PROJECTION ZONES OF DENDRITES OF PHRENIC MOTONEURONS IN CATS

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The phrenic nucleus in the spinal cord, which performs an extremely important role in the regulation of respiration, stretches from the 4th to the 6th cervical segments in the form of a compact formation, which differs sharply form all other nuclei. It consists of about 30 groups of neurons, through which run bundles of longitudinal dendrites of motoneurons; in the spaces between the groups, these dendrites are tightly packed into bundles. Previously [1] the quantitative characteristics of neuronal structures of the phrenic nucleus were given and its three-dimensional reconstruction was described. The nucleus is described as the lateromedial nucleus of lamina IX in Rexed's atlas [8].

In the investigation described below, to obtain a fuller understanding of the structure of the phrenic nucleus and the functional role of its dendrites, their distribution was traced and their protection zones (terminal ramifications) were studied.

EXPERIMENTAL METHOD

Portions of the cervical segments with the phrenic nucleus were removed from 48 adult cats after various acute experiments, which were performed under pentobarbital anesthesia (40 mg/kg, intraperitoneally). Pieces of brain were processed by Golgi's method in the modifications of Kopsch or Bubenaite [2]. Frontal, horizontal, and sagittal serial sections 100 μ thick were used. The reconstruction was carried out on the basis of two to six serial sections with the aid of the RA-6 drawing apparatus.

EXPERIMENTAL RESULTS

As a rule phrenic motoneurons have 6-8 principal dendrites. Radial dendrites emerge from the phrenic nucleus, penetrate into all laminae and nuclei of the ventral horn, and also into the various white columns.

A scheme of a frontal section passing through the rostral part of the 6th cervical segment is shown in Fig. 1a; the boundaries of the laminae and nuclei and, in particular, the lateromedial nucleus, are indicated. Reconstruction of four motoneurons with their radial dendrites was done on sections at the same level of the spinal cord (Fig. 1b, d). The largest dendrite of motoneuron 1 (Fig. 1b) branches into two processes, one of which runs diametrically across the whole of the gray matter, to emerge at its boundary and to terminate in the ventrolateral funiculus. The second dendrite gives off branches into lamina VII, into the most dorsal of the lateral motor nuclei, and into the ventrolateral funiculus. A dendrite which enters the ventromedial funiculus can be seen in the same motoneuron. The third dendrite divides into branches and penetrates into the region of the lateral nuclei and into the ventral funiculus. Four radial dendrites can be clearly distinguished on motoneuron 2, two of them running in the medial direction, two in the lateral. Dendrites running in the medial direction terminate in different regions of the ventromedial funiculus and in the ventromedial nucleus, but one of the main branches runs into the anterior commissure. Motoneuron 3, with a group of processes which branch in laminae VIII and VII (Fig. 1d) is very interesting. Such motoneurons are quite rare. The length of the radial dendrites reaches 1-1.5 mm. A reconstruction based on horizontal sections through four phrenic moto-

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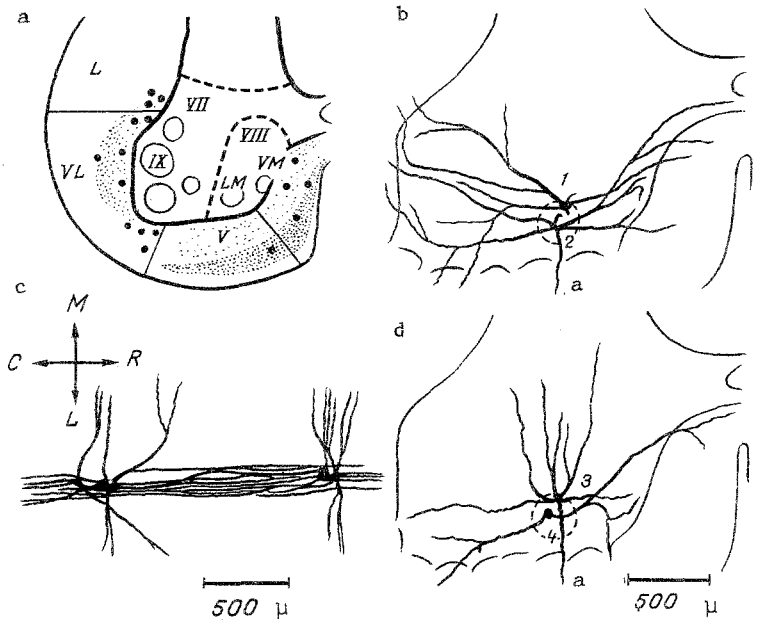

Fig. 1. Reconstruction of radial and longitudinal dendrites of phrenic motoneurons on the basis of frontal and horizontal sections: a) scheme of frontal section C6: LM) lateromedial nucleus, VM) ventromedial nucleus and ventromedial funiculus, L, VL, and V) lateral, ventrolateral, and ventral funiculi, respectively, dots indicate fibers of reticulospinal tract, circles show descending respiratory fibers; b, d) reconstruction of radial dendrites of phrenic motoneurons. Orientation of sections the same; c) reconstruction of longitudinal dendrites: M, L, R, C) medial, lateral, rostral, and caudal directions respectively. Magnification: a, b) 44; c) 63. Explanation in text.

