AN ATTEMPT TO PRODUCE AUTOMATISM IN A SPINAL CENTER

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Little information is at present available on the causes and conditions of formation of one of the more important properties of the central nervous system, its constant rhythmic activity. A matter of particular interest, therefore, is the study of the continuous flow of afferent impulses from the various receptor zones to the brain, which may be responsible for the permanent background pattern of excitation of the nervous centers. In this connection important work has been published [4, 6], showing that the automatism of the respiratory center of fishes and frogs ceases after division of the aortic nerve, which carries impulses from the receptor zone in the region of the bifurcation of the aorta. Our experiments on frogs [2] led to the conclusion that the automatism of the respiratory center of the frog is determined by the constant background excitation of the nerve cells of the inspiratory region of the center, due to a continuous stream of impulses from these receptors. Exclusion of the latter leads to a sharp lowering of the functional activity in this area alone, whereas similar changes are not observed in the expiratory and motor regions. Exclusion of the receptors of the lungs or the proprioceptors of the respiratory muscles is followed only by a disturbance of respiration and the appearance of oscillatory respiration, and no arrest of respiration occurs. Exclusion of other receptor zones has no effect on respiration. The impression is gained that the automatic activity of the frog's respiratory center is based on a constant level of background excitation of the inspiratory center resulting from a continuous flow of impulses from the aortic receptors. The increasing flow of impulses from the lungs and proprioceptors of the respiratory muscles developing in the course of excitation of this center creates additional excitation therein, as a result of which, by the laws of parabiosis, the initial excitation is either reinforced or inhibited, depending on the actual level of excitation of the inspiratory center at the time.

This view is supported by the results of experiments in which a single stimulus from a cathode is superimposed on the inspiratory center at various moments of the respiratory cycle [3]. Similar hypotheses regarding the conditions of development of the automatism of the respiratory center on the basis of initial background excitation in warm-blooded animals have been put forward by other writers [7, 8], although the cause responsible for the background excitation in warm-blooded animals has not yet been discovered.

The conditions of the onset of automatism in the respiratory center of the frog may serve as an example of one of the principles of the formation of automatism in the central nervous system. In the present paper we describe the results of experiments in which similar conditions of activity were created in a spinal center in a frog in order to develop an automatic function in that center, similar to the mechanism described above of the activity of the respiratory center.

EXPERIMENTAL METHOD

Experiments were carried out on spinal frogs of the species Rana esculenta and R. ridibunda. The basic principle of the experiment was that a continuous stream of impulses was sent to the spinal center of the frog from one of the sensory nerves, which must have the effect of creating an initial "background" excitation of this center similar to that occurring in the inspiratory center. An additional stimulus was then periodically added from another nerve, either a synergist or an antagonist.

In one series of experiments we used the exciting action of synergistic nerves (tibial and peroneal) in relation to their common center for the semitendinosus muscles (stimulation of these nerves causes a contradiction of the semitendinosus muscle). After the nerves had been dissected before the beginning of the experiment, the frog was allowed to rest for 1.5-2 h. Chloride electrodes (stimulating) were then introduced beneath the nerves and connected to the output of a stimulator, specially assembled by E. V. Sinyakov and giving rhythmic discharges with frequencies within the range from 10 to 200 cps. The shape of the output impulse from this generator was similar to that of the "break" impulse in a secondary induction coil. The amplitude of this impulse was regulated by a potentiometer, included in parallel with the secondary winding of the transformer. The stimulator had two such circuits. Furthermore, the resistors, capacitors, and transformers were so selected that at the same frequency equal amplitudes could be obtained in both circuits. A special feature of the stimulator was that a change in the frequency caused hardly any change in amplitude; at the same frequency, moreover, the amplitude of the stimulus could be varied. The supply for both circuits was a BAS-90 unit.

The frog was laid dorsum uppermost on a board. The semitendinosus muscle was connected to the pen of a vertical myograph. The amplitudes of the reflex contraction of the semitendinosus muscle during stimulation of the tibial nerve and then during stimulation of the peroneal nerve or vice versa were recorded separately. In each case the strength of stimulation and the frequency were so selected that the reflex responses of the muscle were close to maximal. After the frog had rested, one of the nerves was subjected to prolonged stimulation (between 30 and 40 sec) of a certain strength and frequency (by analogy with the prolonged, continuous stimulation of the center, creating the background excitation). When a steady contraction of the muscle resembling continuous tetany had developed, an additional stimulus was applied periodically to the second, synergistic nerve, with a pre-selected frequency. The amplitude of this stimulation was gradually varied each time it was applied successively from zero to a maximum, thus imitating the inclusion of a gradually increasing stream of impulses (such as may develop during the stretching of the lungs in inspiration). Each additional stimulus was applied at the time when the muscles had reached the maximal level of their initial (background) reflex contraction. As soon as depression of the existing reflex began to appear (as could be judged by the fact that the amplitude of the contraction began to fall), the additional stimulus was applied to the synergistic nerve, and when the contraction had returned to its initial level, another additional stimulus was applied. These additional stimuli were reapplied several times. When the experimental results were analyzed, only those were considered in which the background reflex stimulation persisting after removal of the additional stimulus maintained the previous initial level. Control experiments in which the nerves were divided showed that the reflex responses described above did not develop, thus proving the absence of an artefact.

