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Review Article

Integrative Processes in the Spinal Cord

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Abstract

The spinal cord, more than any other part of the central ¬nervous system, has retained the features of the embryonic structure in the form of a continuous brain tube, relatively uniform throughout its length. Only in terrestrial vertebrates, which have limbs with well-developed muscles, are two thickenings (cervical and lumbar) distinguished in the spinal cord, which contain a greater number of nerve elements than its other parts. A characteristic feature of the organization of the spinal cord is the regular periodicity in the exit of spinal roots containing afferent and efferent fibers. Each pair of roots (with some exceptions) corresponds to one of the vertebrae and leaves the spinal canal through the opening between them. Therefore, the spinal cord is divided into segments, the number of which is equal to the number of vertebrae and which are designated accordingly to the vertebrae. There are no morphological boundaries between the segments. The segments of the spinal cord are divided into cervical, thoracic, lumbar ¬and sacral; their number in each section varies greatly among different classes of vertebrates.

Keywords: integrative processes; spinal cord; neurons

Introduction

The spinal cord, more than any other part of the central nervous system, has retained the features of the embryonic structure in the form of a continuous brain tube, relatively uniform throughout its length. Only in terrestrial vertebrates, which have limbs with well-developed muscles, are two thickenings (cervical and lumbar) distinguished in the spinal cord, which contain a greater number of nerve elements than its other parts. A characteristic feature of the organization of the spinal cord is the regular periodicity in the exit of spinal roots containing afferent and efferent fibers. Each pair of roots (with some exceptions) corresponds to one of the vertebrae and leaves the spinal canal through the opening between them. Therefore, the spinal cord is divided into segments, the number of which is equal to the number of vertebrae and which are designated accordingly to the vertebrae. There are no morphological boundaries between the segments. The segments of the spinal cord are divided into cervical, thoracic, lumbar and sacral; their number in each section varies greatly among different classes of vertebrates [1-4].

Almost all afferent influences enter the spinal cord via the dorsal root fibers, which are the central branches of the axons of the neurons of the spinal ganglia. After entering the spinal cord, the afferent fibers divide into two bundles - lateral and medial. The medial bundle is dominated by thicker fibers; they mainly enter through the dorsal horn into the dorsal funiculus, where they divide in a T-shape, forming a shorter descending and a longer ascending branch. The latter can pass through the entire spinal cord and end in the Goll and Burdach nuclei of the medulla oblongata. From the branches passing in the dorsal funiculi, in turn, collaterals depart, directed ventrally into the gray matter . The lateral branch, which contains finer afferents, enters directly into the gray matter of the dorsal horn, where its fibers form both longitudinal bundles and collaterals to various types of spinal neuronal elements. Thus, all afferent fibers entering the spinal cord have essentially a dual function: they activate neurons in their own part of the spinal cord and simultaneously send information to other parts of the spinal cord and the brain [10-12].

In the overwhelming majority of cases, the collaterals of the afferent fibers establish synaptic contacts with intermediate neurons (i.e., neurons whose axons do not extend beyond the central nervous system). Only one type of afferents — the afferents of the muscle spindles—along with collaterals to intermediate cells , give collaterals directly to the motor nuclei. Recently, Kirkwood and Sears presented data on the presence of monosynaptic connections with motor neurons in the thoracic and lumbar regions also in group II muscle afferents [21].

Neural Composition

The total number of neuronal elements in one segment of the spinal cord is very large. According to Gelfan , it is about 375,000 in the lumbar region of the dog's brain. The distribution of neurons across the gray matter is very uneven, and they are collected in groups (nuclei). In the spinal cord, the nuclei are elongated along the length in the form of a column or spindle ; in the middle, they usually contain more cells and are therefore thicker. Most of the nuclei of the spinal cord occupy several segments, and accordingly,

the afferent and efferent fibers associated with them enter and exit the spinal cord not through one, but through several roots [13].

The most important nuclei of the spinal cord are located in the ventral horn and contain motor neurons (motor neurons), the axons of which exit as efferent fibers through the ventral roots. Motor neurons associated with a particular muscle are grouped in the ventral horn, forming their own column of cells [12].

In the intermediate zone of the gray matter there is also a more compactly located group of cells, forming the nucleus of Cajal. Here there are relatively small neurons, the axons of which can extend over one or two segments, giving off collaterals mainly in the ventral direction and ending on other neurons of the ipsi- or contralateral side. In this nucleus it is not possible to morphologically distinguish cell groups of a certain functional affiliation, as it is possible to do for the motor nuclei, since it is difficult to trace with which subsequent elements the intertwined short-axon cells are connected [11].

The apex of the dorsal horn is occupied by a group of very small cells with short, densely branching processes that are closely intertwined with each other and form a plexus (the gelatinous substance of Rolando). The processes of these cells either end in the same segment or extend to one or two neighboring ones as part of the Lissauer tract [17].

Along with the isolation of individual nuclei in the gray matter, the cellular elements of the spinal cord are widely described according to the principle proposed by Rexed. The gray matter is divided in the dorsoventral direction into a number of plates, in each of WHICH there is a predominance of neurons of the same type. The neurons of the gelatinous substance form plates II and III, the neurons of the intermediate nucleus form plates IV—VI, and motor neurons form plates IX [19].

A recent morphometric study of intermediate neurons in the cat spinal cord has shown that the total number of such neurons is greatest in the medial gray matter. The maxima of their observed numbers shift from the lateral part of lamina IV to the medial part of lamina VIII in accordance with the zones of distribution of the axon terminals of the main spinopetal tracts. In the medial and dorsal part of the gray matter, spindle-shaped neurons are most often observed, and in the lateral and ventral parts, multipolar cells. A gradual - increase in the size of all elements in the lateral and ventral directions is observed; in some cases, statistically significant differences in size and shape were established between neurons of adjacent laminae. However, a comparison of quantitative data for different segments indicates a single plan for their architectonics [18].

All neurons of the spinal cord which, by the nature of the distribution of their processes, can exert a synaptic action only within one or two segments, are united under the name segmental. In addition to segmental neurons, which form the bulk of the cells of the spinal cord, the spinal cord contains neurons that have long axons that exit into the white matter and then spread along it over significant distances. These neurons create conducting pathways of the spinal cord, connecting its segmental structures with other parts of the central nervous system. *Propriospinal* conducting pathways connect distant segments of one section (short pathways) or segments of different sections (long pathways) of the spinal cord. Neurons that form such pathways are located mainly in the intermediate zone of the gray matter; their axons pass either in the lateral funiculus or in the medial part of the ventral funiculus. After returning to the gray matter, they establish contacts with segmental intermediate and motor neurons. *The spinocerebral tracts* connect the structures of the spinal cord with various structures of the brain. In addition to the already mentioned tracts of the dorsal funiculus, which are essentially formed not by spinal but by peripheral neurons, a number of tracts are formed by neurons of the gray matter, located among the segmental neurons; their main mass passes in the lateral funiculus. These include the spinothalamic, spinocerebral (straight and crossed) and spinoreticular tracts, each of which differs in the localization of the spinal neurons that form them, the course of the fibers and the method of ending in the brain. The *cerebrospinal tracts,* on the contrary, are formed by neurons of the structures of the brain, and the axons descend along the white matter to various spinal segments, enter the gray matter there and end in terminal branches on certain segmental or propriospinal cell groups. This includes the corticospinal tract, which exists only in mammals and is formed by the axons of the pyramidal neurons of the cerebral cortex, the rubrospinal, vestibulospinal, reticulospinal, tectospinal and some other tracts [17].