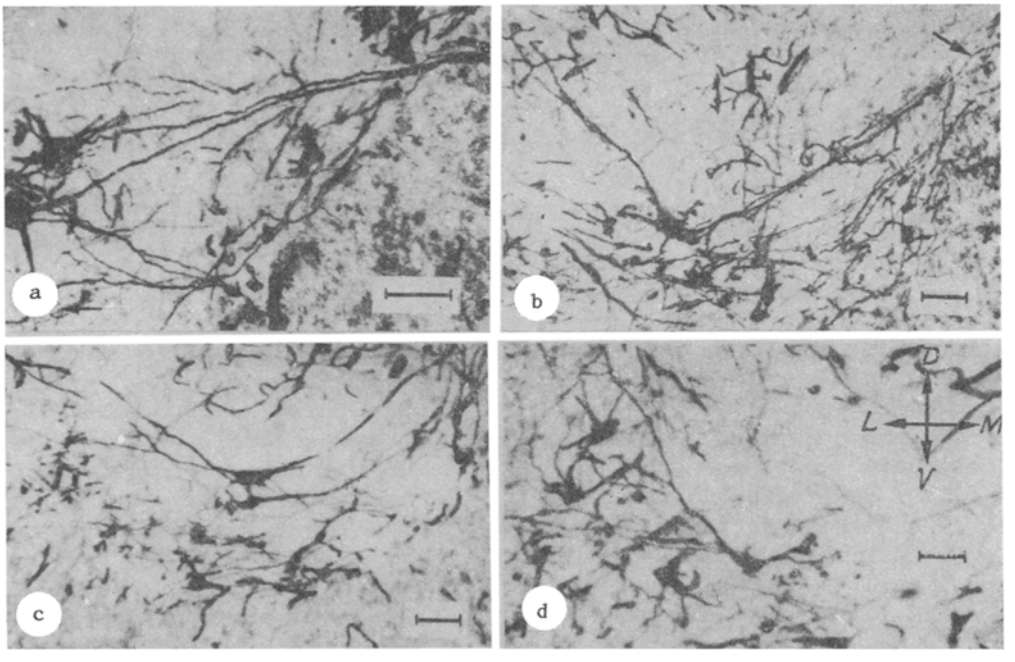

Fig. 2. Fragments of radial dendrites of phrenic motoneurons. Scale 100 μ. Golgi's stain. Magnification: a) 82; b, c, d) 20. Explanation in text.

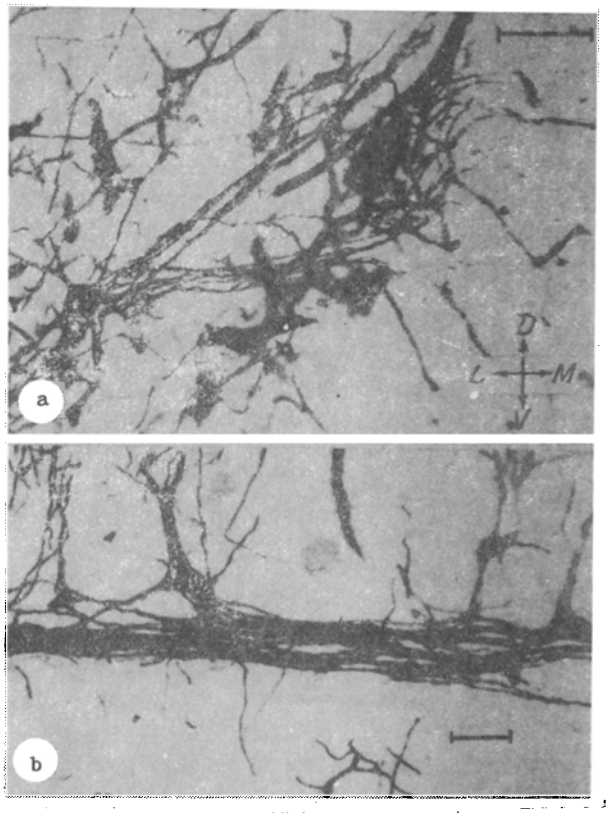

Fig. 3. Fragments of bands of radial and longitudinal dendrites of phrenic motoneurons: a) top band includes type 2 dendrites, bottom band type 3 (frontal section). 82×; b) longitudinal band of dendrites (type 6, horizontal section), radial dendrites running into ventromedial nucleus also can be seen. 20×. Scale 100 μ. Golgi's stain. Explanation in text.

