THE DOMINANT FOCUS OF EXCITATION IN THE FORMATION OF A CONDITIONED REFLEX

M. Ya. Rabinovich and L. G. Trofimov

Electrophysiologic Laboratory (Head -- Professor L. G. Trofimov), Institute of the Brain (Director -- Full Member of the USSR Academy of Medical Sciences, Professor S. A. Sarkisov)

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As the result of studies of the mechanisms of cortical function by means of electroencephalography made in recent years some new facts have emerged concerning the relation between a dominant focus of excitation in the cortex and the mechanism of temporary connection formation. I. P. Pavlov [6] suggested that the formation of a conditioned reflex could be based on the ability of an adequately excited cortical focus to direct towards itself weaker stimuli arriving from the outer and inner environments; this concept brought together the mechanism of the formation of temporary connections and the properties of a dominant focus.

Electrophysiologic facts now available indicate the existence of a dominant focus of excitation in the cortex during the formation of a conditioned reflex. There is, however, not a single opinion on the location of this focus. Some workers [1, 7, 8] consider that the dominant focus arises, as suggested by Pavlov, in the cortical representation of unconditioned reflex activity. According to the data of others [4, 10] the formation of a dominant focus occurs at that point of the cortex on which the stimulating signals impinge.

The present work reports certain data obtained during the study of electrical phenomena in the cortex of the motor, auditory and visual analysors during the formation of a motor-defense conditioned reflex to sound and light; these data are relevant to the question of a dominant focus in the formation of temporary connections.

EXPERIMENTAL METHODS

Experiments were carried out on dogs with implanted electrodes according to the method usually employed in this laboratory [2]. A conditioned motor-defense reflex (flexion of the hind limb) was established in the animals to rhythmic auditory and visual stimuli which were reinforced by electric stimulation of the hind limb skin with a lag of 3-4 seconds.

Records were taken from the cortical terminations of the motor (g. cruciatus post.), auditory (g. ectosylvius med.) and visual (g. lateralis and g. ectolateralis) analysors on the hemisphere contralateral to the limb being stimulated.

DISCUSSION OF RESULTS

An analysis of the electroencephalograms (EEG) recorded during the formation of a conditioned reflex (present and previous studies [3]) shows even at the beginning of the formation of a temporary connection the conditioned stimulus evoked a definite increase in the amplitude and frequency of potentials in all the areas investigated -- motor, auditory and visual. These changes appear with the first few combinations of the conditioned and unconditioned stimuli and precede the appearance of the conditioned motor reaction. Similar generalized changes of potentials towards excitation are noted in the period when the stimulus signal begins to elicit a definite motor reaction.

Later, as the conditioned reflex becomes more firmly established, the stimulus signal evokes changes of potential predominantly in those cortical zones between which a temporary connection is being formed. Figure 1 shows that definite increases of the amplitude and frequency of potentials in the cortical terminations of the motor and auditory analysors are seen when a sufficiently firm motor-defense reflex to sound had been established (144 combinations). The amplitudes in the motor cortex increase from 10-20 μV in the "background" record to 35 μV at the moment when the signal stimulus begins to act and up to 35-55 μV at the moment associated with the conditioned motor reaction. In the case of the auditory cortex the amplitudes increase from 20 to 40 μV at the moment of the sound stimulus and up to 60 μV during the motor reaction. The frequency rises from 35-36 to 40 per second in the motor cortex and from 25-27 to 32 per second in the auditory cortex. The first period of enhanced amplitude and frequency recorded from the motor and auditory cortex at the moment when the signal stimulus begins to act has a small latent period and lasts about 0.5 seconds.

