THE INTERSEGMENTAL PATHWAYS OF THE VISCEROMOTOR REFLEXES OF THE SPINAL CORD

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The results of recordings of the synaptic reactions of the motor neurons in the lumbar segments of the spinal cord in response to visceral influences demonstrate the complex character of the intraspinal and segmentary pathways of the visceromotor reflexes [1,2,4].

During stimulation of the splanchnic nerves, the ascending impulses are known to spread along the fibers of the lateral and dorsal columns of the spinal cord [6,8-10,13], where they are located alongside the fibers of the somatic afferent pathways [3,5,13]. Possibly the descending visceromotor influences are transmitted by the collateral fibers both of the dorsal and of the ventro-lateral pathways, forming synaptic endings on the internuncial and motor neurons of the nuclei in the thoracic and lumbar segments of the spinal cord.

The object of the present investigation was to test this hypothesis and to determine the order of excitation of the various neuronal groups within one of the lumbar segments of the spinal cord in response to visceromotor influences.

EXPERIMENTAL METHOD

No concrete information is available regarding the pathways of conduction of visceromotor influences in the lower segments of the spinal cord, and for this reason an attempt was made to choose a simple method for determining the localization of the pathways carrying these influences. The method used was the focal recording of potentials from various points of the spinal cord by means of low-ohmic microelectrodes, enabling the localization of the activated structures in the substance of the spinal cord to be determined with reasonable accuracy depending on the intensity of the electric field which they create.

Experiments were carried out on cats with an intact nervous system, anesthetized with chloralose and Nembutal (45 and 15 mg/kg body weight, respectively). The operation to enable the electrical activity of the spinal cord to be recorded, the dissection, and the stimulation of the ipsilateral splanchnic nerve were carried out by the method described previously [1,2]. In a series of experiments, the sympathetic chain was divided below the point of entry of the splanchnic nerve. The spinal cord was exposed at the level of the 4th-5th lumbar segment. The focal potentials were picked up by glass microelectrodes filled with a 2.5 M solution of NaCl, with a resistance of 0.5-1 mΩ.

The microelectrodes were implanted in a transverse plane of the 5th lumbar segment; the implantation channels of the microelectrodes were situated 250-300 μ apart. The focal potentials were recorded in each channel every 250-300 μ as the microelectrode was pushed deeper.

At the end of the experiment, the microelectrode was cut off and left in one of the channels for subsequent verification of the direction of its implantation. The segment of the spinal cord with the microelectrode was extracted and fixed in 10% formalin solution. Serial sections 30-60 μ in thickness were cut on a freezing microtome. From the oscillograms thus obtained charts showing the distribution of the latent period and the amplitude of the focal potentials over the transverse section of the spinal cord, and charts of the inflow and outflow densities of the current were plotted (by the method of Howland, Lettvin, and co-workers [22]).

EXPERIMENTAL RESULTS

The focal potentials recorded at different depths of the spinal cord during stimulation of the ipsilateral splanchnic nerve consisted of a positive or negative wave, changing its sign depending on the position of the points of the microelectrode in the spinal cord.

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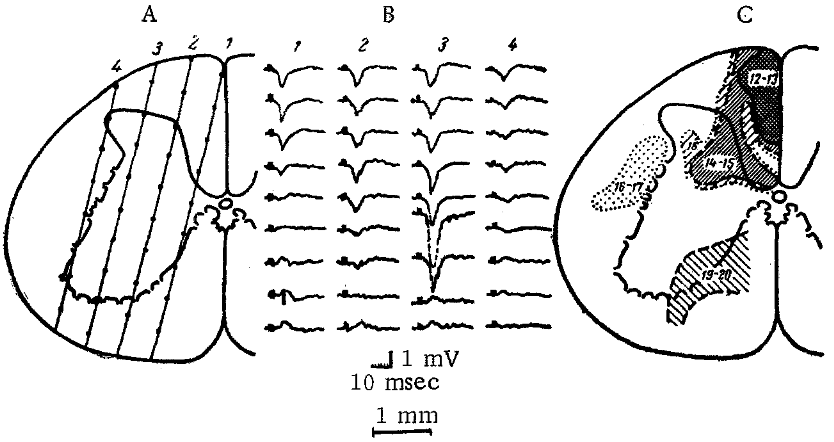

