PSEUDOUNIPOLAR NEURONS OF THE SPINAL CORD AND ITS ANTERIOR AND POSTERIOR ROOTS

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Extensive and varied evidence is now available to show that cells of the type of pseudounipolar neurons are found not only in the spinal and the corresponding cranial ganglia, but also, and sometimes in large numbers, in some other structures of the central and peripheral nervous systems.

The presence of nerve cells in the roots of the spinal cord was first demonstrated by Schäfer [16] and Hyrtl [13]. However, details of their fine histological structure were obtained considerably later. A detailed description of these neurons was given by Piolti [14], who used Cajal's impregnation and Nissl's staining methods on guinea pigs, cats, dogs and man, and convincingly demonstrated the sensory nature of these elements. Sensory cells were also found in the initial parts of the spinal nerves [9], in the grey matter of the posterior and anterior horns, and in the intermediate zone of the spinal cord [8]. Cells of this type were found with great regularity at the anterior periphery of the white matter of human fetuses [12] and in adults [2, 6].

It is evident that various factors affect the formation of heterotopic sensory neurons. In some cases the appearance of some such cells is brought about by disturbance of the normal course of the processes of embryogenesis, especially in the period of neurulation, which leads to displacement of the anlagen of the sensory cells from the ganglionic crest to the neural tube [8]. In other cases, as a result of definite functional relationships in the fetus, they are formed from the neural tube [15].

According to Humphrey [12], these cells in human embryos are responsible for early reflex activity, and are proprioceptive. Subsequently, intramedullary [12] and radicular [18] heterotopic elements are doomed to degeneration and disappearance. Only a few of these elements, losing their peripheral connections, are reorganized into, possibly, association elements of the spinal cord [12].

However, the discovery of typical pseudounipolar neurons in adults [2], as mentioned above, contradicts this complete degeneration and reorganization. Some time ago, B. S. Doinikov [3], who studied the sensory cells in the roots of the oculomotor, accessory, and other nerves, expressed disagreement with this point of view [18]. Yet this eminent Soviet researcher was at a loss to interpret the functional significance of these cells because of their great variability in number. In Doinikov's opinion [3], further observations and experiments were necessary to elucidate this problem.

In the present investigation our object was to discover whether heterotopic elements of the roots and spinal cord send their processes into the peripheral nerve, or whether, as Humphrey [12] claims, they take on associative functions in the postnatal period. In order to solve this problem we chose the method of dividing a peripheral nerve and then conducting a retrograde search for reacting heterotopic cells.

EXPERIMENTAL METHOD

Heterotopic cells were studied in the lumbosacral segment of the spinal cord and in the roots in 15 newborn kittens and 8 fully grown cats over 1 year old. Bilateral division of the sciatic nerve at its outlet from the pelvis was performed on 10 adult cats. The material was fixed in alcohol, and embedded in celloidin, and sections were cut on a microtome to a thickness of 12 μ and stained by Nissl's method. The roots were studied together with the ganglia, mainly in longitudinal sections, either separately or in conjunction with the corresponding parts of the spinal cord. The spinal cord was investigated in series of transverse and longitudinal sections. Part of our material was impregnated by Cajal's method.

EXPERIMENTAL RESULTS

The whole series of animals studied (15 kittens and 18 cats) could be divided into three groups. The first group comprised 4 newborn kittens and 6 fully grown cats in which no heterotopic cells were found; the second – 5 newborn kittens and 7 fully grown cats in which these neurons were observed only in the posterior of anterior roots or in both together; and the third group included the newborn kittens and cats in which heterotopic cells were found in all the structures studied.