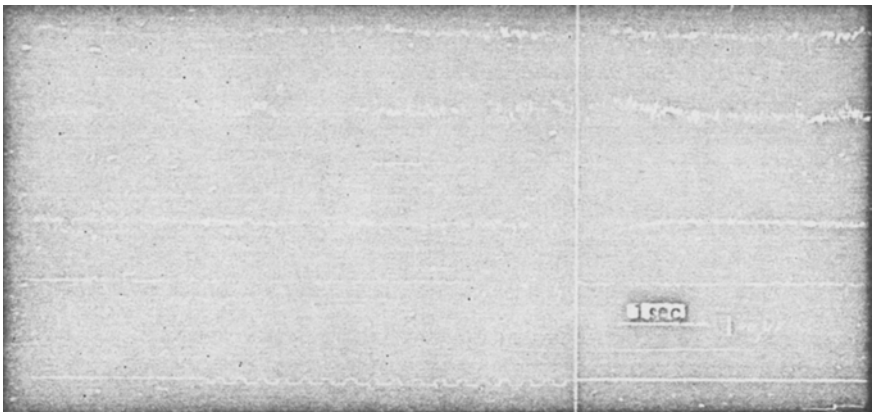

Fig. 1. Electrical activity of the cortical terminations of the motor, auditory and visual analysors during a conditioned defense reflex to sound. Dog Zhuk. Right hemisphere. Bipolar record.
Records from above downward; cortical electrogram of motor analysor; same, auditory analysor same, visual analysor; record of movement of the hind leg. Signal marker of the auditory stimulus (sound 500 cps with frequency interval 4 per second). Artefact from electric stimulation of skin excluded from all records.

In other words, the cortical centers of the analysors directly involved are in a state of excitation which, in the present case, begins almost simultaneously with the action of the signal stimulus, becomes stronger at the moment of the motor reaction and ends after the discharging event—movement. No changes of this nature are observed in the potentials of the visual cortex which, in this particular case, is not directly involved in the formation of the temporary connection. In fact, during the formation of the conditioned defensive reflex to sound the amplitude of the waves on the visual cortex was diminished even in the "background" records.

If the establishment of a firm conditioned defensive reflex to sound is followed by the development of a defensive reflex to light, the changes in the cortical motor and auditory analysors during the action of the new signal stimulus remain the same in character as during the action of sound. Figure 2 shows records of the electrical activity of the motor, auditory and visual cortex in the same dog but using a light signal stimulus started 5 minutes after the 140th combination with sound. The potentials in the motor cortex showed an increase in amplitude from 15-20 μV in the "background" record to 40-45 μV under the action of the light stimulus, while the frequency rose from 35-38 to 44-45 cycles per second. In the cortical auditory analysor the amplitudes increased from 20 to 50-60 μV and the frequencies from 26-28 to 35-38 cycles per second.

In the cortical visual analysor on which the signal stimulus impinged directly there was barely perceptible increase in the amplitude of the waves, while the frequencies remained the same as in the "background" record. Judging by the character of the EEG changes, a state of excitation is produced in the motor and auditory

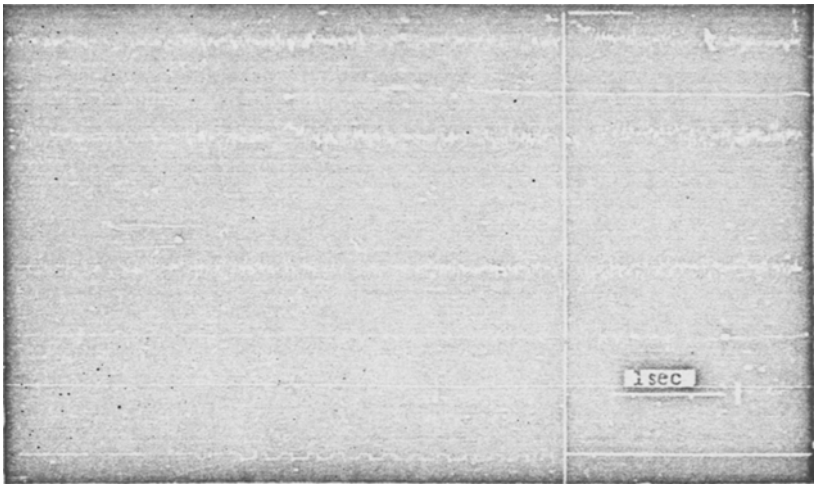

Fig. 2. Changes in the electrical activity of cortical motor, auditory and visual analysors under the action of light signal stimulation. Dog. Zhuk. Right hemisphere. Bipolar recording.
Records from above downward: four upper records same as in Fig. 1. Lower record – signal marker for conditioned light stimulus (electric lamp with flicker frequency 4 per second).

analysors, evoked by impulses from other cortical areas, and this focus of excitation can inhibit the responses from other cortical areas to stimulation directed to them. When a conditioned reflex reaction to light is established, then an analogous state of excitation to that described for the association of the motor and auditory analysors arises in the motor and visual areas.

