ELECTROPHYSIOLOGICAL ANALYSIS OF THE CENTRAL MECHANISMS CORRELATING INTEROCEPTIVE INFLUENCES ON SKELETAL MUSCLES

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Experimental data concerning the mechanisms correlating interoceptive influences on the skeletal muscles have been obtained mainly by means of the myographic recording of the reflex reactions of the skeletal muscles [1-3, 5, 6]. However, this method of investigation does not give a complete picture of the functional changes arising under the influence of interoceptive stimulation in the various structures (internuncial and motor neurons) of the spinal cord.

A more detailed analysis of the interoceptive influences on the skeletal muscles has shown [8] that stretching the urinary bladder leads to an initial depression of the monosynaptic responses of the motor neurons of the spinal cord, followed by their stimulation. The polysynaptic responses are depressed independently of the monosynaptic. In addition, it has been found that the application of single stimuli to the splanchnic and pelvic nerves, and also to the sympathetic chain, with a test interval of 50-150 msec causes facilitation, and with an interval of 150-250 msec, inhibition of the monosynaptic potentials [9]. In these circumstances, polysynaptic reflexes with a short latent period are facilitated, but the polysynaptic responses with a longer latent period are inhibited. During stimulation of the interoceptors, besides changes in the reflex responses of the spinal cord, depression of the potentials on the dorsal surface of the spinal cord is also observed [4]. As the results described show, the central mechanisms correlating the interoceptive influences on the skeletal musculature remain unexplained.

In the present investigation of the effect of stimulation of the mechanoceptors of the rectum on the monoand polysynaptic reflex reactions of the motor neurons of the flexors was studied, and the importance of the dorsal roots and the suprasegmental portions of the central nervous system in the transmission of interoceptive impulses to the spinal cord was examined.

EXPERIMENTAL METHOD

Acute experiments were carried out on cats lightly anesthetized with urethane (1 g/kg) and also on spinal cats. The spinal cord was exposed in the region of the lumbo-sacral enlargement.

The potentials were fed into a cathode-ray oscillograph with an ac amplifier from the peroneal nerve at the point where it enters the tibialis muscle. Reflex responses were evoked by stimulation of the central end of the divided dorsal root (L_5 - L_6) or of the spinal cord directly (the dorsal roots were intact) by means of a focal microelectrode (Nichrome, diameter 30 μ) in glass insulation, buried in the spinal cord to a depth of 0.5 mm from the dorsal surface at the point of entry of the dorsal roots into the cord.

For stimulation a dc source was used, gated through a distributive transformer.

The mechanoceptors of the rectum were stimulated by inflating a rubber balloon introduced into its ampulla to a pressure of 60-120 mm Hg. For the duration of the experiment the animal's body temperature was kept between

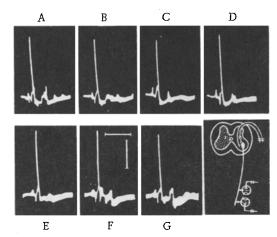


Fig. 1. Changes in reflex discharges of the spinal cord during interoceptive stimulation. Experiment on April 13, 1963. A) Reflex discharge in response to over-threshold stimulation of the central end of a Y-shaped dorsal root of the lumbar division of the spinal cord; B-E) 10 sec, and 1, 2, and 5 min after the beginning of stimulation; F and G) 20 sec and 10 min after stimulation stopped (pressure 100 mm Hg). Calibration 50 μ V, time marker 10 msec.

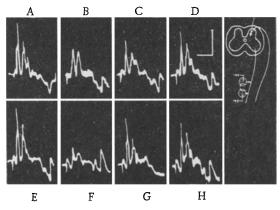


Fig. 2. Changes in reflex discharges of the spinal cord during interoceptive stimulation. Experiment dated January 17, 1963. A) Reflex discharges during over-threshold stimulation of the spinal cord through a focal microelectrode buried to a depth of 0.5 mm from the dorsal surface of the cord; B-E) 5 and 45 sec, 2 and 6 min after beginning of stimulation; F-H) 5 and 45 sec, and 10 min after its end (pressure 120 mm Hg). Calibration 100 μ V, time marker 10 msec.

