THE INFLUENCE OF INTEROCEPTIVE STIMULATION ON THE DEVELOPMENT OF A DOMINANT FOCUS IN THE SPINAL CORD

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Investigation of the development of stable foci of excitation in the central nervous system [3, 5-8, 10-14, 18-20, 23] gives grounds for the suggestion that the formation of a dominant focus is associated with a change in the functional state of the center and is important in the coordination of the activity of the animal.

In a previous paper we showed that stimulation of the diencephalon of the frog (by the action of adrenalin), which has a controlling influence over the spinal cord, causes changes in the functional state of the dominant focus and strengthens the dominant [9]. It was thus shown that factors changing the functional condition of the centers affect the development of the dominant.

Many investigations [1, 2, 4, 15-17, 21, 22] have established that interceptive stimuli affect the functional condition of the central nervous system, causing changes in the excitation of the centers.

Arising from the notion of the importance of the functional condition of the center during the formation of a dominant within it, and in view of the great importance to the body of afferent impulses reaching the central nervous system from the internal organs, we considered it important to study the influence of interoceptive stimulation on the development of a dominant focus in the spinal cord. This was the purpose of the present investigation.

EXPERIMENTAL METHOD

Experiments were carried out on cold-blooded animals (frogs). In order to produce interoceptive stimulation we used the distended walls of the urinary bladder, by raising the pressure inside the organ. The formation of the dominant focus was carried out in the flexor center of the spinal cord. The criterion of the dominant state of the center was strengthening of the reflex contraction of the semitendinosus muscle under the influence of additional stimuli from other sensory nerves. Under these circumstances we recorded the contraction and the action potentials of the muscle. In all 147 experiments were performed.

The cerebral hemispheres were removed from a frog (Rana ridibunda), and the peroneal nerve and semitendinosus muscle were dissected out on one side, and the peroneal and ulnar nerves on the opposite side. Through the cloaca and into the urinary bladder was introduced a cannula, connected by means of a three-way tube to a rubber bulb (used for inflating the urinary bladder) and to a mercury manometer for recording the pressure inside the urinary bladder. The frog was fixed to a cork mat and placed in a humid chamber. The ipsi- and contralateral peroneal nerves and the ulnar nerve were placed on Dubois-Raymond electrodes which acted as stimuli. These nerves were stimulated with the current from an induction coil or from a thyratron stimulator. Application of the stimulus was recorded on the myogram and on the oscillogram. The action currents were taken from the semitendinosus muscle by silver needle electrodes, through an amplifier (with a range of 1 to 1500 cps) to a six-channel oscillograph. The action currents of the muscle were recorder with a No. 4 loop. The time marker was a sinusoidal line with a frequency of 50 cps.

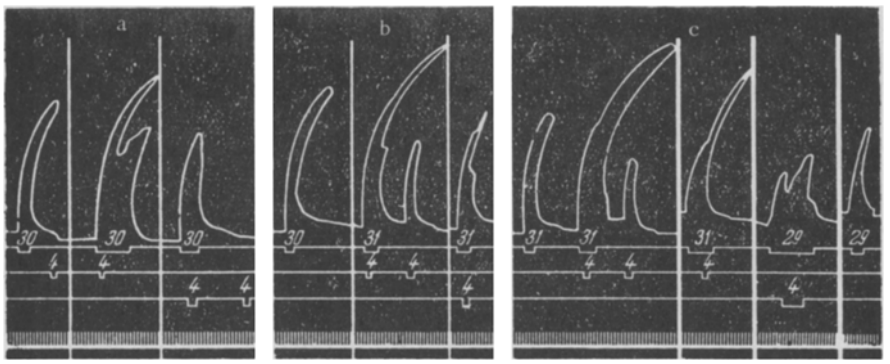

Fig. 1. The influence of interoceptive stimulation (as a result of stimulation of the mechanoreceptors of the urinary bladder) on a spinal cord dominant (experiment No. 26 – Rana ridibunda).
a) Reflex contractions of the semitendinosus muscle at the beginning of the experiment, before formation of the dominant; b) the same, after formation of a dominant in the flexor center of the spinal cord by the influence of subthreshold stimulation of a sensory nerve (2 cm below the threshold of stimulation); c) the same, 5 minutes after inclusion of interoceptive stimulation (stretching of the musculature of the urinary bladder by an increase of 10 mm of mercury of the intravesical pressure) in association with the dominant. Significance of the curves (from above down): myogram of reflex contraction of the semitendinosus muscle; marker of stimulation of the ipsilateral peroneal nerve; marker of stimulation of the contralateral peroneal nerve; marker of stimulation of the ulnar nerve; time marker (1 second).

