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Review Article

Impulse Activity of Neurons of The Substance Gelatinosus and Neurons of the Posterior Horn of The Spinal Cord (Layers Iv And V)

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Abstract

The study of the impulse activity of neurons of the gelatinous substance and neurons of the posterior horn of the spinal cord in layers IV and V is aimed at studying the mechanisms of processing pain and sensory signals. The gelatinous substance and the posterior horn of the spinal cord play a key role in the perception of pain and regulation of sensory information. Analysis of the impulse activity of neurons in these areas will allow a deeper understanding of the neurophysiological processes underlying pain syndromes and other neurological disorders, and will also help develop new approaches to the treatment of pain disorders and neuropathies.

Kew Words: impulse activity; neurons; gelatinous substance; posterior horn; pain information

Introduction

The electrophysiological properties of neurons in this area have been studied extremely insufficiently at present. This is due to a number of factors, the most important of which are the difficulty of stable (even extracellular) recording of neuronal discharges and the lack of reliable indicators that the recorded potentials actually reflect the activity of neurons of the gelatinous substance. It has been shown that some neurons of the gelatinous substance do not have spontaneous activity, while other cells generate rhythmic discharges with a frequency of 10–30 imp. /sec. It should be noted that deep chloralose-nembutal anesthesia was used in the experiments [1,2]

According to data obtained on non-anesthetized cats, most elements of the gelatinous substance are characterized by low-frequency, irregular discharges with independent time distribution. Localization of elements with different discharge frequencies in the cross section of the dorsal horn of the spinal cord. It is evident that units with a similar average frequency are concentrated in certain zones of the dorsal horn. Most elements of the gelatinous substance exhibit spontaneous activity with a frequency of 1–20 impulses/sec, and the discharge frequency of layer II neurons was lower (4.5±1.45 impulses/sec) compared to layer III cells (8.3±1.2 impulses/sec) [2].

The dorsal horn elements had different temporal distributions of background discharges. The type of discharges, or the so-called structure of background impulse activity (BIA), was determined on the basis of inter-impulse intervals. In most elements localized in the gelatinous substance, BIA was characterized by irregular discharges. Elements with group discharges were very rare. It was not possible to find any relationship between the average BIA frequency and the type of background discharges [1,3].

In order to establish whether there are certain forms of statistical interrelation of background discharges or the nature of their distribution is random (independent), the expected density function (EDF) of the distribution of discharges after each previous discharge was determined for each element. In accordance with the EDF, all elements were divided into two groups. In the first group of elements, the EDF is represented by a curve located parallel to the abscissa axis at the level of the average frequency: deviations from it, occurring without a certain sequence. Such a uniform EDF was found in most elements of the gelatinous substance. Uniform EDF is more typical for elements with an irregular type of background discharges, but can also be found in the case of regular activity [3,5].

In the second group of elements localized in the gelatinous substance zone and at the base of the posterior horn, the EDF was graphically depicted as a curve with periodic wave-like changes from the average frequency level. The EDF deviation was considered reliable if the wave amplitude exceeded the average level by a double fundamental deviation at 8 = 2\1π, where (π is the number of impulses in a given matrix cell). In some elements, only the initial maximum deviation with a duration of 20–40 ms was detected. In other cases, 2–3 regular waves with a duration of 50–200 ms were detected. Such uneven EDF was observed in neurons with different discharge frequencies, but significantly more often in elements with regular and group BIA [1].

In accordance with the EDF theory, it is assumed that the presence of 2–3 periodic waves in the function graph indicates a statistical dependence of the distribution of intervals both within impulse groups and between individual groups of discharges. Such statistical dependence is probably inherent in elements experiencing strong synchronous synaptic bombardment, at the apex of which action potentials arise. As follows from the data, gelatinous

elements with uneven EDF are localized in those areas of the posterior horn (layers II–III) where a large number of cutaneous terminals terminate. The uneven nature of EDF is apparently due to the independent, random distribution of discharges that arise as a result of asynchronous synaptic bombardment [1,6].

