LOCALIZATION IN THE CEREBRAL CORTEX OF THE RAT

COMMUNICATION II. CONDITIONED REFLEX ACTIVITY OF RATS AFTER REMOVAL OF THE OCCIPITAL CORTEX

Dang-Tkhu

Department of Normal Physiology (Head, Professor G. I. Kositskii, N. I. Pirogov II Moscow Medical Institute)
Director, Corresponding Member USSR Academy of Sciences E. A. Asratyan
(Presented by Active Member AMN SSSR V. V. Parin)
Translated from Byulleten' Éksperimental'noi i Meditsiny, Vol. 33, No. 6,
pp. 19-24, June, 1963
Original article submitted April 28, 1962

The aim and method of the present work are similar to those described previously in Communication I [3]. The difference was only that previously we investigated in the rat the effect of extirpation of the temporal cortex, and in the present instance it is the occipital region which was removed.

FIRST SET OF EXPERIMENTS

Changes in Positive Conditioned Reflexes (to a Bell and to Light) After the Operation. The work was carried out on 12 rats aged 5 months. The reflexes became fairly stable after 20-25 experiments. To obtain more stable reflexes we carried out a further 25-35 experiments. Before the operation, the animals responded correctly on 90-100% occasions to positive stimuli (bell and light) and gave 85-95% correct responses to the negative signals (intermittent bell and intermittent light). There were two deaths from the operation.

In the first experiment (five days after the operation) there was no reflex response to sound in three of the rats, and none to light in six. The positive conditioned reflex to light had been weakened more than the response to sound. The response to the light developed before the response to sound; in three rats the time difference was four days, and in two it was 1-2 days (Fig. 1). In the remaining animals, although the conditioned reflexes to light and to the bell recovered simultaneously (on the fifth day after operation), there were fewer correct responses to the light than to the bell. One rat gave four correct conditioned responses during the whole post-operational period, and all were to the

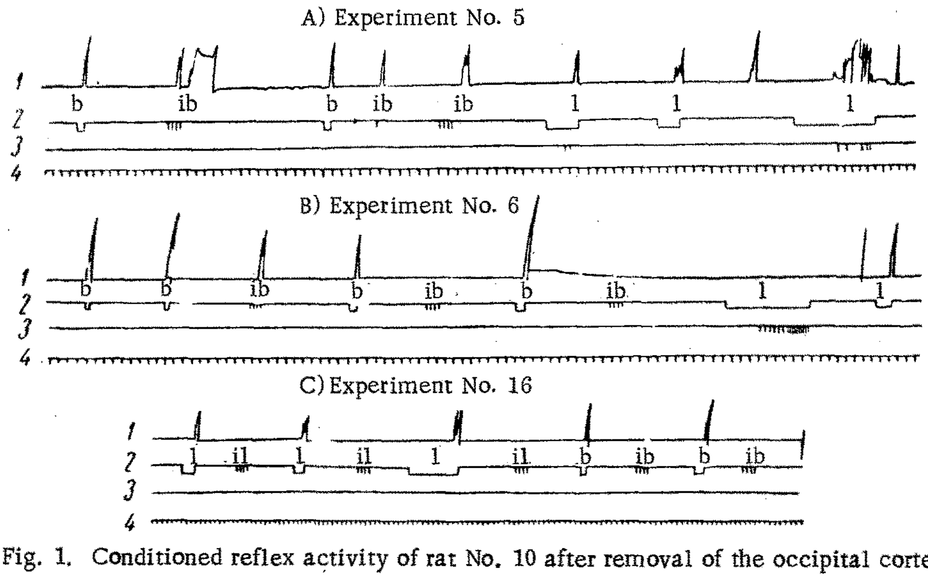

Fig. 1. Conditioned reflex activity of rat No. 10 after removal of the occipital cortex. 1) Defensive conditioned reflex; 2) conditioned stimuli: b—bell, ib—interrupted bell (differentiation); l—light, il—interrupted light (differentiation); 3) unconditioned stimulus (electric current); 4) time marker (two seconds).

