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AFFERENT CONNECTIONS OF POSTERIOR COLUMN NUCLEI OF THE SPINAL CORD

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Electrical stimulation of the forelimb or its nerves in cats is known to induce evoked potentials (EP) in nuclei of the posterior columns of the spinal cord (NPC) not only on the side of stimulation [5], but also on the opposite side [2-4]. This observation contradicted the classical view that the posterior columns of the spinal cord have unilateral connections with NPC and are responsible for generation of the EP-complex in response to stimulation of the corresponding forelimb.

The aim of this investigation was to study the spread of posterior-column afferent projections to contralateral NPC, to compare ipsilatefal and contralateral EP in these structures, and to look for the structural sources of conduction of afferent projections of the posterior spinal columns to the contralateral NPC.

EXPERIMENTAL METHOD

Experiments were carried out on adult cats. There were two methods of investigation: electrophysiological and electron-microscopic, both described in detail previously [3]. The first method consisted of recording and analyzing EP at different points of symmetrically opposite NPC during stimulation of the forelimbs in intact cats and after preliminary hemisection of the tegmentum mesencephali under acute experimental conditions. For electron-microscopic investigation of the afferent connections of the posterior columns of the spinal cord with NPC unilateral damage was inflicted on the posterior columns of the spinal cord in the animals of Group 3 at the level of cervical segments 3-5. For this purpose, after removal of the covering cervical spinal muscles the corresponding part of the spinal cord was exposed for a distance of 3-5 cm. The posterior arches of the vertebrae were nibbled away, the dura mater was divided sagittally, and the posterior columns of the spinal cord were identified and then divided.

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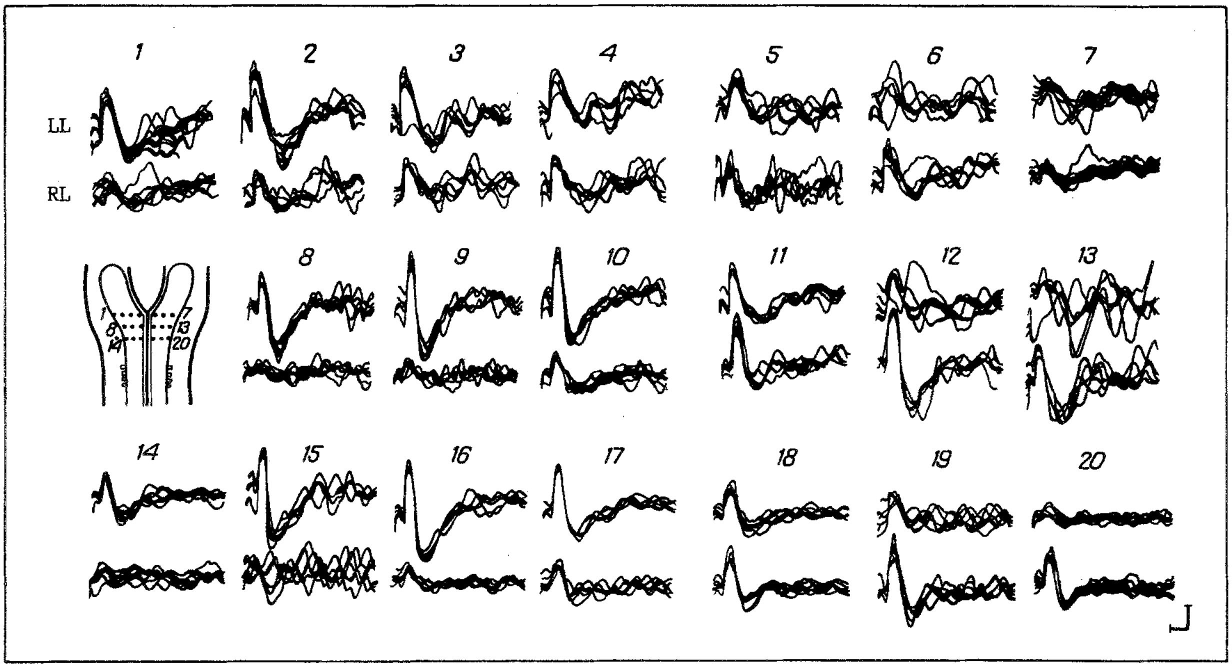

Fig. 1. EP recorded in response to electrical stimulation of the forelimb in intact cats and in animals with hemisection of the tegmentum mesencephali.