An interesting fact was noted in the course of the experiments. If a random movement occurred in the animal's hind leg (the limb under investigation) unconnected with any of the stimuli being used, changes in the EEG potentials could be detected which depended on the particular conditioned stimulus which preceded the random movement. If, for example, the random movement occurred directly after the conditioned reflex response to sound (Fig. 3,a) the EEG changes were similar to those which took place during the conditioned reflex to sound, i.e., the motor and auditory areas showed increased amplitudes and frequency of the waves, while the changes in the visual area were much less pronounced. If, however, the random movement occurred following the conditioned reflex reaction to light (Fig. 3,b) excitation took place in the cortical components of the motor and visual analysors, while the cortical components of the auditory analysor showed signs of active inhibition – appearance of slow waves.

The facts described demonstrate that when a conditioned reflex is formed, a focus of excitation appears in the cortex; this focus has a number of distinctive features. It appears every time under the action of a conditional stimulus and disappears after the discharging act – the conditioned reflex reaction. The focus of excitation, arising under the action of the signal stimulus, embodies both cortical areas involved in the association and inhibits the third area which is not directly concerned in the formation of a given temporary connection (see Fig. 1). The same focus of excitation can arise in response to impulses from other sources and it then reduces the ability of other cortical areas to respond to stimuli aimed directly at them (Fig. 2). And, finally, this focus of excitation possesses certain inertia as shown by the fact that random movements of the limb under investigation can reproduce the distinctive EEG changes which preceded these random movements (see Fig. 3).

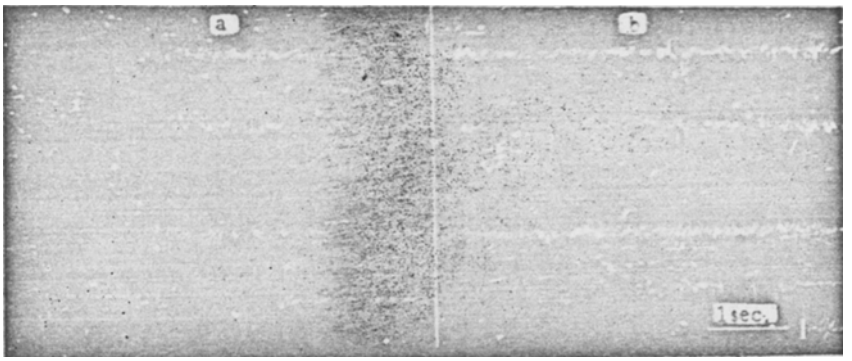

Fig. 3. Changes in the electrical activity of cortical motor, auditory and visual analysors during random movements of the hind leg being studied, after the use of conditional stimuli.
a) auditory stimulus; b) (right) light stimulus. Dog Zhuk. Right hemisphere. Bipolar record. Records from above downward same as in Fig. 1.

These distinctive features of the focus of excitation which appear during the formation of a conditioned reflex show that the focus has some properties of dominance. As can be seen from the encephalograms a dominant focus is not formed at some one point on the cortex but extends to and includes those cortical structures between which the connection is being established. The EEG s show that all the changes undergone by this focus under the influence of various signal stimuli characterize it as a functional entity; its structural components, however, can be different, and often widely separated, areas of the cortex. This is in complete agreement with the views of A. A. Ukhtomsky, who defined dominance as a phenomenon based on the excitation of a whole constellation of centers.

