ENDINGS OF PRESYNAPTIC FIBERS ON MOTOR NEURONS OF THE SPINAL CORD OF THE HUMAN FETUS

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The influence of the reticular formation on spinal reflexes was described in the earliest reports of the study of the physiology of this region of the brain [28-30]. In the course of subsequent physiological investigations the more intimate mechanisms of the reticulo-spinal interrelationships were discovered, and it was shown that the reticular structures directly control the activity of the spinal neurons [16, 17]. Meanwhile, information has been gathered concerning the morphological basis of these processes [5, 6, 25, 35, 15, 27]. So far, however, no clear idea has yet been formulated of the actual localization of the endings of the reticular fibers in the gray matter of the spinal cord [33, 22, 37, 38]. Thus the terminal pathway of the reticulo-spinal flow of excitation has not been structurally defined.

We have attempted to investigate this problem by using the ontogenetic method. Long before the discovery of the role of the reticular formation in the integrative activity of the brain, Windle and Fitzgerald [39] showed that the first descending fibers of the white matter of the spinal cord of the fetus are reticulo-spinal fibers. These findings were subsequently confirmed [8, 9, 11, 12, 13, 14, 19, 20, 40, 39]. We postulated that it would be possible to trace the advancing course and the localization of the endings of the presynaptic reticular axons, for at this period the picture has not yet been complicated by the interneuronal fibers from other origins, which develop later.

In our previous investigations [9, 11, 12] fibers were described which appeared in the gray matter of the 1st-3rd, 5th, and 8th cervical segments in the early periods of development of the human fetus (7.5-8.5 weeks). The fibers emerged from the region of the funiculus anterior and passed towards the groups of motor neurons of the lateral part of the horn. We suggested that these fibers are axons of the reticulo-spinal tracts.

In the present study additional methods were used to investigate these fibers (axons) and to determine the tracts to which they belong, their final course, and the site of their synaptic contacts in the gray matter of these segments of the cord.

EXPERIMENTAL METHOD

Material from the 1st-3rd, 5th, and 8th cervical segments of the spinal cord of 13 human fetuses between the periods of 7.5 and 21 weeks of development was used. The age of the fetus was determined from Schultz's table [36]. The preparations were treated by silver-protein impregnation by Peters' method [29, 30] and by Golgi's method of chrome-silver impregnation.

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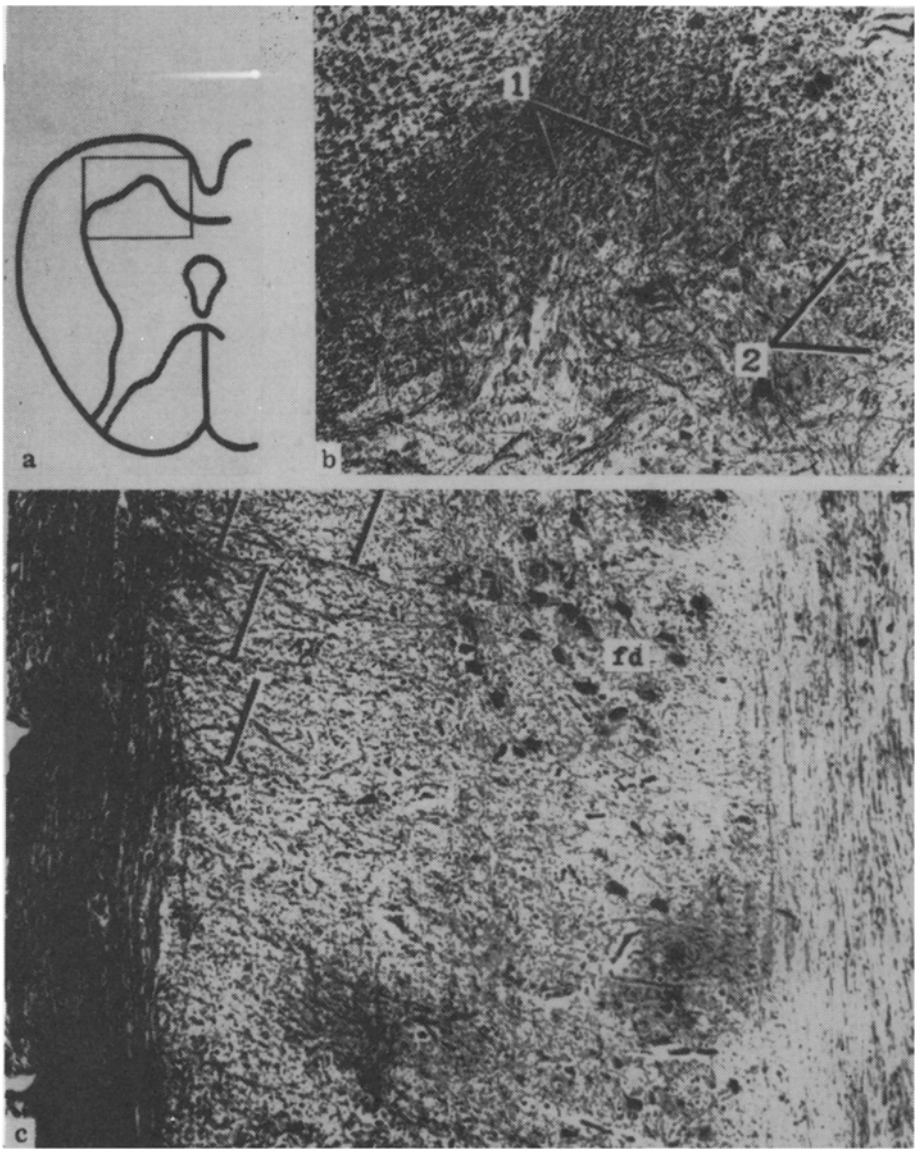

