PERSISTENCE OF AUTONOMIC CONDITIONED REFLEXES IN CATS AFTER REMOVAL OF NEOCORTEX

(UDC 612.833.81-06 : 612.822.6]-084)

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Presented by the late Academician P. S. Kupalov
Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 59, No. 3, pp. 3-5, March, 1965
Original article submitted October 10, 1962

It has been established that conditioned reflexes can be elaborated in decorticate rabbits [4, 12], cats [1, 2, 3, 6, 11] and dogs [7, 9, 10]. It has not, however, been proved that subcortical structures are directly concerned in the closure of reflexes in normal animals. Some time ago the author drew attention to the persistence of conditioned reflex changes in cardiac activity in cats after decortication [8]. Specific investigations were, however, necessary for any final conclusions.

METHOD AND RESULTS

The experiments were carried out on two cats with the cortex of the left hemisphere already removed. Two conditioned reflexes with responses of opposite nature were elaborated in each animal. In the case of cat No. 30, a sound of frequency 300 cps was reinforced by the inhalation of ammonia vapor and a sound of 1000 cps was reinforced with raw meat; for cat No. 36 the sound of 300 cps was paired with the feeding of raw meat and the 1000 cps sound with the inhalation of ammonia vapor. The inhalation of ammonia produces bradycardia and apnea and the ingestion of meat, tachycardia and tachypnea. The ammonia-conditioned signals acted alone for 5 sec, and the food-conditioned, for 20 sec.

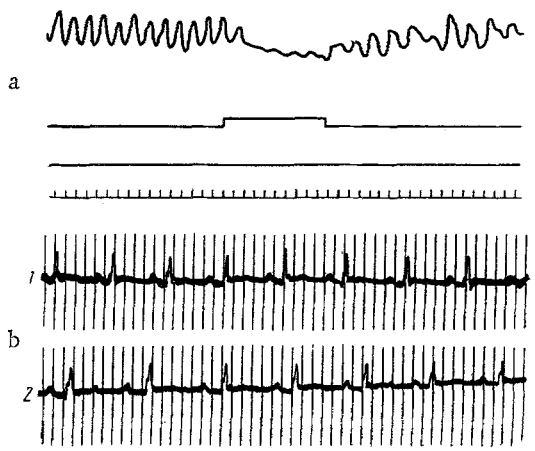

Fig. 1. Conditioned reflex retardation of respiration and slowing of heart by conditioned signal (sound of 300 cps) on 26th day after decortication of second (right) hemisphere. a) Pneumogram. From above down: pneumogram; conditioned signal; unconditioned signal; time (1 sec). b) ECG before acoustic stimulation (sound of 300 cps) heart rate 193/min (1) and during acoustic stimulation, heart rate 166 beats/min (2).

Cardiac activity was recorded electrocardiographically and respiration, kymographically.

The experiments for the production of conditioned reflexes in cat No. 30 were started a month after removal of the cortex of the left hemisphere. The reflex of tachycardia and tachypnea to the 1000 cps sound was elaborated first. In all 135 combinations were required for its formation and firm establishment. Conditioned reflex bradycardia and apnea were then elaborated to the sound of 300 cps. Firm establishment of these conditioned reflex changes, in contrast to the preceding changes of opposite type, required only 22 combinations. From the sixth day of work for the formation of the ammonia-conditioned reflexes, a start was made with the application of both conditioned signals (300 and 1000 cps), together with their appropriate reinforcements, in the same experiment. A somewhat greater number of food-reinforced conditioned signals were administered in the course of an experiment as the cardiac and respiratory conditioned reflexes to these stimuli were less intense than responses to the 300 cps sound. At first, cat No. 30 was seldom able to distinguish the sounds, but after

