CONNECTIONS OF THE RUBROSPINAL TRACT WITH NEURON GROUPS IN THE LUMBAR DIVISION OF THE SPINAL CORD

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Electrophysiological and morphological methods were used to investigate the distribution of endings of fibers of the rubrospinal tract among groups of neurons in the lumbar division of the spinal cord. Most endings of the rubrospinal fibers are located in the lateral part of Rexed's layer VII, and a very small number in layer VI; no endings were found near the bodies of motoneurons. The arrival of rubrospinal impulses leads to the development of a focus of early electronegativity in the gray matter of the spinal cord. Its localization corresponds precisely with the localization of most endings of rubrospinal fibers.

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The rubrospinal tract is one of the principal pathways transmitting cortical and cerebellar motor impulses to the spinal cord. Although the character of ending of the rubrospinal fibers in the spinal cord has been studied by many investigators [9-11], there is still no general agreement on this problem. Morphological investigations [10], for instance, revealed degenerating fibers in layer IX of the gray matter, but no direct connection could be shown between the rubrospinal fibers and motoneurons of the spinal cord. These results suggest that impulses from the tract reach motoneurons only via internuncial cells. This hypothesis is in agreement with results of most electrophysiological investigations of responses of single motoneurons and of their global activity evoked by impulses arriving from the red nucleus during isolated stimulation of that structure [1, 3, 6, 12]. However, some workers [6] obtained motoneuron responses with a latency indicating the possibility of monosynaptic connections between rubrospinal fibers and motoneurons. The possibility that such connections exist has also been mentioned by Sasaki and co-workers [12].

The principles governing connections between rubrospinal fibers and interneurons likewise are unexplained. Some workers consider that these fibers converge on those same interneurons which receive peripheral afferent fibers [8]. Other investigators, however, have demonstrated the presence of special interneurons in the spinal cord, activated only by the rubrospinal tract [4].

It was therefore decided to make a parallel study, using electrophysiological and morphological methods, of the character of connections between fibers of the rubrospinal tract and various neuron groups of the spinal cord.

EXPERIMENTAL METHOD

Experiments were carried out on adult cats anesthetized with chloralose (45 mg/kg) and nembutal (15 mg/kg). The red nucleus was stimulated through a bipolar electrode with a series of pulses 0.1 msec in duration. To rule out the possibility of transmission of descending impulses along the pyramidal system, the pyramids were divided. In the electrophysiological investigation focal potentials were recorded from a large number of points in the cross section of segment L7 of the spinal cord. Electrical activity was recorded by microelectrodes filled with 3 M NaCl solution, with an impedance of about 5 mΩ. The tracks of insertion of the microelectrode were 500 μ apart, and focal potentials were recorded every 200 μ as the microelectrodes were inserted deeper into the spinal cord. After the end of the experiment the thin part of the microelectrode was cut off and left in the investigated segment, which was then excised and immersed in 10% formalin solution for fixation. The track of insertion of the microelectrode was determined in histological sections, after which all the preceding channels of insertion and points of

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recording of the focal potentials were recreated. From the results obtained, diagrammatic maps were drawn showing the distribution of electrical activity through the cross section of segment L7 at intervals of 8, 20, and 40 msec after the beginning of stimulation of the red nucleus.

To determine the localization of endings of fibers of the rubrospinal tract in the lumbar segment morphologically, electrolytic destruction of the red nucleus was carried out by application of a current of 6 mA for 30 sec. The animal was perfused with physiological saline and 10% formalin solution through the heart 6 days later, after which the spinal cord was removed. Serial sections 30 μ in thickness were cut on a freezing microtome, stained by the Nauta—Laidlaw method, and drawn on a drawing apparatus. Superposition of the drawn sections gave a composite picture of the distribution of degenerating endings of rubrospinal tract fibers.