Thus, the presented data show that neuronal elements of the dorsal part of the posterior horn have an uneven EDF character and can differ significantly in frequency and type of discharge distribution, and elements with the same type of impulse activity and similar frequency have a certain localization in the posterior horn, which is probably due to the morphological features of these elements and cyanization of their connections [2,3,6]. The uneven EDF, most often found in elements located in the lateral region of the dorsal horn, apparently indicates the existence of some specific pathways of their activation, the effects of which are presented in the form of odic, intense and synchronous impulses [2]. It was found that in response to a single irritation of the cutaneous nerve, in which long-term (80–150 msec) electrotonic dorsal root potential were recorded in the dorsal roots with a latent period of 2–4 msec, most neurons in the dorsal part of the dorsal horn generated group discharges. As in the case of interneurons in other areas of the spinal cord, the frequency and duration of multiple discharges were in direct dependence on the intensity of the afferent stimulation [1,2,5].

In neurons localized in the lateral part of the II and III layers of the spinal cord, in which the initial BIA was absent or low-frequency, with a tendency for impulses to group (this was revealed during the analysis of the EDF), the response to a single irritation of the cutaneous nerve consisted of 5–7 action potentials (AP). The latent period of the first AP varied within 1.5–4 ms. The group discharge was divided into an initial burst lasting 15–40 ms and consisting of 3–5 AP with an inter-pulse interval of 5–10 ms, which corresponds to a frequency of 100–200 imp. /sec., and a more delayed group of impulses (latent period 40–60, sometimes more than 80 ms), consisting of 2–3 AP [2].

The second type of response reaction, found in elements with regular BIA, was characterized by a high-frequency (300–1400 imp./sec.) group discharge with a duration of 30–50 ms, which arose with a latent period of 1–1.5 ms. The magnitude of the latent period, time and frequency characteristics allow us to assume that the recording in this case was made not from the afferent fiber, but from the soma or axon of the cell, activated monosynaptically [3–7].As shown by the comparison of the parameters of the group discharges of these elements with the development of AP, the temporal and frequency organization of the evoked activity of these elements corresponds to the temporal course of posterior root potentials. Consequently, neurons of the gelatinous formation participate in the occurrence of the depolarization potential (DP) of the cutaneous nerve [2,3]. Other elements of the dorsal part of the dorsal horn that do not have BIA, in response to stimulation generated only 1–3 AP with a latent period of the first AP of 40–60 ms, and intervals between subsequent APs of 15–30 ms. The appearance of response APs corresponds to the descending part of the posterior root potentials. It follows that these elements cannot participate in its formation [2,3,4].

In elements with an irregular type of BIA, in response to a single irritation of the cutaneous nerve, as a rule, single APs were detected, arising with a latent period of 5–10 ms, after which an inhibitory aftereffect developed. With rhythmic stimulation (1–5 stim. /sec.) there was an increase in the number of APs for each subsequent stimulus [2]. With a single stimulation of the muscle nerve, in response to which posterior root potentials (PRP) arose with a latent period of 3–5 ms and an amplitude 2–3 times smaller than PRP caused by stimulation of the cutaneous nerve, we did not detect short-latency discharges of the elements of the studied area. As a rule, only 1–2 PRPs with a variable pulse interval and a latent period of the first equal to 10 ms were recorded. These observations give reason to believe that PRP of muscle fibers is not associated with the activation of gelatinous cells, which is in good agreement with the assumption that PRP of muscle afferents occurs as a result of the activity of deeper cells [1,2,3].