38 and 39° by means of an ultrathermostat. To prevent the exposed surface of the spinal cord from drying, it was flooded with mineral oil warmed to 37-38°. Altogether 44 cats were used in the experiments,

RESULTS

In the overwhelming majority of experiments the monosynaptic reactions were modified only very slightly by the influence of the interoceptors. Stimulation of the mechanoceptors of the rectum led after 5-10 sec to depression of the monosynaptic potential (Fig. 1B); after 30 sec or (more often) 2 min the depression reached its maximum (Fig. 1C). Later the amplitude of the monosynaptic peak potential returned to its initial level (Fig. 1D) or remained slightly below it. In two experiments at the beginning of interoceptive stimulation the monosynaptic discharge increased very slightly in amplitude. In eight experiments there was no change in the monosynaptic discharge in response to interoceptive stimulation.

More substantial changes took place in the polysynaptic reflex responses during interoceptive stimulation. In all the experiments stimulation of the mechanoceptors of the rectum led to depression of the polysynaptic discharges. Even in cases when the monosynaptic potentials were unchanged or strengthened in response to interoceptive stimulation, the polysynaptic discharges were still inhibited. In no case was an increase in the amplitude of the polysynaptic discharges observed.

Depression of the polysynaptic discharges appeared 5-10 sec after the beginning of stimulation of the mechanoceptors of the rectum, and it then deepened slightly. Their maximal depression, like that of the monosynaptic potentials, took place after 30 sec or 1 min of interoceptive stimulation. Depression then gradually weakened and the amplitude of the potentials sometimes reached the initial level.

It is clear from Fig. 1A that after a well-defined monosynaptic peak potential came a series of polysynaptic discharges of low amplitude. At the 10th second of interoceptive stimulation (see Fig. 1B) the polysynaptic potentials were considerably depressed, and at the end of the first minute, instead of the series of polysynaptic potentials, only one potential was recorded (see Fig. 1C), and the rest were considerably inhibited. After 2 min the depression of the polysynaptic discharges still remained considerable (see Fig. 1D). Meanwhile, the changes in the monosynaptic potential were insignificant.

Stopping the interoceptive stimulation caused a "secondary" brief depression of the mono- and polysynaptic reflex reactions. However, in some experiments it lasted longer

than during the actual interoceptive stimulation. Usually maximal depression of the reflex responses was observed 10-30 sec or 1-2 min after stopping stimulation of the rectal mechanoceptors. Most frequently the reflex reactions were restored after 4-5 min.

These experiments showed that with an increase in the strength of stimulation of the mechanoceptors of the rectum there was a corresponding increase in the degree and duration of inhibition of the recorded reflex responses.

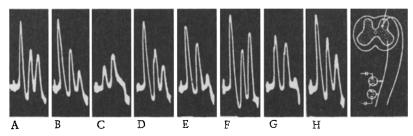


Fig. 3. Changes in reflex discharges of the spinal cord during interoceptive stimulation. "Spinal" cat. Experiment on January 28, 1963. A) Reflex discharges during submaximal stimulation of the spinal cord through a focal microelectrode buried to a depth of 0.5 mm from the dorsal surface of the cord; B-F) 3 and 45 sec, 2, 3, and 5 min after stimulation began; G and H) 60 sec and 2 min after stimulation ended (pressure 100 mm Hg). Calibration 1 mV, time marker 10 msec.

