CONDITIONED REFLEXES IN DECORTICATE RABBITS

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There is now no doubt that in the higher animals, at any rate, conditioned reflexes are developed in the cerebral cortex. However, the question has frequently been raised as to whether the cortex is the only area in which such reflex connections can be established.

On this point, I. P. Pavlov said that "it is possible that at certain times and under certain conditions conditioned reflexes may be formed in parts of the brain outside the cerebral hemispheres. It is not possible to make a categorical statement, because all our classifications and laws are to some extent provisional and apply only to a particular time, to particular methods, and to the material at hand" [12].

It has frequently been pointed out [1, 2, 10, and others] that conditioned reflexes may be formed in decorticate guinea pigs, cats, and dogs. It is true that, as several investigators have pointed out, these reflexes differ considerably from those formed in intact animals. Thus, N. F. Popov [13], working on decorticate dogs, was able to develop a positive response to a metronome after presenting it more than 200 times in combination with an electric shock. However, the raising of the foot to the sound of the metronome did not take the form of an isolated reflex, but there was a generalized response in the form of disorderly movements not only of the leg but of all the other legs and the rest of the body.

According to E. Kuller and F. Mettler [14], and F. Mettler, S. Mettler, and E. Kuller [15], in response to the conditioned stimulus the decorticate animal merely raised the whole of the hind portion of the body from time to time, so bearing the whole of its weight on its front legs, i.e., it simply made a jumping movement.

S. I. Lebedinskaya and S. I. Rozental' [10], when forming a feeding conditioned reflex by I. P. Pavlov's classical secretory method, found no essential difference between decorticate and normal animals in the rate of formation or the character of the conditioned reflexes.

Evolutionary physiology confirms the possibility that conditioned reflexes may develop in decorticate animals. It is known that the lower and less highly organized animals which have no cortex are nevertheless capable of forming conditioned reflexes, i.e., temporary connections [5, 6, 7, 8, 9, 11, and others].

However, in the higher animals, the ability of the subcortical structures to form temporary connections has not been sufficiently studied. In some animals, such as the rabbit, no investigations of this type have been made. The present work on decorticate rabbits, represents an attempt to determine the method of development and the changes occurring in conditioned defensive reflexes involving shaking off the stimulus.

METHODS

The experiments were performed on 10 rabbits, of which 2 were used as control and 8 were decorticate. The cortex was removed from the upper and lateral areas of the cerebral hemispheres. Parts of the cortical areas

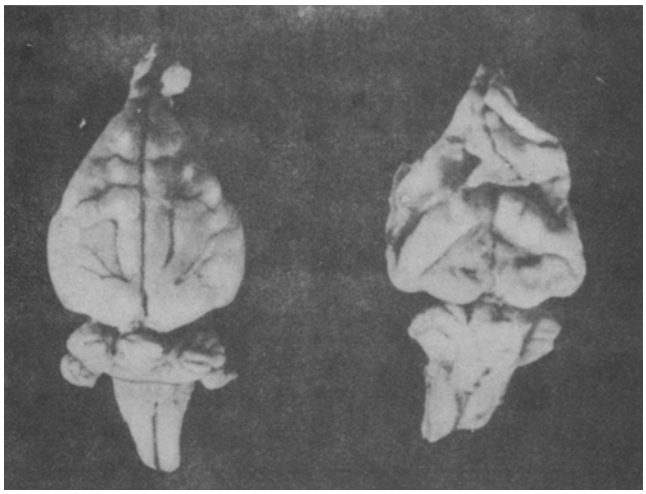

Fig. 1. On left, brain of normal rabbit, and on right, that of decorticate animal (seen from above)

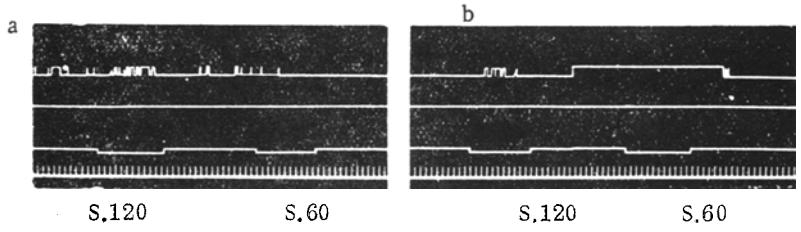

Fig. 2. First experiment (2 1/2 months after decortication) using a conditioned and a differentiated stimulus in (a) a decorticate rabbit, and (b) in a control animal.
Curves, from above downwards: "shaking off" movements; time of action of unconditioned stimulus; time of action of conditioned stimulus; time marker (1 second); s.120-conditioned positive signal, s.60-differentiation.