EXPERIMENTAL RESULTS

A map of the distribution of focal activity 8 msec after the beginning of stimulation of the red nucleus is shown in Fig. 1A. Short-latency electropositivity located in the regions of the lateral column of the spinal cord and evidently reflecting activity of rubrospinal fibers can be clearly seen on this map. The latency of its appearance averaged 4.7 msec (varying between 3 and 5.9 msec). Activity of the rubrospinal tract could also be recorded by an electrode placed on the lateral surface of the spinal cord. When a single stimulus was applied to the red nucleus, a rubrospinal wave was recorded in the lumbar segment in the form of a triphasic potential. An increase in the number of stimuli in the series led to the appearance of the corresponding number of waves. The latency of the potentials thus recorded was 4.9 msec, the same as the mean latency of electropositivity recorded in the tract by the microelectrode.

A focus of negativity developed after a somewhat longer latent period (6.3 msec, variation between 4.5 and 7.6 msec) in the lateral part of Rexed's layer VII (at a depth of 2.4-2.6 mm from the dorsal surface). This focus appeared in response to stimulation of the red nucleus by a single stimulus, and an increase in the number of stimuli in the series caused an increase in the amplitude of the focal potential. Since electrical activity developed in other areas of the gray matter after a longer latent period, the lateral part of layer VII must be regarded as the region of localization of postsynaptic activity of the neurons activated primarily by rubrospinal fibers.

To confirm that this activity was connected only with excitation of the rubrospinal tract, experiments were carried out in which the dorsal part of the lateral column was divided in the upper lumbar segments, interrupting the rubrospinal tract but leaving the reticulospinal tracts intact. Division in this manner led to complete disappearance of the focal potentials in the lateral part of layer VII (Fig. 2).

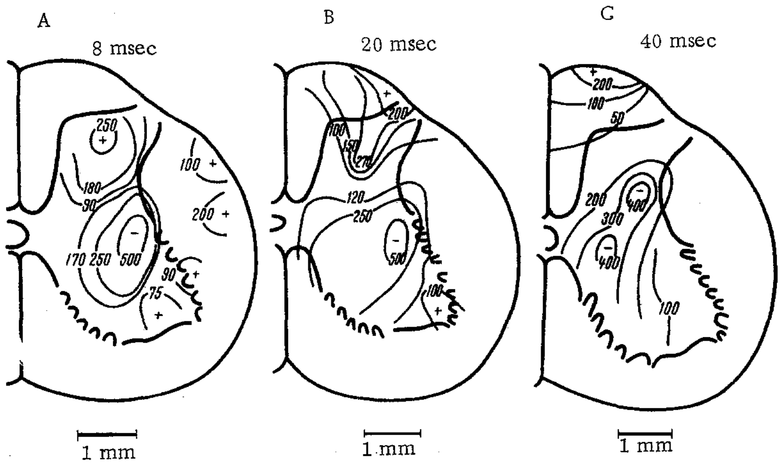

Fig. 1. Schemes of distribution of electrical activity in cross section of spinal cord after stimulation of red nucleus. A) 8 msec; B) 20 msec; C) 40 msec after beginning of stimulation of red nucleus by series of 4 stimuli. Amplitude of potentials shown in microvolts.

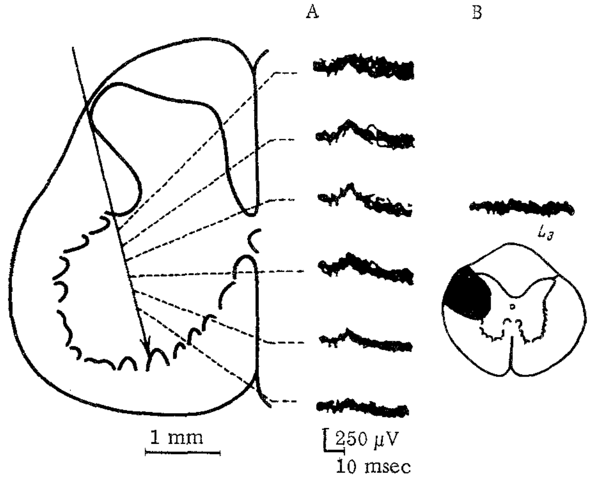

Fig. 2. Focal potentials recorded in Rexed's layer VII during application of two stimuli to the red nucleus. A) Before; B) after division of dorsal part of lateral column in L3. Each tracing obtained by superposition of 5 sweeps of the beam.