neurons with their longitudinal dendrites is shown in Fig. 1c. Each motoneuron gives off several well-developed dendrites, which extend over long distances (up to 2 mm) in rostral or caudal directions. Longitudinal dendrites ramify along their course but, as a rule, do not go outside the phrenic nucleus. Several motoneurons with fragments of their radial dendrites, crossing the gray matter in lateral (Fig. 2c, d) and medial (Fig. 2a-c) directions, are shown in Fig. 2. Some dendrites go outside the gray matter and give off branches in the various funiculi of white matter: in the ventrolateral (Fig. 2c, d), ventral (Fig. 2a), and also the ventral, medial, and dorsal parts of the ventromedial funiculus (Fig. 2a-c). One of the dendrites runs into the anterior commissure (Fig. 2b, arrow). Branches of dendrites in the ventromedial nucleus are clearly visible in Fig. 2a, and in the lateral motor nuclei in Fig. 2c, d. The left dendrite of the motoneuron (Fig. 2b) loses itself in lamina VII (arrow). It can be concluded from examination of a large number of sections that most dendrites run in rostrocaudal, medial, dorsomedial, and lateral directions. Dorosomedial dendrites give off terminal branches in the dorsal part of the ventromedial funiculus close to the anterior commissure or actually penetrate it, whereas the ventromedial dendrites ramify in the ventromedial nucleus or terminate in the more medial and ventral parts of the ventromedial funiculus. The above-mentioned types of dendrites tend to be gathered into bundles or bands; the density of the dendrites is so great that the bands can be seen in single sections. Figure 3 may serve as an example, for bands running in the dorsomedial and ventromedial directions can be clearly seen in it (Fig. 3a), as well as the rostrocaudal, which is the most powerful band of all (Fig. 3b). We were unable to observe any bands of radial dendrites, running into laminae VII and VIII or into the ventral funiculi.

This investigation showed that dendrites of motoneurons of the phrenic nucleus penetrate into all structures of the anterior horn at the level of segment C4-6 of the spinal cord. Six types of dendrites can be distinguished (four of them, as already mentioned, form bands),

differing in the pathways which they follow and the zones of terminal ramifications or projections. There are five types of radial dendrites: 1) ventrolateral, with projection zones in lateral motor nuclei of lamina IX, and also in the ventrolateral funiculus; 2) dorsomedial, for commissural, running into the dorsal part of the ventromedial funiculus or into the anterior commissure; 3) ventromedial with projection zones in the ventromedial nucleus or ventromedial funiculus; 4) ventral with projection zone in the ventral funiculus; 5) dorsal with projection zones in laminae VIII and VII. There is also a sixth type of dendrite, which runs along the spinal cord, in either rostral or caudal directions, and virtually does not go outside the phrenic nucleus.

Penetration of dendrites of the phrenic motoneurons into the ventral, ventrolateral, and ventromedial funiculi, and also into laminae VIII and VII is functionally justified and understandable. Here they obtain information from reticulospinal tracts from the medulla and pons, among which there are respiratory fibers performing different functions [3, 4, 6, 7]. It can be tentatively suggested that dendrites of phrenic motoneurons running into the commissure are responsible for correcting the synchronized working of the phrenic nuclei in the two halves of the spinal cord. The functional significance of the numerous branches of dendrites of the phrenic motoneurons in the ventromedial nucleus, revealed by this investigation, is not yet clear. Ramifications of dendrites of phrenic motoneurons in the region of the lateral motor nuclei are of great interest. They most probably do not begin to function until their supraspinal inhibition is removed under certain conditions. We know, for example that after spinalization of rabbits the rhythm of their respiration follows that of the spinal locomotor generator [9]. Our results are in good agreement with data in [5], although unfortunately bands of dendrites are not described in it.

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ULTRASTRUCTURAL CHANGES IN DENDRITES DURING AGING

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A detailed study of the response of dendrites during aging is of great theoretical and practical importance in view of their role in the synaptic mechanisms of brain activity as the receptive apparatus of nerve cells that are responsible for integrating information reaching the neuron. During aging in man and animals various changes have been demonstrated (mainly at the light-optical level) in dendrites. A reduction in the number of successive branchings, in the number of branches, and in the total length of both basal and apical dendrites has been noted [6, 8]. In the neocortex of old dogs the horizontal branches and, in some neurons, the basal branches of the dendrites also are lost [2]. A marked decrease in arborization density of the basal dendrites has been found in the auditory cortex of old

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