A widespread method of grouping descending tracts (based mainly on clinical data) is to isolate the pyramidal (corticospinal) system and combine all other systems into an extrapyramidal group. However, as experimental data on their neural organization and, in particular, experimental-morphological data on the principles of their connection with the neural structures of the spinal cord accumulated, a certain artificiality of such a combination became clear. Therefore, Kuipers proposed dividing the descending tracts by the organization of their spinal connections into lateral (cortico- and rubrospinal) and medial (vestibulospinal and reticulospinal). A common feature of the lateral systems is the location of the descending fibers in the dorsolateral funiculus and the predominant connection of the terminals through the interneuron apparatus of the lateral part of the dorsal horn with the lateral groups of motor neurons. They are also united by the fact that both of them represent new systems in an evolutionary sense. The reticulospinal and vestibulospinal systems, which are part of the medial group, are united by a common course in the ventral funiculus and a common method of giving off terminals to the segmental neural apparatus. All of them are evolutionarily ancient systems and are developed in all classes of vertebrates [11-19].

Afferent Inputs of The Spinal Cord

The success of modern analysis of the neural mechanisms of spinal cord activity was facilitated by a detailed study of the fiber composition of peripheral nerves and the creation of a classification of sensory fibers according to the threshold of electrical stimulation and the speed of excitation conduction. These classifications do not always coincide with the division originally proposed by Erlanger and Gasser, and therefore it is advisable to dwell on them specifically [11]. Classification proposed by Lloyd and Chang and Rexed and Terman has found wide acceptance , according to which they are divided into groups I, II, and II. Group I includes fibers with a diameter of 12-20 μm with a maximum conduction velocity of 110-120 m/s. The thickest of them (group Iα), already mentioned earlier, originate from the primary (annul -spiral) endings of muscle spindles, and the somewhat thinner ones (subgroup IB) originate from the Golgi tendon receptors. Group II includes fibers with a diameter of 4-12 μm (conduction velocity 35-70 m/s), which originate mainly from the secondary endings of muscle spindles. Group III includes afferents with a diameter of 1-4 μm, which are apparently associated with Pacinian corpuscles and free nerve endings . Afferents of group III are activated by strong pressure on the muscle and its chemical stimulation and have a conduction velocity of 10-24 m/s. Some authors also distinguish group IV muscle afferents, corresponding to group C according to the classification of Erlanger and Gasser and associated with blood vessel receptors, as well as some encapsulated receptors [11-19]. It is generally accepted that when the stimulation strength of a muscle nerve exceeds 1.6 times the threshold for the most excitable - fibers, practically all afferents of group Ia are activated and fibers of group IB begin to be excited; the latter are completely activated at a stimulation strength of 2.4-2.5 above the threshold. However, in some nerves, the multimodal excitation of these groups of fibers by electrical stimulation is difficult, which creates uncertainty in isolating the central effects they cause . Fibers of group II are excited at stimulation strengths in the range from two to five to eight thresholds. Group III is excited quite effectively at a current strength 10 times exceeding the threshold and is completely activated at 23-26 thresholds [17]. Muscle afferents of groups II and III are often also referred to as afferents. flexor reflex (FRA) by the basic nature of the reflex reaction that occurs when they are stimulated (see below). The FRA also includes high-threshold articular afferents and groups of skin fibers that correspond in effect . A certain artificiality of such a combination will be shown in the following presentation. In contrast to the classification of muscle nerve afferents, the division of cutaneous afferents into groups α and

δ is widely used. In the cat, fibers of group α have a diameter of 6-17 μm and an average conduction velocity of 66 m/s, i.e., they correspond to Aβ fibers and only partly to Aα and Aγ fibers according to the Erlanger and Gasser classification. Fibers δ have a diameter of 1-(1 μm and an average conduction velocity of 21 m/s. Fibers α begin from the low-threshold mechanoreceptors activated by hair displacement, touch, and light pressure on the skin. δ fibers are associated with high-threshold receptors that are excited by temperature and strong mechanical stimulation of the skin surface. Some afferents of this group are involved in the transmission of signals about pain stimuli [16].

The cutaneous nerves also contain a large group of non-myelinated fibers of group C. A certain part of them is connected with mechanoreceptors of the skin, while another part starts from thermoreceptors. The speed of conduction of C-fibers varies from 0.5 to 1.5 m/s. Many C-fibers are excited only by damaging irritations of the skin. The threshold of their electrical excitation exceeds the threshold of activation of fibers of group A α by 30 or more times [14].

It should be noted that at present some authors have begun to use a classification for cutaneous fibers similar to that given above for muscle afferents. In this case, group α is designated as group II, and group δ as group III. Group I is absent from cutaneous nerves. However, it is necessary to keep in mind that the spectrum of fibers included in the corresponding groups of muscle and cutaneous afferents does not coincide. The thickest cutaneous afferents exceed in diameter the limits of group I of muscle afferents, the upper limit for which is set at 12μm. Only for the visceral nerves is the classification of afferent fibers mainly used, corresponding to the original one. In the splanchnic nerve, fibers of the group are distinguished A β, A γ and C; these groups are subdivided in some cases into subgroups (β_1, β_2, β_3, δ_1, δ_2). Group A β often includes more rapidly conducting fibers, so it can be designated as group A γ δ, as well as slowly conducting fibers, which correspond to group B. This division is also valid for other visceral nerves - hypogastric, pelvic , although the fiber composition in them has been less accurately studied. Visceral afferents of group A β have a special origin - they are associated with the Vaterpacinian corpuscles of the mesentery, which are unique mechanoreceptors. Afferents mechanoreceptors of hollow organs have a conduction velocity of 3.5-14 m/s and, therefore, fall into group Aδ (B). Finally, afferents transmitting impulses from chemoreceptors and stretch receptors of the gastric and intestinal walls are included in group C [1-14].It should be noted that some authors suggest the possibility of the entry into the spinal cord of visceral afferents of a special type, which are not axons of neurons of the spinal ganglia, but processes of Dogel cells of type II, located in the peripheral vegetative ganglia and sending one of their processes to the periphery to the receptor structures, and the other - in the direction of the sympathetic chain. After sectioning the vegetative nerves, a number of authors found intact thin unmyelinated fibers in their peripheral ends, and degenerated fibers of the same caliber in the central ends. Electrophysiologically, in some visceral nerves, after degeneration of afferents coming from the spinal ganglia, it was possible to record pulsation in response to irritation of the receptors of internal afferents, which spread at a speed of about 0.5 m / s and, therefore, corresponded to the activity of the fibers of the group. It is usually believed that such afferents are related to peripheral reflex arcs that close in the autonomic ganglia. However, Bulygin proposed to consider them as true "sympathetic" afferents in contrast to the usual "somatic" afferents. At present, there is no precise data on the properties of the afferents of the few fibers of this type and the possibility of their influence on processes in the spinal cord [10-14].