In another series of experiments the additional stimulus was applied to the contralateral nerve in sufficient strength to influence the spinal center, yet no visible contraction of the contralateral muscle was permissible. The remaining experimental conditions were the same as in the experiments with ipsilateral stimulation.

EXPERIMENTAL RESULTS

It is clear from Fig. 1 that during test stimulation of the tibial nerve, a persistent optimal reflex response of the semitendinosus muscle was recorded. A similar response was also recorded during stimulation of the second synergistic nerve (the peroneal). Against the background of prolonged stimulation of the tibial nerve, causing a continuous reflex contraction of the muscle, additional periodic stimulation of the peroneal nerve at a frequency of 40 cps and with gradually increasing amplitude of each stimulus from zero to its maximum, and withdrawal of stimulation at the first signs of depression of the reflex, led to modification of the effect. At the moment of the first application of the additional stimulus to the peroneal nerve, slight reinforcement of the existing reflex was observed. In response to the second stimulus, however, a slight depression of the reflex took place initially, which ceased as soon as the additional stimulation of the peroneal nerve was discontinued. Each succeeding additional stimulus from the peroneal nerve caused a more prolonged temporary depression of the existing maximal tetany in response to progressively shorter applications of the additional temporary stimulus. Hence, although depression of the existing reflex was at first difficult to elicit, it subsequently became progressively easier to obtain and more obvious in its manifestation, and it developed in response to progressively shorter periods of stimulation (see stimulus marker). However, this did not take place as a result of increasing fatigue of the center, for after withdrawal of the additional stimuli from the peroneal nerve, the level of the existing reflex response remained

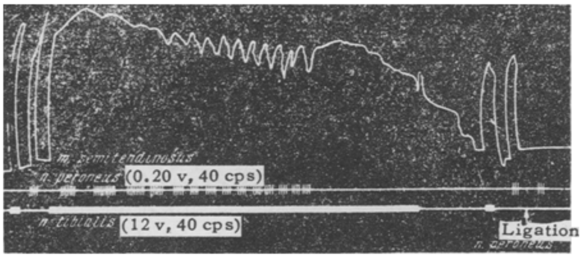

Fig. 1. Response reaction of the spinal center of the semitendinosus muscle to stimulation of synergetic nerves. Significance of the curves (reading down); responses of the muscle to stimulation of the nerves; marker of stimuli from peroneal nerve; marker of stimuli from tibial nerve.

the same as at the beginning of the experiment. Consequently, under the conditions of stimulation provided, the nerve center assimilated the rhythm of interchange of excitation and inhibition fairly quickly. In some experiments prolonged after-effects were observed in the form of a periodic interchange of excitation and inhibition during the continuing action of the background stimulus alone.

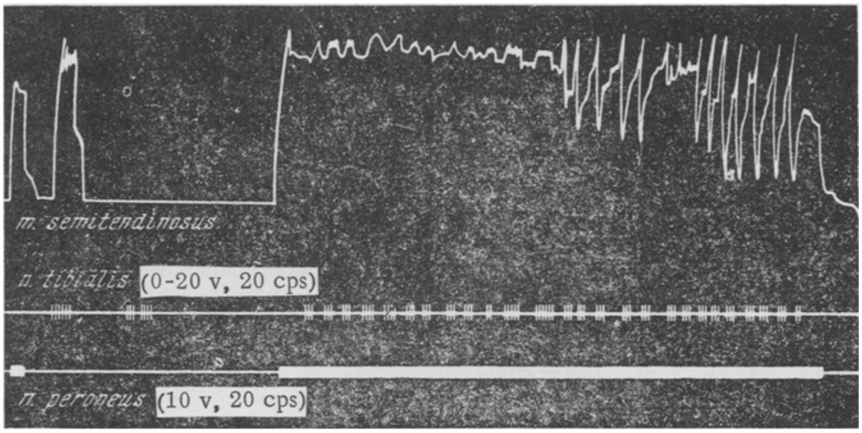

Fig. 2. Reflex responses of the semitendinosus muscle to stimulation of synergistic nerves. Significance of the curves (reading down); muscle responses; marker of stimuli from tibial nerve; marker of stimuli from peroneal nerve.

Similar results were also observed in the remaining experiments (in the presence of almost maximal initial reflex responses to stimulation of the synergistic nerves). If, however, they were slightly below optimal, reinforcement of the reflex was observed. The experimental results confirmed the fundamental principle of the Vvedenskii--Ukhtomskii school, that the same sensory nerve may cause either excitation or inhibition of the center, depending on the actual state of the latter and on the intensity of the stimuli arriving from the nerve. If the stimuli are weak, the nerve will reinforce the initial excitation, but if strong, it will inhibit it. This evidently happens as a result of the periodic action of the receptors during stretching of the lungs, sending impulses via the vagus nerve, the effect of which on the respiratory center is known to depend on the strength and frequency of stimulation [1].