Fig. 1. Focal potentials of the 5th lumbar segment of the spinal cord during stimulation of the ipsilateral splanchnic nerve: A) scheme of transverse section of the 5th lumbar segment of the spinal cord with the channels of implantation of the microelectrode traced on it; B) focal potentials recorded in these channels at depths denoted by points; C) time sequence of excitation of different neuronal structures of the 5th lumbar segment of the spinal cord in response to visceral influences.

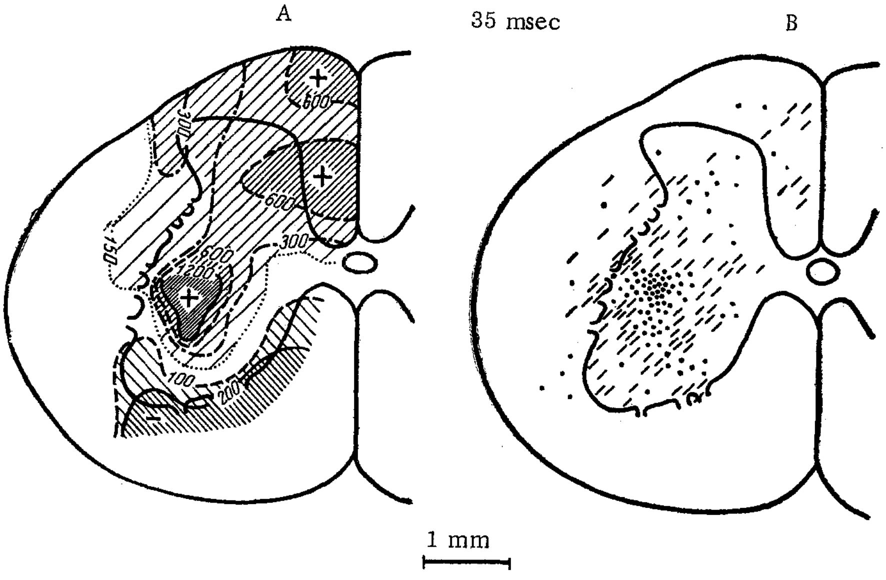

Fig. 2. Distribution of amplitudes of focal potentials (in μV) over the transverse section of the spinal cord (A) and charts of density of sources (strokes) and inflows (dots) of current into the 5th lumbar segment of the spinal cord 35 msec after stimulation of the ipsilateral splanchnic nerve (B).

An example of the distribution of these reactions in the 5th lumbar segment of the spinal cord is given in Fig. 1A and B. Most of the focal potentials arising during stimulation of the ipsilateral splanchnic nerve were complex in form, so that two or more components could be distinguished.

At different recording points, these potentials possessed a different latent period. The scheme of distribution of the latent periods of the focal potentials over the transverse section of the 5th lumbar segment of the spinal cord illustrated in Fig. 1C revealed the time sequence of activation of the different structures of the spinal cord in response to stimulation of the ipsilateral splanchnic nerve. The earliest focal potentials, with a positive sign and a latent period of 12-13 msec, were found in the region of the dorsal columns. After 16-17 msec, signs of similar activity appeared in the region of the lateral columns; however, the amplitude of the focal potentials here was much less than in the region of the dorsal column.

