PROPRIOCEPTOR REFLEX CARDIAC EFFECTS

PROPRIOCEPTOR REFLEXES AFTER SECTION OF THE POSTERIOR COLUMNS

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It is known that the afferent pathways associated with motor control pass through the white matter of the posterior columns of the spinal cord. Various investigators [1,2,3,4,5,6], who have attempted to explain the mechanism of motor conditioned reflexes, have damaged the white matter of the posterior columns and then made observations on these reflexes after motor control had been re-established.

At present two contradictory views are held. I.M. Apter [1] and V.P. Protopopov [5] found that after section of the posterior columns previously elaborated conditioned reflexes disappeared and failed to recover. On the other hand, L.S. Gambaryan [2,3,4] maintains that not only section of the posterior columns but their total destruction over several segments does not destroy previously elaborated conditioned reflexes or prevent the formation of new ones.

It must be noted that these authors did not study proprioceptor reflexes. They investigated the motor reaction in response to electrical stimulation or to food offered by hand. Consequently, there is no foundation for the conclusion based on the elimination of the afferent pathways from the muscles and joints of the limbs [3] as in these cases the motor reaction is adequately mediated by the lateral and anterior columns.

I.M. Sechenov [7] and M. Schiff [9] in experiments on frogs, showed that after section of the posterior columns, proprioceptor impulses may pass through the damaged portion; this is possible because of the internuncial connections of the grey matter of the spinal cord.

This has been confirmed by E.D. Gardner and F. Morin [8] in experiments on apes, using an electrophysiological method. Here it was found that after section of the posterior columns, the passage of proprioceptor impulses to higher levels of the central nervous system was greatly impaired.

EXPERIMENTAL METHODS

In one of the dogs, 14 months after section of the posterior columns between C_2 and C_3,* we investigated

* A histological investigation carried out at the end of the experiments showed that there were very considerable changes in the posterior columns of the spinal cord. At the site of the section there was a fine scar which stained dark red with picrofuchsin. Above the scar in the region of the posterior columns the myelin coats and axis cylinders of most of the nerve fibers had disappeared. In places where the nerve fibers had disappeared, a finely fibrous tissue could be seen, which gave a negative reaction for myelin. (The investigations were made in the Department of Pathological Anatomy with the cooperation of D.S. Sarkisov).

the effect of proprioceptor action on the heart, using the method described by us previously. Before the operation the animal had become familiar with the bench on which it stood, and had been trained to support on its back for 10 minutes a load equal to its own weight, and it was not until the end of this period that it began to shift its weight from one foot to another and to whimper. Fourteen months after the operation, there was almost complete compensation of motor function, externally. But even then, the animal would sometimes stand for long periods on the dorsal surface of the paw. It was unable to support a load equal to its own weight, and fell being unable to rise with the load. The animal could support a load of 80% of its own weight for not more than 3-4 minutes, and could stand quietly with this load for only about 2 minutes. This load of 80% of the body weight applied for 2 minutes was then used as an unconditioned stimulus. Positive conditioned stimuli: light (60 w electric lamp) and a metronome giving 120 beats per minute (M_{120}), and as a differentiated stimulus a metronome at 60 beats per minute was used (M_{60}).

EXPERIMENTAL RESULTS

In the first experiments a static load by itself caused a considerable change of heart rate which lasted from the time the load was applied until 12-15 minutes after its removal; however, after the sixth trial this effect occurred only during the action of the unconditioned stimulus. This change became very small and was sharply augmented only when the animal moved with the load. The static effect had disappeared. No acquired skill in carrying the load could be observed.

In unoperated animals before conditioned reflexes were formed, the stimuli of light, M_{120}, M_{60}, and bell caused changes in heart rate only in 1-4 tests with the isolated stimuli, and after that were ineffective. After removal of the posterior columns these stimuli caused a considerable increase in heart rate and changes in the electrocardiogram both of which lasted for quite a long time. The reaction of the heart associated with the orientating reaction of the animal to the bell remained, and was not extinguished after repeated tests with this stimulus over a period of 4 months. The following differences were also noted (see Table).

TABLE

Changes in the Conditioned Reflexes in Dogs after Section of the Posterior Columns of the Spinal Cord caused by Operation

Conditioned reflex	Number of combinations	
	in unoperated healthy dogs	in dogs after section of the posterior columns
Formation of conditioned reflex to light	—	18-25
Formation of conditioned reflex to M_{120}	5-10	25-36
Extinction of the conditioned reflex to M_{120}	3-4	19
Re-establishment of conditioned reflex to M_{120}	1-2	21
Development of differentiation to M_{60}	1	6
Alteration of the significance of a pair of conditioned stimuli.	3-4	30

From the results shown in the table it can be seen that the conditioned reflex effect on the heart is formed earlier by a weak stimulus (light) than by a strong one (M_{120}).

