CONNECTIONS BETWEEN NERVE CELLS IN PERIPHERAL AUTONOMIC GANGLIA

I. STRUCTURE AND FORM OF THE INTRAGANGLIONIC SYNAPSES

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The original basis for the structure of the autonomic nervous system as proposed by Langley, which postulated a single peripheral synapse, has recently been reviewed. In addition to the preganglionic connections, synapses have been described between the neurones which make up the ganglion, i.e., intraganglionic connections. However, this last type of connection has not been sufficiently studied. There have been very few investigations [1,2,5,6,7,9], and we have therefore been led to make a study of the intraganglionic connections in abdominal sympathetic ganglia deprived of preganglionic fibers and terminations.

METHOD

The work was carried out on cats which readily tolerate an operation on the ganglia of the solar plexus. The experiments were divided into two main groups.

In the first group, consisting of 42 cats, the following two-stage operation was performed. In order to produce complete degeneration of the preganglionic fibers, in the first stage we divided all fibers running to the solar plexus in the splanchnic nerves, in the branch connecting the solar plexus with the vagus, in the thin branch which frequently passes from the aortic plexus, and even the branch running from it to the renal plexus. The cats were kept for 20, 25, or 30 days, in order for complete degeneration of the preganglionic and sensory fibers and their terminations to occur. For better demonstration of the pericellular terminations, we decided to use a method best suited to their easy and effective impregnation. We therefore carried out the following additional operation: we removed the edge of the left celiac ganglion, which received (chiefly) the splanchnic nerve, or any other portion of the ganglion, so as to separate the cell bodies (trophic centers) from their outgrowths.

Because 20, 25, and 30 days after the first operation all the sensory and preganglionic fibers entering the ganglion and their endings had degenerated, the pericellular apparatuses could only be formed from fibers (outgrowths) of cells in the ganglion itself; no other kinds of fibers survived the operation. The material was taken 24, 48, 72, 96 h, and up to 12 days after the second operation (mostly during the first three days); it was fixed in 12% neutral formol, impregnated by Bielschowsky-Gros, impregnated with gold, and counterstained with carmine.

For comparison, control, and the demonstration of possible effects of stimulation, we made a simultaneous study at the same times of ganglia of animals on which only the first operation had been performed.

For the simultaneous demonstration of the preganglionic and intraganglionic connections, in the second set of experiments on 30 cats, the edge of the ganglion was extirpated at the same time that the preganglionic fibers were divided, and for comparison we studied ganglia in which only the preganglionic fibers had been divided. The material was collected at the same times as in the first experiment, chiefly within the first three days.

RESULTS

In the experiments in which the preganglionic fibers had been divided and the edge of the ganglion extirpated, we constantly found a number of endings which resembled those found in the two-stage operation. In the experiments where only the preganglionic fibers had been divided, such fibers were found seldom and were very few. This fact confirmed that the endings revealed originated from cells lying within the ganglia.

The most favorable times were 24, 48, and 72 h, and the following descriptions will be based on them. At this

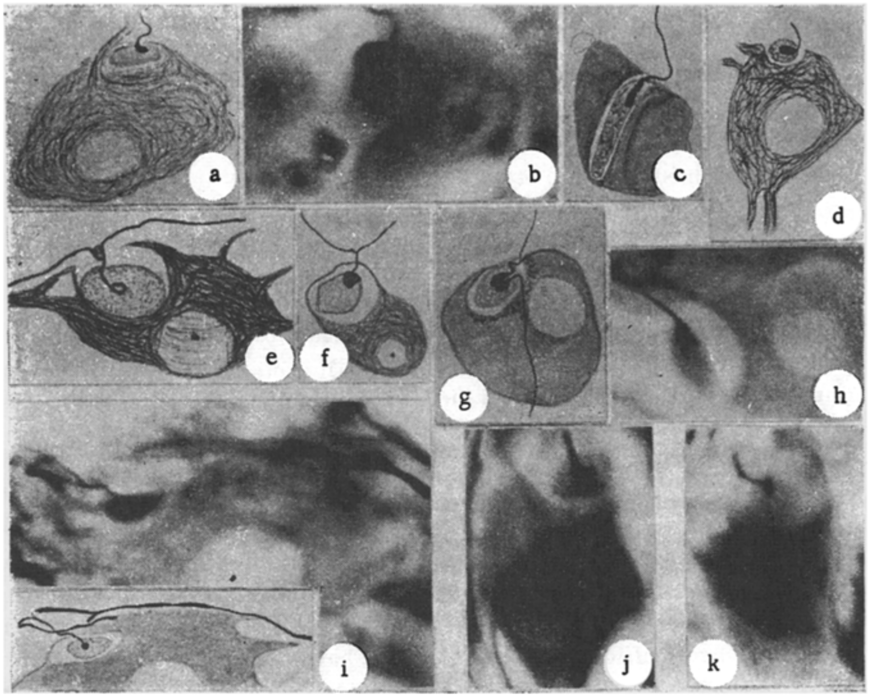

Fig. 1. Different forms of solitary intraganglionic synapses on neurones of the ganglia of the feline solar plexus. Impregnation Bielschowsky-Gros.