In the next series of experiments reflex reactions of the motor neurons of the flexors were evoked by direct stimulation of the gray matter of the spinal cord through a microelectrode implanted in the region of the motor nucleus of the tibialis muscle (segments L_5 - L_6). In these experiments the dorsal roots were not divided. When the stimulating microelectrode was buried to a depth of 0.5 mm from the dorsal surface of the spinal cord, mono- and polysynaptic discharges arose in the nerve to the muscle. As in the preceding series of experiments, stimulation of the rectal mechanoceptors led to depression of these discharges, starting 5-30 sec after it began (Fig. 2B); after reaching maximal intensity, despite the continuing interoceptive stimulation, the depression gradually weakened (Fig. 2C), and after 5-7 min the amplitude of the discharges returned to its original level (Fig. 2E). After interoceptive stimulation had ended, a further depression of the reflex reactions developed, starting at the 5th second (Fig. 2F). At the 45th second the monosynaptic potential was almost back to its initial level, whereas the polysynaptic discharges were still sharply depressed (Fig. 2G). The same was observed at the 45th second of interoceptive stimulation (see Fig. 2C).

In these experiments attention was drawn to the fact that the mono- and polysynaptic reflex responses of the flexor motor neurons caused by stimulation of the spinal cord were much more strongly inhibited when the ipsilateral dorsal roots were intact than the reflex reactions associated with stimulation of the central end of the divided dorsal root. Evidently this was because afferent interoceptive impulses may travel to the spinal cord along both the ipsilateral and the contralateral dorsal roots. If they could travel only along the latter, as E. F. Bogovarova [2] asserts, the reflex reactions of the spinal cord caused by stimulation of the divided dorsal root would be modified in the same way as the reactions associated with stimulation of the spinal cord (when the dorsal roots were intact), but this was not observed in any of the experiments.

The series of experiments carried out on spinal cats showed that there was no essential difference in the direction and character of the interoceptive effects on the reflex reactions of the flexor motor neurons in these animals by comparison with cats with an intact central nervous system.

Distension of the rectum, as in the previous series of experiments, caused a clear and consistent depression of the mono- and polysynaptic discharges of the spinal cord, starting at the 5th-10th second after the beginning of stimulation and reaching its maximum at the 45th-60th second (Fig. 3C). Later the reflex reactions gradually recovered and their initial level was restored after 3-5 min (Fig. 3F). Ending interoceptive stimulation led to repeated depression of the mono- and polysynaptic reactions of the motor neurons of the flexor muscles (Fig. 3G), which returned to their initial level after 2-3 min (Fig. 3H).

The facts described above, together with findings reported by other authors [1-6], thus demonstrate that the interoceptive corrective influences from the receptors of the rectum on the reflex reactions of the spinal cord may act at the level of the spinal cord itself, without involving the participation of the suprasegmental portions of the central nervous system.

It is important to note that during interoceptive stimulation the polysynaptic reflex reactions are more strongly depressed than the monosynaptic. In some experiments in which the amplitude of the monosynaptic peak was unchanged, the polysynaptic discharges were obviously depressed. It may be supposed that the interoceptive influences affect the motor neurons mainly through certain internuncial neurons, possessing synaptic connections with the

primary afferent axons, as a result of which presynaptic inhibition of the excitatory postsynaptic potentials takes place. A similar conclusion was reached by O. I. Evtushenko [4] on the basis of the study of changes in the potentials on the dorsal surface of the spinal cord.

Since at the level of the internuncial neurons there are no mechanisms of inhibition analogous to the mechanisms of reciprocal inhibition involving the participation of Renshaw's cells [7], there are grounds for regarding the interoceptive inhibition of the polysynaptic reflex response as presynaptic inhibition.

SUMMARY

Acute experiments on cats were used to study the influence of stimulation of the mechanoreceptors of the rectum on the mono- and polysynaptic reflex responses from the flexor motor neurons.

It was found that reflex monosynaptic potentials in the overwhelming majority of experiments were insignificantly inhibited or remained unchanged, whereas the polysynaptic discharges were inhibited in all cases irrespective of the monosynaptic ones. Experiments proved that the interoceptive afferent impulses may be conveyed to the spinal cord both through the ipsi- and contralateral dorsal roots. In addition, it was found that the corrective interoceptive influences may be exercised at the level of the spinal cord, without the participation of the suprasegmental formations of the central nervous system.

On the basis of an analysis of the results obtained and literature data it is supposed that the interoceptive inhibition is presynaptic in character.

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