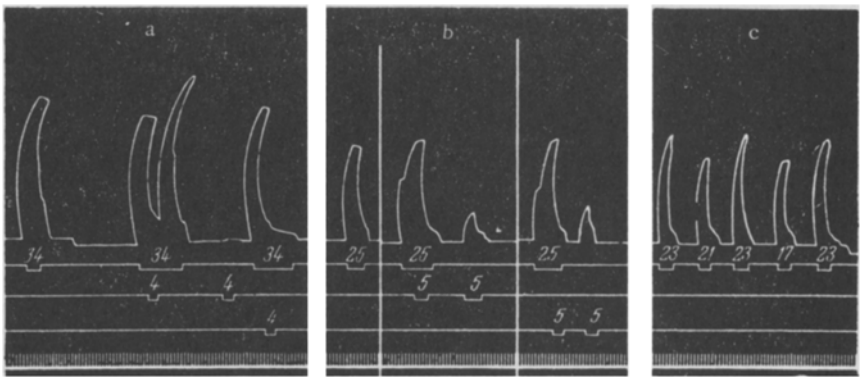

Fig. 2. Formation of a dominant focus in the spinal cord under the influence of interoceptive stimulation (in response to stimulation of the mechanoreceptors of the urinary bladder (experiment No. 84 – Rana ridibunda).
a) Reflex contractions of the semitendinosus muscle at the beginning of the experiment, before formation of the dominant; b) the same, after formation of the dominant in the spinal cord under the influence of interoceptive stimulation (stimulation of the mechanoreceptors by an increase of pressure inside the urinary bladder of 10 mm of mercury); c) development of a paradoxical stage as a result of the prolonged action of interoceptive stimulation. Significance of the curves as in Fig. 1.

The threshold of the reflex was determined and the reflex contractions of the semitendinosus muscle traced, and on this background was superimposed stimulation of the ulnar and contralateral peroneal nerves.

In the first series of experiments a dominant focus was produced in the flexor center of the spinal cord by subthreshold stimulation of the ipsilateral peroneal nerve. After definite intervals of time (10 minutes) the subthreshold stimulation was interrupted, and all the tests mentioned above were carried out. After the formation of the dominant the urinary bladder was inflated with air until the pressure within it reached 8 - 10 mm of mercury above the original.

In the second series of experiments the subthreshold stimuli were not applied, but the condition of the flexor center of the spinal cord was changed by the action of interoceptive stimulation alone, and the tests were applied under these conditions. In order to prevent adaptation of the mechanoreceptors to prolonged stimulation, a short time after inflation of the urinary bladder (15 – 20 minutes) the pressure inside the organ was reduced, and then raised once more to the initial level. In this way the prolonged action of interoceptive stimulation on the functional condition of the centers of the spinal cord was secured.

EXPERIMENTAL RESULTS

The results obtained showed that interoceptive stimuli arising in consequence of raising the pressure inside the urinary bladder may have a biphasic action on the functional state of the flexor center of the spinal cord, at first causing an increase (the shorter phase) and then a decrease of reflex excitation.

Inclusion of the interoceptive stimulation (by raising the pressure inside the urinary bladder by 8 – 10 mm of mercury) in association with the dominant already formed in the flexor center of the spinal cord by subthreshold stimulation of a sensory nerve, leads to strengthening of the dominant. By the continued action of the interoceptive stimulation the dominant state of the center is considerably enhanced and at the same time a fall in the amplitude of reflex contraction of the muscle is produced, as is illustrated by the myogram of experiment No. 26 (Fig. 1).

It can be seen from the myogram that as a result of subthreshold stimulation (coil distance 2 cm below threshold) the reciprocal inhibition, clearly observed at the beginning of the experiment (see Fig. 1,a) disappeared and was replaced by the converse effect of increase of reflex contraction of the muscle as a result of stimulation of the contralateral peroneal nerve (see Fig. 1,b). Furthermore, stimulation of the contralateral peroneal nerve alone after subthreshold stimulation began to cause contraction of the ipsilateral semitendinosus muscle (see Fig. 1,b). Stimulation of the ulnar nerve in association with reflex contraction of the semitendinosus muscle, which had no effect on the reflex contraction at the beginning of the experiment (see Fig. 1,a), also began to cause an increase in this reflex contraction of the muscle after the action of the subthreshold stimulation (see Fig. 1,b). The changes produced indicate the formation of a dominant focus in the flexor center of the spinal cord as a result of the subthreshold stimulation. The addition to interoceptive stimulation to this background (raising the pressure inside the urinary bladder by 10 mm of mercury) led to enhancement of the dominant state of the center.

Meanwhile the reflex excitation fell, since the amplitude of the reflex contraction of the semitendinosus muscle in response to stimulation by an induction current (coil distance – 29 cm) in association with inflation of the urinary bladder (see Fig. 1,c) is considerable lower than before inflation, with weaker stimulation by the induction current (intercoil distance – 30 cm; see Fig. 1,a).

