MORPHOLOGY AND PATHOMORPHOLOGY

CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF THE PERIPHERAL NERVOUS SYSTEM

PART II. FUNCTION NATURE OF DOGEL'S TYPE II CELLS

V. I. Pilipenko

From the B. I. Lavrentyev Neurohistology Laboratory (Director : E. K. Plechkova), Institute of Normal and Pathological Physiology (Director: Prof. V. N. Chernigovsky, Member Acad. Med. Sci. USSR), Acad. Med. Sci. USSR, Moscow

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The study of the morphology of Dogel's Type II cells, and of their function and relations with other nerve formations, is of considerable importance for the comprehension of the nervous mechanisms assuring the regulation of some of the body functions, as well as for the development of general concepts of the structure and functional characteristics of the nervous system.

As far back as 1896, A. S. Dogel [1], who had made a study of the morphology of the nerve cells of the intestinal and cardiac ganglions, proposed a classification of neurons, which was accepted by the majority of workers. According to this classification, cells possessing a small number of long processes with few ramifications, which emerge from the ganglions, were called Type II cells, and Dogel expressed the opinion that they are peripherally distributed sensory neurons.

The sensory nature of these cells is still, however, not universally accepted, notwithstanding indirect and direct evidence in favor of this view presented by a number of authors.

I. F. Ivanov [3], who performed experiments involving severing of the intestinal nerves, showed that degeneration of the nerve takes place centrad to the transection, whereas the peripheral portion remains intact, from which he drew the conclusion that the latter represent centripetal axons of Type II cells. Further evidence in support of this view is afforded by other findings of this author, viz, that the quantitative gradient of intact fibers in the peripheral portion of the severed nerve corresponds with the gradient of distribution of Type II cells found in the intestinal wall by B. I. Lavrentyev [6]. The dendrites of these cells form ramifications, typical of receptor formations, in the intestine of lower vertebrates, such as the frog (A. A. Nemilov) and the lamprey [8].

Evidence has been presented by M. D. Zaidenberg, and also by T. S. Ivanova [4], which permits of the characterization of the ramifications of the dendrites of Dogel's Type II cells as receptor formations. I. A. Chervova [10], who made an experimental study of the morphology of cardiac ganglions, concluded from her findings that the Type II cells have a sensory function.

We have made a study of Dogel's Type II cells of ganglions of the intermuscular plexus of various sections of the intestinal tract, chiefly of the small intestine of guinea pigs, rabbits, cats, and dogs. Type II cells of the cardiac ganglions of rabbits, cats, dogs, pigs, bulls, and horses were also studied.

Nerve tissues were stained with methylene blue according to Dogel, and also impregnated with silver.

Thick sections (up to 120μ) and whole preparations of separated layers of intestinal wall were particularly useful for our purposes, as was also the epicardium of the auricle, separated from the myocardium. For silver staining we applied the method of differentiation of impregnated preparations with potassium bromide solutions. After washing the impregnated slices or delaminated fragments with distilled water they were immersed in 25% KBr solution, and the degree of differentiation was checked under a microscope. After differentiation the slices were washed thoroughly with several changes of distilled water (KBr reacts violently with sulfuric acid, which should be borne in mind when washing the vessels).

Apart from the generally known peculiarities distinguishing Type II cells from other nerve cells of the alimentary tract, the most striking is the intensity of staining with silver salts. Thus, only Type II cells are usually selectively stained in the intestinal wall.

Like other workers, we were unable to see any pericellular formations on Type II cells, and this may be considered to constitute a second characteristic feature distinguishing them from Type I cells. With methylene blue staining the contours of Type I cells often appear very distinct, owing to development of their pericellular apparatus.

