SYNAPTIC PROCESSES IN MOTOR NEURONS DURING VISCERO-SOMATIC REFLEXES

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The visceromotor reflexes occupy an important place in the reflex activity of the spinal cord [1, 3-6, 8, 18]. The results of the electrophysiological investigation of the responses of the spinal roots in such reflexes have shown that motor reactions evoked by stimulation of, for example, the splanchnic nerve are widespread and involve, not merely all the thoracic, but the lumbar segments also [7, 9-14, 16].

However, the results of the study of the root reactions demonstrate only the complex, polysynaptic character of the excitation of the motor neurons, and they do not provide a more detailed explanation of the functional organization of the visceromotor reflexes, or still less of the synaptic processes lying at their basis. To solve these problems the synaptic potentials of individual neurons of the spinal cord must be recorded; the results of such recordings are described in this paper.

EXPERIMENTAL METHOD

Experiments were conducted on 18 cats with an intact central nervous system, anesthetized by intraperitoneal injection of a mixture of chloralose (45 mg/kg) and Nembutal (15 mg/kg).

The potentials were recorded intracellularly by the usual method [2], principally at the level of the 5th-6th lumbar segments. For identification on the basis of antidromic excitation of the motor neurons, the main muscular nerves of the corresponding hind limb were dissected (nerves to the posterior biceps, semitendinosus, and quadriceps), and stimulating electrodes were fixed to them; the dorsal roots usually were not divided, for antidromic excitation of the cell appears after a shorter latent period than orthodromic monosynaptic excitation, and can easily be differentiated from it. A constant check on the excitability of the nerves was made on the basis of recordings of the action potential of the afferent wave from the dorsal surface of the brain. This wave was recorded on the oscillograph in step with the intracellular response.

A flow of afferent impulses was evoked by electrical stimulation of the central end of the splanchnic nerve. For this purpose the splanchnic nerve was dissected from the loose tissue of the abdominal and thoracic cavities as far as its point of entry into the sympathetic chain, and it was divided at the coeliac ganglion. The dissected end of the splanchnic nerve was brought out to the dorsal surface of the animal's body and buried, like the limb nerves, in an oil bath formed from the surrounding tissues.

The splanchnic nerve was stimulated not more frequently than once per second, for at a higher frequency of stimulation rapid attenuation of the visceromotor reflexes took place [13, 15]. In some experiments for comparison one of the intercostal nerves also was stimulated. The strength of stimulation of the splanchnic nerve varied from 1 to 20 V. To determine the groups of fibers excited by a current of this voltage, recordings were made of the monophasic action potentials of the splanchnic nerve, isolated together with the sympathetic chain and placed in oxygen-enriched Ringer's solution. Recordings were made from the nerve immersed in mineral oil at 37°.

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Characteristics of Reactions of Flexor and Extensor Motor Neurons of the Spinal Cord to Stimulation of the Central End of the Splanchnic Nerve

Motor neurons	Ipsilateral stimulation							Contralateral stimulation						
	no. of neurons tested	component I			component II			no. of neurons tested	component I			component II		
		character of PSP	responding cells (in %)	latent period (msec)	character of PSP	responding cells (in %)	latent period (msec)		character of PSP	responding cells (in%)	latent period (msec)	character of PSP	responding cells (in %)	latent period (msec)
Flexor	17	EPSP	71	31.0±1.5	EPSP	77	61.5±2.9	10	EPSP	70	25.7±1.7	EPSP	90	56.0±2.4
		IPSP	—	—	IPSP	6	Not measured		IPSP	—	—	IPSP	10	Not measured
Extensor	24	EPSP	58	37.3±2.7	EPSP	—	—	14	EPSP	71	37.7±3.6	EPSP	21	65.0±4.9
		IPSP	37	28.2±2.8	IPSP	96	60.5±4.7		IPSP	29	31.0±6.6	IPSP	79	73.2±7.4

Legend. PSP—postsynaptic potential.

EXPERIMENTAL RESULTS

The results of the intracellular recording of the potentials of 50 identified flexor and extensor motor neurons in the lumbar portion of the spinal cord showed that each of these groups was characterized by postsynaptic potentials of relatively constant type, found in nearly all the investigated neurons. The results of the recording are given in the table, and they show the character of the developing postsynaptic reaction and the percentage of cells in which it was found, together with the mean length of the latent period of the reaction.

The postsynaptic changes in the flexor motor neurons took the form of a fairly intensive and very prolonged depolarization (excitatory postsynaptic potentials—EPSP). The course of depolarization was very irregular in character; however, among the waves of synaptic depolarization it was still possible to distinguish fairly clearly components with a latent period of development and with maximal intensity (Fig. 1). This difference was seen more clearly during weak stimulation of the splanchnic nerve, when the individual components of the EPSP often appeared to be separate and did not merge with one another.

