ABSENCE OF CONVERGENCE IN SENSORY ZONES OF POSTERIOR HORNS OF THE SPINAL CORD

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UDC 612.831

Absence of convergence has been found in some sensory neurons of the posterior horns of the spinal cord.

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The work of Sherrington and his collaborators [6] showed that different afferent nerves terminate on the same motor cells, thereby creating overlapping of motor zones. This phenomenon is at the basis of the convergence principle, which in turn serves as the basis for coordination of functions of the spinal cord. Occlusion is a measure of convergence. The question arises whether convergence exists in the sensory zones of the posterior horns, especially in zones formed by neurons of what has been called the spino-bulbar system, the activity of which is easily recorded from the dorsal surface or from the depth of the posterior horns of the spinal cord. If convergence is the rule in the motor zones, this nevertheless does not mean that it is also the rule for sensory zones.

The present investigation showed that convergence is absent in some sensory neurons of the posterior horns.

EXPERIMENTAL METHOD

Experiments were conducted on rats and cats anesthetized with pentobarbital sodium (30 mg/kg). Monopolar recordings were made of the posterior horn potentials by means of a cotton wool wick applied to the surface of segment L_7 in cats and L_5 in rats, strictly in the midline. The indifferent electrode was placed on neighboring muscles. In some experiments on cats the active electrode was a glass microelectrode (diameter 5 μ), inserted into the spinal cord to a depth of 0.5-1 mm in a dorso-ventral direction. The animals were fixed tightly in a special frame. The microelectrode was inserted into the spinal cord of the cats by means of a special micromanipulator, securely fixed to the spinous processes. Posterior horn potentials were evoked by stimulation of purely cutaneous (plantar and sural) and mixed (peroneal, tibial, and sciatic) nerves. The ventral roots were divided. The nerves were stimulated with square pulses 0.1 msec in duration; the responses were fed into a UBP1-01 amplifier and recorded on a loop oscillograph.

EXPERIMENTAL RESULTS

During simultaneous stimulation of the left peroneal and tibial nerves of the rats, the amplitude of the combined response was equal to the sum of amplitudes of responses to individually stimulated nerves (see Fig. 1a). This means that afferent nerve fibers running into the spinal cord in these nerve trunks do not converge on the same neurons whose activities were recorded.

During stimulation of the ipsilateral sural and plantar nerves, the combined response also was equal to the sum of responses of the individually stimulated nerves (see Fig. 1b). Similar results were obtained during stimulation of other homolateral and contralateral nerves in various combinations.

If the stimulation did not coincide strictly, the amplitude was slightly diminished (see Fig. 1c). However, this does not mean occlusion, for in cases when stimuli do not coincide there is no such thing as a combined response, because each stimulus evokes its own response. Whatever the interval between stimuli, the test response was neither diminished nor increased, i.e., neither occlusion nor facilitation took place during conditioning.

Institute of Higher Nervous Activity and Neurophysiology, Academy of Sciences of the USSR, Moscow (Presented by Academician V. V. Parin). Translated from Byulleten Éksperimental'noi Biologii i Meditsiny, Vol. 65, No. 1, pp. 9-12, January, 1968. Original article submitted August 10, 1966.

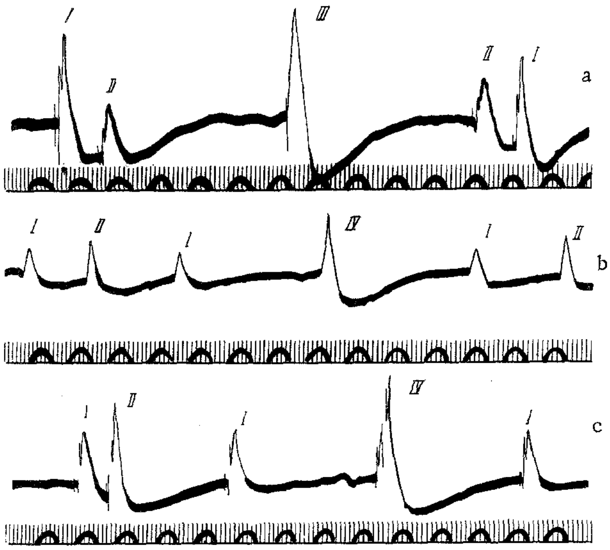

Fig. 1. Responses of posterior horns of spinal cord at level of segments L_5-L_6 to electrical stimulation of mixed (a, c) and cutaneous (b) nerves in a rat. a) combined response (III) is equal in amplitude to sum of responses to stimulation of peroneal (I) and tibial (II) nerves; b) combined response (IV) is equal to sum of responses during stimulation of sural (I) and plantar (II) nerves. c) Combined response (IV) is slightly smaller than sum of responses to stimulation of peroneal (I) and tibilal (II) nerves. Time markers 20 and 2 msec.

