LOCALIZATION OF FUNCTIONS IN THE CEREBRAL CORTEX OF THE RAT

REPORT 1. CONDITIONED REFLEX ACTIVITY IN THE RAT AFTER EXTIRPATION OF THE TEMPORAL CORTEX

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One of the principal supporters of the theory of equipotentialism was Lashley. On the basis of his own findings, obtained mainly from experiments on albino rats taught to pass through mazes of varying complexity, he concluded that extirpation of not less than 15% of the cerebral cortex adversely affected the animals' ability to learn [18]. This interference with learning was the more marked the greater the destruction to the cerebral hemispheres; in Lashley's opinion the part of the brain to suffer injury was completely irrelevant.

Opposing Lashley's views, I. P. Pavlov [10] pointed out that, when given the task of walking through the maze, "the rat may make use of smell, hearing, sight, and cutaneous and kinesthetic simuli. Since the special areas for these receptors are situated at various places throughout the hemispheres, and their elements are represented at scattered points throughout the whole mass of the hemispheres, the animal will always be able to accomplish its task provided that the whole mass of the hemispheres has not been removed, but the difficulty will naturally be greater the less intact cortical tissue remains." Pavlov pointed to the need for studying the behavior of the rat in conditions in which it uses only one or a few receptors.

Several non-Soviet experimental researchers who have studied the localization of functions in the cortex of rats [14, 16, 19-28] have expressed their disagreement with Lashley's theory of equipotentialism [21, 22, 28], while others have supported it wholly or in part [16, 23, 24].

Although Lashley himself also found that vision is localized in the occipital lobes of the cerebral cortex and motor function in the fore-brain in rats, he nevertheless continues to believe that the whole cerebral cortex is functionally homonymous [17].

Many Soviet workers [5, 6, 7, 12] have drawn attention to the unsoundness of Lashley's theory of equipotentialism, but apparently without possessing experimental proof obtained with rats. Some researches [3, 4, 8], in which the cerebral cortex was extirpated, were carried out on rats, but the question of the localization of fucntions was not specially studied in these investigations.

We carried out an experimental investigation to elucidate some aspects of the problem of localization of functions in the cerebral cortex of the rat. We used the technique of production of conditioned reflexes and habit formation in a maze.

EXPERIMENTAL METHOD

In this research we used L. I. Kotlyarevskii's conditioned-reflex chamber, as slightly modified by V. P. Podachin [11]. This chamber has two compartments, separated by a partition with an opening through which the two halves communicate. Each compartment contains one feeding bowl. This chamber may be used to produce both defensive (motor) and alimentary (motor) conditioned reflexes. The presence of a defensive conditioned reflex was indicated by the fact that the rat ran from one half of the chamber to the other during the action of the conditioned stimulus

