

CONVERGENCE IN THE SENSORY ZONES OF THE DORSAL ROOTS OF THE SPINAL CORD DURING STIMULATION OF MUSCULAR AFFERENT NERVES

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When the muscular afferent nerves are stimulated, two types of responses can be detected from the surface of the spinal cord: the first appears immediately after the spike potential expressing the activity of the fibers of the posterior columns, the second some 9-11 msec later [2].

Unlike the responses to stimulation of the cutaneous and mixed nerves and the roots, the potentials arising during stimulation of the muscular afferent nerves have received inadequate study.

The object of this investigation was to study some properties of these potentials in the hope that this would facilitate the understanding of the functional organization of the spinal cord.

EXPERIMENTAL

Experiments were carried out on 16 rats weighing 150-180 g, anesthetized with pentobarbital sodium (30 mg/kg body weight). The potentials were picked up from the dorsal surface of the spinal cord with thin wicks of cotton wool soaked in physiological saline, at the level of segment L5, where their amplitude was greatest. The indifferent electrode was placed on the neighboring muscles. To evoke the potentials the nerves to the lateral and medial heads of the gastrocnemius muscle were stimulated by means of a two-channel stimulator. The duration of each stimulus was 0.05 msec. The potentials were recorded on a loop oscillograph.

EXPERIMENTAL RESULTS

The responses to stimulation of the nerves to the medial (M) and lateral (L) heads of the gastrocnemius muscle at different intervals are shown in the figure. If the stimuli coincided, the amplitude of the combined response (C) was much less than the sum of the amplitudes of the responses to stimulation of the nerves separately. In that case, the response to stimulation of the lateral nerve (L) was 350 μ V, the medial (M) 250 μ V, and the combined response (C) 300 μ V. The loss of amplitude of the combined response was thus 300 μ V (50%).

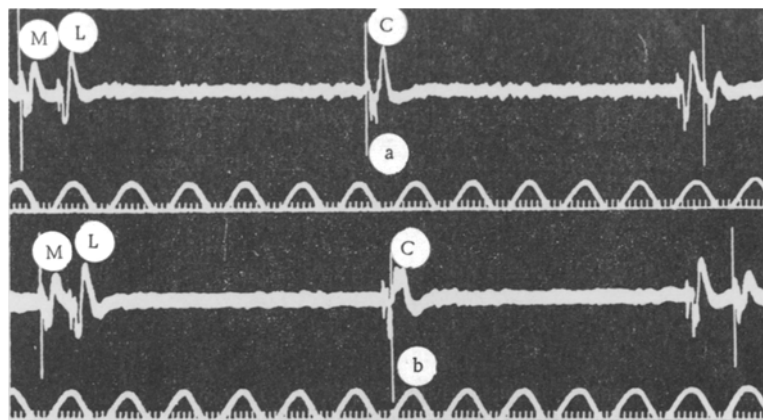
If the test stimulus coincided with the descending phase of the negative slow potential evoked by the conditioning stimulus (see figure, a, responses on the right), the amplitude of the test response fell appreciably. If the interval between the test stimulus and the conditioning stimulus was longer than 15-20 msec, no loss of amplitude took place.

Total occlusion of the response of the nerve to the lateral head of gastrocnemius, when the interval between the conditioning and test stimuli was 2 msec, is illustrated in the figure, b. Occlusion of the responses was observed in all 16 experiments and it ranged from 52 to 65%, except in one case when it was 80% (see table).

The table also shows that the amplitude of the L responses in all 16 experiments was greater than the amplitude of the M responses, presumably in association with the greater weight of the lateral head than of the medial head of the muscle and the correspondingly larger number of spindles which it contains.

It was, thus, found that when two muscular nerves are stimulated, the total response is less the sum of the responses to stimulation of the nerves separately. In some cases the occlusion was so considerable that one response completely abolished the other. Since occlusion is the yardstick of convergence, it can be concluded that the muscular afferent nerves converge on the same neurons of the posterior horns.

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Surface potentials of the spinal cord in response to stimulation of the lateral (L) and medial (M) nerves to the gastrocnemius muscle in rats. The common response (C) is much smaller than the sum of the responses to stimulation of each nerve separately. Time) 2 and 20 msec. a) Partial occlusion of the response; b) total occlusion of the response.

