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DENDRITIC SYNAPSES OF CAT PHRENIC MOTONEURONS

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KEY WORDS: phrenic nucleus; motoneurons; dendrites; spines.

The onset of respiratory rhythmic activity in neurons of the phrenic nucleus in the spinal cord of intact animals is determined by descending pathways from the medullary respiratory center. We know that central respiratory neurons have monosynaptic connections with motoneurons of the diaphragm [4, 6]; all motoneurons, moreover, receive the same synaptic excitatory inflow [2]. As a result of supraspinal influences synchronous activity of phrenic motoneurons takes place, and is manifested as a slow depolarization wave, in phase with inspiration. The problem of the structural basis of this synchronous activation has not yet been solved. It was suggested some time ago that descending respiratory fibers terminate on dendrites of phrenic motoneurons, which form tightly packed bands [1]. If junctions of any kind exist between dendrites, a small number of fibers approaching them may trigger all the motoneurons of the nucleus. The existence of electrical synapses has not previously been discovered in the phrenic nucleus [5].

This paper describes various formations which may be responsible for junctions between dendrites of motoneurons and, in the writers' opinion, which may be the basis for their synchronous activation.

EXPERIMENTAL METHOD

Regions consisting of 4-6 cervical segments were excised after acute experiments on 48 adult cats. Pieces of spinal cord were stained by Golgi's method in the modification of Kopsch or Bubenaite. Frontal, horizontal, and sagittal serial sections 100 μ thick were used.

EXPERIMENTAL RESULTS

Dendrites of phrenic motoneurons can be divided into six types depending on the zones of their terminal ramifications (projections). Most radial dendrites and also rostrocaudal dendrites form bundles or bands. Spines were found on widely different segments of dendrites in all bands. Most frequently projections, located very close together and resembling a comb, could be seen on the surface of the dendrite. Spines resembling long rods without thickenings, or with various kinds of thickenings in the form of simple or more complex plaques also were seen. Regions of interweaving dendrites, with single projections clearly visible on their surface, are shown in Fig. 1a, and well-marked spines resembling rods with plaques at their ends are shown in Fig. 1b, c — in this case one plaque sits on a curved rod (high degree of differentiation). Various types of well-organized spines can be seen in Fig. 1d, between dendrites running into lamina VIII. Projections whose tips are arranged opposite one another can also be seen on dendrites of a ventrolateral band (Fig. 1e). The same picture also is observed in a band running in the ventromedial direction (Fig. 1f); a spine in contact with a neighboring dendrite can be seen here. Often one dendrite could be seen to run toward the neighboring group of cells of the nucleus and, when followed further, to form an *en passant* synapse with the initial segment of the dendrite of a certain motoneuron. These synapses are indicated in Fig. 2a, b by arrows; in Fig. 2a the right dendrite of a large cell forms

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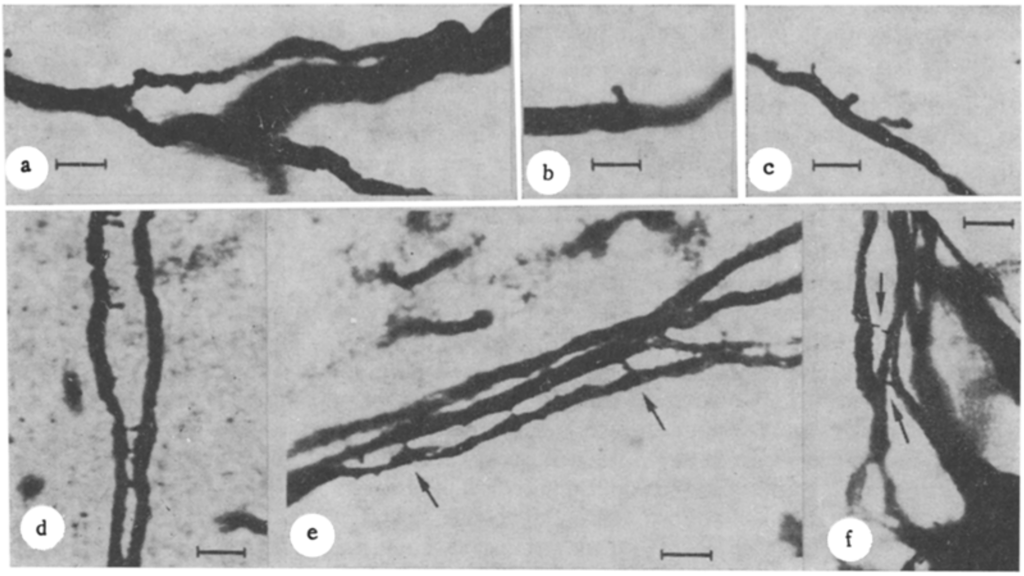

Fig. 1. Structure of spines of different types on dendrites of phrenic motoneurons: a) fragment of dendrite with single projections, 400×; b, c) fragments of dendrites with spines of different shapes, 400×; d) spines on dendrites running into lamina VIII, 200×; e) fragments of dendrites of ventrolateral band, projections opposite one another seen on neighboring dendrites 400×; f) spines on dendrites on ventromedial band, 200×. Scale 10 μ. Golgi's method.