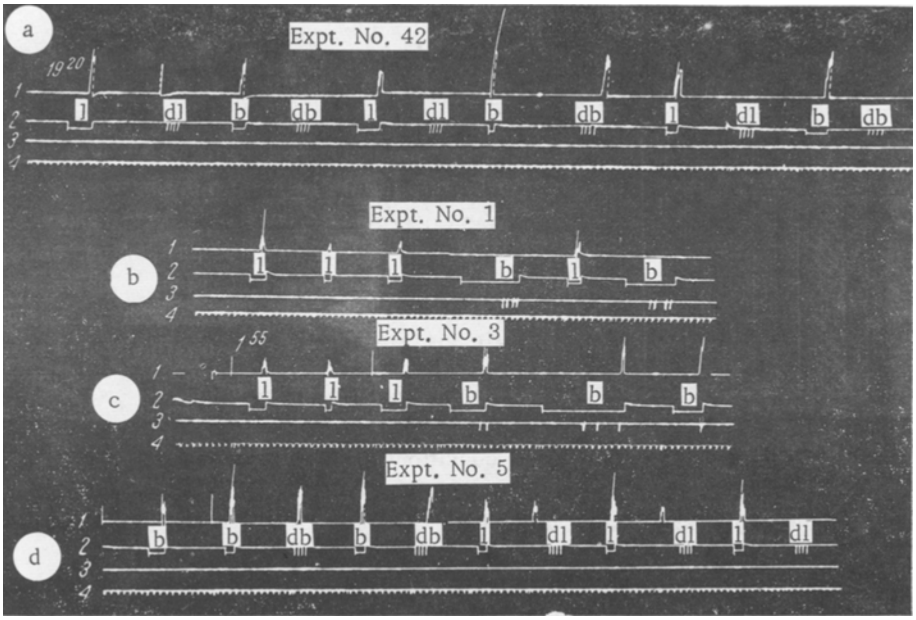

Fig. 1. State of the conditioned-reflex activity of rat No. 12B before (a) and after (b, c, d) removal of the temporal cortex. 1) Defensive conditioned reflex; 2) conditioned stimuli; B) bell, DB) intermittent bell (differential), L) light, DL) interrupted light (differential); 3) unconditioned stimulus (electric current); 4) time marker (2 sec).

without reinforcement. As conditioned stimuli in these experiments we used the light from a 6 W electric lamp, a bell, and a buzzer (400 cps, 50 db). The differential stimuli were an intermittent bell and an interrupted light. As unconditioned stimuli we used sunflower seeds and the current from the secondary coil of an induction apparatus.

EXPERIMENTAL RESULTS

Series 1. Changes in positive and negative conditioned reflexes to a bell and light after operation.

Positive conditioned reflexes to the bell and the light (duration of action of stimulus 3 sec) and differentiation to the intermittent bell and interrupted light were formed in 13 rats aged 2 months. The conditioned reflexes were established in the course of 15-18 experiments, but they were not firmly consolidated, especially differentiation. Before operation from 55 to 76 experiments were undertaken on each rat.

Taking as our guide the cytoarchitectonic chart of the rat's brain [15], we extirpated the cortex from both temporal lobes simultaneously, under ether anesthesia and in semisterile conditions. Four rats died as a result of the operation. Results were obtained from nine rats, in three of which differentiation could not be formed. We found the following changes in the conditioned-reflex activity of the animals.

In the first experiment (3rd day after operation) there was no conditioned reflex to light in two rats and none to sound in six rats. The positive conditioned reflex to the bell was weakened to a greater degree than the positive conditioned reflex to light. The conditioned reflex to the bell was restored later than the conditioned reflex to the light, by 3 days in two rats and by 2 days in three rats (the results of the experiments on one of the rats are illustrated in Fig. 1). In the remaining rats the conditioned reflex to the bell appeared simultaneously with the conditioned reflex to the light, but the adequate conditioned reactions to the bell were less in magnitude than those to the light.

The positive conditioned reflex to the light reached its preoperative level on the 3rd day after operation in four rats, on the 7th day in one rat, and on the 9th day in four rats. The positive conditioned reflex to the bell reached its preoperative level on the 6th-7th day in three rats, and on the 8th-10th day in three rats. On the 8th day after operation the conditioned reflexes to the bell had become the same in the rats as the conditioned reflexes to the light. The positive reflexes both to the light and to the bell reached their preoperative level at the same time (Fig. 2).

The differential reactions to the bell and light were disinhibited immediately after restoration of the positive conditioned reflexes. Differentiation to the bell became weaker than to the light when the positive conditioned reflex