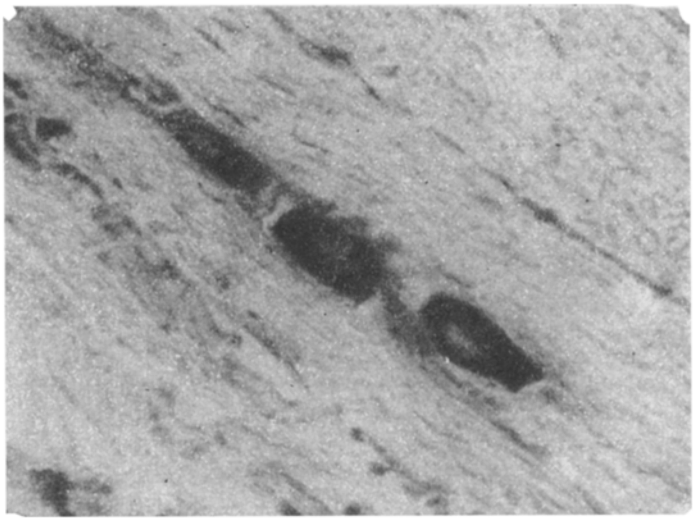

Fig. 1. A group of sensory nerve cells of small size in the anterior periphery of the white matter of the spinal cord of an adult cat. Photomicrograph. Stained by Nissl's method. Magnification: objective 40 ×, eye-piece 7 ×.

In the animals of the last group the number of heterotopic cells fell as the distance from the spinal ganglia increased. This was readily established by studying series of longitudinal sections of the whole lumbosacral portion of the spinal cord with the adjacent roots and ganglia from newborn animals. In the posterior roots the nerve cells were arranged wither individually or in groups of 3-4. Cell groups were encountered in the proximal and distal segments of the roots. At the point where the root entered directly into the spinal cord, heterotopic cells were less numerous. In the while matter of the spinal cord, unipolar cells and groups of 2-3 neurons were scattered throughout the extent of the lumbosacral segment, lying both at the periphery and in the depth of the anterior funiculi, in areas lying next to the intramedullary fibers of the anterior root, and among them (Fig. 1). Along the course of the ventral roots as far as the ganglia these heterotopic elements consisted of single cells. In one newborn kitten these elements were present in the grey matter, where they lay at the side of the anterior grey commissure beneath the ependyma of the central canal.

These cells were less numerous in the sections from the fully grown cats than in those from newborn kittens. The decrease was particularly noticeable in preparations from the spinal cord. At the same time changes were never found in the cytoplasm and nuclei of the cells that might indicate their necrosis or death. It is more likely that the decrease in the number of cells was relative, and associated with an increase in the mass of the spinal cord and the thinning out of its neurons.

By their morphology, the heterotopic cells were typical pseudounipolar neurons, which are highly characteristic of the spinal ganglia. In the young animals the size of the cells, when measured in two directions, varied from 12 × 15 to 25 × 30 μ, and in adult cats – from 15 × 20 to 40 × 50μ. In the center of the cell lay an oval nucleus. In the adult animals the nucleus contained a single, central nucleolus, whereas in the newborn kittens the presence of 2 or 3 nucleoli was not a rarity. In the latter case the nucleoli could be the same size, or one could be larger than the others. The cytoplasm of the cell in the newborn kittens was filled with a finely granular tigroid. In the adult animals, the chromatophilic substance of the largest cells consisted of irregularity shaped masses. The cytoplasm of some nerve cells of the adult cats also contained lipofuscin. The neurofibrillary apparatus of the cells consisted of a delicate, narrow-looped plexus of almost uniform density. The single process of the cell formed an initial glomerulus, which in the newborn animals took the form of only a single turn or a slight bend; in the adults there were 6 or 7 such turns.

Changes in the structure of the neurons (an increase in the size of the cells, a decrease in the number of nucleoli, the deposition of pigment, coarsening of the tigroid, an increase in the complexity of the structure of the initial glomerulus) are characteristic features of the morphology of aging of the spinal ganglia [1]. The common pattern of differentiation is undoubtedly due to identity of function, and is suggestive of the participation of heterotopic elements in the sensory innervation of the periphery of the body. This is convincingly demonstrated by using the test of the retrograde reaction caused by division of the sciatic nerve. This, the largest nerve trunk, is formed by processes in the cells of the lumbosacral segment, from which it can be assumed to contain dendrites of heterotopic cells.