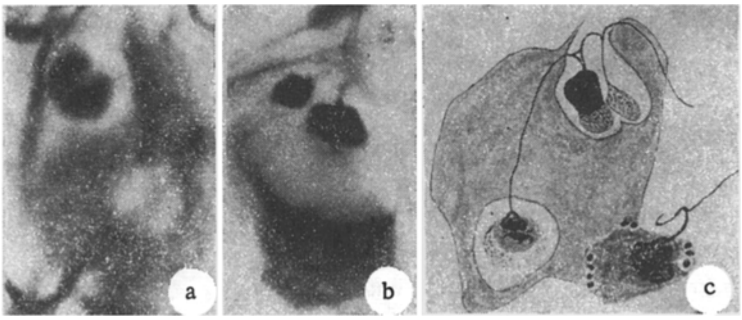

Fig. 2. Numerous synaptic endings on neurones of ganglia of the feline solar plexus. Impregnation Bielschowsky-Gros.

time, the endings are shown quite easily and very clearly, and have not undergone any abnormal changes. Changes take the form chiefly of some increase in the amount of perifibrillar substance at the terminations. The later changes are more extensive.

Remembering the results of I. F. Ivanov [4], who described nerve fibers ascending from the intestine to the ganglia of the solar plexus, in some of the experiments we divided the nerves of the cranial mesenteric plexus.

The experiments showed that after the operation in the ganglia there are tens and hundreds of terminations which lie on the body of the nerve cells, forming a pericellular apparatus, as well as endings in the connective tissue, glia, in the connective tissue sheath of the ganglion, along the nerve trunks within the ganglion, and in the nerves running from the plexus to the organs. We carried out the same experiments on the superior cervical and caudal mesenteric ganglia, with the same results.

The endings forming the intraganglionic connections may be divided into single and multiple types, as has been done in presenting the results of the indirect observations [8]. The single endings are the most common, and constitute the main mass of those observed by us in the experiment.

The structure of the precellular apparatus found within the ganglia is the same as that of the preganglionic terminations: each ending consists of two components, a perifibrillar substance which makes direct contact with the body of the cell, and a neurofibrillar framework enclosed in the perifibrillar substance.

The neurofibrillar framework of individual endings may have various forms, as follows: a small delicate button, club, loop, ring, two clubs joined together, or a fibrillar ball or cap and several joined rings presenting an appearance resembling the first stage of formation of a ball.

The cytoplasm (perifibrillar substance) of the ending of the intraganglionic connections appears in various states. Most frequently it has a granular structure (Fig. 1c,d,e,g,i).

In the endings where the neurofibrillar framework has the form of a loop or ring, the perifibrillar substance is differentiated into two zones – a peripheral granular and an inner agranular zone lying within the fibrillar ring. Besides presenting a granular appearance, it may take the form of a homogeneous mass impregnated with a color of various depths varying from pale grey to intensè black. In the latter case, the neurofibrillar framework is hidden by the stain of the perifibrillar substance, and the end portions of the terminations show up as dark homogeneous spheres. Sometimes only the outline of the perifibrillar substance is impregnated, and frequently it does not show at all, and then its point of junction with the nerve cell remains unstained. In this case, if there is a large amount of perifibrillar substance, the neurofibrillar framework lying in its center appears to be situated extracellularly.

The form of the perifibrillar substance (which determines the shape of the end portion) varies. Usually it is round (see Fig. 1b, e) or oval, and less frequently it may take the form of a flattened or elongated drop.

Its amount varies also in the different terminations. On stimulation, in many of the end portions it is increased, as is easily shown in material collected at various times.

The perifibrillar substance of the intraganglionic endings lies on the cytoplasm of the cell body, just as it does on the endings of the preganglionic fibers (see Fig. 1e), but it is distinguished from the cytoplasm by many properties, and remains clearly delimited from it and from the fibrils of the neurone at all points of contact. Also, there are no intermediate structures between the cell body of the neurone and the perifibrillar substance. Consequently, this type of connection also is of the neuronal type.