Functional characteristics spinal cord neurons

Functional properties motor neurons

An accurate determination of the functional properties of motor neurons was made possible by using the above-mentioned feature of the central course of group Iα afferents —the establishment of direct (monosynaptic) connections with motor neurons. Since the thickest afferent fibers also have the lowest threshold, they can be excited in isolation by an electrical stimulus applied to the muscle nerve, and cause a synchronous afferent wave in them, which will also synchronously excite motor neurons. Since the refractoriness of such afferents (like the refractoriness of motor fibers) is very short, all temporary changes in the central transmission along the monosynaptic reflex arc can be attributed to motor neurons. This circumstance was used by Lloyd, who conducted the first accurate measurements of synaptic processes in motor neurons. Using time-shifted single stimulations of the Ta fibers of two closely related synergistic muscles that largely converge on the same motor neurons, Lloyd made the important conclusion that the afferent wave causes a local process in the motor neurons that cannot by itself cause the cell to discharge. This process, unlike the propagating impulse, is not refractory and can be summed with another such process, causing a propagating impulse upon reaching a certain critical level. The duration of the local process after a single afferent wave is about 10 ms [11]. After the creation of the method of intracellular recording using glass electrodes, the possibility of direct study of processes in the nerve cell opened up; it was the motor neurons of the spinal cord that were the first to be subjected to such study in the works of Eccles. In this case, a local electrical reaction was discovered that underlies synaptic excitation (excitatory postsynaptic potential - EPSP). When the EPSP is summed up to a critical level, an action potential arises with characteristic components in the ascending phase, which make it possible to isolate in it the action potential of the initial segment of the axon (NS peak) and the soma and dendrites (SD peak). An examination of the features of these components of the action potential with a change in the frequency of antidromic excitation of the motor neuron showed that the properties of the nerve impulse in different parts of the cell are not the same. At a low frequency, the action potential has all the components. When the frequency increases to approximately 100/s, the SD peak ceases to be reproduced and only the NS peak is retained, and with an even greater increase, only a small M peak is retained, which indicates a lower lability of the motor neuron soma compared to the initial segment of the axon and a lower lability of the initial part of the axon compared to its myelinated part [19]. It is important to note that the same sequence of the SD and NS components of the motor neuron action potential is observed both when the discharge occurs as a result of synaptic action (orthodromically) and when the cell is excited antidromically as a result of electrical stimulation of its axon. This indicates that in both cases the same part of the cell, namely the initial segment of the axon, is initially excited. During synaptic excitation, local currents created by depolarized postsynaptic parts of the somatodendritic membrane apparently reach the initial segment and, having brought its depolarization to a critical level, cause the appearance of an NS peak in it. The NS peak, in turn, forms an action potential that propagates along the axon and also penetrates in the antidromic direction into the cell body and dendrites (to an as yet unknown distance). As the action potential propagates along the dendrites, its speed probably slows down and its temporal characteristics change accordingly [18]. Direct attempts to determine the characteristics of the action potential in the dendrites of the motor neuron were made using two fastened microelectrodes with a tip spacing of 10-20 μm, which were repeatedly inserted into the motor nucleus with the aim of simultaneously hitting the soma and dendrite of the same cell. In a very small number of cases, it was possible to record in-phase action potentials with both microelectrodes, apparently reflecting the propagation of the action potential from the soma to the dendrite. In this case, one of the electrodes recorded a normal SD peak, and the second an action potential of longer duration [17].

A characteristic feature of excitation of the soma of motor neurons is the presence of a strongly expressed and prolonged trace hyperpolarization, the amplitude of which is approximately 10 times greater than the amplitude of such in the axon. The presence of such hyperpolarization, naturally, reduces the ability of motor neurons to reproduce high-frequency impulses, keeping it at a level of several tens of impulses per second [16]. The severity of the afterhyperpolarization and, accordingly, the frequency of impulses are not the same in different motor neurons, and the latter can therefore be divided into two groups - fast (physical) and slow (tonic). Intracellular recording showed that the afterhyperpolarization of slow motor neurons lasts 130 ms or more, and that of fast motor neurons does not exceed 110ms. Accordingly, the frequency of impulses of fast motor neurons with their constant synaptic

excitation can reach 30-60 imp /s, and that of slow motor neurons - only 10-20 imp /s. However, with prolonged excitation (for example, with muscle stretching), the discharge frequency of slow motor neurons increases for a long time, while the discharge frequency of fast neurons does not increase. These features of excitation of the two types of motor neurons correlate with the functional properties of the muscles they innervate. Faster “white” muscles are innervated by fast motor neurons, and slower “red” muscles are innervated by slow motor neurons [15]. A special place in functional terms is occupied by small motor neurons, the axons of which belong to the fibers of group A γ (gamma motor neurons). The number of gamma fibers can be up to $^{1}/_{3}$ of all the fibers of the ventral root. In mammals, gamma fibers innervate intrafusal muscle fibers that are part of muscle spindles. Contraction of intrafusal fibers does not lead to the appearance of a motor response, but significantly increases the frequency of the afferent discharge coming from the stretch receptors. Gamma motor neurons are scattered between alpha motor neurons and have a tendency to background impulse activity; under reflex influences, their discharge is distinguished by a higher frequency, which may be associated with their higher excitability to synaptic influences [9-14]. Unlike mammals, in lower vertebrates (amphibians) small motor neurons innervate the motor muscles, but of a special type - tonic muscles, the fibers of which do not have a mechanism for generating spreading excitation and directly respond to the synaptic action of motor endings with slow contraction (contracture) [11]. The problem of the mechanism of central inhibition was first solved in the motor neurons of the spinal cord. In intracellular recording from cells through which synaptic transmission was suppressed by direct inhibition (i.e. by sending a preliminary afferent wave along the fastest conducting afferent fibers of the antagonist muscle, according to Lloyd) a local hyperpolarization reaction (inhibitory postsynaptic potential - IPSP) of approximately the same duration as the EPSP was recorded. The occurrence of IPSP is a characteristic feature of motor neurons; in all cases they are created not directly by afferent fibers, but by the action of the synaptic endings of interneurons synthesizing and releasing the corresponding inhibitory mediator (for more detailed information on the characteristics and mechanisms of EPSP and IPSP, see the volume "General Physiology of the Central Nervous System") [14-19].