Rhythmic stimulation of cutaneous and muscle afferents led to a change in the BIA of neuronal elements. This change was detected both at stimulations sufficient for generating AP and at subthreshold stimulations, which corresponds to well-known facts showing the ability of rhythmically evoked subthreshold PSP to modulate spontaneous cellular activity. Increased BIA was observed in neurons localized in different zones and having different parameters of impulse activity. Increased rhythm occurs simultaneously with a change in the type of impulse. At rhythmic stimulation, the values of impulse activity caused by synchronous and intensive synaptic bombardment in the same cases when the nature of the EDF graph, and not rhythmic activation, probably only increased the change in the depolarization wave without changing the periodicity of their change in neurons generating AP with a small constant frequency. It can be assumed that at rhythmic stimulation, the autogenous rhythm of these elements disappears and the impulse activity is caused by steeply increasing periodic waves of synaptic depolarization. The importance of simultaneous activation of the autogenous and synaptic mechanisms of AP generation cannot be ruled out. The change in neuronal activity could occur without the participation of the EDF. In this case, inhibition of impulse activity was achieved not only with stimulation of the cutaneous neuron, but also of the muscle neuron. The data obtained show the possibility of convergence of the inhibitory effects of various afferent sources on the first neuron of the dorsal part of the dorsal horn. Inhibition of impulse activity in these cases can occur as a result of hyperpolarization or is associated with changes in presynaptic structures [1,3,7]. Most neurons located in layer II did not respond to rhythmic stimulation by changing the discharge frequency. However, the absence of frequency changes did not mean the effectiveness of afferent stimulation, since the nature of the EDF changed in some elements. Apparently, in these cases, despite the previous number of generated impulses, the informational nature of the impulse activity changes due to their different distribution in time [6,7].

Thus, the neuronal elements of the dorsal part of the horn react differently to rhythmic afferent stimulation. No dependence of the change in impulse activity during rhythmic stimulation on the localization of the elements and the type of BIA was found. Analysis of the EDF allows us to assume the presence of different and, probably, separately existing mechanisms that change impulse activity during rhythmic stimulation. Comparison of the frequency-time parameters with the time course of the ZSP allows us to assume that some neurons of the gelatinous formation (neurons responding to afferent stimulation with a short-latency high-frequency group discharge) can be the source of generation of the DP of the cutaneous nerves. Consequently, these neurons can participate in the modulation of the afferent flow, carried out due to the mechanism postulated by Melzack and Wallach. On the other hand, it can be considered that the existing disagreements in explaining the mechanisms of presynaptic inhibition are apparently not fundamental, since the DP of the cutaneous and muscle nerves can have different neuronal sources of generation [5,6,7].

The key point of the "gate" theory of pain is the assertion that the activation of unmyelinated conductors causes hyperpolarization of the primary afferents of fast-conducting myelinated fibers, as a result of which the synaptic efficiency of impulses arriving along these fibers increases, i.e. presynaptic facilitation occurs, which underlies the "opening" of the afferent input. This assertion is based on electrophysiological data showing that isolated activation of C-fibers (conduction in group A fibers was disrupted by an anodal block) causes positive PRP. The connection of positive PRP with hyperpolarization of afferent fibers is argued by a decrease in the excitability of cutaneous terminals during positive PRP. However, in a number of studies, negative and negative-positive PRP were found under anodal block. Manfredi, studying changes in postsynaptic output in the anterolateral columns with combined stimulation of afferents of different calibers, did not find a facilitatory effect of C-fibers [3–7].

Thus, there are certain disagreements regarding the central presynaptic effects of C-fibers. These disagreements may be due to differences in experimental models (anesthetized, decerebrated, spinal animals) and

methodological techniques (nature of stimulation, features of the anode block, type of electrodes, etc.).

Currently, there are two alternatives in explaining the neuronal mechanisms of hyperpolarization of primary afferents: either it is caused by the direct hyperpolarizing effect of a certain neuronal source, or it occurs as a result of inhibition of neurons that depolarize afferent terminals. According to the hypothesis of Melzack and Wall, hyperpolarization at the segmental level is caused by inhibition of neurons of the gelatinous substance and, consequently, a decrease in the presynaptic polarization of the A-fiber terminals. However, such a mechanism of hyperpolarization is based only on the assumption that both our and thick fibers, which have different localizations of synaptic contacts on neurons of the gelatinous substance (ventral and dorsal, respectively), should have oppositely directed (excitatory and inhibitory) synaptic effects on them [5,7].