It can be seen from the myogram in Fig. 1 that the increase in the reflex contraction of the semitendinosus muscle as a result of stimulation of the contralateral peroneal nerve in association with interoceptive stimulation is considerably greater (119%; see Fig. 1,c) than the effect observed before addition of the interoceptive stimulation (53.6%; see Fig. 1,b). Increase in the reflex contraction of the semitendinosus muscle in response to stimulation of the ulnar nerve is also greater in association with interoceptive stimulation (36%; see Fig. 1,c) than the effect observed before addition of the interoceptive stimulation (21.7%; see Fig. 1,b). Thus the results obtained showed that interoceptive stimulation causes enhancement of the dominant focus in the spinal cord arising as a result of subthreshold stimulation of a sensory nerve.

In the next series of experiments we studied the changes in reflex activity of the center under the influence of interoceptive stimulation. In this case subthreshold stimulation was absent, and the contraction of the muscle in response to application of all the tests was recorded before and then during the action of interoceptive stimulation. The experiments showed that in response to interoceptive stimulation a dominant focus may appear in the spinal cord, its constellation of centers including the flexor center of the spinal cord. The question of how

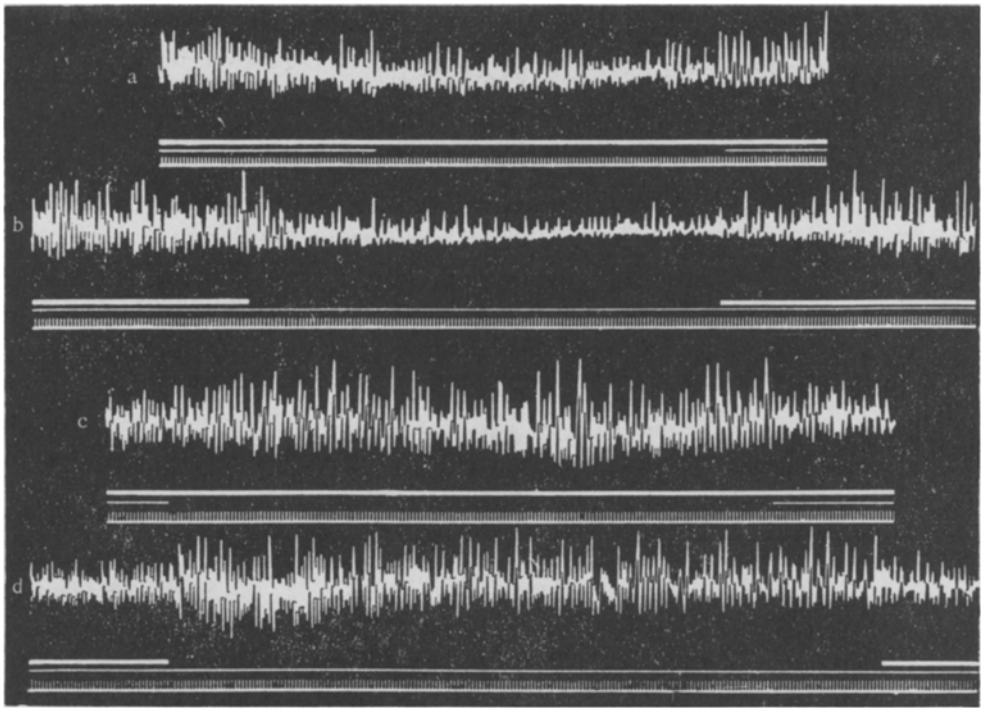

Fig. 3. Changes in the action currents of the semitendinosus muscle arising during reflex contraction of the muscle in the formation of a dominant focus in the spinal cord under the influence of interoceptive stimulation (stimulation of the mechanoreceptors of the urinary bladder).

a) Changes in the action currents of the semitendinosus muscle in response to the addition of stimulation of the ulnar nerve to reflex contraction of the muscle at the beginning of the experiment, before the action of interoceptive stimulation; b) changes in the action currents of the semitendinosus muscle in response to the addition of stimulation of the contralateral peroneal nerve to reflex contraction of the muscle at the beginning of the experiment, before the action of interoceptive stimulation; c) changes in the action currents of the semitendinosus muscle in response to the addition of stimulation of the ulnar nerve to reflex contraction of the muscle during the action of interoceptive stimulation; d) changes in the action currents of the semitendinosus muscle in response to the addition of stimulation of the contralateral peroneal nerve to reflex contraction of the muscle during the action of interoceptive stimulation. Significance of the curves (from above down): action currents of the semitendinosus muscle, marker of stimulation of the contralateral peroneal nerve, marker of stimulation of the ulnar nerve, time marker (0.02 seconds).

widely spread is the dominant focus in the spinal cord in response to distension of the urinary bladder remains unsolved and demands further study.

