

## CONNECTIONS BETWEEN NERVE CELLS IN PERIPHERAL AUTONOMIC GANGLIA. COMMUNICATION II. COMPLEX FORMS OF INTRAGANGLIONIC CONNECTIONS

G. A. Koblov

Department of Histology (Head, Professor G. A. Koblov) Saratov Medical Institute

(Presented by Active Member AMN SSSR V. N. Temnovskii)

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Previously we have reported the presence of intraganglionic connections in the solar plexus.

In our study of the nature of the intraganglionic connections between neurones we were also concerned to find whether the neurones were connected in groups of two or in larger groups and how the connections were arranged. We also wanted to find the relationship between the preganglionic and the intraganglionic connections.

The method of investigation has been described in Communication I.

The results obtained showed that the branches of a single fiber may make connection with several neurones within the ganglia, and that the organization of such connections may be of several types.

In the simplest case the nerve fiber approaches the cell, forms a single ending on it, and then proceeds to one of the adjacent cells where it forms another ending, so connecting the two neurones in series (Fig. 1, A). Now turn to Fig. 1, B: the main fiber leaving the fine bundle and passing into the intercellular plexus forms in succession endings on three neurones remote from each other, and so connects them. This fiber with its endings is interesting also because all three endings are different in size and constitution. The observed differences show that the reactive changes they have undergone are different and that the different endings formed by a single fiber have not been affected simultaneously. Apparently in pathological conditions a loss or alteration of function of different endings of a single fiber may also occur to different extents and at different times.

This type of connection is of quite wide occurrence in the autonomic ganglia we have studied, but besides this form there is also another which is more complex (Fig. 1, C). After it has formed an ending on a neurone the fiber proceeds further to terminate in a fibrillar sole plate or foot on the body of another neurone, i.e., the organization of the connections here is analogous to the one illustrated in Fig. 1, B. However, from the other side another fiber approaches the same neurone; it divides into three branches each of which forms a termination. One branch divides, forms a multiple ending on the neurone, while the other forms a single ending on an adjacent neurone, and the third terminates in the surrounding glia. Here there is also termination a which leaves the main neurone. Quite a complex system of connections is established involving a whole group of closely related neurones (neuronal field); we may therefore refer to this form as the "field" connection.

This observation is interesting for the further reason that the presence of two endings from different neurones on the body of one neurone (screen structures) was previously thought to be a special property of the central nervous system. However such structures are present also in the peripheral autonomic ganglia, and in this particular case in the ganglia of the solar plexus [4, 5].

In most cases, in the ganglia we have investigated the screen structures from two different fibers form two solitary endings typical of intraganglionic connections on the body of the neurone they approach.

Particular attention should be paid to the relationship between the endings in the screen structure (Fig. 1, D), observed in normal material. On the body of the neurone at the point at which the outgrowth leaves it there is quite a large club-shaped ending characteristic of intraganglionic connections. Adjacent to it and distinguished by the degree of impregnation there is a very fine fiber which winds round the club-shaped ending and terminates both on it