Fig. 1. Scheme (a) and frontal section of the region of the anterior horn at the level of the 3rd cervical segment (b). Age of fetus 19 weeks. 1) Group of fibers leaving medial reticulo-spinal tract; 2) group of fibers leaving posterior longitudinal bundle. Impregnation by Peters' method. Magnification 10 × 20. c) Sagittal section in the plane of passage of the medial reticulo-spinal tract. Age of fetus 21 weeks. The arrows denote the presynaptic collaterals leaving the medial reticulo spinal tract and running towards the motor neurons in the region of the motor center of the flexores digitorum (fd). Photomicrograph. Impregnation by Peters' method. Magnification 7 × 20.

EXPERIMENTAL RESULTS

Studies of frontal sections of the spinal cord treated by Peters' method showed that two groups of axons leave the region of the funiculus anterior and run into the gray matter of each of the segments (Fig. 1, b). The axons of the first group appear in the first cervical segments in the 7.5 week fetus (CR = 20 mm) and they emerge from the medio-ventral part of the funiculus anterior. The axons of the other group, appearing in the segments C_1-C_3 at 8.5 weeks (CR = 26 mm), emerge from the medio-dorsal region of the white matter, in direct contact with the anterior commissure. Both groups of fibers are shown in Fig. 1, b in a section of the spinal cord of a 19-week fetus (CR = 150 mm). Comparison of the topography of these fibers with the known facts of the anatomy of the spinal

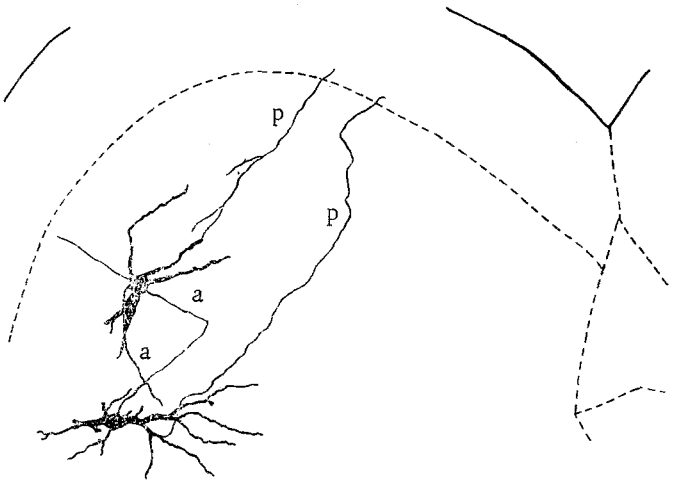

Fig. 2. Frontal section at the level of the 3rd cervical segment of a 10-week fetus. Presynaptic collaterals in contact with motor neurons in the region of the spinal nucleus of the accessory nerve. a) Axon; p) presynaptic collateral. Impregnation by Golgi's method. Figure prepared by drawing apparatus. Magnification 10 × 20.

cord showed that the point of emergence of the fibers of group 1 corresponds to the position of the medial reticulo-spinal tract [15, 26, 28, 32], and that of the fibers of group 2 to the position of the posterior longitudinal bundle [3, 7, 32, 34].

In order to show conclusively that the above fibers are in fact the axons of these descending tracts, series of sagittal sections were cut after preliminary marking of the region of origin of the posterior longitudinal bundle and medial reticulo-spinal tract. It is clear from Fig. 1, c that some of the fibers of the medial reticulo-spinal tract change their descending course and turn at a right angle to enter the gray matter of the segment, which they intersect transversely. A similar picture was also observed in relation to the fibers of the posterior longitudinal bundle. Hence, it could be concluded that the fibers which we described previously belong to two systems of descending tracts (the medial reticulo-spinal tract and the posterior longitudinal bundle) and pursue an independent course in the segment.