In the unoperated animals, M_{120} begins to cause changes in heart rate after 5 combinations of the conditioned and unconditioned stimuli, and by the 10th combination it is completely effective. In dogs with section of the posterior columns changes in the heart rate can be induced by the M_{120} alone after 25 combinations though the conditioned reflex continues to grow after 36 combinations (Fig. 1). The differentiated stimulus applied to the unoperated animals caused changes in the heart rate and a broadening of the QRS complex after only 1-4 times. After section of the posterior columns, the same stimulus caused changes in the heart rate which occurred in two phases: when first applied there was an increase in heart rate, and when applied subsequently there was a decrease; differentiation was established after 6 applications of the M_{60} stimulus.

The extinction of the proprioceptor conditioned reflex effect on the heart in dogs after section of the posterior columns takes place 5-6 times more slowly than in nonoperated animals, and its restoration takes place in a manner which is similar to that of forming the conditioned reflex for the first time (Fig. 2).

Simultaneous alteration of the significance of a pair of conditioned stimuli takes place in unoperated animals after 3-4 trials of the stimuli having an altered significance, but takes place differently according to the phase of the training * to carrying the static load: if it occurs in phase IV, a neurosis develops, while if the conditioned reflexes are altered in phases II and III there is no change in the background level of the heart rate. In the operated animals recognition of the altered significance of a pair of conditioned stimuli requires a period 7-10 times longer than in controls, and at a certain period in the alteration there is a considerable change in the background level of the heart rate (Fig. 3).

These results show the great difference between the effects of proprioceptor impulses on the heart in the two groups of animals.

The long time for which the reaction of the heart associated with the orientation reaction of the animal is preserved, and the more rapid formation of a conditioned reflex to a weak stimulus than to a strong one, may be explained in terms of a reduction in tone of cortical cells which results from the elimination of the stream of impulses falling on them from the receptors in the muscles. The less well-shown unconditioned reflex reaction on the heart of the static load, applied to the animal standing still on the bench, and the considerable associated change in the properties of the proprioceptor conditioned reflex effect on the heart indicate an interference in the transmission of impulses, after section of the posterior columns.

The marked and prolonged changes in the heart rate which occur when the static load alone is applied, may be ascribed to changes in the orientation reaction of the animal to this stimulus. At the same time however, in view of other facts, we may suppose that in normal animals the motor apparatus plays a part in the reaction of the animal to the various stimuli in the surrounding medium, and the resulting stimulation of the proprioceptors exerts a correcting effect on the work of the heart.

The absence of the phenomenon of "static effort" and training phases in animals after section of the posterior columns is one more indication that Lindhardt's phenomenon and its changes during the training process are due primarily to the reaction of the central nervous system, conditioned by stimulation of the proprioceptors.

Proprioceptor action on the heart is not completely excluded by high section of the posterior columns.

This may be due to internuncial connections in the grey matter and to spinocerebellar pathways in the lateral columns of the spinal cord. However in normal animals the posterior columns of the spinal cord are the chief pathways along which the proprioceptor impulses which are responsible for the changes in cardiac activity travel to the brain.

* Details of the phases of training to carrying a static load have been given by us in the Byull. Eksptl. Biol. i Med., 1957, 43, No. 1, 14-20.

In our experiments the static load was inevitably associated with stimulation of the tactile receptors over a wide area of the skin of the feet. Experiments on dogs with a transection of the posterior columns of the spinal cord, which leaves the spinothalamic tracts containing some of the tactile fibers intact, may indicate that changes in heart rate in normal animals in response to the application of a static load, are due chiefly to proprioceptor and not to tactile stimulation.