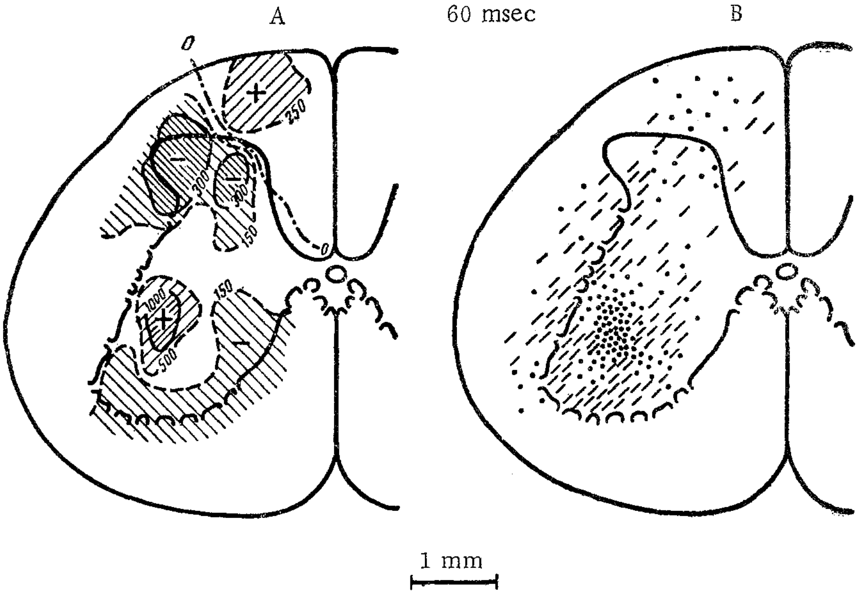

Fig. 3. Schemes of distribution of amplitudes of focal potentials over the transverse section of the spinal cord (A) and of the density of the sources and inflows of the currents (B) 60 msec after stimulation of the splanchnic nerve. Remainder of legend as in Fig. 2.

After a further 19-20 msec, negative focal potentials appeared in the medial part of the ventral horns and the adjacent white matter, against the background of which synchronized discharges of individual cells were frequently observed. The duration of these reactions was 65-80 msec.

Finally, in the region of the motor nuclei of the ventral horn, complex electrical reactions were recorded, consisting of low-voltage components with a short latent period and later high-voltage components, reaching their maximal values after 50 msec. The duration of these focal potentials was 90-120 msec. In the lateral part of the ventral horn, approximately coincident with the region of localization of the flexor motor neurons, negative potentials were recorded while in the dorso-medial part, containing mainly extensor motor neurons, positive focal potentials were recorded, and the latent periods of these potentials were 17-18 and 18-19 msec, respectively.

In order to localize these zones of maximal activity of the neuronal structures of the spinal cord excited by interoceptive impulses, schematic charts were plotted showing the distribution of amplitudes of the electrical reaction at various time intervals after stimulation of the ipsilateral splanchnic nerve. A scheme of the transverse section of the 5th lumbar segment of the spinal cord is shown in Fig. 2A, and on it are inscribed the regions of maximal amplitude of the investigated reaction 35 msec after stimulation of the splanchnic nerve. The interval of 35 msec corresponds to the first phase of the postsynaptic processes in the motor neuron [1]. At this period considerable activity is still preserved in the white matter of the dorsal columns of the spinal cord. At the same time, a powerful focus of positivity was observed in the region of the extensor motor neurons and one of negativity in the zone of localization of the flexor motor neuron, and also of the commissural cells, embracing also the white matter of the ventral horn.

Calculations of the density of the current at the different points of the transverse section of the spinal cord (Fig. 2B) showed that the region of localization of the extensor motor neuron of the ventral horn was the most powerful focus of sources of current. This agrees with the results of intracellular recordings of the postsynaptic potentials (PSP) in the motor neurons during stimulation of the splanchnic nerve [1], revealing intensive inhibitory postsynaptic potentials (IPSP) in these cells.