The object of the next part of the investigation was to demonstrate the site of the endings of these fibers. Preparations treated by Golgi's method were used for this purpose. A section of the 3rd cervical segment of a 13-week fetus (CR = 70 mm) is shown in Fig. 2. Motor neurons (2) are situated in the region of the nucleus of the accesory nerve; the first sends its axon along the course of the root of the accesory nerve, and the second sends its axon towards the white matter of the lateral part of the funiculus anterior. Two presynaptic fibers leave the medio-ventral region of the funiculus anterior, each of which ends on a dendrite of the corresponding neuron.

The next drawing (Fig. 3) is taken from a section of the 8th cervical segment of a 10-week fetus (CR = 39 mm). In the region of the motor center of the flexores digitorum a motor neuron can be seen which sends its axon into the lateral part of the white matter. A presynaptic fiber leaves the medio-ventral region of the funiculus and terminates on the body of the cell.

The contacts as described above are similar in character to Szentagothai's Type 1 presynaptic collaterals [37], among which this author includes the reticular fibers. A similar picture was observed by G. P. Zhukova [4], who described the presynaptic fibers of the funiculus anterior of adult and young animals. The fact that, according to our findings, the reticular fibers established synaptic connections directly with the motor neurons suggests that this type of communication is possible. It should be recalled here that the descending axons of most of the other tracts do not terminate in the anterior horns, but on the neurons of the intermediate zone [38]. Consequently, the mode of formation of synaptic contacts of the reticular fibers is distinguished by certain special features.

So far we have not specially emphasized to what groups of motor neurons the fibers we have described are described are addressed. As we have previously shown [11, 12], the reticular fibers come into contact with the

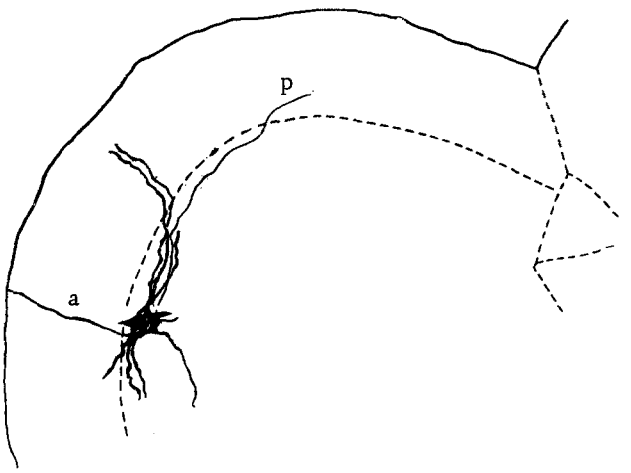

Fig. 3. Frontal section at the level of the 8th cervical segment of a 13-week fetus. Presynaptic collateral in contact with a motor neuron in the region of the motor center of the flexores digitorum. Legend and conditions of production of drawing as in Fig. 2.

neurons of the spinal centers of lateral flexion of the neck and of the grasping reflex. The commencement of reflex function coincides in time with the invasion of the reticular fibers [10]. What are the reasons for this early reticular control over the motor neurons of these centers?

We know that by the 6th-7th week the main structural links of the above-mentioned reflexes have been formed [10, 14, 18, 20, 21, 39, 41], although reflex activity has not yet started. If it is remembered that the fibers of the medial reticulo-spinal tract belong to Magoun's facilitating system [23, 26] it may be postulated that contact with the reticular fiber raises the excitability of the as yet immature embryonic motor neuron to a level high enough for perception of sensory information and for sending impulses to the working organ. The terminal mechanism of closure of the embryonic reflex arcs is probably of this type.

The next descending axon, converging on the spinal neurons, belongs to the system of the posterior lontigudinal bundle. The difference between the times of penetration of these two systems of fibers is small and it varies, at the levels which we studied, between limits of 1-2 weeks. Penetration of the axons of the posterior longitudinal bundle may be interpreted as the establishment of descending control by the extrapyramidal system. It should be remembered that, according to recent findings, the posterior longitudinal bundle is also in direct communication with the reticular formation of the brain [25, 33, 35, 15].

Since the penetration of these fibers affects different segments selectively, neurons receiving descending control acquire the facility for preferential function, and this, in turn, determines the times and order of appearance of the reflexes. These relationships are evidently the structural expression of the principle of consolidation enunciated by P. K. Anokhin in his theory of systemogenesis [1, 2].

It may be concluded from the results obtained that the reticular structures are directly concerned in the organization of reflex activity in early embryogenesis. This investigation supplements the information obtained from general neurophysiology concerning the terminal pathways of the reticulo-spinal flow of excitation and the place of the reticular formation in the integrative activity of the brain.

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