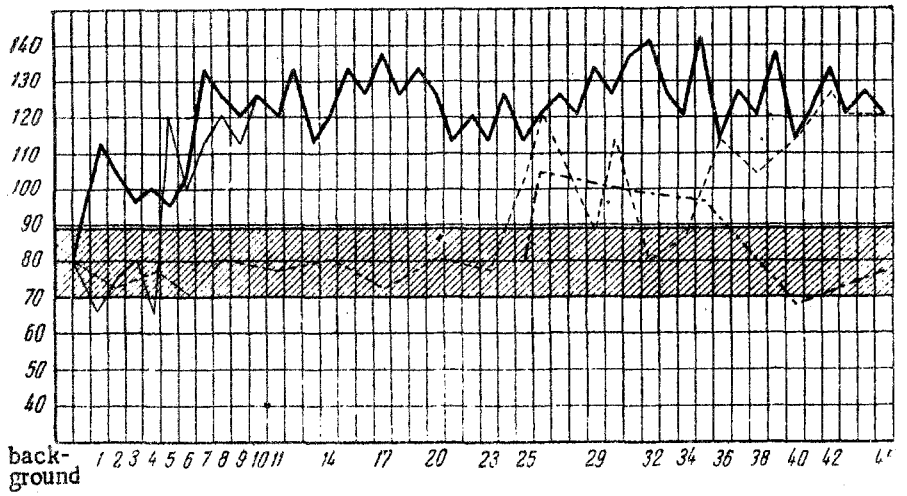

Fig. 1. Formation of conditioned reflexes. Vertically) heart rate, horizontally) number of coincidences of the stimuli. Changes in the heart rate under the influence of: ——— combination of static load with M_{120}, -------- M_{120} alone, — — — M_{60}, —·—· M_{120} in a normal animal. Shaded area) variation of heart rate in absence of stimuli.

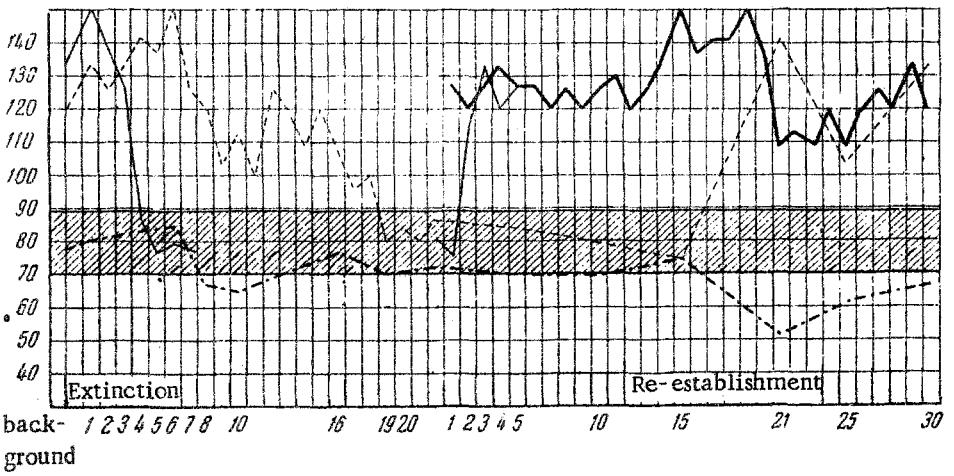

Fig. 2. Extinction and reformation of conditioned reflexes. Traces as in Fig. 1.

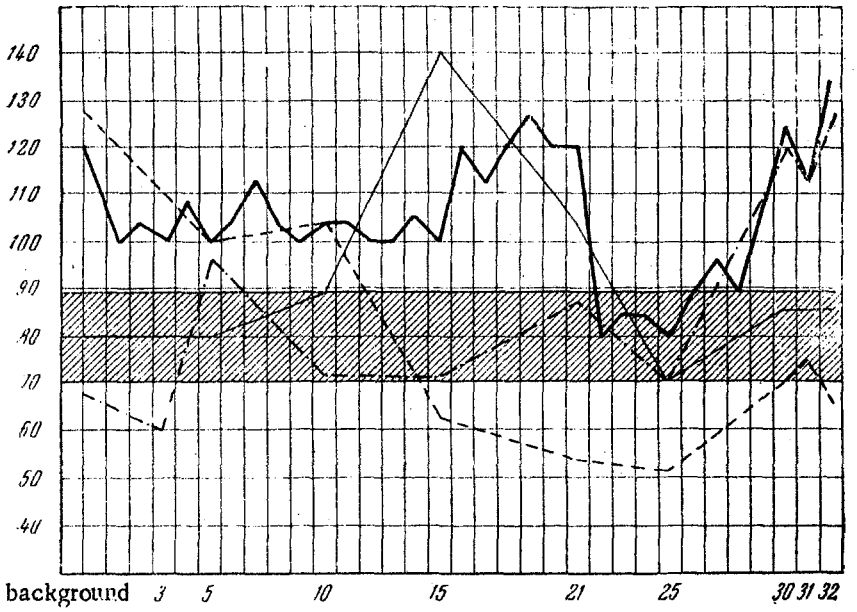

Fig. 3. Alteration of the significance of a pair of conditioned stimuli. Traces as in Fig. 1; ▬▬ combination of static load with M_{60} shaded area -- variation in the heart rate before the alteration, ——— changes in the background level of the heart rate during the process of alteration of the conditioned reflexes.

SUMMARY

The following phenomena were noted in dogs 14 months after section of the posterior trunks of the spinal cord in comparison with intact animals: the value of the time of retaining of the load decreases, the effect of unconditioned reflexes from the proprioceptors on the heart decreases, Lindhardt's phenomenon and training to static load are absent. However, the orientation reaction of the heart to light and sound stimuli is retained for a long time. Formation, extinguishing, restoration and change of conditioned reflexes are 4 to 10 times slower.

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