Occlusion of Surface Potentials of the Spinal Cord Evoked by Stimulation of the Nerves to the Lateral and Medial Heads of the Gastrocnemius Muscle in Rats

Amplitude of responses (in μV) to stimulation of

n. gastrocn. lat.	n. gastrocn. med.	both nerves together	occlusion (in %)
420	273	310	55.2
381	250	310	58
470	360	346	58
685	430	470	83
450	285	350	55
494	330	330	57
375	225	248	58
489	358	305	65
364	170	249	53
425	250	280	56
375	267	257	62
345	162	193	61
450	210	330	52
430	240	290	56
481	285	310	53
470	430	348	61

Occlusion in relation to the potentials of the posterior surface of the spinal cord was first described by Gasser and Graham [5]. Their findings were confirmed by Hughes, McCouch, and Stewart [7]. However, to evoke responses in the spinal cord these workers stimulated the roots or mixed nerves. It was not clear, therefore, which nerve fibers were responsible for the observed occlusion—muscular or the cutaneous. Attention to this point was first directed by Bernhard, who showed in special experiments that the early response is not occluded, and that occlusion develops only for the late response.

The results of the present experiments showed that simultaneous stimulation of two muscular afferent nerves evokes an electrical response whose amplitude is 50–60% less than the amplitude of the responses to the nerves stimulated separately. This means that the muscular afferent nerves converge on the same neurons. This fact becomes understandable in the light of observations reported in the literature. When the tibial and peroneal nerves were stimulated simultaneously, a high degree of convergence was observed on the cells of Clarke's columns [6]. Although in these experiments mixed nerves were stimulated, it must be assumed that the effect was due to muscle afferent fibers and not to cutaneous fibers. Since the cells of Clarke's columns are activated by afferent fibers from muscle and tendon receptors [4, 8], it may be concluded that these fibers are the ones which converge on them. Hence, not one afferent fiber from the muscles and tendons, but several fibers must converge on each cell of Clarke's columns. If this line of reasoning is followed, the ultimate question must be: which structures of the spinal cord generate slow potentials in response to stimulation of the muscular nerves. The participation of the motor neurons in the genesis of the

potentials recorded in the present experiments is excluded on the grounds that when muscle efferent fibers are stimulated no negative slow potential is recorded from the dorsal surface [3]. Consequently, the source of these potentials may be certain internuncial neurons in the posterior horns or the cells of Clarke's columns.

Observations which help to elucidate the genesis of these potentials have been reported. The muscular afferent fibers, stimulation of which gives rise to a slow potential, are known to have a high threshold [2] and a diameter of 2–4 μ . It is also known that only the thick muscular afferent fibers terminate on the cells of Clarke's columns monosynaptically [8]. The thin fibers with a high threshold evidently communicate

polysynaptically. In that case, it seems probable that the slow potential evoked by stimulation of a high-threshold muscular afferent nerve is generated by sensory neurons intercalated in the pathways of these high-threshold nerve fibers. The absence of accurate information on the generator of the slow potentials evoked by stimulation of the muscular nerves does not mean that the facts discovered in the present experiments should not be discussed from another aspect. The point is that convergence exists for muscular afferent fibers and does not exist for cutaneous fibers. This difference in the organization of the sensory neurons is evidently based on the wide peripheral divergence of the cutaneous fibers and the tactile neurons in the spinal cord [9, 10], ruling out the possibility of central convergence. So far as the muscular afferent fibers are concerned, these do not diverge at the periphery. Each intrafusal muscle fiber at the periphery receives one thick afferent fiber for the innervation of the nuclear envelope and one or two thinner fibers for the muscle tube. Since occlusion does not occur during stimulation of the cutaneous nerves, but is well marked during stimulation of the muscular nerves, it can be concluded that this difference in the central organization is due to a difference in the distribution of the cutaneous and muscular nerves at the periphery. The cutaneous nerves are characterized by wide divergence at the periphery, but the muscular nerves do not diverge. The absence of peripheral divergence of the afferent nerve fibers in the muscles makes it necessary for them to converge in the centers.

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