Cases where the action of a new signal stimulus reproduces cortical changes associated with a state of excitation characteristic for the preceding temporary connection but does not elicit the conditioned reflex reaction merit particular attention (see Fig. 2). It would seem that the excitation of the cortical components of the motor and auditory analysors clearly reflected in the EEG should evoke a corresponding motor reaction. The absence of such reaction can be explained by the new signal stimulus restoring only part of the previous dominance. A. A. Ukhtomsky [9] supposed that cortical and somatic components should be distinguished in the dominant entity, and that in connection with this "the preceding dominance is restored either in a very contracted way with very small inertia—only by the cerebral components, or with the full previous inertia, occupying the centers for a long time and displacing from them other reactions." Since under the influence of a new signal stimulus—light—the previous dominance expressed itself only in excitation of the motor and auditory areas of the cortex the new signal stimulus evidently restored only the cortical components "with barely perceptible excitation in the muscles" [9]. The somatic components of the previous dominance (motor reaction) remained inhibited.

Application of electrophysiologic methods to the study of conditioned reflex activity in animals has revealed that the electrographic evidence of excitation of the corresponding cortical areas is not always associated with a motor reaction even in those cases when an effective and firmly linked signal stimulus is used.

On the other hand, it is not infrequently observed that a conditioned motor reaction may be very definite and pronounced with no discernible changes (or only very small changes) in the EEG from the corresponding areas (Fig. 4). Such "unsuccessful" records are encountered particularly frequently when the conditioned reflex is firmly established, and investigators tend to disregard them and omit them from demonstrations. Yet they could be taken as evidence of the possibility of restoring only the somatic components of the dominance with "barely discernible" participation of the cortical components. These findings coincide with the observations of L. A. Novikova, V. S. Rusinov, and A. F. Semiokhina [5]. The latter were studying cortical association (or connection) under the influence of an artificially induced (direct current) dominant focus and found that in some cases the stimulus elicited movement of the limb without perceptible change in the electrical activity of the cortex, while in other cases stimulation produced definite changes in the EEG without reflex movement of the limb.

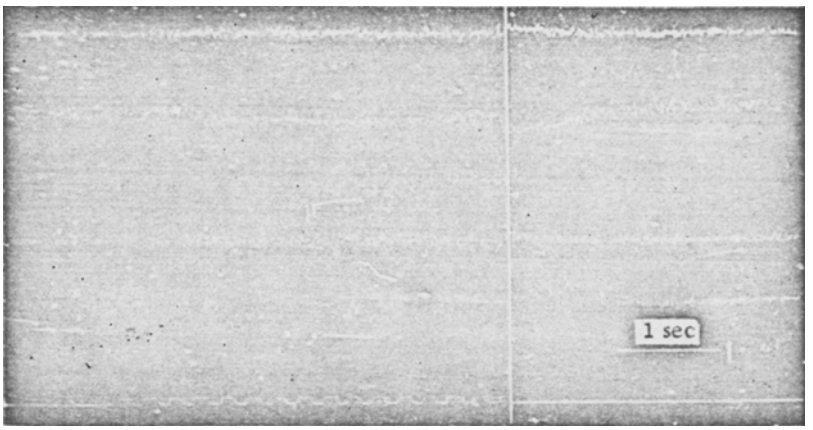

Fig. 4. Electrical activity of cortical components of the motor, auditory and visual analysors during a conditioned defense reflex to sound. 136th combination. Dog Zhuk.
Records from above downward same as in Fig.

The present authors realize that the facts submitted are far from solving this important neurophysiologic problem. The aim of this work was not so much the solution as the re-posing of the question of interrelations between the properties of dominance and physiologic mechanisms of the formation of temporary connections.

SUMMARY

Electroencephalographic data on the formation of a dominant focus of excitation during the development of defense conditioned reflexes provoked by light or sound were analyzed. The experiments were performed on dogs with permanently implanted electrodes.

It has been established that during the development of conditioned reflex connections the formation of a focus of excitation of the dominant type is taking place in the cerebral cortex. The dominant focus incloses cortical structures involved in the formation of the conditioned reflex bonds.

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