EXPERIMENTAL RESULTS

EP recorded in response to electrical stimulation of the forelimb in intact cats and in animals with hemisection of the tegmentum mesencephali were of greater amplitude in NPC on the side of stimulation (Fig. 1). However, EP in these animals were recorded not only above the ipsilateral (relative to the stimulated forelimb) nucleus of the fasciculus cuneatus (NFC), but also above the nucleus of the ipsilateral fasciculus gracilis (Goll's bundle) and beyond the sagittal plane above NPC of the opposite side of the medulla. Admittedly, all EP were lower in amplitude and gradually decreased as the recording microelectrode was shifted in the opposite direction relative to the stimulated forelimb. Thus functional projections of the forelimb to NPC, which we described, do not have the strict ipsilateral relations postulated by the classical view of the conducting systems of the spinal cord. After hemisection of the tegmentum mesencephali (3-8 days or more), changes in characteristics (amplitude, time, location) of EP in the symmetrical NPC were closely similar to changes in the corresponding characteristics of responses in these same structures seen immediately after the operation on the midbrain. The only point to be mentioned is that the second positive component of the EP showed a greater increase and was spread more widely over the surface of NPC. It will be clear from Fig. 1 that the EP predominated above NPC ipsilaterally, but they could also be seen on the opposite side of the spinal cord, beyond the sagittal plane. These contralateral responses were not the "leaking," of the current from its own ipsilateral half of the brain stem. The enlargement of the first negative component of EP 8 days after the operation on the midbrain is visible in Fig. 1, and most marked in the caudal portions of NPC. As regards the second positive component of EP, it was considerably enlarged in both caudal and rostral zones of NPC.

Electron-microscopic investigation of animals with division of the posterior columns of the spinal cord revealed degeneration of axons and, in particular, of large synaptic terminals not only on the side of operation, but also on the contralateral side (Fig. 2). Degeneration of axons of both "dark" (with an increase in electron density of the matrix and the appearance of cytolysis and of large granular vesicles) and "pale" types was observed in the rostral and caudal levels of NFC. Cases of "pale" degeneration were more frequent and were characterized by a floccular matrix, by a decrease in the size and number of the synaptic vesicles, and by their agglutination. The synaptic population in NFC after division of the posterior columns showed no significant changes from the quantitative aspect, in our view, on the side contralateral to the operation. Degeneration affected individual synaptic endings and, in particular, axo-axonal junctions. Numerous glycogen granules were observed in large and medium-sized axon terminals and also in processes of glial cells, especially astrocytes; moreover, they were more characteristic of

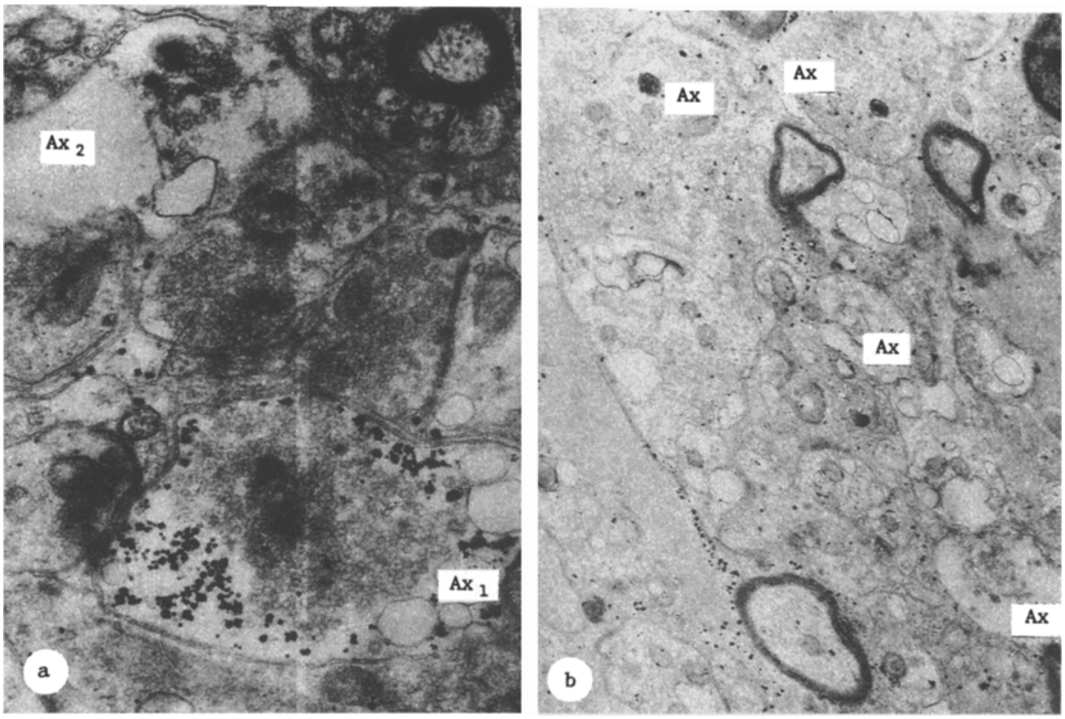

Fig. 2. Structure of synapses in contralateral nucleus of fasciculus cuneatus after division of posterior columns of spinal cord: a) glycogen accumulation in axon ending (Ax_1) and changes in axon of "pale" type (Ax_2; 25,000×), b) multiple signs of degeneration in axon endings (Ax), glycogen accumulation in processes of nerve and glial cells (8000×).