The earliest EPSP regularly appeared in the motor neurons with a latent period of 25-30 msec. This postsynaptic activity, however, was of very low amplitude and it rarely led to the generation of a spreading impulse. After 50-60 msec another, much more intensive, wave of postsynaptic activity appeared, marked by considerable duration (as much as 100 msec or more) and variability. After reaching the threshold level, the synaptic depolarization at this period often led to the generation of one, and sometimes of two or three spreading impulses (Fig. 1A). The appearance of an action potential was associated with the subsequent weakening of the synaptic depolarization, although it was usually not abolished completely and it soon began to increase again.

In a very few investigated motor neurons, during stimulation of the splanchnic nerve a very weak activity arising much sooner than the two principal phases described above, and with a latent period of about 12-15 msec, was recorded. It was difficult to differentiate from the extracellular field; its intensity did not exceed 200-500 μV.

The changes evoked in the same motor neuron by stimulation of the ipsi- and contralateral splanchnic nerve were of the same sign; no evidence of the reciprocity of the synaptic changes was observed (Fig. 2). In some cases the latent period of the postsynaptic changes produced by impulses from the contralateral nerve was a few milliseconds shorter than the latent period of the ipsilateral changes, while their amplitude was slightly larger; however, no statistically significant difference could be found between these changes.

The application of a series of stimuli (frequency 100 pulses/sec) instead of a single stimulus to the splanchnic nerve was rather more effective in evoking synaptic processes in the motor neuron, especially in relation to the weaker initial component of the reaction (Fig. 1B).

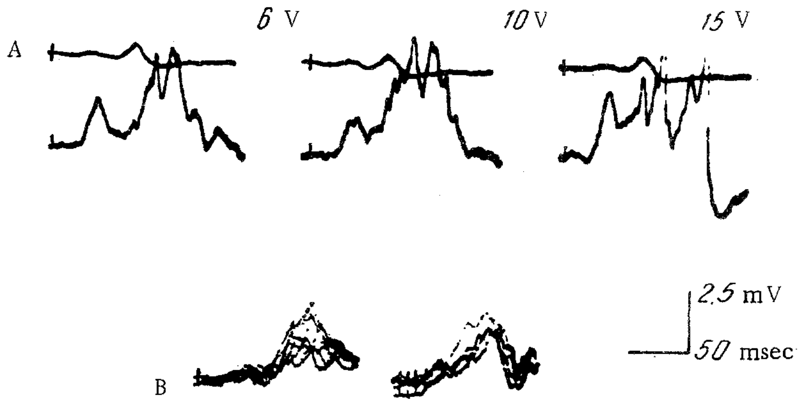

Fig. 1. Postsynaptic potentials of flexor motor neurons during stimulation of the splanchnic nerve. A) Application of a single stimulus of different strength to the splanchnic nerve; top curve—potential of dorsal surface of the spinal cord, bottom—synaptic potential of motor neuron; B) postsynaptic potential of another motor neuron arising during stimulation of the splanchnic nerve with a single pulse and a series of pulses. The oscillograms were obtained by superposing several paths of the beam in step with the stimulus.

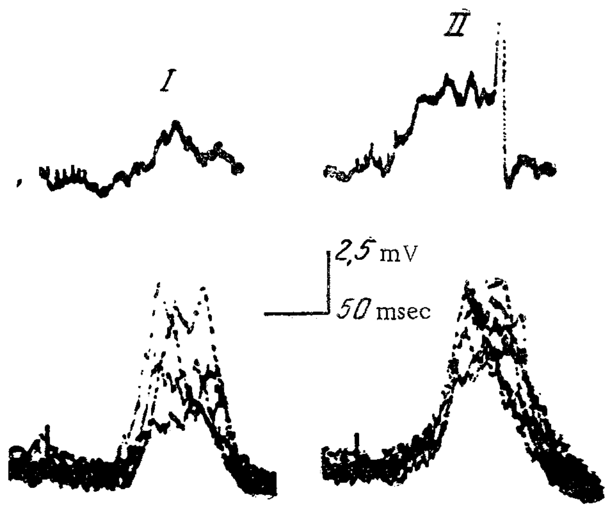

Fig. 2. Postsynaptic potential of two flexor motor neurons during stimulation of the ipsi-(I) and contralateral (II) splanchnic nerves. Top oscillograms—a single path of the beam and stimulation with a series of pulses; bottom—superposition of several paths of the beam and stimulation with a single pulse.

Comparison of the threshold strength of stimulation of the splanchnic nerves required for the appearance of a synaptic reaction with the action potentials of the isolated nerve and of the sympathetic chain showed that both components of the synaptic reaction were connected with excitation of the fibers of group A γ. δ.

The postsynaptic changes in the extensor motor neurons consisted of the same phases as those found in the flexor motor neurons, but the character of the changes of polarization of the postsynaptic membrane in this case differed substantially from that in the preceding case. The first component of the postsynaptic changes, which in this case had a slightly longer latent period than the analogous component in the flexor motor neurons, could be either depolarized or hyperpolarized; the relative frequency in percent with which these components appeared is given in the table. The oscillograms obtained when recordings were made from two different extensor motor neurons (Fig. 3) clearly reveal the differences in the character of the first components of the postsynaptic changes.