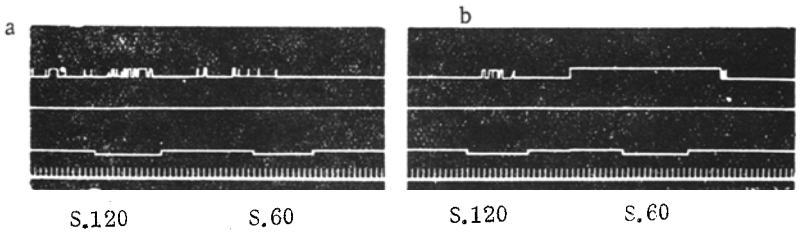

Fig. 3. Conditioned reflex shaking and its differentiation in decorticate rabbits No. 3 (a) and 4 (b). Notation as in Fig. 2.

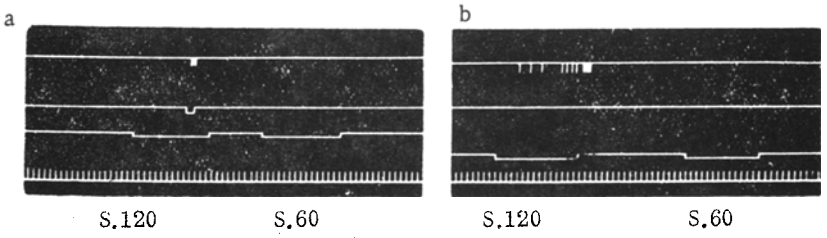

Fig. 4. Conditioned "shaking off" reflexes in a) decorticate and b) control rabbits after a 9-month interval. Notation as in Fig. 2.

adjacent to the cerebellum, and at the base of the brain, were left intact. Of the 8 operated animals, 4 perished a few days after the operation, 2 lived for half a year, while the remaining 2 survived for more than 1½ years before being killed for histological examination.

Examination with the naked eye revealed that 60-80% of the cortex had been removed; the parietal areas had been removed completely, the only parts of the frontal areas remaining were those in the neighborhood of the olfactory bulbs and the base of the brain. The temporal portions remaining were found only at the base of the brain, where a very thin portion remained. Small parts of the occipital areas were preserved close to the base of the brain and the cerebellum. The lateral ventricles were greatly enlarged and opened (Fig. 1). Before and after decortication, the conditioned motor defensive "shaking off" reflex was developed using the method of A. A. Volokhov and G. A. Obraztsova [4].

Conditioned stimuli consisting of a flickering light or the intermittent sound of a bell ringing at 120 strokes per minute were given for 10 seconds at each stimulus. The stimulating electrodes were placed on the outer ear.

The strength of the current was somewhat above threshold. The induced "shaking off" movement was recorded using a mercury interruptor attached to the parietal region of the skull by "Mendeleev's" cement. Electrical reinforcement was used only when no shaking occurred in response to the conditioned stimulus; if the shaking did occur, no reinforcement was given. A bell operating at 60 strokes per minute was used as a differentiated stimulus.

The animal was allowed to move freely about the compartment during the test. The conditioned stimuli were applied every 2 minutes. They were given in the following sequence: light 120+, bell 120+ , and bell 60-, bell 120+, light 120+, bell 120+, bell 601, bell 120+. The "shaking off" movements, the time of application of the conditioned and the unconditioned stimuli, and the time marker were all recorded on the kymograph.

RESULTS

In the control experiment, the conditioned reflex was usually established by the second or third day, or sometimes not until the fourth. At first it took the form of a generalized motor reaction in which the animal ran away. Shaking occurred only in response to the unconditioned stimulus.

From the 10-15th day onwards, in addition to the simple evasive response, a conditioned reflex "shaking off" reaction also developed. In most cases, and in all the subsequent experiments, this conditioned reflex "shaking off" occurred at the same time as the animal made its escape. Only in rabbits Nos. 5 and 7 was the response confined to the "shaking off" movements.

The differential stimuli were applied on the 13th day, the first response followed on the 15-17th day, and became stable by the 21-27th day.

The positive and negative conditioned reflexes were "learnt" very thoroughly. In all, 70 experiments were carried out on each rabbit, i.e., more than 400 positive and over 100 negative conditioned reflexes were evoked. Subsequently, 8 animals (Nos. 3-10) were decorticated. Two (Nos. 1 and 2) were kept as controls.

For the first few days after the operation, the rabbits sat motionless. They were artificially fed by placing of carrot in the mouth, and they could be made to feed only in this way. Later, those which survived (Nos. 3, 4, 7,and 9) began to move about, and fed themselves.

In order to avoid any effect on the conditioned reflexes from purely traumatic causes, the experiments were not resumed until 2½ months after the operation. In the operated animals, the conditioned reflexes had disappeared entirely, while in the control animals both positive and negative reflexes were well preserved (Fig. 2).