Functional Organization Motor Nuclei

The motor nucleus (polymotor neurons) is not simply a set of cells innervating the fibers of the same muscle, but a specific system, the inclusion of elements in the activity of which is determined by a number of factors. As was first established by Sherrington, when a reflex motor reaction occurs, a relatively small number of motor neurons of the nucleus enter the discharge; the remaining cells remain in a state of subthreshold synaptic excitation, forming a subthreshold fringe. The presence of a subthreshold fringe is the basis for the phenomena of summation (facilitation) during the interaction of reflex influences, since the neurons included in it can be more easily involved in the discharge when additional synaptic influences arrive at them [19]. Microelectrode studies have shown that subthreshold excited Motor neurons do not form a spatially limited group, but are scattered throughout the nucleus. At the same time, the ability to pass into a discharge, determined by the threshold of electrical excitability, is not the same for different motor neurons. Larger motor neurons have lower excitability than smaller motor neurons, which is possibly determined by differences in the size of their surface. This difference in size is related to the number of muscle fibers innervated by the neuron's axon: large motor neurons innervate a large number of them, which possibly reflects the need to maintain a larger volume of trophic influences [15].

The effectiveness of inhibitory influences on the motor nucleus is also probably differentiated, although there is no direct evidence for this. The final result of inhibitory influences is the cessation of discharges in a certain number of motor neurons and their transition to a state of subthreshold synaptic excitation [10].

It might be thought that the order and speed of involvement of the motor neurons of the nucleus in the discharge are also determined by the uneven distribution of synaptic inputs among them. The precise determination of this possibility presents great difficulties. Both general considerations and data concerning the branching of afferent fibers in the motor nucleus can be cited against it. In experiments on stimulation of a single afferent fibers of group Iα and the recording of the resulting "single " EPSPs in motor neurons, it was established that such a fiber forms synaptic connections with virtually all motor neurons of the corresponding motor nucleus. On the other hand , each individual motor neuron can be monosynaptically activated by all the fibers of this group studied. In the presence of such an all-encompassing overlap of the projections of individual afferent fibers, it is difficult to expect significant variations in the effectiveness of the synaptic action on individual motor neurons. A similar test cannot be carried out with respect to polysynaptic influences exerted through intermediate cells, but there are no reasonable grounds for assuming that in this case the nature of the distribution of terminals in the motor nucleus will be fundamentally different. In experiments with direct stimulation of a single interneuron and recording of the evoked synaptic reactions in motor neurons, it was shown that in this case, too, a large number of motor neurons can be activated through one axon [19]. The following general consideration should also be taken into account : If there really were a noticeable difference in the effectiveness of possible synaptic influences on different motor neurons within the nucleus, due to the anatomical features of the branching of presynaptic fibers, then it would be impossible to identify a regular difference in synaptic excitability associated with the sizes of individual motor neurons [21]. An important functional feature of the organization of motor nuclei is the presence of a negative feedback system in motor neurons formed by axon collaterals and a special inhibitory interneuron (Renshaw cells). As was first shown by Renshaw, excitation of axon collaterals causes a rather prolonged high-frequency discharge of such cells; in parallel, a prolonged IPSP develops in motor - neurons, which can be differentiated from after hyperpolarization. On each Renshaw neuron converges a number of axon collaterals from many motor neurons; in turn, Renshaw cells, as shown by morphological and electrophysiological data, can also cover with their synaptic influences large groupsof not only motor but also interneurons. Using direct local stimulation of various points of the white and gray matter, it was possible to evoke antidromic responses of Renshaw cells at a distance of up to 12 mm from the location of the cell, and the conduction velocity along the axon exceeded 30 m/s. The axon terminals of these neurons could be traced in the same way both in the motor nuclei and in more dorsomedial areas of the gray matter [20]. The presence of such a widespread negative feedback system places the motor nucleus under distributed inhibitory control, which affects not only those motor neurons that generated the discharge and set the axon collaterals in action, but also the motor neurons that form the subthreshold fringe. Apparently, as a result of the action of such a system, the motor nucleus can be maintained in a state of low activity more effectively than on the basis of trace processes, sufficient for the implementation of normal motor activity and at the same time preserving large reserve capacities in the event of a sharp increase in the demands on the musculature [19].

Functional Properties Intermediate Neurons

Direct investigation of the activity of interneurons (abbreviated interneurons) of the spinal cord began soon after the successful microelectrode recording of motor neuron responses. All cells that can be antidromically excited by stimulation of the ventral roots are identified as interneurons. The electrophysiological characteristics of interneurons are fundamentally no different from those of motor neurons. Synaptic influences on them are also mediated through EPSP and IPSP, the summation of which, upon reaching a critical level, leads to the appearance of a propagating action potential. The duration of the action potential in interneurons, however, is shorter than in motor neurons, and the peak is not accompanied by such a developed afterhyperpolarization. Therefore, interneurons can generate discharges of impulses of a higher frequency - up to 500 and even 1000 imp /s. In most cases, the action potential cannot be separated into distinct components even by differentiation, which apparently indicates more uniform functional characteristics of the soma of such cells and the absence of a clearly defined zone of high excitability in the initial segment of the axon. Very often, background impulse activity is characteristic of interneurons [18].

Since interneurons cannot be so easily divided by antidromic excitation from one or another motor nerve, the basis for their functional division is often the determination of the characteristics of responses to signals coming from different types of afferent fibers. The possibility of such a division was established by Eccles et al., who were the first to show that different types of muscle afferents and cutaneous afferents selectively excite monosynaptically different groups of interneurons. The discovery of this feature formed the basis for all subsequent analysis of the systemic organization of the interneuron apparatus of the spinal cord [17].

Successful intracellular recording of synaptic responses of interneurons became possible after mastering methods of working with thinner and sharper microelectrodes. It made it possible to give a detailed characterization of interneurons according to the above-mentioned feature. Along with interneurons monosynaptically connected with low-threshold muscle or low-threshold cutaneous afferents, a large group of cells receiving synaptic high-threshold muscle, cutaneous and articular afferents, which, according to the nature of the basic reflex reaction they cause , are combined into so-called afferents flexion reflex (FPR). Such afferents can also evoke EPSPs and/or IPSPs in the interneurons of the first two groups, but only di- or polysynaptically. Thus, the division of interneurons by the nature of the afferent inputs turns out to be As Wall first showed, interneurons associated with low-threshold cutaneous receptors form a well-defined horizontal plate in the central part of the dorsal horn; neurons in this area do not respond to muscle stretch. Cells excited by such stretch are located in the form of a plate ventral. This topographic differentiation, consistent with data on the distribution of focal potentials evoked by electrical stimulation of different types of primary afferents in the gray matter, turned out to correspond quite well in the lumbar spinal cord to the histological division of the gray matter into the plates described above, according to Roxed. This correspondence also takes place in the thoracic region [10].

With some clarifications, the diagram of the connection of spinal interneurons with primary afferents looks like this [16].

Low-threshold cutaneous afferents associated with tactile receptors monosynaptically activate interneurons of lamina IV, polysynaptically - interneurons of lamina V. Low-threshold afferents monosynaptically excite cells located in the V plate, and polysynaptically excite cells of the IV plate; among the neurons of this plate, several subtypes can be distinguished , differing in the nature of polysynaptic effects from high-threshold one's afferents. Low-threshold muscle afferents monosynaptically excite interneurons of lamina VI [12].