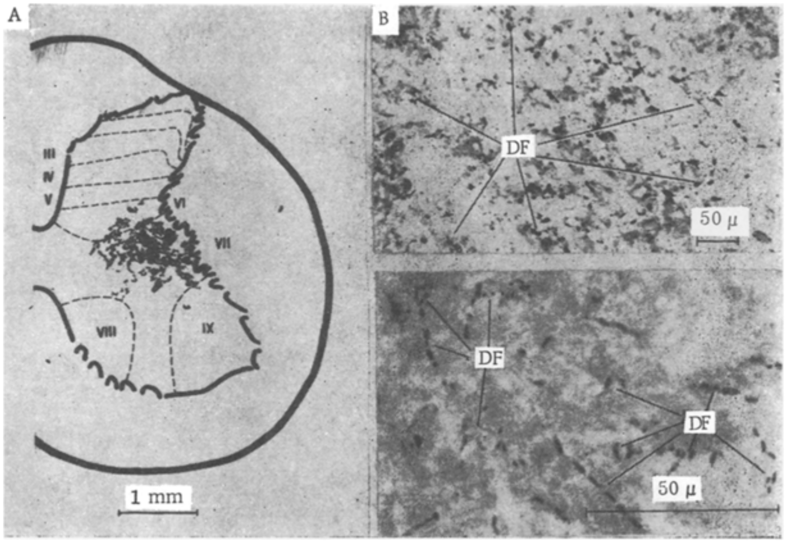

Fig. 3. Map-diagram showing distribution degenerated fibers (DF) of the rubrospinal tract in segment L5 of the cat spinal cord after destruction of the red nucleus (A) and photomicrograph of the gray matter of layer VII of segment L5 under different magnification (B).

Morphological investigations of the localization of degenerating fibers of the rubrospinal tract in the gray matter of segment L5 after artificial destruction of the red nucleus (Fig. 3) showed that most are concentrated in Rexed's layer VII, and that their number in layer VI is much smaller. The greatest density of degenerated fibers was observed in the lateral part of layer VII; the region of maximal density coincided exactly with the point of recording of maximal short-latency electronegativity. Only a very small number of degenerated fibers were found in the gray matter of layer IX, and the region of the bodies of the motoneurons contained no fibers of the rubrospinal tract. It is important to note that the zone of endings of the rubrospinal fibers on internuncial neurons lies ventrally to the zone of endings of the pyramidal fibers [2]. Although some overlapping of these zones occurs in Rexed's layer VI, this does not mean that the two systems may converge here on the same neurons. There is electrophysiological evidence to suggest that the two systems are connected monosynaptically with different cells [2, 4, 5].

At long intervals after stimulation, electronegativity appeared in the region of the nucleus intermedius of Cajal and the motoneurons of the spinal cord (Fig. 1B). The mean latency of the response in these nuclei was 8.7 msec (variation from 7.7 to 9.8 msec), evidently indicating activation of the corresponding neurons through additional synaptic delays (probably in interneurons of the lateral part of layer VII). The possibility of direct activation of more medially situated interneurons by slow-conducting rubrospinal fibers cannot, of course, be ruled out.

During analysis of focal potentials 40 msec after the beginning of stimulation of the red nucleus, a different type of distribution of potentials over the cross section of the spinal cord was observed (Fig. 1C), coinciding in its general features with the distribution of focal potentials in the spinal cord during prolonged depolarization of presynaptic endings of primary afferent fibers [7]. These findings are in agreement with the results of investigations by Hongo, Jankowska, and Lundberg [8], who showed that rubrospinal impulses can produce presynaptic depolarization of group 1B and cutaneous afferent fibers.

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