Absence of convergence in the sensory zones of the posterior horns was also seen when high-frequency repetitive stimulation of one afferent nerve was combined with low-frequency stimulation of another. These experiments revealed that the responses evoked by each afferent nerve were independent, for after "exhaustion" of the sensory zone of one nerve, the addition of low-frequency stimulation of the other again evoked high responses.

The synaptic organization of the neurons of the spino-bulbar transmission system is evidently such that only one afferent fiber converges on each neuron of this system. According to some data, the sensory neurons of this sytem receive inhibitory influences from the cerebral and cerebellar cortex [4]. This means that inhibitory descending fibers, but not excitatory, converge on them.

Hence, whereas convergence is well-developed in the motor system of the spinal cord, it is absent in the sensory sphere, at least in the neurons of the spino-bulbar system. Sensory neurons cannot, in principle, be the end point for convergence of many afferent nerve fibers because their principal function is to discriminate between stimuli and to analyze them into their component parts for further processing of the information at higher levels. If the neurons of the sensory zones allowed convergence, they would be overloaded with peripheral information, which would be most undesirable from the point of view of economy of design of the nervous system.

Gasser and Graham [2] did not observe occlusion during stimulation of symmetrical roots (L_7, S_1), but observed it only during stimulation of homolateral roots, and even then, not in all experiments. Bernhard [1] found occlusion during combined stimulation of only one pair of cutaneous nerves (the sural and dorsal femoral cutaneous nerves) but occlusion was absent during stimulation of three other pairs of nerves. Occlusion in the experiments of Gasser and Graham was evidently due to the fact that these authors stimulated mixed nerves or roots. Since occlusion is always present during stimulation of nerves to muscles, its development in the experiments of Gasser and Graham was obviously due to excitation of nerves to muscles. It must be assumed that convergence is a feature of the central sensory zones of muscle afferent fibers. So far as cutaneous afferent fibers are concerned, no convergence takes place in their sensory zones.

Every point of the skin is supplied by two or three roots [5], which results in wide overlapping of the peripheral sensory zones.

Each neuron of the upper layers of the posterior horns of the spinal cord supplies its own cutaneous zone with an area of 30×15 mm, or sometimes even 60×30 mm [7]. The tactile receptors of the skin—Meissner's corpuscles—are grouped so that many cells are innervated by a single afferent fiber [8]. This wide peripheral divergence of the cutaneous afferent fibers evidently makes their wide convergence on the central cells of the sensory system unnecessary. If many cutaneous afferent fibers converge on one sensory neuron, ability to discriminate between peripheral stimuli would be limited and the sensory neurons would be overloaded with peripheral information.

The absence of convergence in the sensory zones of cutaneous afferent fibers formed by neurons of the spino-bulbar system does not justify the conclusions that this phenomenon is a characteristic feature of sensory zones in general. However, there is some evidence in the literature to suggest that convergence is the exception rather than the rule for many sensory zones (for example, in the visual cortex) [3].

Even a cursory examination of the organization of sensory zones in the somatosensory cortex reveals the territorial independence of neurons activated by stimulation of the skin from neurons activated by stimulation of receptors of deep sensation. Along the latter, further specialization is observed, with a distinction between the fast adapting and the nonadapting [5]. This spatial organization of sensory systems at the level of spinal cord, nuclei of the dorsal columns, and somatosensory cortex, is evidently directly related to stimulus discrimination. New experimental findings suggest not only that convergence on sensory neurons of the somatosensory cortex is reduced to a minimum, but that something directly opposite to convergence takes place, at least on the lemniscus neurons of the cortex: it is not the excitatory, but the inhibitory afferent ending from the inhibitory annular zones of the skin which converges on these neurons. The claim is made that such convergence facilitates localization of the site of stimulation [5]. Afferent inhibition apparently prevents the neuron from responding to other excitatory impulses, as a result of which it responds only to the excitatory impulses of its own receptive zone.

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