In order to obtain a closer analogy between the automatic activity of the respiratory and spinal centers, we attempted to create conditions in which a second, additional stimulus applied to the spinal center in the conditions described above would have a dual effect: initially of reinforcing the existing excitation, and subsequently giving way to inhibition. We succeeded in our purpose in a few experiments. For instance, in the experiment depicted in Fig. 2, the background stimulation of the peroneal nerve was only just below maximal, while additional stimulation of the tibial nerve was maximal. During the first moments of application of the additional stimulus to the tibial nerve, only a slight reinforcement of the existing reflex was observed. This was later accompanied by the subsequent phase of depression. Withdrawal of the additional stimulation from the tibial nerve led to restoration of the level of the existing tetany. It is interesting that we sometimes observed a similar picture when recording the respiratory movements of frogs: in one case "inspiration" was followed immediately by its depression, while in the other case "expiration" was followed by the apparent restoration of the original level, after which an additional "inspiration" appeared, accompanied by inhibition.

In the experiments in which additional stimulation was applied to the contralateral homonymous nerve, when tetany of the semitendinosus muscle was elicited by stimulation of the ipsilateral nerve, we obtained similar results which are described above, but we never succeeded in observing a dual response to the additional stimulus (Fig. 3). Here too, the reaction of the center to the additional contralateral stimulation (right tibial nerve) was at first hardly perceptible, and it then became more obvious in the form of a periodic depression. It is interesting to note that in this case the after-effect following withdrawal of the additional contralateral stimulation, in the form of a periodic interchange between excitation and inhibition, developed more frequently, more clearly, and for a longer time.

If, therefore, we compare the results of these experiments with those of our previous investigations [2, 3] on the respiratory center of the frog, we can see that the spinal center, if placed in the same conditions of stimulation as the respiratory center, also displays an automatic function. In this particular case the conditions were, on the one hand, a continuous initial background excitation of one of the centers formed as a result of a constant influx of afferent impulses from a definite sensory zone; and on the other hand an additional, periodic afferent stimulation from any other receptor zone, arising in the course of this background excitation.

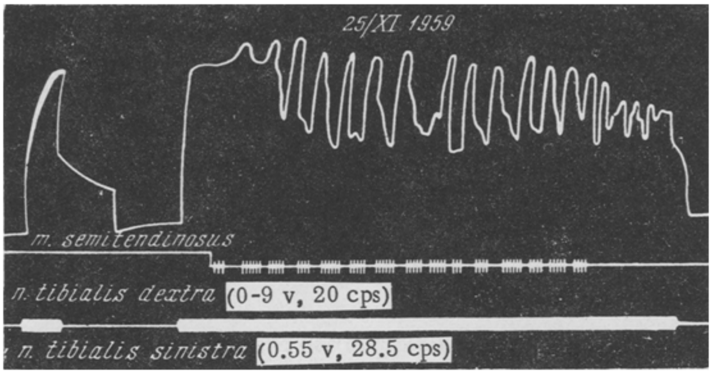

Fig. 3. Reflex responses of the semitendinosus muscle to stimulation of the ipsi- and contralateral nerves. Significance of the curves: contradiction of the semitendinosus muscle: marker of stimuli from right tibial nerve; marker of stimuli from left tibial nerve.

It is interesting that the initial responses of the spinal center to the stimulation we have described, in unusual conditions of functioning, were slightly inert, but that the center subsequently assimilated progressively rapidly the new working rhythm, and the reactions became increasingly marked. Several features in common with the activity of the respiratory center were observed here. For instance, the initial background excitation of the spinal center must be of adequate intensity (as shown by maintenance of a steady optimal tetany). Our previous experimental studies of the respiratory center of the frog showed that the automatism of this center requires for its functioning a relatively high functional level of its inspiratory region, for if a continuous arrival of afferent impulses from the aortic receptor zone is interrupted, not only is respiration arrested, but this is accompanied by a loss of tone of the respiratory muscles. This suggests that when the respiratory center carries on its automatic function, the respiratory musculature is in a state of continuous background contraction, which may be simply the reflection of background excitation of the respiratory center. We also found that a dual reaction of the already excited spinal center can only be elicited by stimulation of a synergistic nerve, causing an initial reinforcement, giving way to inhibition. This phenomenon is analogous to the well known reactions of the respiratory center to stimulation of the pulmonary branches of the vagus.

SUMMARY

Experiments were conducted on frog spinal cord center with the creation of conditions for its activity analogous to those for the frog respiratory center activity. For this purpose one of the nerves was stimulated for a prolonged period, thus creating a background lengthy optimal excitation in the spinal cord nervous centers; then the synergetic nerve was subjected to periodical brief stimulation which led to a transitory depression of the initial excitation. In another series of experiments an attempt was made at inhibition of the initial central excitation from the same contralateral nerve. The main principles, governing conditions of activity of some automatically working centers (particularly of the frog respiratory center), were disclosed, permitting it to be modelled in other nonautomatic centers.

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