Of particular interest in terms of the participation of the gelatinous substance in the occurrence of hyperpolarization and the validity of the basic position of the "gate" theory of pain are data on changes in the impulse activity of cells of the gelatinous substance during natural nociceptive stimulation. In experiments on non-anesthetized animals, it was established that natural nociceptive stimulation (skin compression with a toothed clamp, causing pain in an animal in free behavior) differently changes the secret impulse activity of neurons of the gelatinous substance and deeper located cells. It was in the area of the gelatinous substance that neurons were found whose impulse activity was suppressed (less often did not change) and nociceptive stimulation causing a sharp (5–10 times) increase in background discharges of cells of the IV–V layers. A more distinct multidirectionality of the nociceptive effect on neurons of different localizations is revealed when comparing the dynamics of changes in their impulse activity. It is noteworthy that the suppression of the impulse activity of neurons of the gelatinous substance and the increase in discharges of cells of the IV and especially V layers during nociceptive effects in most cases had a similar development over time [2,5,7].

Recently, data have appeared showing that presynaptic hyperpolarization is of greater importance in the regulation of the motor function of the spinal cord, in particular in the implementation of the high-threshold flexor reflex, than in the formation of an ascending pain flow. This confirmation is postulated on the basis of experimental material showing that activation of the flexor reflexes afferent system causes significantly greater hyperpolarization in proprioceptive (flexor) intraspinal terminals than in cutaneous ones. The high-threshold flexor reflex in its physiological significance is a nociceptive reaction that is sharply suppressed by analgesics. Based on this, one can assume that the contradictions between Mendel's and Melzack's and Wall's data. Moreover, it seems to us that when it activates the threshold nociceptive fibers, along with the inclusion of I and II, forming an ascending high-threshold flow, the systems that create conditions for the fastest implementation of responses to pain stimulation should be temporarily activated [5,6.7].

Thus, it should be recognized that the gelatinous substance, which embodies the presynaptic control of the segmental afferent input, plays a significant role in the transmission and threshold impulses to the first relay neurons of the segmental level.

Neurons of the posterior horn of the spinal cord (layers IV and V), their properties and sources of activation. According to modern concepts, neurons are functionally the first link of the spinal cord transmitting afferent innervation (including high-threshold "nociceptive") in the ascending direction.

Neurons of layer IV differ from cells of the gelatinous substance by their large size (20–60 μm in diameter) and a well-defined dendritic tree oriented in the ventrodorsal direction. Dendrites penetrate the gelatinous substance, penetrating it with secondary branches in the radial direction, where they form synapses (zone of synaptic contacts) with axons of gelatinous neurons. Dendrites are equipped with spines, which are important loci of postcontacts and play a significant role in the processes of reading. Cells of layer IV also have numerous axosomatic synapses (second zone of synaptic contacts), through which the modulating effects of afferent terminals and propriospinal fibers are realized. The same synapses are located on the proximal parts of the dendrites [8,9].

Functionally, layer IV of the gray matter of the posterior horn of the spinal cord is represented by cells on which afferent signals from all types of cutaneous fibers converge, arising not only from mechanical but also chemical and thermal irritations of the skin. These neurons do not respond to stimulation of visceral and muscular afferents. This is in good agreement with the available data on the more dorsal ending of cutaneous fibers, compared to proprioceptive ones, within the posterior horn of the spinal cord. Axons of layer IV cells form the spinocervical tract ascending within the dorsal part of the lateral funiculus [8,10].

As follows from a number of detailed studies, all neurons of layer IV, depending on the type of converging afferents, the size of the receptive field and the nature of the response to natural irritation of varying intensity, can be divided into two groups: neurons with a narrow dynamic range and neurons with a wide dynamic range. Neurons of the first group usually have low-frequency (up to 5 impulses/sec) background activity. They are monosynaptically activated by low-threshold cutaneous fibers, generating in response a short-latency, high-frequency burst of 4–30 impulses, followed by an inhibitory pause lasting 50–100 ms. Neurons of this group are characterized by a small (1–2 cm), sharply defined receptive field: its shape and size practically do not vary with artificial changes in neuron excitability, which gave grounds to assume the absence of a subthreshold border in the field. An adequate stimulus for these neurons is touching the receptive field. Cell responses adapt rather quickly and, what is especially important, do not increase with an increase in the intensity of skin irritation up to pain. It is believed that such neurons are well specialized in relation to low-threshold cutaneous afferents and do not play a significant role in the formation of the ascending nociceptive flow [10].