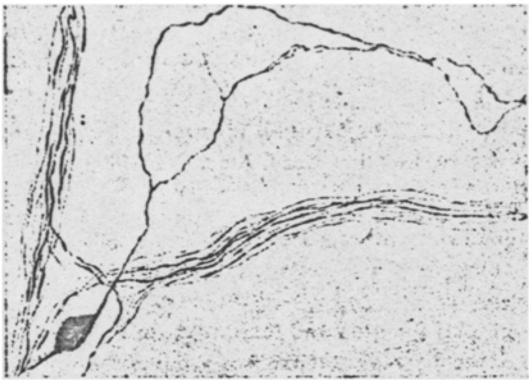

Fig. 1. Ramification of dendrites of a Type II cell from the myenteric plexus of the small intestine of a cat.
Whole preparation, silver impregnated.

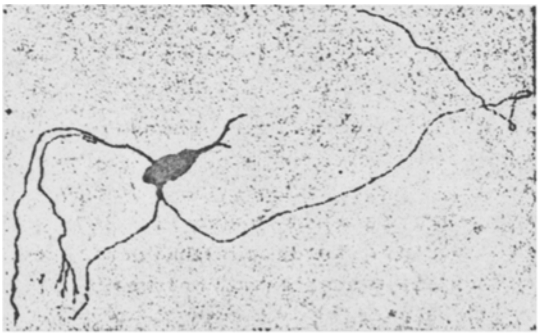

Fig 2. Arborizations of a Type II cell dendrite, from the auricular epicardium of a dog.
Whole preparation, stained with methylene blue.

Type II cells are also distinguished by their somewhat larger size; this applies particularly to the small intestine of the guinea pig, as has been shown by M. D. Zaidenberg [2].

These cells are usually to be found in ganglions, most often of the peripheral parts of the myenteric plexus, but they may also be found singly, outside of a ganglion. In such cases, and when its processes are sufficiently well-defined, it is possible to follow the branchings of its axons, and to see that they enter into and branch within ganglions, while the dendrites proceed from the adjacent tissue. Individual dendrites may be followed for a certain distance within the nerve trunks of the plexus, to emerge later into the muscular tissue.

It is sometimes possible, with whole preparations, to follow the ramifications of dendrites over a considerable distance. The dendrites often bifurcate, to give thinner and thinner branches, which finally disappear in the intestinal wall. Triangular plates or large varicosities are frequently to be seen at the points of branching. The very fine terminal fibrils often exhibit minute varicosities, which are always revealed by staining with methylene blue, and in some cases with silver. This closely resembles the familiar pictures of branching systems of so-called diffuse sensory terminations (see Fig. 1).

The same remarks apply to Type II cells of the cardiac ganglions, which may form aggregations in the epicardium, in the form of microscopic nodes.

A considerable number of these cells are also distributed outside the ganglions. They usually possess two or three processes, the dendrites of which form typical sensory arborizations, and the axons proceed to the ganglions (Fig. 2). Unipolar cells are also encountered, in which the axon does not emerge directly from the cell, but from a common process with the dendrite. In such cases, too, the general feature of dendrite ramifications, of terminating in very fine varicose fibrils, permits of their recognition as receptor formations.

It is known that physiological methods can in many cases make important contributions to the solution of complex problems of morphology. We have applied physiological experiments to the study of the functional significance of cells of Dogel's Type II.

If these cells are in fact sensory neurons, and if the intact nerve fibers found by I. F. Ivanova in the peripheral section of a cut mesenteric nerve represent their axons, then it should be expected that they display action potentials when the receptors constituted by the dendrites are stimulated in any way.

It was essential, in order to investigate this possibility, to exclude impulses from the peripheral sections of the processes of spinal ganglion cells, entering into the composition of the mesenteric nerves. This was achieved in our experiments by registering impulses from the peripheral ends of mesenteric nerves at sufficiently long times after their transection for the degeneration of the peripheral ends of sensory nerve fibers of central origin.

The experiments were perfomed on rabbits and cats. A number of mesenteric nerves (every other one) were severed at the root of the mesentery of cats, and after the lapse of 14 to 27 days we stimulated the intestinal receptors by distending the appropriate loop by means of a needle joined through a 3-way connection to an oncometer, and registered the impulses proceeding from the peripheral ends of the severed nerves, using an oscillograph (Type OB-2, from the experimental factory, Academy of Medical Sciences).