Unlike the first, the principal second component of the postsynaptic changes was always hyperpolarized (inhibitory): the inhibitory postsynaptic potential in this case was of very considerable duration and amplitude.

The postsynaptic changes in the extensor motor neurons similarly depended on the number of stimulating pulses applied and the strength of stimulation of the splanchnic nerve, like the changes in the flexor cells. The ipsi- and contralateral effects likewise were practically identical.

The postsynaptic potentials thus demonstrated are the basis of the visceromotor activity previously investigated by many authors.

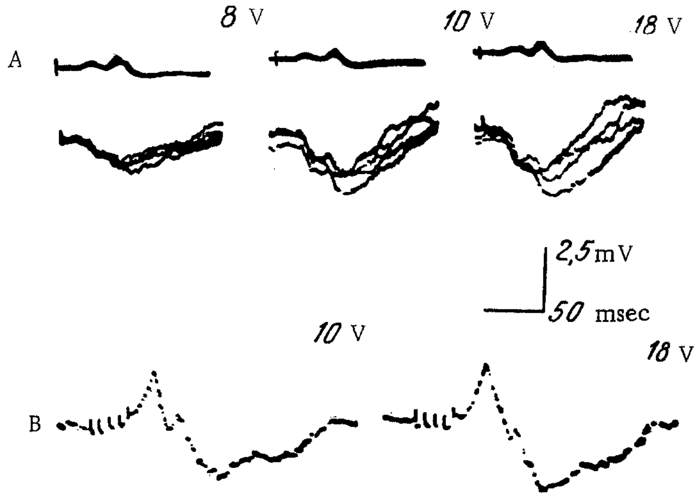

Fig. 3. Postsynaptic potentials of extensor motor neurons during stimulation of the splanchnic nerve. A) A single stimulus applied to the ipsilateral splanchnic nerve in different strengths; top curve—potential on the dorsal surface of the spinal cord, bottom—synaptic potential of the motor neuron. The oscillograms were obtained by superposition of several paths of the beam; B) postsynaptic potential of an extensor motor neuron of another type. The oscillograms were obtained by a single path of the beam and stimulation of the ipsilateral splanchnic nerve by a series of pulses.

Measurements of the latent period of the polysynaptic discharges arising in the ventral roots of the lumbar portion of the spinal cord in response to stimulation of the splanchnic nerve, undertaken in different laboratories, have led to similar, but not absolutely identical results. Evans and McPherson [15] give the latent period of the polysynaptic discharge in the ipsilateral 6th ventral lumbar root as 15-30 msec. According to Duda [14], the latent period of the discharge in the same region during maximal stimulation of the splanchnic nerve is 20-30 msec, and during submaximal stimulation, 35-40 msec; in these circumstances, as the present results have show, the reflex discharge is often subdivided into two components.

The results of the intracellular recordings from identified motor neurons described above demonstrate the synaptic organization and functional structure of the motor activity evoked by impulses from the splanchnic nerve. These impulses evidently activate two systems of synaptic influences on the motor neurons. One of these, the stronger and, judging by the longer latent period, the more complex, activates the flexor and inhibits the extensor motor neurons. The prolonged nature of the postsynaptic processes arising during activation of this system by a single afferent wave from the splanchnic nerve, predisposing to asynchronism of the motor discharge, must be responsible for the tonic character of the motor activity.

The other synaptic system is faster but less effective and it shows no clearly defined organization on the reciprocal principle. Evidently the determination of the principles of its functional organization requires a more detailed differentiation of the motor neurons, for example into phased and tonic, which was not done in this investigation.

Finally, there is reason to postulate the existence of yet another system of transmission of influences to the motor neurons of the lumbar segment, functioning with an especially short latent period (of the order of 15 msec). However, in the conditions of the present experiments (an intact nervous system and general anesthesia), its effectiveness was so low that in most cases it could not be demonstrated in practice. It may be supposed that this lowering of the effectiveness of this system was associated with its active depression by the descending tonic influences from the higher levels of the central nervous system, and in particular with depression of the transmission from the internuncial neurons to the lumbar motor neurons. Internuncial neurons were discovered in the lumbar segment which responded to stimulation of the splanchnic nerve with a very short latent period. The more precise solution of this problem must await investigations of the synaptic processes in the motor neurons during exclusion of descending influences (for example, by transection of the spinal cord).

The synaptic processes discovered in this present study are dependent on activation of the A, γ, and δ fibers in the splanchnic nerve, which coincides with the analogous dependence of the polysynaptic discharge in the intercostal nerves and the ventral roots [11].

The intraspinal pathways of these influences call for special study. All that is known is that the visceromotor influences from the splanchnic nerve are transmitted to the lower segments by propriospinal pathways, independently of a disturbance of the sympathetic trunk in these segments [13], and the transfer of activity to the contralateral side may take place through intraspinal pathways in segments situated proximally to the point of entry of the afferent fibers of the splanchnic nerve into the spinal cord [11, 16].

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. ***Some or all of this periodical literature may well be available in English translation.*** **A complete list of the cover-to-cover English translations appears at the back of the first issue of this year.**
