SYNAPTIC CONNECTIONS BETWEEN THE NEURONS OF THE INTRAMURAL GANGLIA OF THE PELVIC ORGANS

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New experimental evidence has been obtained recently, supporting the view that closure of peripheral reflex arcs takes place within the ganglia of the peripheral segment of the autonomic nervous system.

The findings of a number of workers [3, 4, 5], as well as our own observations [8, 9, 10], have established that Dogel's type II cells, the functional significance of which was until very recently unknown, are in fact peripheral sensory neurons, as A. S. Dogel' himself supposed [2]. The results of the morphological studies of a number of authors [1, 3, 4, 5], as well as our own findings [7, 9, 10], have provided evidence that these cells are, through their dendrites, in synaptic connection with effector neurons, thus forming reflex arcs which are closed within the limits of the peripheral ganglia.

We have worked out a technique for the removal of the spinal cord of cats, with the object of investigating interneuronic connections in the peripheral autonomic nervous system. In our preceding communication [10] we presented evidence that intact synapses persist after a lapse of time sufficient for degeneration of preganglionic fibers of central origin in the solar plexus.

In the present communication we present the results of a study of interneuronic connections in ganglia innervating the pelvic organs, after their total decentralization. Such studies are of special interest inasmuch as many of these ganglia differ from those of the solar plexus in belonging to the parasympathetic branch of the autonomic nervous system.

EXPERIMENTAL METHODS

We applied the methylene blue and silver impregnation method of Kampos, and Cajal's pyridine method, to the investigation of the nerve ganglia of the urinary bladder, urethra, prostate gland, and uterine cervix of cats, at various times after removal of the spinal cord.

EXPERIMENTAL RESULTS

Our experimental material was derived from 18 cats, killed between the 12th and the 34th day after total ablation of the spinal cord below the level of the 6-7th thoracic segment. A second operation, involving division of the splanchnic nerves, with subdiaphragmatic vagotomy, and division of the lumbosacral trunk, was performed on 4 of the cats. We found that after a time such animals begin to feed themselves, actively to catch mice placed in front of them, try to leave their cage when the opportunity presents itself, and to wash themselves, etc.; they behave like quite normal animals. In most cases, the fluid motion change into formed stools by the 5-7th day; this is evidence of a certain normalization of the activities of the alimentary tract, including also partial evacuation of the rectum. Periodic release of small amounts of urine from the

overdistended bladder is also noted. In one of our first experiments, on a cat which was found to be pregnant, we evidently damaged a fetus during one of the routine toilet operations (emptying of the urinary bladder and the rectum). During the night, the cat aborted a fetus, together with some blood clots.

Similar cases have been reported in the literature [13], and provide strong evidience of the existence of peripheral reflex mechanisms affecting the activities of the uterus.

A superficial survey of our sections showed the presence in the ganglia of nerve cells which could, from their dimensions, morphological features, and staining properties, be recognized beyond doubt as being Dogel's type II cells. They are distinguished in the first place by their large size, which approaches that of the average cell of a dorsal root ganglion (30-50 μ), and in the second place by the intensity of their staining or silver impregnation, in contrast to the weakly stained small cells (Fig. 1). There are several score small cells to each Dogel's type II cell seen in sections of large ganglia.

A characteristic feature of the small ganglia, made up of 10-15 small cells, is that there is usually a single large, intensively staining cell present. We noticed that such cells seen in preparations of the ganglia of the urinary bladder, of the cervix, and of the prostate gland differed somewhat in the nature of their dendrites from the Dogel's type II cells of the alimentary tract. As a general rule, the majority of the dendrites do not extend beyond the ganglion, but remain in intimate connection with the small cells of the ganglion.

Synaptic terminations are to be seen in all the above nerve ganglia, including also the intramural ganglia of the colon and rectum, at the motor nerve cells, in the form of very fine pericellular nerve fibrils entwined around the cells.

The nerve fibrils of which the synaptic apparatus is made up do not as a rule terminate around a single cell, but proceed further to other adjacent cells. Another characteristic feature is that this pericellular apparatus is usually to be encountered around cells situated toward the periphery of a ganglion, as has been previously found in the solar plexus.