This very orderly lamellar organization is disrupted in more ventral areas of the gray matter. In laminae VII and VIII, interneurons with a variety of afferent input characteristics are found. In more dorsal areas (laminas II-III), which form the gelatinous substance, the characterization of neurons in terms of afferent inputs has until recently remained difficult due to the considerable difficulty of microelectrode recording of their activity , caused by the very small size of the cells and their packing in a dense longitudinal cord. Recently, however, Cervero et al. and Narotsky and Kerr have published the first data on the synaptic activation characteristics of identified neurons in these laminae [15].

Spinal interneurons can be functionally divided according to the type of their connections with the main long descending tracts. It has been found that the spinal cord contains interneurons monosynaptically connected with various cerebrospinal systems, and in this case, too, their spatial distribution varies. As shown by Vasilenko and Kostyumok, interneurons directly connected with corticospinal fibers are localized in the most lateral areas of laminae V–VI; the bulk of pyramidal fiber terminals are also localized there. Interneurons directly connected with rubrospinal fibers are located in the same area, but somewhat more ventral —in laminae VI–VII. At the same time, interneurons specialized in connections with fibers of the lateral descending systems lack direct inputs from primary afferents. These cells are also distinguished by the peculiarities of the course of their axons, which allows us to classify most of them as short propriospinal neurons [14].

Interneurons monosynaptically connected with fibers of the medial descending tracts (vestibulo- and reticulospinal), are localized in the medial parts of the VII-VIII laminae. As in the case of interneurons associated with lateral systems, there are no direct influences from primary afferents on the neurons of this region. Their axons as part of the ventral funiculus can extend over several segments, which allows us to consider such neurons as short propriospinal neurons [16].

The currently undoubted specialization of spinal interneurons by the type of their main synaptic inputs allows us to formulate the position that the entire mass of cells of this type is divided into a number of functional groups, each of which takes part in the implementation of a certain type of reflex activity determined by signals from the corresponding peripheral receptor systems or (and) the receipt of descending commands from the suprasegmental centers. At the same time, the extensive convergence of excitatory and inhibitory synaptic influences of interneurons of one type on interneurons of other types can be considered as the basis for the interaction of these functional groups in the case of their simultaneous activation. Thus, it is the system of spinal interneurons that determines the specificity of the effector activity of the spinal cord, then including the motor nuclei necessary for its implementation according to the principle of the common final motor pathway [18].

Characteristics Various Functional Groups Interneurons

In connection with the above-mentioned important functional role of spinal interneurons, one of the most pressing problems of spinal cord physiology at the present time is to obtain more precise information about the projections of the corresponding neuronal groups and the methods of their connection with subsequent structures, as well as information about the methods of including these groups in certain natural forms of spinal cord activity. For some types of interneurons such information already exists, but for others it is not yet available [17].

Particularly convenient for research in this direction were interneurons monosynaptically activated by muscle afferents of group Iα (Iα interneurons) . These neurons have a direct inhibitory effect on motor neurons and are responsible for the direct inhibition of motor neurons by an afferent wave from stretch receptors of the antagonist muscle, which was already discovered by Lloyd. An important additional criterion for the functional - identification of such interneurons is the presence of inhibitory inputs from Renshaw cells in some of them, which in turn are activated by axon collaterals of motor neurons . As noted above, axonal Renshaw cell terminals extend partly into the gray matter region of the dorsomedial motor nuclei, where the Iα interneurons synaptically connected to them are localized. The axons of I and interneurons can cover a significant number of motor neurons with their action. This is evident at least from the fact that it is possible to induce antidromic activation of these interneurons from both the ventral and lateral funiculi at a distance of many millimeters from their location; the - antidromic conduction velocity reaches 70 m/s. Using direct stimulation of an individual Iα interneuron through an intracellular microelectrode, it was possible to evoke single monosynaptic IPSPs in motor neurons with an amplitude of 8 to 220 μV. Since such values are 10 to 200 times smaller than the magnitude of the maximum Iα -IPSPs in the same cells upon stimulation of afferent fibers, it is undoubtedly true that, in addition to the wide divergence along the motor nuclei, the axons of Iα - interneurons also widely converge to individual motor neurons. The advent of the technique of microelectrode injection of dyes and enzymes (procyon yellow and horseradish peroxidase) into central neurons made it possible to verify and refine the above data obtained using microstimulation. These studies also showed that the axons of Ia interneurons are myelinated and can divide into ascending and descending branches in the white matter, and sometimes be directed to the contralateral side; their terminals are directed both to motor neurons and to other interneurons [10-19].

Obtaining such precise information about the projections of Iα interneurons and, accordingly, about the methods of creating Iα IPSP in motor neurons provided a material basis for interpreting the data on the interaction of various synaptic inputs on Ia interneurons. This interaction was determined

by the mutual facilitation or suppression of Iα IPSP recorded in motor - neurons, as well as by the direct recording of PSP in interneurons, and basically consists of the following. Low-threshold Iα afferents from several synergistic muscles converge on the same interneurons, and their excitatory synaptic influences facilitate each other. Recurrent influences from Renshaw cells in turn inhibit descending effects on Iα interneurons. Excitatory influences from the vestibular nucleus of Deiters and the medial longitudinal fasciculus (i.e., from reticular neurons) also converge on Iα interneurons. The remaining types of primary afferents (low-threshold cutaneous, high - threshold cutaneous, and muscle) exert a facilitatory synaptic effect on Iα interneurons, probably only through other interneurons. It is curious that such a facilitatory effect from the contralateral side is observed only in spinal animals under chloralose anesthesia, while in decerebrated animals it is replaced by suppression. Apparently, tonic descending influences from the brainstem may have a depressing effect on excitatory interneurons associated with Iα interneurons, thereby unmasking the weaker action of inhibitory connections. Finally, Iα interneurons themselves are confirmed Iα- inhibition during excitation of muscle afferents strictly antagonistic to the muscles that are the source of excitatory Ia-afferents; this inhibition is facilitated by the action of various ipsi- and contralateral primary afferents, as well as a number of descending pathways [13].

All the data presented allow us to consider Iα - interneurons as a system that is always activated in parallel with the motor neurons of the corresponding muscle and has an inhibitory effect on a number of antagonist muscles. At the same time, this system does not function by itself, but is regulated in a certain way by inhibitory feedback from motor neurons (through Renshaw cells) and the same systems of Iα - interneurons of antagonist muscles. Apparently, a quantitative model of the Iα -system operation can already be created, reflecting all the described interactions, but for this it is still necessary to obtain quantitative characteristics of the activity of Ia-interneurons at different levels of motor neuron activation [17].