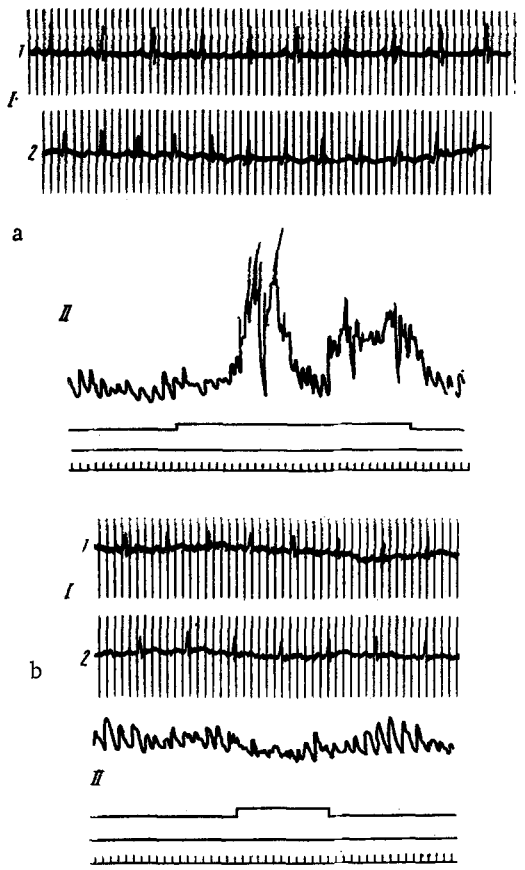

Fig. 2. Ability to distinguish sounds of 300 cps and 1000 cps the first time applied, 15 days after decortication of second (right) hemisphere. a) Conditioned reflex acceleration of heart and respiration by sound of 300 cps. I) ECG before conditioned stimulation-heart rate 196/min (1) and during conditioned stimulation-heart rate 240/min (2). II) Pneumogram (tracings in same order as in Fig. 1). b) Conditioned reflex bradycardia and slowing of respiration by sound of 1000 cps. I) ECG before conditioned stimulation-heart rate 200/min (1) and during conditioned stimulation-heart beat 190/min (2). II) pneumogram (tracings in same order as in Fig. 1).

five days, the ability to differentiate was quite definitely established, as a result of a total of 194 combinations with food reinforcement and 56 with reinforcement by ammonia. The cortex of the right hemisphere was then removed. Experiments were resumed 24 days later, when the cat's condition was quite satisfactory.

The first application of the sound of 300 cps produced conditioned reflex apnea and slowing of the heart by 23 beats/min in cat No. 30. The food-conditioned signal (1000 cps) was tested the following day, the response being merely a slight increase in heart rate and respiration rate. The sound of 300 cps was given as a second stimulus on the same day, and it produced intense apnea (Fig. 1a) and bradycardia (Fig. 1b). To make absolutely certain, the conditioned signals were used without reinforcement in these experiments.

The most definite reaction, namely that to the ammonia-conditioned signal, was extinguished in order to confirm the conditioned reflex nature of the autonomic responses observed. Extinction was achieved in the course of a single experimental day by the application of stimuli, with intervals of two minutes.

The conditioned respiratory reaction was completely extinguished after 14 unreinforced applications of the signal. The cardiac conditioned reflex was extinguished after 30 applications. These reflexes were restored independently the following day.

In the case of cat No. 36, as with No. 30, experiments were started after left-sided decortication. Conditioned reflex bradycardia and apnea to the sound of frequency 1000 cps were elaborated first in this animal. When these reactions were reasonably well established, conditioned reflex acceleration of cardiac action and respiration was elaborated to the sound of 300 cps reinforced with food. Effective differentiation was established after 129 food-conditioned and 143 ammonia-conditioned signals; the neocortex of the right hemisphere was then removed. Experiments were resumed after two weeks, when the cat's condition was again satisfactory.

The first application of the sound of 1000 cps produced only slight bradycardia and slightly more frequent respiration of reduced amplitude. On the following day the food-conditioned signal (300 cps) was used first. It produced considerable tachycardia (Fig. 2a) and considerable tachypnea (Fig. 2b); the respiratory rate was increased by 20/min.

Applied on the same day, the sound of 1000 cps produced appreciable conditioned reflex slowing of the heart and respiration. As in the case of cat No. 30, the conditioned signals were used in these first experiments after the operation without reinforcement.

It may be mentioned that the primitive somatic components of the reflexes (general alimentary excitation or defensive motor reaction) were retained along with the autonomic conditioned reactions after decortication.

Subsequent examination of the animal brains revealed that the decortication had been almost complete. Microscopic examination of the small fragments of the proreal, genual and orbital gyri, left behind in cat No. 36, revealed secondary changes in the cell elements, which could not have functioned normally. The small remaining

fragments of cortex could not, therefore,be regarded as providing a substrate for conditioned reflex activity in this cat. This was confirmed by examination of the brain of cat No. 30, in which the neocortex had been removed completely; its conditioned reflex activity differed in no respect from that of cat No. 36, in which small sections of cortex remained.

The results obtained with cat No. 30, cat No. 36 and a third cat described in an earlier paper [8] may be considered identical. Conditioned reflex changes in cardiac activity and respiration, elaborated in these animals after unilateral decortication, could still be produced after removal of the remaining cortex. Nor did the cats lose their ability to differentiate. Conditioned autonomic reflexes can thus be closed in subcortical formations when the neocortex remains inactive, as well as after its removal.

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