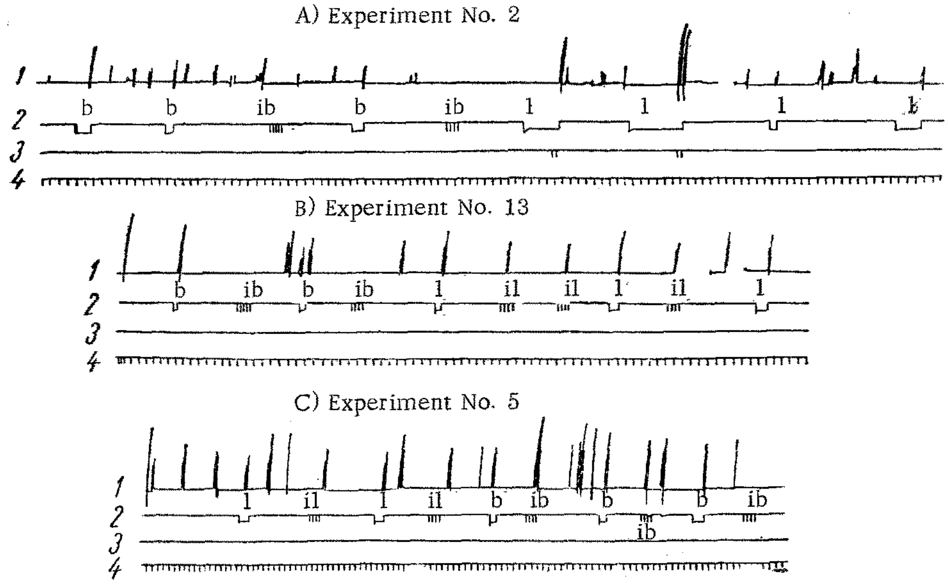

Fig. 2. Disinhihibition and increase of activity in rat No. 12 at an early period (a and b) and three months (c) after removal of the occipital cortex. Indications as in Fig. 1 (each notch indicates the passage of the rat from one half of the enclosure to the other).

bell. Only in one rat was there no change in the conditioned reflex to light or to thte bell, but the negative conditioned reflex to the light was weaker in this animal than was the corresponding reflex to the bell.

The positive conditioned reflex to light was completely restored to the preoperational level by the 17-20th day after operation, and in some rats it was restored by the 7th or 15th day. In general, the conditioned reflex to the bell reached the preoperational level by the 10th day, and in some rats this level was reached by the 5th or 7th day after the operation.

Differentiation to light was impaired more than to the bell; the former recovered later (on the 6th day in one rat, on the 4th day in one, and on the 1-2nd day in five). In two rats no difference was noted in the differentiation as between light and bell.

Relative recovery to the preoperational level of the conditioned response to the light differential stimulus was observed in two rats, and it started on the 12th day after the operation. Differentiation to the bell recovered to the same level in five rats on the 6th-9th day after operation. In the remaining animals there was no recovery of the differentiation to the light or to the bell. A strong disinhibition of the process of differentiation was found to last for the 2-4 days immediately following recovery of the positive reflex, and then disinhibition was frequently repeated in the succeeding experiments (Fig. 2).

After a break of 36 days, the positive conditioned reflexes to light and bell were as strong as they were before the operation. But there was a severe disturbance of differentiation (Fig. 2, c). During this period there was no difference in the conditioned reflex activity (positive and negative reflexes) to light and bell.

After the operation, in many rats we observed an increased spontaneous activity. The number of times the rats passed from one half of the room to the other during the experiment in between signals compared with the number of times they did so before the operation was increased two-fold in the immediate postoperational period, and three-fold in the third month after the operation; the mean figures were: before the operation 2.1 transitions, after the operation 4.1, and in the third month 7.7 transitions (see Fig. 2).

SECOND SET OF EXPERIMENTS

Change in conditioned-reflex elimination of different kinds of reflexes after the operation. In seven rats we developed initially defensive conditioned reflexes to a buzzer and to light, and next feeding conditioned reflexes to the same stimuli. After these reflexes had become established, we elaborated their

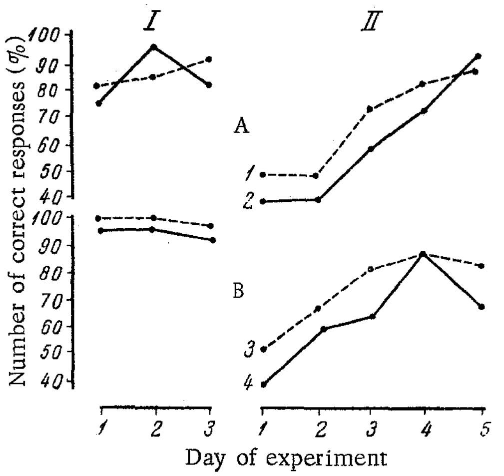

Fig. 3. Elimination of conditioned reflexes from rats (mean results of experiments on seven animals (I) before operation, (II) after removal of the occipital lobes. A—Experiment A (at 16.00 hours); B—experiment B (at 19.00 hours). 1) Defensive conditioned reflex to buzzer; 2) feeding conditioned reflex to light; 3) feeding conditioned reflex to buzzer; 4) defensive conditioned reflex to light.

conditioned elimination (Fig. 3); i.e., in 16 experiments (experiment A) we reinforced the feeding conditioned reflex to light and the defensive conditioned reflex to the buzzer, but at 19.00 hours (experiment B) the procedure was reversed and we then reinforced the feeding conditioned reflex to the buzzer and the defensive conditioned reflex to light. The signal of the feeding reflex acted for one second, and that for the defensive reflex for three seconds. After the conditioned elimination of these reflexes had become fairly stable, we carried out the operation. On the third day after the operation, the rats were tested.