Effects caused by muscle afferent fibers of group Ib , originating from tendon receptors, have been studied in considerable detail at present . When they are excited, motor neurons of the same and synergistic muscles are subject to disynaptic inhibition ("autogenic" inhibition); in the motor neurons of antagonist muscles, on the contrary, excitatory effects may arise. Group II muscle afferents, carrying signals from the secondary endings of muscle spindles, di- and polysynaptically excite motor neurons flexor muscles and inhibit the motor neurons of the extensor muscles. Certain methodological difficulties arise in analyzing the interneuron systems associated with these types of afferents. Although group Ib fibers have a somewhat higher threshold than group Iα fibers, in a number of cases this difference is insufficient for convincingly separating them when their isolated electrical stimulation is necessary. Group II fibers, judging by the extent of the reflex responses that arise when they are stimulated, including vegetative ones, probably cannot be considered homogeneous and originating only from the receptors of muscle spindles; it is possible that the thinner of them are more likely to be related to nociceptive sensitivity [2-8].

Nevertheless, it is possible to distinguish interneuron populations that are predominantly associated with afferents of group Ib (Ib - interneurons) and group II (II- interneurons). Based on the study of changes in disynaptic EPSPs arising in motor neurons upon stimulation of afferents of group Ib, it was concluded that Ib - interneurons converge afferents of various muscles. These interneurons are also subject to facilitatory influences from other types of afferents and descending systems; in particular, cutaneous afferents have disynaptic excitatory connections with them. However, the question of whether the fibers of group Ib exert their inhibitory action independently of the system of Iα -interneurons or use , at least in part, the latter is still unclear. On II- interneurons converges a large number of afferents of this group from various muscles. They do not change their activity under the influence of the antidromic wave in the ventral roots, but are divided into 2 groups according to the presence or absence of excitatory inputs from afferents of group III [1-8].

Apparently, the most extensive system of interneurons is formed by cells primarily associated with high-threshold cutaneous and muscular afferents (HTA). The validity of combining all afferents of this kind into one functional group has been repeatedly questioned, since their various subgroups can undoubtedly transmit signals about stimuli of different modalities; it is known that many thin afferents, including group C, do not belong to the pain sensitivity system, but are associated with mechanoreceptors and thermoreceptors. Nevertheless, the dominant type of spinal reaction to excitation of all these afferents is still generalized - excitation of the flexor motor neurons, which allows using such classification when studying the activity of spinal neural mechanisms [18].

AFR interneurons receive extensive ipsilateral and contralateral afferent influences and also project bilaterally. An extraordinary increase in their activity occurs after the removal of tonic descending inhibitory influences emanating from some (apparently reticular) structures of the brainstem. It is known that the flexion reflex is well manifested in a spinal animal, but is significantly suppressed in a decerebrate animal. To restore the flexion reflex, in the latter case it is necessary to make another transection in the caudal part of the medulla oblongata. The path along which the inhibitory center carries out its action passes in the dorsal part of the lateral funiculus [17].

The action of the descending system, inhibiting the activation of AFR interneurons, can be imitated by administering DOPA (L -3,4-dihydroxyphenylamine, a metabolic precursor of norepinephrine) to the animal. In cats subjected to spinalization, the administration of this substance causes the suppression of all the usual postsynaptic effects associated with the activity of high-threshold cutaneous and muscular afferents (polysynaptic excitation of flexor and inhibition of extensor motor neurons, depolarization of terminals of primary afferents, etc.). Since DOPA is captured by monoaminergic fibers and accordingly stimulates their release of the mediator, it is assumed that the corresponding inhibitory descending pathway is formed by monoaminergic neurons. Indeed, using a combination of histochemical techniques and the method of tracing the retrograde transport of peroxidase the entry of descending monoaminergic pathways from Locus is shown coeruleus et subcoeruleus of the brainstem into various parts of the spinal cord. The terminals of these fibers are distributed in the dorsal part of the gray matter and the intermediolateral nucleus [9-15].

A characteristic feature of the functional organization of AFR neurons is the ability to create very delayed and prolonged activity against the background of excitation of the above-mentioned descending inhibitory pathways. As Anden et al. have shown, after the introduction of DOPA, stimulation of high- threshold afferents begin to cause prolonged excitation of AFR interneurons and flexor neurons on the ipsilateral side with a long latent period motor neuron. In parallel, a similar long-term contralateral extensor reaction develops; along with this, polysynaptic excitation of the contralateral flexor neurons is inhibited. motor neurons. This inhibition is not associated with the development of the latter IPSP and, therefore, develops in contralateral interneurons . Excitation of the AFR under such conditions is also accompanied by an unusually prolonged depolarization of the afferent terminals [13]. All these phenomena indicate the presence of reciprocal relationships between the AFR- interneuron systems of each half of the brain, which creates real opportunities for the emergence of rhythmic alternations of flexor and extensor motor reactions of the limbs, i.e., one of the essential components of locomotion. The synaptic mechanisms that lead to the suppression of prolonged forms of activity are still unknown [12].

Apparently, a special group of intermediate neurons is formed by cells located in the marginal zone of the dorsal horn. They are specifically activated by painful (mechanical and thermal) irritations of the skin and are probably involved in the transmission of corresponding signals in the ascending direction [11].

Interneurons in terms of functionality are the neurons of the gelatinous - substance (GS interneurons) [16]. As already indicated in the anatomical - review, GS interneurons project into a dense bundle of fibers running in the

longitudinal direction; from this bundle they also receive a number of synaptic inputs. Recent electrophysiological studies have confirmed that when the Lissauer tract is stimulated, rostral to the abduction site, both antidromic and synaptic excitation of the GS interneurons can be evoked. The conduction velocity along their axons varies from 4 to 10 m/s; apparently, after traveling some distance, the latter terminate in synaptic endings on other GS interneurons. EPSPs in GS interneurons can also be evoked by high-threshold cutaneous and muscle afferents (groups Aδ or Aβ+C). Lower -threshold afferents (cutaneous and muscle groups II) have a long-term inhibitory effect on their activity. Such an organization of the GS interneuron system can be the basis for long-term reverberation of impulse activity in it, which in turn can provide tonic effects of the gelatinous substance on other spinal structures. The intersegmental transmission of the activity of the GS interneurons apparently occurs not through the Lissauer tract, but through the system of propriospinal neurons. In particular, it is assumed that the GS interneurons participate in the mechanism of presynaptic inhibition . In connection with the significant duration of this inhibition caused by a single afferent wave, it can be thought that its generation requires activation of cells that generate a very long discharge of impulses (similar to Renshaw cells during recurrent inhibition) [15]. Eccles, Kostyuk and Schmidt discovered cells of this kind at a depth of 1.65-2.55 mm from the dorsal surface of the brain, which corresponds to the IV-V laminae according to Rexed. These cells were excited with a central latent period of more than 1.5 ms (i.e., disynaptically) by all groups of primary afferents causing presynaptic depolarization, including very effectively by AFR, and generated a prolonged (10-20 ms) discharge of fairly high frequency (over 1000 imp /s - "D-neurons"). However, Wall, based on an analysis of focal potentials arising in the dorsal horn, 20-30 ms after the arrival of the afferent wave, came to the conclusion that presynaptic depolarization is associated with the activity of GS interneurons. Electron microscopic studies by Rethely and Szentagothai presented a description of synaptic structures that are consistent with the possibility of participation of GS neurons in the creation of presynaptic depolarization. They found special pyramidal interneurons at the border of the III-IV laminae, which give off short varicose branching axons in the dorsal direction into the gelatinous substance, where they form complex synaptic complexes with the dendrites of the GS interneurons and the terminals of the primary afferents. In this case, the ending of the axon of the "pyramidal" neuron is always presynaptic in axo -axonal contacts with many endings of the primary afferents and axo-dendritic contacts with the GS interneurons. Thus, the GS interneurons together with the “pyramidal” neurons they form a feedback chain with the terminals of the primary afferents. The GS interneurons (and also, possibly, the primary afferents and descending fibers directly) activate the “pyramidal” neurons, and they, through their varicose endings, again act on primary afferents and additionally activate deuterates of the GS interneurons, creating opportunities for successful reverberation of impulses in this circuit [14]. It has recently been shown that axo- axonal terminals at the endings of primary afferents are GABAergic. In view of all these morphological data, the contradictions between the assumptions of Eccles et al. and Wall are perhaps only apparent, and both GS interneurons and interneurons located more ventrally in the dorsal horn may simultaneously participate in the creation of presynaptic depolarization [5-9].