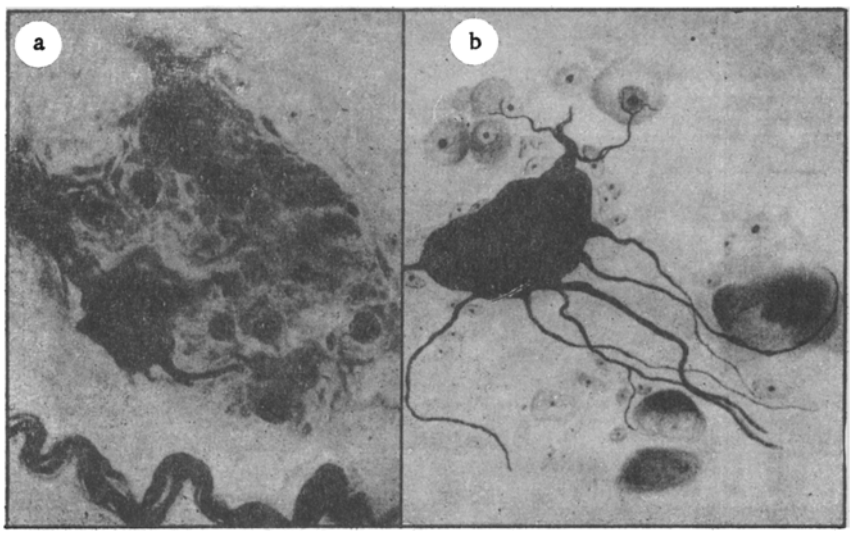

Fig. 1. Single sensory neurons in small ganglia: a) in a ganglion of the uterine cervix; b) in a ganglion of the urinary bladder (sketches of preparations).

Similar synaptic structures, made up of ultrafine pericellular nerve fibrils entwined around nerve cells, were also found in the intramural ganglia of the urinary bladder and of the cervix (Fig. 2). This type of synaptic apparatus exists not only in ganglia, but also at isolated nerve cells.

The form of synaptic apparatus described above is characteristic of the ganglia of animal from which the spinal cord has been removed.

In no cases did we find any synaptic structures in the forms of loops or rings, such as have been described by numerous authors for the synapses of the autonomic nervous system. Our results afford additional support for our previously expressed view that peripheral sensory neurons enter, through their axons, into synaptic connection with effector neurons, forming peripheral reflex arcs.

Morphologically, the synapses formed by the dendrites of Dogel's type II cells represent a system of pericellular nerve fibrils, belonging, according to W. Kirsche's classification [14], to the class of synapses "with a large field of transmission".

Special attention needs to be paid to the connections between neurons effected by dendrites of large cells, terminating within the same ganglion. As is known from A. S. Dogel's classical description [2], cells of ganglia of the autonomic nervous system with dendrites which ramify within the same ganglion within which the cell is situated are classified as type III cells. Similar cells have been described by numerous authors, in particular by F. de Castro [12], as being in intimate connection, through their processes, with other cells of the same ganglion, entwining their bodies and dendrites; this description corresponds very closely with that of A. S. Dogel'. Similar formations have recently been found in ganglia of the human autonomic nervous system by N. G. Kolosov [5] and his collaborator Yu. I. Slepkov [11]. These connections are particularly well defined in the ganglia of large animals and of humans (Fig. 3).

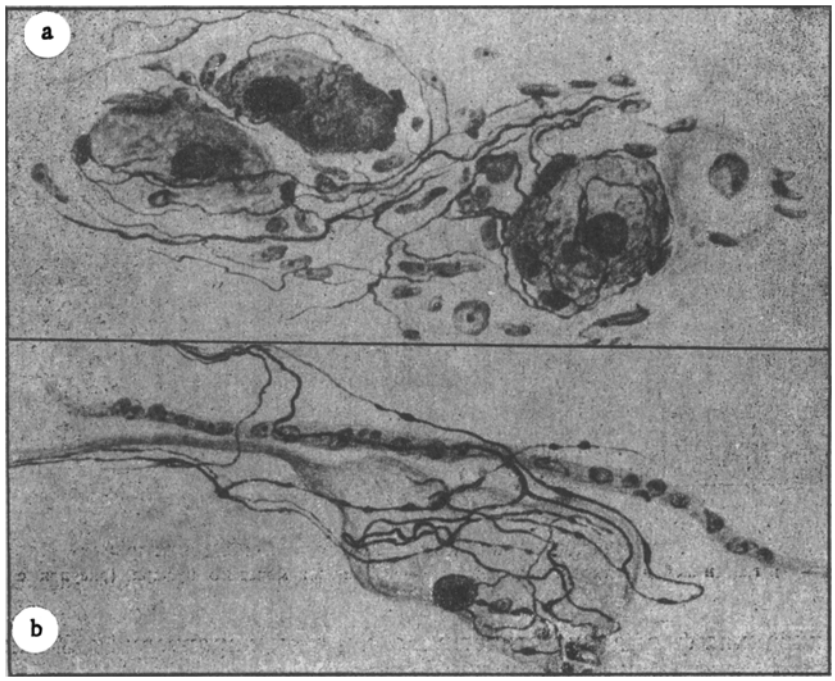

Fig. 2. Pericellular structures: a) in the uterine cervical gland (25 days after removal of the spinal cord, and 13 days after division of the splanchnic nerves, subdiaphragmatic vagotomy, and transection of the sacrolumbar trunk); b) pericellular apparatus of a single nerve cell of the urinary bladder (20 days after removal of the spinal cord, and 10 days after division of the splanchnic nerves and subdiaphragmatic vagotomy).