In experiment A the feeding conditioned reflex to light became weaker than the defensive conditioned reflex to the buzzer, and in experiment B the defensive conditioned reflex to light became weaker than the feeding conditioned reflex to the buzzer (see Fig. 3). The conditioned reflexes to light were more seriously disturbed than were those to sound.

Conditioned reflexes to the buzzer recovered rather earlier and more strongly than did those to light. In four rats by the 5-6th day after the operation the latter ceased to be weaker than the conditioned responses to the buzzer, while in other rats the same state was reached by the 10-11th day.

Relative recovery of the conditioned elimination to the preoperational level was found in four rats on the 6th, 7th, and 9th days after the operation. In the other animals it recovered later, or else there was no recovery.

The results obtained in the first set of experiments show that after removal of about 20% of the neocortex in the occipital region the conditioned reflexes were impaired more in response to light than to sound. The difference was statistically significant (3.85 times the mean error), so we may therefore assume a localization of visual function in the occipital lobes.

The results of the second set of experiments agree with those of the first. The simple reflexes attained the preoperational level on the 15-16th day after the operation, but negative conditioned reflexes were not restored. The results agree with those obtained on dogs by the followers of the I. P. Pavlov school [1, 4, 6-9], and also with what has been found for rats [2]. Lashley taught rats to distinguish the brightness of a color, and then inflicted various kinds of cortical damage.

As a net result of his experiments, he found that after removal of the occipital cortex the habit was lost, but after damage to other parts it was not impaired.

Our conclusion of the localization of hearing and vision in the rat cerebral cortex is based on the state of two conditioned reflexes, one to sound and one to light in each rat. It was found that with damage inflicted at a certain point one of the reflexes disappeared while the other was maintained, while the reverse effect was maintained with the damage at a different point.

Lashley, in his book "The Brain and the Mind" [5, p. 179] wrote: "Arguments in favor of distinct localization of two functions have as their foundation that one function continues to operate despite the damage which has destroyed the other. The possibility of a correspondence between the mass of the brain or mass of the functional area and the complexity of possible actions throws doubt on the principal assumption of the doctrine of localization. . . .". From this it follows that if in cerebral damage a certain function (action) is destroyed, then this function is not complex and related to the smaller removed portion, while the other function is related not only to the part that has been removed but also to the portion that remains intact. In this way Lashley denies the localization of function in the cortex.

As far as our experiments are concerned, we cannot assert that the defensive reflex (running from one half of the room to the other) in response to sound is any more complex than the defensive reflex to light. Lashley's conception does not answer the problem of why this function disappears when the occipital cortex is removed, if it is conditionally associated with the light stimulus, and does not fail when it is associated with sound stimulation; the same thing is true when the function disappears on removal of the temporal cortex, when it is conditionally associated with sound, and is maintained when it is related to a light stimulus.

Lashley [5, p. 119] denies the theory of diaschisis: "According to Monakow (1914), symptoms of cerebral damage are to be attributed to two principal causes: firstly, damage of the nerve elements leads to a loss of those specific functions with which these elements are associated; secondly, it brings about a temporary depression in other cells with which the destroyed elements were functionally related...." Later he writes: "The theory of diaschisis in this form allows no possibility of experimental test." As can be seen from our experiments, there is no difficulty in testing this theory if a comparison is made of the conditioned reflex to light and to sound after damage to the temporal or occipital cortical regions. But for this purpose we must at least consider the simple activity which under certain circumstances is principally related to one receptor, and under other circumstances to others. Lashley was concerned only with one habit elaborated in the maze and the habit was not principally related to any one of the analyzers. In opposing the theory of diaschisis, Lashley used his standpoint to study the vicarious functions of the organism. He found that in cases where a visual habit had been acquired, after damage to the visual centers, no kind of damage to other parts of the cortex could cause a loss of this habit: "Thus, the experiments exclude any possibility of a depression of a single cortical center brought about by destruction of another in this kind of situation." According to our results, depression of one center through destruction of another disappears even 3,5, or at latest 9 days after the operation. Lashley tested his rats at times later than 10 days after the operation.