Occasional endings take the form of spheres or clubs formed by fine fibers which are sometimes somewhat dilated just before the end portion. Some of these solitary endings have a characteristic form; the approaching nerve fiber changes over into a termination, forming a terminal region, while directly from it (see Fig. 1g), or from various levels of its terminal fiber (see Fig. 1e,i; Fig. 1f), a new fiber originates which either proceeds further or forms new terminal portions in the same way.

Many endings acquire in this way the form of an extended spiral (Fig. 2c); then the approaching fiber forms not one, but several end portions on the cell body (Fig. 2c).

Unlike the preganglionic terminations, where there are usually a number of end branches, in the intraganglionic connections there are comparatively few terminal portions lying on the cell body, and as far as we have observed, apart from a few exceptions, there are never more than four. The main mass consists of solitary endings of the type shown in Fig. 1b, d, i,l, next come endings with 2-terminal portions, and last of all endings with more than two terminal portions. This arrangement is very characteristic of the intraganglionic connections, and contrasts with that for the central preganglionic connections.

The numerous pericellular apparatuses may be divided into two groups. Those of the first group have a fine terminal fiber which runs up to the cell and forms on it successively two terminal portions or more of the same or of different sizes (Fig. 2). Some of the endings of this group (see Fig. 2c) have a method of formation which is characteristic, and which have been described above. Other endings of the first group are formed by normal branching (Fig. 2b), but in this case also the number of terminals is small.

In the endings of the second group, along the path of the main thick fiber, very fine lateral outgrowths arise, and then immediately change into massive endings which hang from a short thin foot. Having given off a number of terminations to the nerve cell, the fiber proceeds further, or else terminates beside the cell in the surrounding glia, enclosing two different substrates in its endings. This kind of ending is very rarely encountered.

For the neurofibrillar framework of the numerous pericellular apparatuses the same shapes are found (rings, clubs, plates, spheres, etc.) as for single terminations.

Such are the main forms of the pericellular apparatuses which form the intraganglionic connections.

From what has been said above it is clear that in the structure of the neurofibrillar framework and the form and properties of the perifibrillar substance and the relationships with the neurones, the terminal portions of the intraganglionic pericellular apparatuses in no way differ from those formed by preganglionic fibers. Nevertheless, in comparing the intraganglionic with the preganglionic terminations, it is essential to notice the following differences: a) The central preganglionic terminations are multiple, having from 40 to 45 terminal portions. The intraganglionic terminations are mostly single. Intraganglionic multiple endings have only three or four terminal portions; b) As a rule, the terminal portions of the intraganglionic connections are larger (6-20μ) than are the central preganglionic connections (1-6μ), and they can be well seen under the medium power of a microscope. These differences enable the preganglionic and local connections to be distinguished from their morphological features, without any experiment.

As far as the shape of the cells on which this description has been based, in all cases where it could be clearly determined it was found that the terminations lie chiefly on the cells of the first type (A. S. Dogiel's classification) [3], which make the main mass of the cells of the ganglion.

A more controversial point is what kind of neurones form the endings which have been described. In previous communications describing the same ganglia, we have reported a connection between the cells of the first and second types, and others between cells of the first type. Z. A. Budrina [1,2] found the same arrangement.

V. I. Pilipenko [9], describing the intraganglionic connections within the ganglia of the canine solar plexus after extirpation of the spinal cord (the branch of the vagus was not divided) thinks that they are formed by fibers of cells of the second type. This arrangement does exist, but is not the only one. The majority of connections are between the neurones of the first type. The following facts support this view: 1) in the ganglia of the solar plexus, the number of cells of the second type is very small, as even A. S. Dogiel [3] pointed out; such a small number would be unable to give rise to such a large number of endings as are observed after operation; 2) in the extirpated edge of the celiac ganglion, only neurones of the first type are found and, therefore, the connections revealed after the operation must be formed from their outgrowths. This conclusion is confirmed by indirect observations, as has been explained above [8]. Therefore, the greater part of the endings observed must form connections between neurones of the first type, some of which may have an associative function.

SUMMARY

To investigate the site and mode of termination of the ganglionic cell processes, the author removed the preganglionic conductors of the solar plexus in cats and, after a period adequate for degeneration of the endings, resected the edge of the ganglion. Examination of the remaining part of the ganglion shows that the cell processes terminate on the ganglionic neurone forming solitary and multiple intraganglionic synaptic connections. Both the intraganglionic and preganglionic connections consist of neurofibrillar framework and perifibrillar substance, being of a larger size and having a lesser number of end portions.

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