All the functional groups of interneurons listed above are usually classified as segmental, since their activity has a limited distribution in the spinal cord, covering one or two segments at the site of receipt of the afferent signal. True, the above data with microinjection of dyes and enzymes into the identified interneurons showed that the axons of some of them, usually considered as typically segmental (for example, Iα interneurons), enter the white matter of the cords and extend along it for a noticeable distance before reentering the gray matter. Therefore, it is hardly possible to draw a clear distinction between segmental and propriospinal neurons. Nevertheless, in most cases it is possible to distinguish, properly speaking, propriospinal neurons (PS neurons), whose axons pass through more than two segments in the white matter [16]. Morphological studies using the Golgi method and retrograde degeneration have shown that a significant proportion of interneurons can be classified as such neurons, the somata of which are located, on the one hand, in the lateral and central parts of the V-VII laminae, according to Rexed, and on the other hand, in the ventromedial parts of the VII laminae and in the VIII laminae. The axons of most of them extend up to 5 segments, forming short propriospinal tracts. Neurons that give rise to long descending and ascending propriospinal tracts connecting the cervical and lumbar regions of the spinal cord are localized mainly in the ventral part of the gray matter, and their axons go in the ventral part of the lateral funiculus and in the ventral funiculus [19].

Conduction velocities along the propriospinal pathways were measured both by recording from individual fibers and by recording mass discharges in the case of selective excitation of such pathways. The possibility of selective excitation can be created by preliminary transections of the corresponding sections of the spinal cord cross-section, leading to subsequent degeneration of the fibers of the long descending (and also, depending on the level of transection, ascending) tracts. The average values of conduction velocities along the short propriospinal pathways of the dorsolateral funiculus in the lumbar region of the cat lie within the range from 35 to 40 m/s, and in the cervical region they are somewhat higher. The fastest fibers of these pathways have a conduction velocity of about 70 m/s. The short propriospinal tracts running in the ventrolateral and ventral funiculus in the cat have higher conduction velocities - 45-65 m/s for the total wave and up to 95-100 m/s in individual fibers. Very similar values were obtained in the monkey. The fibers of the long propriospinal tracts running in the central parts of the lateral funiculus and in the ventral funiculus are the fastest conducting (up to 100-110 m/s) [14-18].

As already indicated above, a characteristic feature of the functional organization of short PS neurons is the predominant connection with the projections of the main cerebrospinal descending systems. "Lateral" PS neurons, localized in the middle lumbar segments and sending their axons to the lower lumbar and sacral segments, are intensively excited by fibers of the pyramidal and (or) rubrospinal tracts, and monosynaptic convergence of these inputs often occurs. A similar picture is observed in the cervical region, where in addition to the two tracts indicated, tectospinal fibers also terminate on lateral PS neurons. In addition, neurons of this group can also receive direct reticulospinal projections through the lateral reticulospinal tract [10-17].

The ventromedial group of short PS neurons is connected with the reticulospinal and vestibulospinal tracts, and in this case, too, some of the neurons are monosynaptically excited by both descending systems. In both this and the previous group, a combination of monosynaptic excitation with accompanying di- or polysynaptic action is typical. It is possible that the latter is created by the propriospinal cells themselves, which establish connections with each other; morphological data show that a significant portion of the axonal projections of short PS neurons are directed to other neurons of the same population [7].

Stimulation of peripheral afferents has only a polysynaptic and often extremely weak effect on the overwhelming majority of PS neurons in the lumbar region. This position has given rise to objections, and it has been suggested that the absence of reactions to peripheral signals may be due to some selective suppression of their synaptic transmission. However, recent detailed studies of synaptic inputs to this group of neurons in the cervical region have shown that even there, although peripheral projections exist, the total intensity of their action is significantly lower than the intensity of descending inputs. A similar preferential connection with suprasegmental pathways has also been shown for the ventromedial group of short PS neurons [4-6].

In PS neurons, after their activation (both antidromic and synaptic), pronounced inhibition is observed. In this connection, it has been suggested that these neurons, in addition to mutually excitatory, also have mutually inhibitory connections, organized similarly to the system of recurrent inhibition in the motor nuclei [1-8].

Direct data on synaptic inputs to PS neurons that form long descending and ascending pathways are still practically absent [11].

Determination of the projections of the propriospinal tracts using experimental degeneration methods showed that short propriospinal axons running in the lateral funiculus terminate almost ipsilaterally in laminae V–VII, with their terminals oriented toward the motor nuclei of the distal muscles of the limbs. Propriospinal axons running in the ventral funiculus (both short and long) terminate largely bilaterally in the medial portions of laminae VII and VIII, oriented toward the motor neurons of the proximal muscles of the limbs and the axial muscles of the body [11-16].

The functional characteristics of these projections have been studied primarily using the above-described method of selectively activating them in the white matter of the funiculi. It has been established that the short lateral propriospinal tracts in the lumbar spinal cord form monosynaptic excitatory connections with the flexor motor neurons and partly with extensor neurons, and also inhibitory neurons with extensor neurons. Consequently, among the short neurons, a certain proportion are inhibitory cells. In the cervical region, the lateral propriospinal tracts have a direct excitatory effect on the overwhelming majority of motor neurons. Lateral propriospinal tracts also project onto segmental interneurons, as evidenced by the presence of intense excitatory and inhibitory polysynaptic responses in motor neurons that accompany the initial monosynaptic PSP. In the cervical region, lateral propriospinal influences on segmental interneurons are even stronger than in the lumbar region.

