observed in the auditory zone of the cortex, where the activity was slightly depressed. In the remaining zones of the cortex the initial moment of action of the sound stimulus coincided with a burst of activity, followed in the cortical structures by restoration of the initial level of activity and a slight decrease, and in the motor and orbital areas by a slight increase.

Hence, the formation of internal inhibition to sound stimuli was not accompanied by the appearance of the changes, as described above, in the electrical activity of the visual cortex.

In Fig. 2, C we show the EEG of the cortical structures during the food conditioned reaction to rhythmic light stimulation (4 per sec). The period when the light acted alone was accompanied by the appearance of induced potentials, following (although not always regularly) the rhythm of stimulation. The induced potentials were similar in shape, duration, and amplitude to those observed in response to the action of the conditioned sound stimulus, but they were irregular in character.

An interesting fact was that rhythmic light stimulation was not accompanied by waves in the auditory zone of the cortex analogous to those arising in the visual cortex in response to the action of the conditioned sound stimulus. Very slight signs of desynchronization were observed in the remaining zones of the cortex. Food reinforcement and the act of eating were accompanied, as also in the case of the conditioned reflex to sound, by an increase in the activity in the orbital and anterior sylvian gyri. At the same time the induced potentials disappeared from the visual cortex and the activity in the other cortical zones fell.

What is the mechanism of development of waves of potentials in the visual cortex resembling the responses to flashes of light ? It seems that excitation arrives here from its origin, either in the optic system only, or in this system and also in other brain structures, but insufficiently detected because of the particular arrangement of the electrodes. The most probable explanation is that changes of the type of induced potentials were more marked in the optic system because the unconditioned and conditioned stimuli were accompanied by a redistribution of the tone of the limb and trunk muscles and by the appearance of a local motor reaction [1]. Both these processes were accompanied by changes in the position of the head and, consequently, in the intensity of the light falling on the eyes. The "positional" and "local" excitation followed one another in a certain order, so that the position of the head (and, consequently, the intensity of light falling on the eyes) varied. Moreover, the defensive reaction led to some degree of motor excitement of the animals, and this also affected the intensity of illumination. During the action of the sound stimulus, frequent waves of the type of induced potentials could therefore be observed in the visual cortex.

It should be noted that a marked desynchronization of activity took place in other parts of the brain during the action of the unconditioned and conditioned defensive reflexes. We think that the diffuse excitation arising in response to the direct action of the light stimulus was brought about by the action of nonspecific structures and intensified by the afferent impulses fed back from various sensory organs. In this paper we have attempted to show that this additional afferent system may be present in the visual analyzer.

SUMMARY

In investigating the dynamics of electrical activity in various zones of the cerebral cortex it was noted that during the elaboration of defense and food conditioned reflexes in dogs in response to the action of unconditioned (defense and food) stimuli or conditioned sound signal oscillations resembling by their appearance induced potentials observed during the action of rhythmic light stimulation appeared in the cortical end of the visual analyzer. The appearance of electrical oscillations in the visual cortex in response to unconditioned and conditioned sound stimuli, is explained by the redistribution of the tone of muscles of the extremity and body, leading to a change of the position of the head and, consequently, of the eye illumination. The results of the present investigation may point to the fact that the reverse afferentation of the visual analyzer may also serve as the source of diffuse changes.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