the caudal zones of NFC, contralateral to the side of the operation. In the opinion of several authorities [6] glycogen accumulation in synaptic terminals is the result of weakening of glycolysis, due to a disturbance of axoplasmatic transport from the perikarya of the neurons as a result of external action. It has been suggested that glycogen is synthesized and accumulates in synapses not working at the particular moment [1]. This fact is evidence of the transition of the synaptic ending to a different pattern of functioning, linked with lower expenditure of energy and aimed primarily at preserving the integrity of the synaptic junction.

As this investigation shows, in response to stimulation of the forelimb EP have a particular kind of distribution in symmetrical NPC, being dominant on the side of stimulation in the case of pointwise recording and continuing to be recorded in the contralateral NPC, then becoming smaller in amplitude toward the lateral part of the brain stem. To study afferent projections of the posterior columns of the spinal cord to structures of NPC we used two groups of animals: intact and after preliminary hemisection of the tegmentum mesencephali. In the animals of Group 2 this operation was no obstacle for the spreading of afferent influences from the stimulated forelimb to the test structures. However, as we have found [2], after hemisection of the tegmentum mesencephali simultaneous blocking of the descending inhibitory projections to NPC from structures of the forebrain and brain stem takes place. This operation thus apparently increases the effectiveness of electrical stimulation of the forelimb, and the EP complex in NPC, with the same parameters of stimulation, is increased bilaterally, which provided us with greater experimental scope for verifying the region of spread of EP.

Our electron-microscopic studies confirmed the electrophysiological data on the existence of bilateral afferent projections of the forelimb to symmetrical NPC. In the case of unilateral damage to the posterior columns of the spinal cord, multiple degenerative changes in the synaptic structures of these formations could be found in the contralateral NPC.

Thus our electrophysiological and electron-microscopic data are evidence of the existence not only of classical afferent projections of the posterior columns of the spinal cord, but also of nonclassical projections to the structures of NPC. Both basic, ipsilateral, afferent projections of the forelimb to structures of NPC, but also additional, contralateral afferent projections of the posterior columns of the spinal cord to the corresponding NPC also exist. What is the functional significance of this phenomenon? In our view, afferent projections of the posterior columns of the spinal cord to structures of NPC on the contralateral side are responsible for the identical sensitivity (kinesthetic and tactile) from the half of the body that is supplied by the principal, ipsilateral connections. This hypothesis is based on the following experimental data and concepts. In a parallel investigation we found that NPC have not only classical (lemniscal), but also nonclassical (extralemniscal) connections with structures of the contralateral ventrobasal nuclear complex of the thalamus [4]; moreover, the latter extralemniscal afferent projections of NPC have an additional decussation in the region of the diencephalon. These extralemniscal connections may perhaps be complemented by connections of a certain number of relay cells of the opposite NPC. On the other hand, bilateral inhibitory control of each half of the forebrain by symmetrical NPC is evidence that the common "targets" of this control (the corresponding lemniscal and extralemniscal neuronal elements of the symmetrical NPC) have closely similar functional properties.

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ANTIDROMIC VASODILATATION INDUCED BY A_δ-AFFERENTS IN THE FROG

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Stimulation of the peripheral end of dorsal roots VII-X in the frog leads to vasodilatation in the hind limb [2, 5, 6]. Since this response is determined by the action of impulses traveling along afferent fibers in the peripheral direction, it is called antidromic vasodilatation [4, 5]. In mammals antidromic vasodilatation is induced by impulses traveling along unmyelinated C-afferents [9, 10] and also, hypothetically, along the most slowly conducting A-afferents [9]. In amphibians, however, antidromic action on blood vessels may be a feature characteristic of impulses of myelinated fibers and, in particular, of fast-conducting A-afferents. In frogs, in fact, in response to stimulation of the submaxillary nerve, dilatation of arterioles develops in the homonymous muscle; this response, moreover, is induced by impulses in the fibers possessing the high excitability that is a feature of fast-conducting A-afferents [1]. Fibers on activation of which vasodilatation takes place in the hind limb also are present in the frog sciatic nerve. These fibers are more excitable than the unmyelinated vasoconstrictor fibers of the same nerve [2, 7]. It maybe that the more excitable fibers are afferent.

The aim of the experiments was to discover if this is in fact true, and if it is, to determine the group of afferents to which they belong and the closeness of the excitability of fibers of the sciatic and submaxillary nerves, which are analogous from the standpoint of their action on vessels.

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