Material from the animals was studied one week after division of the sciatic nerve. At this time the retrograde reaction could be demonstrated most convincingly from a considerable number of heterotopic cells simultaneously. In each individual case, moreover, completely intact cells were seen, sometimes lying side by side with modified elements. The character of the reaction of the neurons is noteworthy and convincingly indicates their sensory origin [4, 5].

In most modified cells we observed a perinuclear concentration of chromatophilic substance (Fig. 2). In the different cells the width of the perinuclear ring and the intensity of its staining varied, probably depending on the degree of injury to the neuron and on its functional state at the moment of trauma. Cells were seen in which the tigroid was arranged in the form of a perinuclear rim. The whole of the remaining peripheral part of the body was homogeneous and did not stain by Nissl's method. In other cells the perinuclear halo was narrow, and the remainder of the cytoplasm contained tiny granules of tigroid. Cells with uniformly distributed tigroid in a much smaller amount were observed. Modified cells were found in all the segments which we studied. They were observed more frequently in the posterior roots and less often in the white matter of the spinal cord.

This experiment shows that many heterotopic neurons send their processes into the peripheral nerve and, consequently, participate in the innervation of definite parts of the body. The presence of intact cells does not mean that they do not carry out these functions. The processes of some cells terminate above the point of division or, having passed through the white commissures, take part in the innervation of the internal organs.

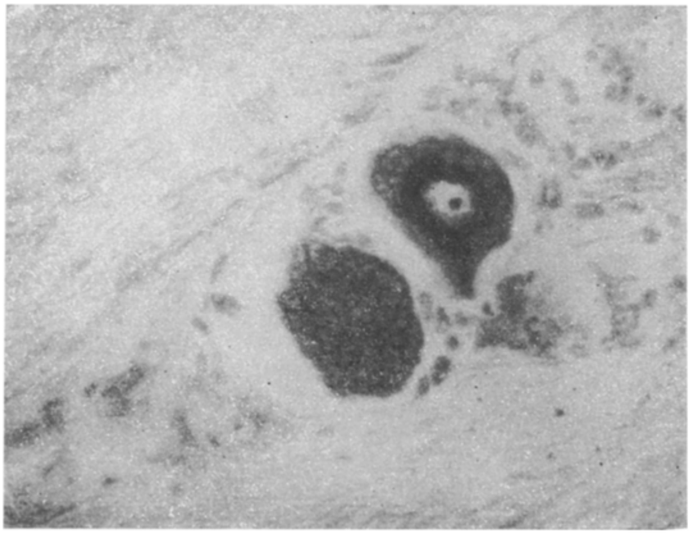

Fig. 2. Two nerve cells in the white matter of the spinal cord among the intramedullary fibers of the anterior root after division of the sciatic nerve in the adult cat at its point of emergence from the pelvis. In one cell a characteristic perinuclear concentration of tigroid can be seen, determining its reaction. In the accompanying neuron the chromatophilic substance has a normal, finely granular structure. Photomicrograph. Stained by Nissl's method. Magnification: objective 40 ×, eye-piece 7 ×.

On the grounds of the structure, the characteristic age differentiation, and the typical retrograde reaction, we can be convinced that the heterotopic cells are sensory in nature. Comparison between the material from the newborn kittens and the adult cats shows that these cells are preserved, if not fully, at least in considerable numbers in adult animals and, consequently, are functioning elements. This is confirmed by the results of the experiment showing that heterotopic cells participate in the innervation of the periphery of the body. Meanwhile, in view of their inconstancy and their great numerical variability in individual animals, the importance of the heterotopic neurons for the organism as a whole cannot yet be assessed.

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