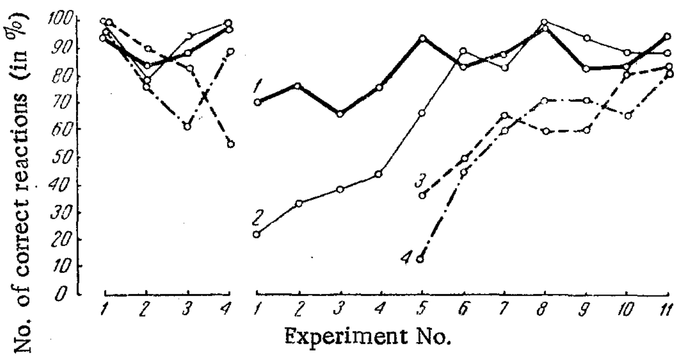

Fig. 2. Conditioned-reflex activity of rats (mean results for 6 animals) before operation (a) and after extirpation of the temporal lobes (b). 1) Defensive conditioned reflex to light; 2) defensive conditioned reflex to the bell; 3) differentiation to light; 4) differentiation to the bell.

to the bell was weaker than to the light. On the 8th day after the operation (after the sixth experiment), when the positive reflexes to the bell had become identical with those to the light, the differential reactions to the bell were also improved and were indistiguishable from the reactions to the light.

The moves of the rats from one half of the chamber to the other during the experiment between the stimuli became more frequent than before the operation. An increased mobility of the animals was observed in the postoperative period, when the positive conditioned reflexes had been restored.

Series 2. Changes in the conditioned-reflex switching from one type of conditioned reflex to another by rats after operation.

Defensive conditioned reflexes to a buzzer and a light were initially formed in 11 rats, followed by alimentary conditioned reflexes to the same stimuli. Afterconsolidation of these reflexes in the rats, a conditioned "switch-over" was developed (see table).

After the conditioned "switch-over" had become relatively stabilized (Fig. 3), the temporal cortex was extirpated bilaterally in the rats. Four rats died from the operation and seven survived. The experiment was performed on the 3rd day after the operation.

In experiment A the defensive conditioned reflex to the buzzer became weaker than the alimentary conditioned reflex to light, while in experiment B the alimentary conditioned reflex to the buzzer became weaker than the de-

Scheme of the Development of a Conditioned "Switch-Over" in Rats

Sequence of experiments	Stimulus Number	Stimulus	Duration of stimulation (in sec)	Reflexes
Experiment A (16 h)	1	Light	1	Alimentary
	2	Light	1	Alimentary
	3	Light	1	Alimentary
	1	Buzzer	3	Defensive
	2	Buzzer	3	Defensive
	3	Buzzer	3	Defensive
Experiment B (19 h)	1	Buzzer	1	Alimentary
	2	Buzzer	1	Alimentary
	3	Buzzer	1	Alimentary
	1	Light	3	Defensive
	2	Light	3	Defensive
	3	Light	3	Defensive

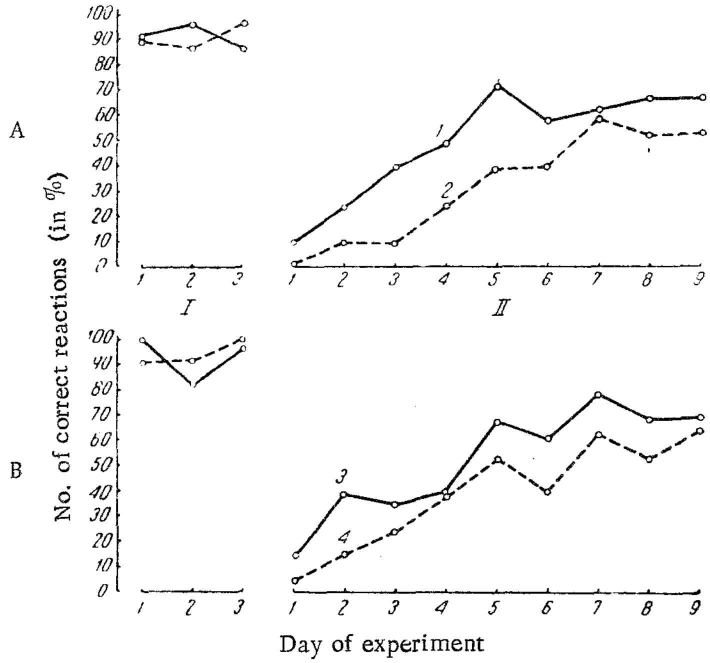

Fig. 3. Conditioned -reflex "switching-over" in rats (mean data for 7 animals) in two experiments conducted 16 h (A) and 19 h (B) before operation (I), and after extirpation of the temporal lobes (II). 1) Alimentary reflex to light; 2) defensive reflex to buzzer; 3) defensive reflex to light; 4) alimentary reflex to buzzer.