Furthermore, according to I. P. Pavlov, after removal of the visual center a visual habit may be formed by virtue of scattered visual elements. In certain rats, in the second set of experiments, a conditioned suppression was obtained after previous removal of the temporal cortex. We expected that there would be a servere impairment of the conditioned suppression in relation to the light stimulus after removal of the occipital cortex. However the destruction was not very great. The idea then arises that after an initial operation (at any point) in rats, adaptation takes place and the scattered elements then begin to play a more important part. Therefore, after the second operation, the conditioned reflexes suffer less.

These results agree to some extent, but not entirely, with Lashley's idea of vicarious functions [13], because, although after a second operation the conditioned reflexes were not severely impaired, nevertheless some depression of the cortical center and some localization of cortical function could be found.

Lashley tested the memory of rats after they had ceased work for 40 days. He found that the operated animals lost none of the habits involved in the discrimination of brightness differences, but made many mistakes in the maze.

In our experiments on rats, after the operation positive conditioned reflexes to sound and to light recovered completely, but differentiation was severely impaired. After a 36-day-interval, positive conditioned reflexes to sound and to light had in no way deteriorated, but differentiation was still further impaired. We are inclined to attribute this result to a disturbance of balance between excitation and inhibition. At an early stage after the operation, the rats became more excitable and by the third month their spontaneous activity had increased still further. This suppression of inhibition and the manifestation of spontaneous activity after cortical damage has been noticed also by many authors [1, 3, 4, 8-12, 14-17]. The results of our experiments on differentiation of stimuli in rats agree with Lashley's findings on habits formed in the maze. It is thought that the main reason for the great disturbances of habit in the maze was the development of spontaneous activity resulting from cortical damage.

SUMMARY

The work was carried out on 19 rats. Positive and negative conditioned reflexes to sound and light, and conditioned changing over of different reflexes to sound and light were elaborated. The occipital cortex was removed after these reflexes had become established. Changes in the conditioned reflex activity occurred after the operation, and demonstrated that in rats visual function is localized in the occipital cortex which is involved not only in the solution of a simple problem, but also in discrimination; it appears also that it is concerned in the change-over of conditioned reflexes. Localization of this function could be demonstrated also after a second injury to the cortex. These results show that a test may be made of the diaschisis theory, support obtained for it in opposition to Lashley's view. After the operation, the rats became more excitable, and their power to differentiate was considerably disturbed. It would appear that the main cause of the marked disturbance of the habit of running in the maze was the development of spontaneous activity as a result of injury to the cerebral cortex.

LITERATURE CITED

1. B. P. Babkich, Transactions of the Society of Russian Physicians in St. Petersburg, 78 (1911), p. 249.
2. V. I. Gunin, Changes of Higher Nervous Activity of Adult Animals (Rabbits, White Mice, and Dogs) Following Extirpation of the Cerebral End of the Visual Analyzer. Author's abstract of Candidate's Dissertation, Moscow (1956).
3. Dang-Tkhu, Byull. éksper. biol., No. 3 (1963), p. 15.
4. A. N. Kudrin, Conditioned Reflexes in Dogs after Removal of the Posterior Halves of the Cerebral Hemisphere, Dissertation, St. Petersburg (1910).
5. K. S. Lashley, The Brain and the Intellect [in Russian], Moscow, Leningrad (1933).
6. T. A. Mering, Conditioned Reflexes in Dogs after Removal of the Nuclear Zone of the Auditory Analyzer. Author's abstract of Candidate's Dissertation, Moscow (1951); Zh. vyssh. nervn. deyat., No. 6 (1952), p. 894.
7. N. F. Popov, In the book: Report of the Seventh All-Union Congress of Physiologists, Biochemists, and Pharmacologists, Moscow (1947), p. 193.
8. N. K. Toporov, Conditioned Reflexes from the Eye after Removal of the Occipital Lobes of the Cerebral Hemispheres from the Dog. Dissertation, St. Petersburg (1908).
9. M. É. El'yasson, Studies of the Auditory Faculty of the Dog under Normal Conditions and after Partial Bilateral Removal of the Auditory Cortical Center. Dissertation, St. Petersburg (1908).
10. J. Delgado and R. Livingston, J. Neurophysiol, 11 (1948), p. 39.
11. J. F. Fulton, A Textbook of Physiology, Philadelphia (1955).
12. O. Langworthy and C. Richter, Am. J. Physiol. 126 (1939), p. 158.
13. K. S. Lashley, Ibid., 59 (1922-23), p. 44.
14. H. W. Magoun and S. W. Ranson, J. Neurophysiol, 1, (1938), p. 39.
15. C. P. Richter and C. D. Hawkes, J. Neurophysiol, 2 (1939), p. 231.
16. T. C. Ruch and H. A. Shenkin, J. Neurophysiol, 6 (1943), p. 349.
17. J. P. Zubek, J. comp. physiol. psychol., 44 (1951), p. 310.

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.