Charts showing the distribution of the amplitudes of the focal potentials (A) and the density of the inflows and outflows of the currents (B) 60 msec after stimulation of the ipsilateral splanchnic nerve are given in Fig. 3. At this period, a completely different type of distribution of the intensity of the electric field over the transverse section of the spinal cord was clearly revealed. In the region of the dorsal columns, positive electrical reactions were recorded, corresponding to the negativity in the region of the dorsal horn. It is clear from Fig. 3B that the region of the dorsal columns was the site of the sources of the current while the region of the dorsal horn was the site of the discharges of the current. This distribution of the electrical fields coincides with their distribution during depolarization of the central endings of the afferent fibers [16-18] and corresponds to the appearance at this period of a considerable electrotonic potential in the dorsal root [2]. Isolated foci of electrical activity in the region of the motor nuclei of the ventral horn in this case were evidently a residue of the postsynaptic processes in the motor neurons.

DISCUSSION OF RESULTS

The recordings of the focal potentials obtained in the present investigation could be used to study the spatial and temporal sequence of excitation of the neuronal structures of the 5th lumbar segment of the spinal cord during stimulation of the splanchnic nerve.

Evidently several pathways exist for the transmission of visceromotor influences to the lumbar motor neurons.

The initial positivity arising in the dorsal column 12-13 msec after stimulation of the ipsilateral splanchnic nerve is evidence of excitation of the fibers in this column conducting visceral impulses in a caudal direction. Excitation of the fibers of the dorsal column is not the result of the visceral impulses arriving here along the dorsal roots from the extraspinal pathways of visceromotor influences [7,11], for according to the present findings and those obtained by Duda [14], division of the ipsilateral sympathetic chain below the point of entry of the splanchnic nerve does not alter the shape or the latent period of the focal potentials recorded.

At the same time, the interoceptive influences spread in a caudal direction also along the lateral columns of the spinal cord. This transmission undoubtedly is interrupted by synapses and is associated with activation of the internuncial neurons of the higher levels of the spinal cord [11,14,15,19]. The low level of activity in this region is possibly associated with the inhibitory action of the supraspinal centers on the transmission of interoceptive impulses to the internuncial neurons of the thoracic and lumbar segments of the spinal cord [4,12,21].

Since the reciprocal organization of the visceromotor reflexes is evidently dependent on the supraspinal regulatory mechanism [4,21], it might be supposed that these influences are conducted in the spinal cord along the reticulo-spinal pathways of the ventral column. It would be natural to expect that, in this region, in the presence of interoceptive influences, positive focal potentials would be recorded, characteristic of the conducting pathways. However, excitation of a large number of commissural internuncial neurons, responsible for the transmission of visceromotor influences from the contralateral side, creating considerable negative focal potentials in this region, masked this defect.

The complex focal potentials of the ventral horn of the spinal cord recorded in the later periods after stimulation of the splanchnic nerve were associated with the simultaneous excitation of several neuronal structures, so that their analysis was more difficult. Evidently, the focal potentials of the ventral horn arise mainly as a result of polysynaptic processes in the motor nuclei of the spinal cord. The signs of these potentials agree well with the results of intracellular recordings in that they show the predominantly excitatory influence of the interoceptive impulses on the flexor motor neurons and inhibitory on the extensor neurons [1]. The electrical fields created by the synaptic processes in the motor neurons may extend also to the region of localization of the nuclei of the internuncial neurons, thereby interfering with the detection of the true sequence of the influence of visceral impulses.

Attention was drawn to the undoubted fact that considerable activity in the region of both the motor neuron and the commissural neurons appeared much later than activity in the region of the dorsal and lateral columns (which is confirmed by the results of intracellular recordings from motor neurons). This agrees with the conclusion that the transmission of interoceptive impulses to the segmental neurons when the spinal cord remains connected with the suprasegmental structures is considerably impaired, as is observed not only at the point of arrival of the interoceptive impulses into the spinal cord (i.e., in the thoracic segments), but also in the lower segments of the spinal cord. Comparison of these results with those of analogous investigations in conditions when the inhibitory control of the suprasegmental formations is excluded would be of considerable interest.

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