For purposes of comparison, we also registered impulses from the peripheral portions of severed nerves immediately after transection, in a few animals (these experiments were done together with T. S. Lagutina, in V. N. Chernigovsky's laboratory).

We found that distension of the appropriate sectors of the intestine led to the appearance of well-marked impulses in the peripheral part of the severed nerves. It is of interest that the impulses were registered not only during distension of the intestine, but also when pressure was released by letting the air out.

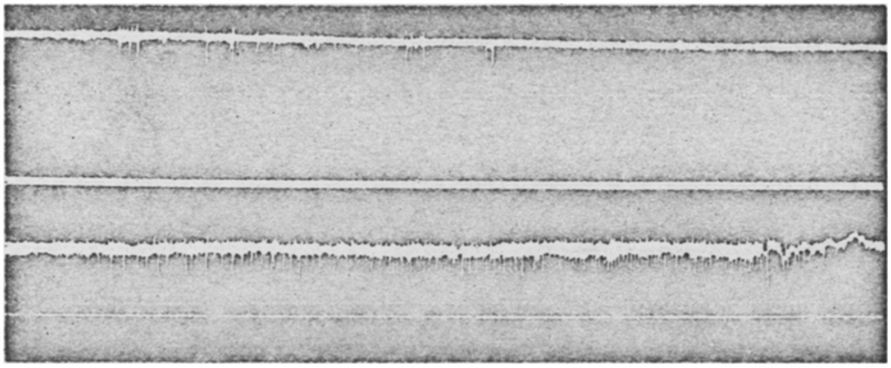

Fig. 3. Impulses from the peripheral ends of a severed mesenteric nerve of a cat, during distension of the intestine with air.
The upper oscillogram was recorded 17 days after transection of the nerve, and the lower one was taken from an intact nerve. The dotted line is a time marker (0.05 sec), and the continuous lines indicate duration of stimulation.

We may relate the appearance of these impulses to stimulation of receptors located in the muscular layer of the intestine. This view is further supported by the appearance of fairly strong impulses when cold physiological saline is introduced into the intestine, due apparently to contraction of the muscles.

Similar experiments, involving transection of the depressor nerve, were performed on rabbits. We found that well-defined impulses, stimulating heart action, could be registered from the peripheral ends of the cut nerves 14, 16, and 27 days after the operation. It follows that axons of Type II cells of the cardiac ganglions enter into the composition of the depressor nerve.

Silver impregnated preparations of the peripheral portions of the severed nerves showed the presence of intact nerve fibers, proceeding singly or in groups.

The qualitative differences between the impulses recorded from the distal ends of the severed nerves immediately after transection, and a long time after, are of interest. Thus, only impulses of low amplitude are recorded from previously severed depressor nerves, whereas the quality of the impulses from the mesenteric nerves remains unchanged, but only their frequency differs (Fig. 3). The latter effect agrees with the experimental morphological observations of E. K. Plechkova [9], relating to the sources of sensory innervation of the heart, and of É. M. Krokhina [5], dealing with the innervation of the small intestine; the data of these authors indicate that the small intestine differs from the heart in that it contains only a small number of nerve terminations originating from the central nervous system. It may, on these grounds, be concluded that the afferent nerves of the small intestine originate from Type II cells.

Our experimental results, taken together with morphological evidence, provide new, and in our opinion, convincing evidence of the sensory nature of Dogel's Type II cells.

We would, in conclusion, like to add the following remarks. V. A. Lebedeva [7] has shown that the sensitivity gradient of the alimentary canal to chemical stimulants coincides with that of distribution of Type II cells, as established by B. I. Lavrentyev, and these cells were on these grounds considered to be chemoceptors. According to our findings, however, they react to mechanical stimulation. It is evident that dendrites of Type II cells give receptors which respond both to chemical and to mechanical stimuli. This view is also supported by the results of morphological studies, according to which dendrites of Type II cells may terminate not only in the muscular layer, but also in the intestinal epithelium (S. Zakusov).

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* In Russian.