The ventral short propriospinal tracts also form mono- and polysynaptic connections with motor neurons; it is possible that the inhibitory polysynaptic effects are realized through Iα interneurons. It is unclear whether the medial PS neurons can exert a direct inhibitory effect on motor neurons. Studies of the intensity of the synaptic action exerted on an individual motor neuron by a single PS neuron have shown that it is small - less than 100 μV. Unlike the lateral PS neurons, the medial ones are connected mainly with motor neurons of the proximal muscles of the limbs, as well as with motor neurons of the body musculature [6-9].

Among the long propriospinal tracts, the descending fibers running in the central parts of the lateral funiculus have direct contacts with motor neurons (not with all of them). In addition, these fibers have direct connections with Iα and AFR interneurons. A similar picture is observed in the case of the long tracts running in the ventral funiculus, but direct connections with motor neurons are less pronounced here, or are absent altogether . The difference in the action of the long descending tracts on the motor neurons of the proximal and distal muscles is less pronounced than in the case of the short propriospinal tracts . The long ascending propriospinal tracts apparently project predominantly onto the motor neurons of the axial muscles , but such information was obtained using indirect methods [9-12].

All of the above allows us to evaluate short PS neurons as a neural system that ensures the transmission of signals arriving along the lateral and medial descending pathways. Long PS pathways undoubtedly play an important role in coordinating the control of the forelimbs and hindlimbs, but it is currently not possible to form a detailed idea of their function [14-19].

Functional properties sympathetic preganglioner neurons

Microelectrode recording of the activity of individual preganglionic sympathetic neurons turned out to be associated with extremely great difficulties, which could not be overcome for a long time. In the region of location of such neurons, i.e. in the intermediolateral nucleus of the thoracic segments of the spinal cord, a number of authors recorded focal potentials in response to antidromic activation of preganglionic axons, indicating the correctness of microelectrode insertion. Focal potentials also arose in this region upon stimulation of high-threshold somatic and visceral afferents. In a number of cases, it was possible to isolate a series of rapid oscillations in the focal potential, reflecting the extracellular activity of individual preganglionic neurons. The most detailed study of the antidromic discharges of these neurons was carried out by Lebedev et al. They showed that preganglionic neurons can be divided into a number of groups based on the speed of propagation of the antidromic wave. The axonal conduction velocities of the main group of neurons located in the intermediolateral nucleus range from 3 to 10 m/s, which allows them to be classified only as group B. They, in turn, can be divided into several smaller subgroups. Along with this main group, neurons with more rapidly conducting B-axons (conduction velocity 10-21 m/s) were found in a limited dorsomedial zone of the ventral horn. In addition, preganglionic cells with slowly conducting and probably unmyelinated axons (conduction velocity up to 1.5 m/s) were found in the lateral part of the intermediate zone. The latter were designated as C- preganglionic neurons [20,21].

A characteristic feature of sympathetic preganglionic neurons is a very low frequency of background activity (no higher than 3-5 impulses /sec). In a significant number of these neurons, background activity is not expressed at all. The discharges of many preganglionic neurons of the intermediolateral nucleus are synchronized with pulse oscillations, and some also with slow oscillations of arterial pressure (waves of the third and fourth orders). In this case, the increase in the frequency of discharges usually precedes the pressor phases. These data are usually considered as an indication of the connection of the corresponding preganglionic neurons with the vasomotor function. At present, there are no data on preganglionic neurons associated with other effector structures (glandular formations, smooth muscles of the gastrointestinal tract, etc.). It is possible that such neurons are localized not in the main nucleus, but in the additional groups described above, and their activity does not correlate with changes in blood pressure [10-19].

Stimulation of afferents causes orthodromic discharges in sympathetic preganglionic neurons, the latent periods of which indicate the polysynaptic nature of the connection between these afferents and sympathetic neurons. The only possible exceptions are B neurons with a high conduction velocity in the axon, which may participate in the generation of the "ultra-early" response, which is distinguished by a very short latent period. Inhibition of background activity may also occur along with activation. Such inhibition is distinguished by a very long duration (several seconds) and may occur without initial excitation. In addition, some neurons exhibit recurrent inhibition; it is manifested in the suppression of antidromic discharges after the preceding antidromic discharge for a time much longer than the refractoriness of the cell soma, as well as in the suppression of an orthodromic discharge by a preceding antidromic one.

Functional properties of parasympathetic preganglioner neurons

Despite the relatively small number of preganglionic parasympathetic neurons localized in the lateral horns of the gray matter of the sacral segments, fairly detailed information has now been obtained regarding their functional properties. Intracellular recording of the activity of these cells has also been carried out.

Parasympathetic neurons are localized in two or three sacral segments and are identified by antidromic activation from the pelvic nerves. Many of them, like sympathetic cells, are in a state of background activity, the increase in frequency of which often coincides with an increase in pressure in the bladder. When visceral (pelvic) or somatic (limb) nerves are stimulated, an evoked discharge occurs in the neurons , characterized by a very long latent period (60-120 ms). Before the evoked discharge, a period of suppression of background activity is observed, which occurs with a short latent period (5 ms) and coincides with hyperpolarization of the neuron in the case of intracellular recording.

There are also grounds to assume the presence of recurrent collaterals for parasympathetic neurons , which exert a recurrent inhibitory effect on them. Stimulation of the ventral roots containing the axons of such neurons at a frequency of 10-20 times per second leads to suppression of their background activity. Interneurons are simultaneously activated, the discharge characteristics of which are similar to those of Renshaw cells [5-15].

Are there specialised "vegetative" interneurons?

In order to clarify the neural mechanisms of reflex reactions carried out through sympathetic and parasympathetic preganglionic neurons of the spinal cord, the question of the presence of specialized interneurons

associated with visceral afferents and projecting in turn onto efferent autonomic neurons is of great interest. As Gokin's studies on the lower thoracic segments have shown, in layer V, according to Rexed, a large number of interneurons are found that respond to stimulation of high-threshold afferents of the splanchnic nerve; however, they are almost always excited by high-threshold somatic afferents and, based on this feature, can be classified as AFR interneurons. Only very rarely are interneurons found in this layer that respond only to somatic or only to visceral impulses. Interneurons with extensive convergence of somatic and visceral influences are also found in more ventral areas of the gray matter - lamina VII. Analysis of the latent periods of responses showed that among these cells, there are cells with very simple (possibly monosynaptic) connections with visceral afferents; other neurons are activated by these afferents through more complex, polysynaptic pathways. Usually, one of the inputs (visceral or somatic) is more effective (more direct) for these neurons, and the other is less effective. Quite rarely are cells registered in which it could be assumed that there are direct connections with afferents of both types. A characteristic feature of neurons of layer VII is also the presence in their discharge caused by stimulation of visceral afferents, in addition to the early response, of an additional late discharge, which coincides in time with the late response of preganglionic neurons. Some of the neurons of this layer generally generate only a late discharge. Apparently, the interneurons of this layer are the structure on which the interaction of segmental and spinobulbospinal visceral and somatic influences caused by high-threshold afferents [5-9].

A certain number of interneurons activated by high-threshold visceral and cutaneous afferents are also found even more ventrally, in lamina VIII; in more dorsal areas of the gray matter, they are absent.

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