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## **The Effect of the Removal of Interprojective Fields of the Cerebral Cortex on the Higher Nervous Activity of Animals**

There is a great body of evidence which indicates that partial ablations of the cerebral cortex, besides specific effects concerning the functions of particular analysers, produce general disturbances of the higher nervous activity. These consist in a more or less pronounced conditioned hypo- or areflexia, disinhibition of inhibitory conditioned reflexes, etc. (cf. Pavlov, 1927, ch. XIX, Voronin, 1948). How far these general disturbances depend on the site of the lesion is still a matter for elucidation. The investigations undertaken in this laboratory, of which the experiments reported here are a first step, try to approach this problem.

The present report represents a comparative study of the effect of the partial frontal and parietal ablations of the cerebral cortex upon the motor alimentary conditioned reflexes (called by us conditioned reflexes of the second type, Konorski and Miller, 1933).

The first stage of the experiments consisted in elaboration in dogs of both excitatory and inhibitory conditioned reflexes to various stimuli (auditory, visual and tactile). The excitatory conditioned reflexes were formed in such a way that the dogs were trained to rise their foreleg and to put it on the foodtray in response to particular stimuli, each movement being reinforced by food. The inhibitory conditioned reflexes were established either by applying, without reinforcement, certain stimuli similar to those reinforced

by food (differentiation), or by combining an additional stimulus (conditioned inhibitor) with a positive conditioned stimulus applied without reinforcement (conditioned inhibition). The procedure of the elaboration of conditioned inhibition was the following; the additional stimulus was applied for a few seconds, and immediately after its cessation the conditioned positive stimulus was applied. When the dog learnt to refrain from the motor reaction to the stimulus preceded by the conditioned inhibitor, the interval

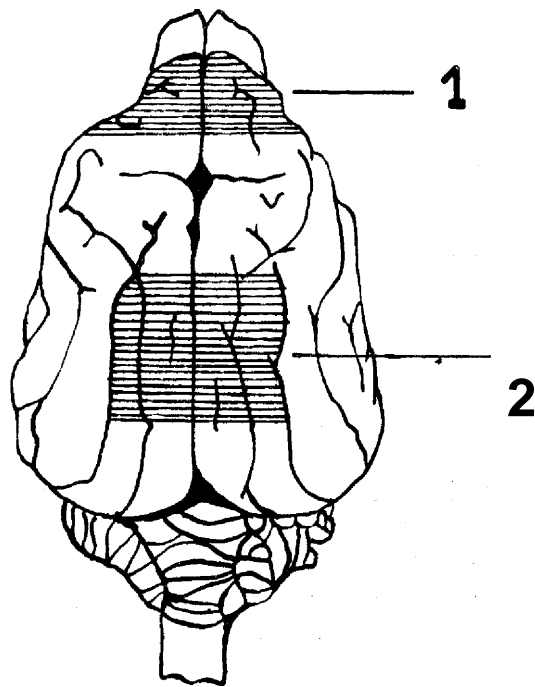


Fig. 1. Cerebral cortex of the dog. The hatched areas represent the site of operations.

between both stimuli was gradually lengthened until the task of inhibiting the motor reaction to this combined and extended stimulus was on the verge of becoming too difficult for the dog. Usually interval was brought to 10-20 seconds.

When all requisite excitatory and inhibitory conditioned flexes were formed and fixed, one of the two cortical ablations

represented in fig. 1 was performed. In the ablation Nr 1 the *gyrus proreus* and *orbitalis* were removed, care being taken to spare the olfactory tracts and bulbs. In the ablation Nr 2 the *gyrus supra-splenialis*, *gyrus entolateralis*, and the anterior part of the *gyrus ectolateralis* were removed. All the operations were bilateral. As soon as the animals improved after operation (which usually took 3-5 days), the effect of the ablation on the conditioned reflex activity was studied.