Two and a half months after the operation, decorticate rabbit No. 3 became even more mobile than before, and more mobile than the controls. The first "shaking off" conditioned reflex appeared in it on the 3rd day of the experiment (after the 18th combined application of the stimuli) and became fairly stable from the 5-7th day onwards (after the 35-45th combined stimulus).

From the times of appearance of the conditioned "shaking off" reflexes, it would appear that the conditioned reflexes were not restored, but were built up again from scratch.

The "shaking off" reaction in Rabbit No. 3 was better shown than in the intact animals. While in the

compartment, it was moving about the whole time (particularly during the first month of the experiments); as a rule it ran in a circle, and frequently made the shaking response in between the signals. When the signal was applied, the shaking became much more vigorous (Fig. 3, a).

Rabbit No. 4 was quieter and reacted less frequently between signals (see Fig. 3, b). In it too, the "shaking off" reaction was better shown than in the controls; the general escape reaction was comparatively weak. Rabbits Nos. 7 and 9 moved about very little after the operation. Usually they sat in the tightly hunched up position. Conditioned reflexes were elaborated only with great difficulty, and did not occur until 50-70 combined stimuli had been given. The conditioned "shaking off" reflex sometimes occurred very violently. However, the responses were very unstable, and occurred only in occasional experiments. There was usually no conditioned escape reaction. They died half a year after the operation, having developed large trophic abscesses on the legs.

Rabbits Nos. 3 and 4 lived for over a year, and remained in good condition. They showed not only a well-developed "shaking off" reflex, but were capable of responding to the differentiated stimuli, though the power to do so developed much more slowly and was somewhat less stable than in the controls.

In the control animals a 9-month break had practically no effect on their conditioned reflexes; in the decorticate group, the "shaking off" reflex disappeared completely (Fig. 4). The conditioned stimulus caused only an orienting and search reflex.

It is therefore possible to develop good positive and negative conditioned reflexes in decorticate rabbits, but they are less stable than those in intact animals.

In spite of the fact that the possibility of forming conditioned reflexes in decorticate animals may now be considered to be established, many workers ignore the formation of temporary connections and the development of conditioned reflexes in subcortical areas. Some, for instance N. F. Popov [13], consider that the responses of decorticate animals to a conditioned stimulus should not be regarded as conditioned reflexes because of their crude nature and diffuse appearance. It is not easy to accept this view, since in Popov's own experiments (using an unconditioned pain stimulus to a dog's foot), the response to conditioned stimulation was just as precise as to the unconditioned stimulus.

In decorticate animals, reflexes which have been integrated at the lower levels of the central nervous system remain unchanged, or , more precisely, less changed. Conditioned reflexes developed from comparatively simple unconditioned reflexes are almost the same in their end result and in their method of development as those in normal animals; such responses include autonomic reflexes, such as salivary secretion in response to a food stimulus [10].

It is known that decorticate rabbits shake themselves much more vigorously than normals [3]. It therefore seems entirely natural that in our experiments the conditioned reflex shaking movements in the decorticate group were shown more definitely than in the controls; the latter had a greater tendency simply to run away, so that it was very difficult to develop the conditioned "shaking off" reflex, which could only gradually be made to replace the generalized escape reaction. It is interesting that young rabbits show first a better unconditioned and then a better conditioned "shaking off" reflex than do adults, and in this way they show some resemblance to decorticate preparations [3].

Nevertheless, we do not consider that differences in the way in which conditioned reflexes develop in normal and decorticate rabbits consist only in differences in their degree of complexity or perfection, or in the level of their integration in the central nervous system. In the decorticate preparation, the conditioned reflex connection is less well made. As had been already pointed out, this weakness is shown by an instability of the differentiated inhibition and in the less stable positive conditioned reflexes, the long break in the experiments eliminating all the connections which had been formed, while no such effect occurred in the normal group.

The conclusion is that both positive and negative conditioned reflexes may be elaborated in the subcortical region of decorticate animals, but that the reflexes are less stable.

SUMMARY

Experiments were performed on rabbits using the conditioned reflex method developed by A. A. Volokhov and G. A. Obraztsova; these showed that in decorticate rabbits it is possible to develop defensive reflexes which

consist of making "shaking off" movements, and that differentiations may be developed (the conditioned defensive signal was either the sound of a bell, or a light flickering at 120 times per minute; a bell striking 60 times per minute served as the differential signal). However, in decorticate rabbits the positive and negative conditioned reflexes are less stable, and become extinct when the experiments are stopped for 9 months, whereas in the intact animals the reflexes are preserved. Both the conditioned and unconditioned "shaking off" reflex is better developed in decorticate than in intact rabbits, the latter showing a greater tendency simply to run away.

In this respect the behavior of the decorticate rabbit is more like that of the young animals.

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