A distinctive feature of neurons of the second group is the convergence of myelinated and unmyelinated fibers on them. These neurons are monosynaptically activated by A-fibers and simultaneously have a polysynaptic C-input. Simultaneous stimulation of A- and C-fibers is manifested by two responses: early and late, occurring with a long latent period (200–300 ms) [11,15].

The intense and prolonged excitatory effect of fibers on layer IV neurons correlates well with their participation in the transmission of pain information. However, this prolonged excitatory effect cannot be fully explained on the basis of presynaptic facilitation, since the duration of step-by-step PSPs (up to 100 ms), reflecting the hyperpolarization of terminals, is significantly less than the response of the neuron. It is assumed that the prolonged activation of layer IV neurons that occurs during stimulation of C-afferents is also due to prolonged postsynaptic judgment of the dendrites of these neurons [10,12,13].

A characteristic functional property of neurons with A and C-inputs is an increase in the intensity and duration of the C-discharge with repeated activation of C-fibers. The nature of this phenomenon, called "winding up", is unlikely, since there is no increase in the C-potential in the neurogram for each subsequent stimulus. The phenomenon of "winding up" is also visible during intracellular recording. In most cells localized not only in layer IV, but also in layers V and VI, the phenomenon of "winding up" was accompanied by the appearance of prolonged depolarization of the membrane. It is also suggested that "winding up" can be caused not only by postsynaptic, but also by presynaptic (hyperpolarizing) changes [9]. An important functional feature of neurons with a wide dynamic level is the increase in their response reactions with an increase in the intensity of natural stimulation of the receptive field, up to pain. However, some authors believe that this property is not at all characteristic of all neurons activated by A- and C-afferents, since they found about 40% of cells that responded only to weak tactile stimulation. It should be noted that those excited by A- and C-fibers

were found in all layers of the posterior horn and even in the anterior horn of the spinal cord [10].

Neurons of layer V. Large, spindle-shaped neurons of this layer are oriented in the mediolateral direction and have a well-developed dendritic tree, penetrating into the gelatinous substance. A characteristic functional feature of neurons of layer V is the convergence of cutaneous, visceral and high-threshold muscle afferents on them. When visceral nerves are stimulated, the response of these neurons can be recorded upon activation of fibers of the A-gamma, A-delta group. The cell response in these cases is presented as a burst consisting of 2–12 AP and lasting for 2–16 ms. It has been established that the excitatory effect of high-threshold visceral afferents is realized not only by polysypaptic pathways, but even di- and moposipaptic. A similar nature of connections has been found for high-threshold muscle afferents [8,9,14]. Neurons of layer V differ significantly from cells of layer IV in the organization of the cutaneous input. It has been shown that neurons of layer V do not have a monosynaptic connection with low-threshold (A-beta) afferents and their activation through this afferent channel is mediated by neurons of layer IV. But at the same time, neurons of layer V are excited by A-delta cutaneous afferents and, what is most curious, the responses of these neurons can be monosynaptic [15].

On neurons of layer V, there is an interaction of afferent information from visceral conductors with impulses from cutaneous and muscle afferents. The nature of this interaction, as follows from the data obtained with grandcellular recording, can be facilitatory and inhibitory. However, in the case of an influx of afferent signals through cutaneous and visceral nerves, the result of the neuronal response is determined by the time relationships between these signals [10–15].

Convergence of multimodal high-threshold afferents involved in the conduction of nociceptive signals on layer V neurons gives grounds to believe that they play a significant role in the formation of a common (somatic-visceral) ascending flow underlying the phenomenon of referred pain. It is possible that the emergence of a non-ascending "pain" flow at the output of the first receptor neuron activated by high-threshold somatic and visceral afferents is carried out with the help of a "gate" mechanism. On the other hand, such functional properties of layer V neurons as a large receptor field, a wide dynamic range of activation by natural stimuli - from touch to damage to myelinated and unmyelinated cutaneous afferents, indicate that these cells (along with a certain group of layer IV neurons) can also be a segmental substrate for the formation of "skin pain" [13,14].