Different authors have ascribed different functions to cells of this type. A. S. Dogel', on the basis of his concept of the reflex function of ganglia, considered them to be associative neurons. F. de Castro [12] considers them to be effector neurons, and he regards the connections between the dendrites of these cells and of other neurons as being merely an adaptation to the transmission of nerve impulses from one preganglionic fiber to a group of effector neurons within the ganglion.

Iu. I. Slepkov [11] believes that these cells are identical with those of Dogel's type II, i.e., they are sensory neurons, forming receptor terminations at the other neurons. N. G. Kolosov [5] regards them as motor cells, although he also endows them with sensory neuron functions.

Such divergent views as to the nature of these cells, and to the physiological function of the connections between their processes and those of other nerve cells may be ascribed to the circumstance that, as is usually the case, the shorter processes which ramify within the ganglion itself are regarded as dendrites, i.e., as processes receiving nerve impulses. However, the classification of nerve cell processes as dendrites or axons is highly arbitrary. Sensory neurons, in particular, are distinguished by the circumstance that the thicker and longer peripheral process has a receptor function, i.e., it is a dendrite, while that proceeding to the brain is shorter and is highly ramified within the brain, but is an axon.

It is in most cases not possible to distinguish an axon from a dendrite of a Dogel's type II cell of the alimentary tract, the sensory nature of which is now beyond dispute. Moreover, the cell processes under discussion are not true dendrites, i.e., protoplasmic processes, but should rather be regarded as processes of the axonal type.

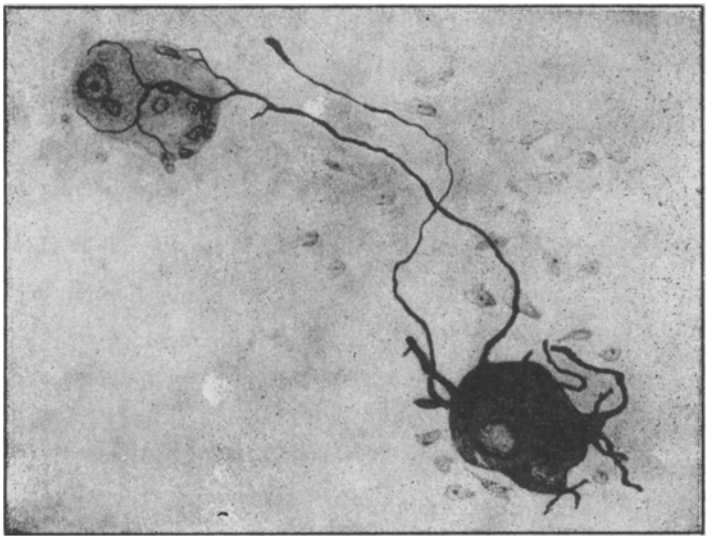

Fig. 3. Synaptic connections between neurons of a peripheral ganglion of the autonomic nervous system (stellate ganglion) of a bull (sketch made from a preparation).

We therefore believe that the contact between the processes of the large intensively staining cells and of the small cells of the ganglia is a real synaptic connection, being the morphological expression of the functional connection between peripheral sensory and effector neurons. In other words, such cases represent a reflex arc, of which the afferent limb is the Dogel's type II cells.

The circumstance that in some cases the processes of the sensory neurons (Dogel's type II cells) emerge from the ganglia, while in other cases they terminate within the ganglion, forming synaptic connections with its cells is evidence merely of special features of the construction of peripheral reflex mechanisms, depending on the functional peculiarities of a given organ.

It is evidently necessary, in order to perform a function of the complexity of intestinal peristalsis, to have nervous connection between remote ganglia of the intramural plexus. Such connections may be achieved by the long processes of the Dogel' type II cells, which emerge from the ganglion within which the cell is located.

In the more compact uterine cervical ganglia, and in those of the prostate gland and the urinary bladder, the sensory cells enter into synaptic connection with other cells of the same ganglion, by means of their

processes; for this reason the corresponding processes are shorter, and this determines the characteristic form of the sensory neuron.

SUMMARY

The functions of the intestine are not totally abolished following removal of the spinal cord of cats, below the level of the 6-7th thoracic segment. Evacuation of formed stools takes place, on a limited scale. Retention of urine is accompanied by periodic voiding of small amounts from the overdistended bladder. An injured fetus was spontaneously expelled from the uterus of one of the cats, showing that uterine function persisted after complete separation from the central nervous system. Synaptic connections could be demonstrated in the peripheral ganglia of the pelvic organs (bladder, urethra, prostate, cervix uteri), between sensory neurons (Dogel's type II cells) and effector neurons of the same ganglion.

Peripheral reflex arcs, with which the different limb is provided by Dogel' type II cells, may thus render possible the functioning of viscera following the total severance of connections with the central nervous system.

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