The experiments were carried out on 5 dogs. In two animals only a frontal ablation was made, in the third dog first a frontal and after a lapse of time a parietal ablation was performed, in the fourth dog the order of ablations was reversed, and in the fifth dog there was first a superficial frontal ablation made, then a parietal ablation, and finally a second, more radical frontal ablation.

The following results were obtained.

The parietal ablations did not produce any disturbance either in excitatory or inhibitory conditioned reflexes. Even the most difficult inhibitory reflex, the one to the conditioned stimulus following at some interval after the conditioned inhibitor, was perfectly preserved.

On the other hand all frontal ablations produced a marked and protracted disinhibition of inhibitory conditioned reflexes. Three degrees of this disinhibition could be discerned. 1) In the period of the strongest disinhibition the dog performed the trained motor reaction incessantly to all stimuli and during the intervals between their application. This form of behaviour was observed only during the first postoperative days and was not present in all dogs. 2) After some time the motor reactions during the intervals disappeared, but the dog reacted positively to both excitatory and inhibitory stimuli. 3) Gradually the inhibitory response to the differentiated stimuli was re-established, but the dog could not inhibit the motor reaction to the conditioned stimulus preceded (even immediately) by the conditioned inhibitor. The restitution of this form of inhibition, especially when the interval between both the stimuli was protracted, was very slow and in some dogs took several months to be complete.

As an especially demonstrative example of these results, the experiments with the dog on which three operations were performed may be adduced.

The first operation in which the dorso-medial parts of the frontal lobes were removed resulted in a marked disinhibition of inhibitory conditioned reflexes. In the first experiment after the operation the dog performed the conditioned motor reaction incessantly throughout the experimental session. In the following sessions the movements during the intervals disappeared, but the dog reacted positively to both excitatory and inhibitory conditioned stimuli. Gradually the inhibitory reflex to the differentiated stimuli was restored, then to the conditioned stimulus preceded immediately by the conditioned inhibitor, and finally, after 11 weeks, the dog succeeded in inhibiting the motor reaction when the interval between these stimuli was 5 seconds.

7 months after the first operation the parietal ablation, according to fig. 1, was performed. This ablation caused no disinhibition the conditioned reflex activity remained completely normal.

Then, R months later, a second frontal operation was made, which the orbital surface of the frontal lobes was removed. This operation again resulted in a strong disinhibition, this time even more prominent than after the first ablation. The period of the maximal disinhibitory effect (when the dog displayed his motor reaction incessantly during a whole experimental session) lasted more than 2 weeks, and full restoration of the conditioned inhibition (with the interval between the stimuli protracted to 5 seconds) is not completed even now, three months after the operation.

The problem arises, whether the additional postoperative training of inhibitory reflexes plays any role in their restoration. To answer this question, in various experiments some (or all) inhibition stimuli were tested only from time to time, in order to avoid, much as possible, their retraining. It was thus established that the inhibitory capacity of the dog was gradually restituted independently of the additional training, although it cannot be excluded that such a training may speed up the process of restoration. But on the other hand it was observed that if an inhibitory stimulus was applied too frequently during the period when the inhibitory power of the dog was strongly

diminished, heavy functional disturbances of the conditioned reflex activity were produced (experimental neuroses), and the inhibitory capacity of the dog became even worse.

According to our results the restoration of the conditioned inhibition is much more difficult for the animal than the restoration of the differential inhibition. Whether it is so because of the greater difficulty of this form of inhibition in general (which is rather doubtful), or because this form of inhibition involves some cortical mechanisms connected with frontal lobes, cannot be definitely answered.

Our results concerning frontal lobes ablations are consistent with many previous investigations which either directly (Afanasjev, 1913, Stanley and Jaynes 1949, Allen 1949) or indirectly (Babkin 1909, Shumilina 1949, Speakman and Babkin 1950, etc.) point out to the impairment, after such operations, of the inhibitory capacity of the animal, especially as far as its motor activity is concerned. The lack of disinhibition after our parietal operations suggests that the form of disturbance of the cortical activity found in our experiments cannot be regarded as a result of every kind of cortical ablation independently of its site.

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