During prolonged action of interoceptive stimulation parabiotic stages arise and the reflex excitation begins to fall sharply. The further action of the interoceptive stimulation leads to the development of inhibition in the spinal cord center and to disappearance of reflex excitation. We give for illustration the results of experiments in which the activity of the muscle was recorded myographically and electrographically.

From the myogram of experiment No. 84 (Fig. 2,a) it can be seen that at the beginning of the experiment stimulation of the contralateral peroneal nerve in association with reflex contraction of the semitendinosus muscle caused a well marked reciprocal inhibition. Stimulation of the ulnar nerve in association with reflex contraction of the muscle had no effect. As seen from the myogram, 10 minutes after raising the pressure inside the urinary bladder by 10 mm of mercury (see Fig. 2,b), the amplitude of reflex contraction of the muscle was reduced, and it responded to stimulation with the induction current (coil distance – 25 cm) by a contraction with

a considerable smaller amplitude than to stimulation with a weaker current (coil distance – 34 cm) at the beginning of the experiment. Stimulation of the contralateral peroneal nerve and also of the ulnar nerve, in association with stimulation of the ipsilateral peroneal nerve, and after the action of interoceptive stimulation, led to a significant increase in the amplitude of the reflex contraction of the muscle, as can be seen from the myogram (see Fig. 2, b). Under these conditions stimulation of the contralateral peroneal nerve and of the ulnar nerve separately caused a contraction of the semitendinosus muscle, whereas at the beginning of the experiment stimulation of these nerves did not cause the muscle to contract. The changes produced demonstrate the formation of a dominant in the flexor center of the spinal cord under the influence of interoceptive stimulation. In response to the prolonged action of interoceptive stimulation, as the experiments showed, the development of parabiotic stages is observed. It can be seen from the myogram (see Fig. 2, c) that one hour after inflation of the urinary bladder, stimulation of the ipsilateral peroneal nerve by the induction current (coil distance – 23 and 21 cm) caused a reflex contraction of the muscle of greater amplitude than in response to stimulation of the nerve by a stronger current (intercoil distance – 17 cm). This shows the presence of a paradoxical stage. 3 hours after increasing the pressure in the urinary bladder in this experiment, complete inhibition developed.

The results of the electrophysiological investigations are shown in Fig. 3 (experiment No. 117). It can be seen from the oscillogram that stimulation of the ulnar nerve in association with reflex contraction of the semitendinosus muscle at the beginning of the experiment (see Fig. 3, a) caused a slight fall in the amplitude of the action currents of the muscle. Stimulation of the contralateral peroneal nerve superimposed on reflex contraction of the muscle led to a sharp fall in the amplitude of the action currents of the muscle (see Fig. 3, b), characteristic of reciprocal inhibition. Forty-five minutes after inflation of the urinary bladder, as seen from the oscillogram (see Fig. 3, c, d), the picture is sharply altered. Under these circumstances stimulation of the ulnar nerve superimposed on reflex contraction of the semitendinosus muscle began to cause not a decrease but an increase in the amplitude of the action currents of the muscle (see Fig. 3, c).

The reversal of the effect was obtained in an even more demonstrative form in response to stimulation of the contralateral peroneal nerve superimposed on reflex contraction of the muscle. Instead of the sharp decrease in the amplitude of the action currents of the muscle, observed at the beginning of the experiment (see Fig. 3, b) a considerable increase took place (see Fig. 3, d). This indicates a considerable increase in the summating power of the center under the influence of interoceptive stimulation.

The results obtained thus show that the action of interoceptive stimulation of a certain intensity, arising as a result of stretching of the musculature of the urinary bladder, causes changes in the spinal cord dominant, and in the absence of such a dominant may lead to the formation of a dominant focus in the flexor center of the spinal cord.

SUMMARY

The authors studied the effect of interoceptive stimulations (in stimulation of the mechanoceptors of the urinary bladder) on the development of a dominant focus in the spinal cord of cold-blooded animals (frog). It was shown that interoceptive stimulations effected on the background of a dominant (already formed in the flexor center of the spinal cord under the effect of subliminal stimulations of the sensory nerve) causes an intensification of the dominant.

It was established that the interoceptive stimulations may cause the formation of the dominant focus in the spinal cord (it may form in the flexor center of the spinal cord).

Parabiotic stages appear, the reflex excitation is depressed and inhibition develops in prolonged action of interoceptive stimulations.

In formation of a dominant focus in the flexor center of the spinal cord under the effect of interoceptive stimulation, the stimulation of the ulnar nerve and of the contralateral peroneal nerve on the background of reflex contraction of the semitendinosus results in increase of the amplitude of the muscular action currents. This points to a pronounced increase of the summation ability of the center.

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