fensive conditioned reflex to light. The reflexes to the buzzer became weaker than the corresponding reflexes to light. The conditioned reflex to light was restored 5 days sooner than the reflex to the buzzer in one rat, and 1-2 days sooner in 3 rats. In the remaining rats the conditioned reflexes to the buzzer and light were restored almost at the same time, but the adequate conditioned reactions to light were of greater magnitude than those to the buzzer. The conditioned reflexes to the buzzer became equal in magnitude to the reaction to light on the 6th day after operation in two rats and on the 8th-9th day in three rats. The conditioned "switch-over" was restored almost to the preoperative level in three rats on the 9th, 10th, and 12th days after operation respectively. In four rats the conditioned "switch-over" did not reach the preoperative level.

The results obtained in the first series of experiments demonstrated that after extirpation of about 20% of the cortex of the temporal lobes (neocortex), the conditioned reflexes to sound were impaired to a greater degree than those to light. The difference was statistically significant (more than 5.7 times greater than the mean error), from which it may be concluded that the function of hearing is localized in rats to the cortex of the temporal lobe. After removal of this area of cortex, the negative conditioned reflex to sound was weakened to a greater degree than the negative conditioned reflex to light. The results of the second series of experiments were in agreement with these findings.

Conditioned "switching-over" is a more complicated problem, and in this case the disturbance of the conditioned reactions to sound was more marked than to light, and was observed for a longer time than the positive reflex to sound in the first series of experiments. The positive conditioned reflexes to sound and light in the first series of experiments were restored to their initial level, whereas the reactions during the conditioned "switch-over" reached their initial level later or, in some rats, not at all.

The results of our experiments on rats are in agreement with the results of numerous investigations on dogs [1, 2, 10, 14], and confirm that Pavlov's view regarding the presence of localization of functions in the cerebral cortex of the rat is correct.

A defect of the technique used by Lashley was that he formed only one skill in the rat in the maze (although a rat in a maze does not utilize any one receptor more than the others). In our experiments, on the other hand, we studied the rat in conditions in which it could utilize each receptor (auditory, optic, tactile) separately. We were, therefore, able to compare some reflexes with others: the positive conditioned reflex to sound with the positive conditioned reflex to light, the negative conditioned reflex to sound with the negative conditioned reflex to light, and so on.

Hence, by means of a conditioned-reflex method, we were able to demonstrate the presence of localization of the hearing function in the cerebral cortex in rats. The advantage of this technique for solving problems concerning the localization of functions in the cerebral hemispheres is apparent.

SUMMARY

The work was done on 24 rats. Positive conditioned reflexes to sound and light were elaborated; differentiation to interrupted sound and light, conditioned switching over of various food and defense reflexes to sound and light were also formed. Once these conditioned reflexes are consolidated the cortex of the temporal lobes is removed. Changes in the conditioned-reflex activity after the operation demonstrated that in rats the auditory function is localized in the temporal cortex, and this not only in solution of a simple task, but also of a differential one, and of a complicated task involving switching over of conditioned reflexes. The available data show that the more complex the task – the later and with the greater difficulty the preoperative reflex level is restored. These data also demonstrate the advantages of the conditioned-reflex methods over the labyrinth one for solving the problem of functional localization in the large hemispheres. The data obtained confirm the correctness of I. P. Pavlov's assumptions on the presence of the functional localizations in the cortex of rat cerebrum, and show the erroneousness of Lashley's theory of equipotentialism.

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