SECOND-ORDER RESPIRATORY CONDITIONED REFLEXES IN CATS

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The possibility of the formation of second-order reflexes was first shown by I. P. Pavlov's associates and was frequently discussed at the Pavlov Wednesdays [5]. These results were subsequently confirmed by B. I. Bayandurov [2] working on birds, L. G. Voronin [4] – on dogs and monkeys, and by K. Khekht [7] working on rats. V. L. Balakshina [1] and I. E. Vasilevskaya [3] showed that second order conditioned reflexes could be established in response to interoceptor stimulation. All these investigations concerned the formation of second-order conditioned reflexes on the basis of first-order food and defense reflexes.

We have made a study of the cortical regulation of respiration in cats, and have demonstrated the possibility of rapidly forming stable first-order respiratory conditioned refexes [6]; we have attempted to find whether it is possible to form second-order respiratory conditioned reflexes, and have tried to study the features of these reflexes qualitatively by observing the rate at which they develop, their stability, and the effects of external and internal inhibition.

METHOD

We have carried out 80 experiments on 3 animals (2 males and 1 female). Initially, a constant stable first-order respiratory conditioned reflex to a bell was formed, the reinforcement being effected with ammonia. When the bell rang, there was a marked reduction in respiratory movements. The second-order respiratory conditioned reflex was developed in response to a 40 w lamp, which was lit for 6-8 seconds; then, when the light had been switched off, or 1-2 seconds later, the bell was turned on for 6-8 seconds. No ammonia was given in this case. To prevent the extinction of the first-order respiratory reflex, the sound of the bell was reinforced from time to time with ammonia. Various intervals between the simultaneous presentation of the two stimuli were used, and these ranged from 30 seconds to 5 minutes. The duration of the experiments varied from 30 to 60 minutes. In each experiment both stimuli were given 4 to 8 times. The respiration was recorded by a pneumograph, with the animal in a sitting position.

The cat Lis was a restless animal which fatigued rapidly, and whose respiration was irregular; it was not found possible to develop a second-order respiratory conditioned reflex in it. When the experiments were repeated, a breakdown of higher nervious function occurred, and this was shown by the appearance of sudden movements and cries, which were followed by complete immobility – the animal sitting frozen in one position with its eyes open. A first-order respiratory conditioned reflex which had been previously elaborated was completely inhibited. When the experiments were discontinued for from 2-3 days to 1 month, the animal did not recover.

The two other animals succeeded in developing second-order respiratory conditioned reflexes. In the cat One-Eye, this reflex was developed in response to the eighth coincidence of the signals and became stable from the time of the seventeenth coincidence. It was manifested by a reduction in the respiratory movements, though this reduction was less than in the case of the first-order reflex. A pneumogram obtained from this animal is given in Fig. 1 by way of illustration.

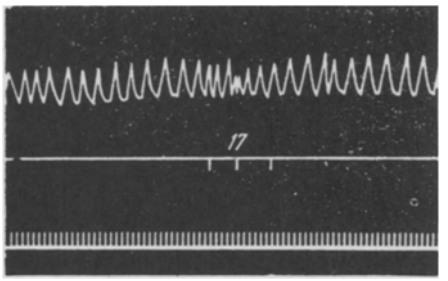

Fig. 1. Formation of a first-order respiratory conditioned reflex in the cat One-Eye.
Curves, from above downwards: pneumogram; record of stimuli: light (second-order reflex) is given between the first and second vertical lines, the bell (first-order reflex) is given between the second and third vertical lines; time marking (1 second).

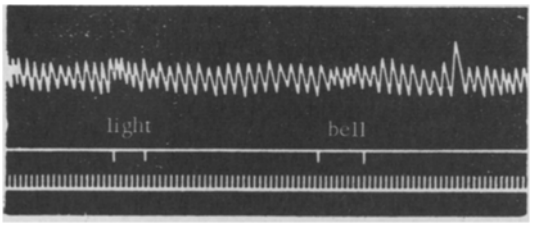

Fig. 3. Second-order respiratory conditioned reflexes when the second stimulus is applied at a definite time interval after the first.
Curves as in Fig. 1.

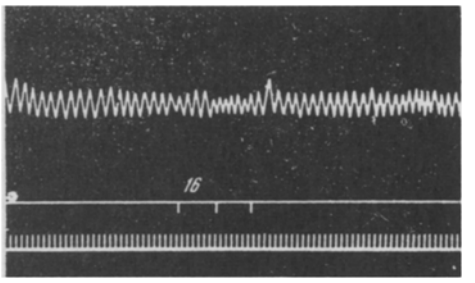

Fig. 2. Development of a second-order respiratory conditioned reflex in the cat Sil'va. Curves as in Fig. 1.

During the whole of the experimental period, both the first-and the second-order reflexes were maintained at a constant level. No extinction of these reflexes occurred when the experiments were interrupted for from 2 to 7 days.

In the cat Sil'va, the second-order conditioned reflex was first observed at the 9th coincidence, and it remained constant until the end of the experiments. In response to the action of the light, which was the second-order conditioned stimulus, the respiration became reduced for 2-3 seconds; after that it gradually increased in strength and returned to its original level by the end of the stimulus period, while in the case of the bell, which was the first-order conditioned stimulus, there was a marked reduction of respiratory movements during the whole of the period of its action.

The points we have mentioned in connection with the first-and second-order respiratory reflexes are shown in the pneumogram of Fig. 2.

Separate application (outside the stereotype) of the first-and second-order conditioned stimuli evokes respiratory changes of the same type and extent as when they are applied immediately in succession. This is shown in the pneumogram of the cat Sil'va (Fig. 3).

After the experiments had been interrupted for from 2 to 7 days, the second-order respiratory conditioned reflex was found to be extinguished, but it returned after 2-3 applications of the combined stimuli. In the cat Sil'va, sometimes a reduction or even a complete inhibition of the second-order respiratory conditioned reflex was found towards the end of an experiment. In many experiments, in both animals, the second-order conditioned reflexes were found to be inhibited as a result of extraneous stimuli such as a dog barking, movements of objects in the field of view, knocking, all of which stimuli appeared to act as external inhibitors.

When the reinforcing stimuli, which included ammonia for the bell, and the bell for the light, were withdrawn, the second order respiratory conditioned reflex became extinguished much more rapidly than did that of the first order. In Sil'va, the extinction occurred at the 4-5th unreinforced application of the stimuli, while in One-Eye, 8-10 unreinforced applications of the stimuli were given before this occurred. The first-order respiratory conditioned reflex was preserved long after complete extinction of the second-order reflex. Occasionally, disinhibition of a completely extinguished second-order respiratory conditioned reflex was observed.

Thus, our experiments have shown that complex temporary connections can be formed between the cerebral cortex and the respiratory center, and that these connections include the cortical areas of several different analysers. The second-order respiratory conditioned reflexes can be elaborated only in animals which have a strong equilibrated type of nervous system. The second-order respiratory conditioned reflexes have the same qualitative characteristics as the second-order food and defense conditioned reflexes, i. e. they are less stable, and less well developed as compared with the corresponding first-order reflexes.

SUMMARY

Conditioned respiratory reflexes of the second order to the light of a 40 watt lamp were developed in 3 animals with reinforcement by conditioned reflexes of the first order (to the bell sound). Conditioned respiratory reflexes of the second order developed in 2 of the 3 animals. They were less stable and less pronounced than the respiratory reflexes of the first order. Therefore, complex temporary associations may form between the respiratory center and the brain cortex, into which several analyzing cortical areas are included simultaneously.

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* In Russian.

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*** See English Translation.