The involvement of layer V neurons in the transmission of nociceptive information is also confirmed by the results of a study showing that bradykinin (a substance that causes pain in humans and pseudo-affective reactions in animals) strongly excites neurons. Moreover, the onset of the activating effect of bradykinin on layer V neurons and its duration correlate well enough with the time parameters of the development of a pseudo-affective reaction [15]. As was shown in studies performed on non-anesthetized curarized cats, most neurons in layers IV–VI of the dorsal horn (48 out of 52) have spontaneous background activity. The highest-frequency discharges (29.1+5.5 mi/sec) are characteristic of neurons scaled in layers V–VI of the gray matter (28 cells). Cells located in layer IV and on the border of layers IV and V (29 neurons) had a lower discharge frequency (14.2+ \.2 imp. /sec.) [13]. A certain differentiation between neurons of diffuse layers in our experiments was revealed when studying their note reactions to natural stimulation and the sizes of receptive fields. Neurons localized in layer IV and on the border of layers IV–V had the smallest receptive fields.

The receptive fields of these neurons were usually located on the dorsum of the foot and the lower third of the shin and had dimensions from 10X30 to 30X40–50 mm. In 6 cases, the receptive field was larger. As examples showing the dimensions of the receptive fields, the response of neurons to tactile stimulation and strong mechanical action in neurons of layers IV and V, the data of two experiments are given. The receptive fields of neurons of layers V–VI were found on the lateral surface of the shin, the lower third of the thigh, and on the foot. The shape and size of the receptive field of these neurons were very diverse: from a strip measuring 20X70 cm to the skin surface of the entire foot or shin. In 6 of 21 neurons of layers V–VI of the posterior horn, the receptive field occupied the entire limb and sometimes extended into the gluteal region. The general physiological properties of neurons are their ability, as revealed in experiments, to respond to electrical stimulation of high-threshold afferents and to natural nociceptive irritation. We found only 8 cells that did not respond to this effect. In addition, all of them had receptive fields of small size. It is believed that such neurons are well specialized in relation to low-threshold cutaneous afferents and do not play a significant role in the formation of an ascending nociceptive flow [12, 13].

All neurons activated in experiments by low- and high-threshold afferents increased their impulse activity with an increase in the intensity of natural irritation up to pain. Compression of the skin with a toothed clamp was used as a nociceptive irritation. The painful nature of such an effect was preliminarily tested under conditions of free behavior of animals. An increase in impulse activity to damaging irritation was found in 32 of 40 neurons studied. 15 of them were located in layer IV and on the border of layers IV–V, 17 – in layers V–VI. It is evident that after nociceptive stimulation of the skin in the area corresponding to the receptive field of a given neuron, the frequency of impulse activity increased by 3–5 times, especially in the first 6–10 sec, and during the following 30–40 sec it exceeded the frequency of background discharges by 2–4 times [8,9,15].

It was found that the neuron's response to nociceptive stimulation could be significantly lower if it was applied against the background (or immediately after) of prolonged rhythmic stimulation of low-threshold fibers. These results indicate that the emergence of an ascending impulse flow at the output of these neurons can be accomplished with the help of a "gate" mechanism. The data on the inhibitory effect of low-threshold fibers on the synaptic efficiency of high-threshold input in relation to neurons of the posterior horn are in good agreement with the results of other authors who have shown an increase in late C-responses of a neuron when stimulating unmyelinated fibers. In our opinion, these gates can be considered as a neurophysiological basis for a number of clinical and experimental observations on the analgesic effect of tactile stimulation applied in the zone surrounding the focus of nociceptive action. Therefore, it can be considered that the cytoarchitectonically isolated in the posterior horn should rather be considered as zones of concentration of neurons with certain properties, and not as absolutely different, functionally specialized neuronal ensembles [12,15].

Thus, neurons of layer IV, activated by pulpal and gelatinous afferents, as well as cells of layer V, as the main neurons of ascending projections from multimodal afferent systems, take the most direct part in the positioning of impulses, which ascend along the dorsolateral and ventrolateral tracts of the spinal cord to the supramedial formations, where the pain sensation is formed and the systems implementing the pain responses are launched. At present, there is a large amount of convincing data allowing us to consider that the emergence of an ascending high-threshold flow at the segmental level can be carried out on the basis of "gate" mechanisms. However, the question of whether there are presynaptic changes in the main operant method of controlling the afferent input, apparently, should not be accepted unambiguously [7,8,13,15].

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