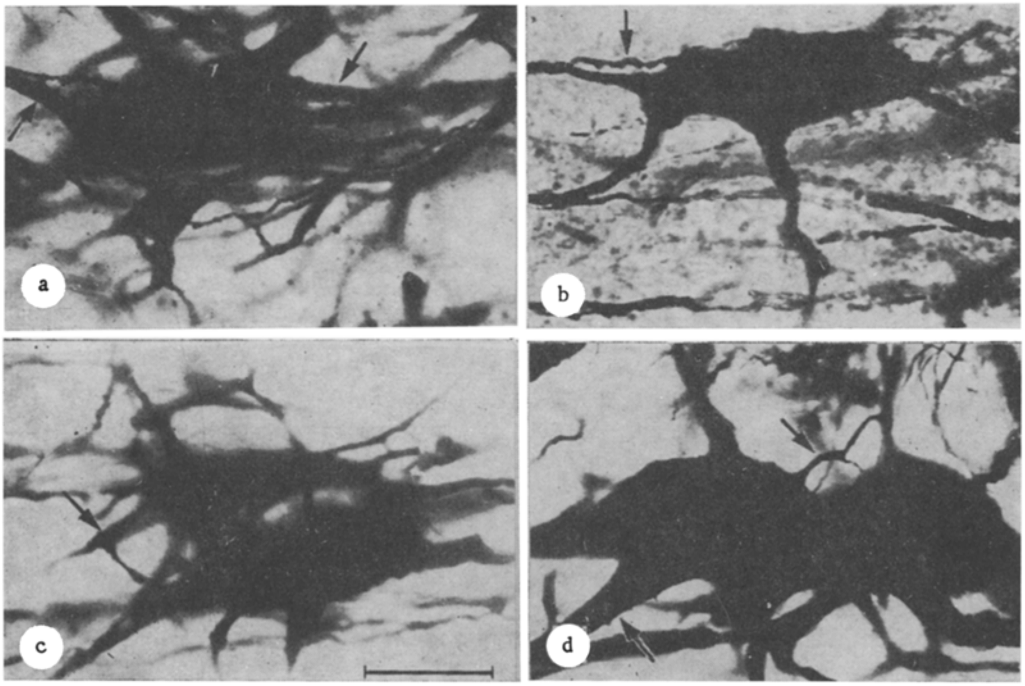

Fig. 2. Different types of *en passant* synapses. Scale 50 μ. Golgi's method. 160×. Explanation in text.

a synapse with the process of a nearby motoneuron, which lies outside the frame. Synapses, one of which is illustrated in Fig. 2c, are quite frequently found. Here the tip of the dendrite of a distant motoneuron can be seen to fuse with the initial segment of the dendrite of a motoneuron (arrow). The best example of yet another type of synapse found in the phrenic nucleus is shown in Fig. 2d. A small dendrite leaves the cell body of the motoneuron on the left and gives rise to two branches: one on the body of the neighboring motoneuron, the other on its axon. Processes of two neighboring cells, running upward or into the ventral zone of white matter, are axons. Spines are clearly visible on the base of the lower dendrite of the motoneuron on the left.

These results, which in our opinion are very important for physiologists, help to explain some functional features distinguishing the phrenic nucleus and, in particular, the mechanism of synchronous activation of phrenic motoneurons. The arrangement of packing of the dendrites in bands itself suggests the existence of connections between them. These connections should be most probably be electrical. However, Lipski [5] failed to find them, although he does not rule out the possibility that his technique was not completely adequate. In the present investigation morphological structures which can form synapses between dendrites are described. Unfortunately, the final conclusion regarding the existence of synapses can be drawn only on the basis of electron microscopy. It is difficult to evaluate the functional significance of the *en passant* synapses and the spinous formations in the phrenic nucleus [3]. Nevertheless, if our hypothesis [1] that respiratory fibers from the pacemaker zone of the respiratory center reach dendrites of the phrenic nucleus is correct, the existence of synapses between dendrites, and perhaps of electrical communications between them, provides the structural basis and a mechanism of synchronous activation of the motoneurons of that nucleus. The view expressed in one publication, that bands of dendrites in the spinal cord can perform the role of substrate for central programs of stereotyped activity [7], must be recalled.

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EFFECT OF HORMONAL AND NEUROTROPHIC FACTORS ON EXPRESSION OF FAST MYOSIN IN SLOW MUSCLE

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It is now generally considered that the phenotypes of skeletal muscle fibers (MF) are controlled by many different factors [2, 3]. The most important of these factors are neurotrophic and hormonal control. Motoneurons, for instance, determine differentiation and maintenance of the differentiated state of different types of MF by means of neurotrophic substances synthesized in the perikaryon and transported intraaxonally to the muscle [3], and also by the character of the spike discharge of motoneurons [10]. It has also been shown that both increased and reduced concentrations of iodine-containing thyroid hormones in the body may lead to changes in muscle phenotype [6, 8, 9]. For instance, after administration of L-thyroxine (T_4) to guinea pigs MF containing fast myosin appear in a slow (the soleus) muscle [1, 8]. Motor denervation of the muscle followed by injection of T_4 caused an increase in the relative number of fast MF in that muscle [1]. Since both axonal transport of substances and nervous impulses cease after division of the motor nerve to a muscle, it was decided to study how T_4 affects the phenotype of a muscle when axonal transport is blocked but when transmission of impulses along axons of motoneurons still continues.

This paper gives the results of a study of the histochemical, morphometric, and immunochemical characteristics of guinea pig slow muscle under the conditions described above.

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