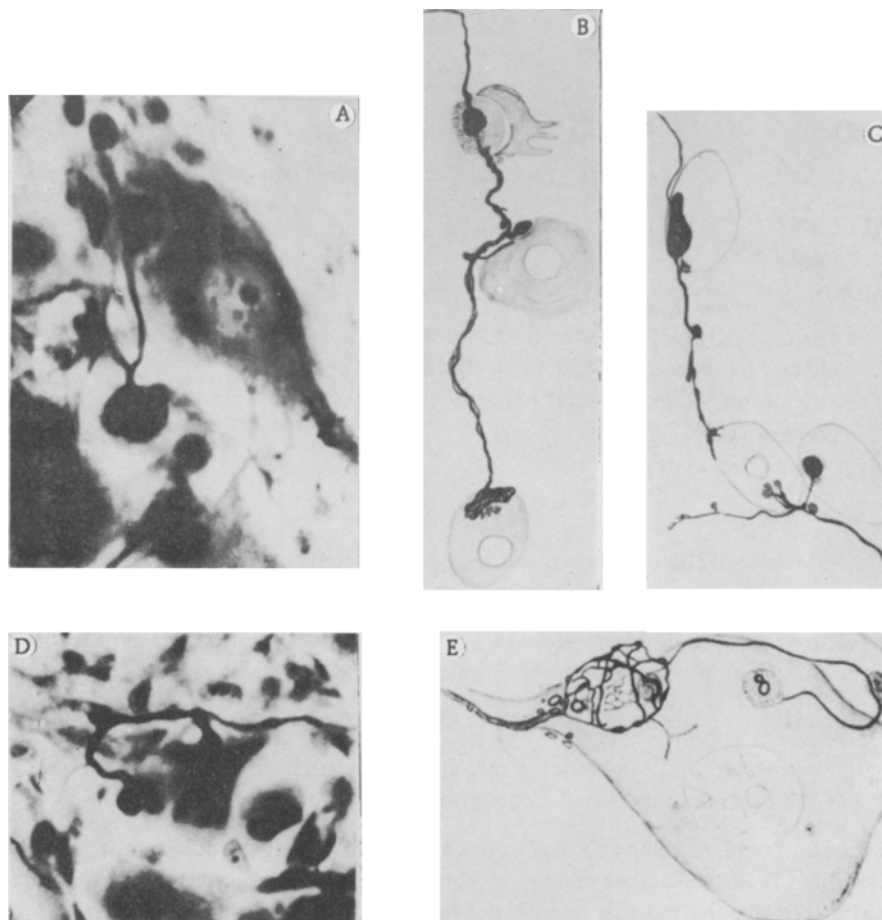


Fig. 1. Principal forms of complex intraganglionic connections. A) The nerve fiber forms endings on two adjacent neurones; B) successive formation of terminations on three neurones; C and D) screening structures; E) relationships between an intraganglionic and a preganglionic termination. Impregnation by Bielschowsky-Gross method. MBI-1.

and on the body of the neurone. One fiber is separated from the plexus, entwines the club-shaped ending, leaves it and at a distance from the other fibers it forms a terminal portion having a granular perifibrillar substance on the body of the same neurone. The multiple pericellular apparatus formed from a fine fiber is typical of preganglionic connections. We will therefore consider it now. The arrangement we have described greatly enhances the interest of this type of connection, because it confirms that direct contact of the terminal portions is possible [3, 5] and shows one of the variants of the mutual relationships of the preganglionic termination with an ending of the intraganglionic connections, while at the same time connection is made with a neurone on which these terminations are distributed.

The screen structure of Fig. 1, E is interesting in another connection. It is formed by two fibers approaching from different sides. One forms a solitary terminal portion, and the other forms two terminations on the body of the same neurone. Alternating with the endings on the neurone, two other terminal portions are given off into the glia from the same fiber. The simultaneous formation of endings in the glia and on the nerve cells is quite common. The terminations in the glia may then be found between the endings on two neurones.

The presence of endings from a single fiber in the glia and on neurones is found in the central nervous system, in the preganglionic connections, and apparently it is a characteristic structure. Intraganglionic connections are no exception either.

In experiments in which first the preganglionic supply was interrupted and then part of the ganglion extirpated we were able to determine where and how the remaining outgrowths of a ganglion cell terminate. Besides forming terminations on neurones and capsules the outgrowths of the cells give rise to a large number of terminations in the



Fig. 2. Some forms of termination of the outgrowths of ganglion cells (A - E). Impregnation by Bielschowsky-Gross method. MBI-1. Obj. 90X, ocul. 10X.

glia, connective tissue, and capsule of the ganglion, and along the bundles within the ganglion, particularly along the path of bundles of fibers emerging from the ganglion, where they are especially numerous [6].

All these endings consist of a neurofibrillar skeleton and of a perifibrillar substance and show the same range of structural variation as occurs in all other terminations, including preganglionic and intraganglionic synapses, i.e., they are organized in the same way as all the other terminations.

Solitary or very simple bushy endings form the main mass of the terminations. Also more complex forms are encountered. The simplest endings are the bunches shown in Fig. 2, A. In structure and arrangement they resemble one of the forms of the typical endings of the outgrowths, because they may be found by direct observation [5, 6], but only at a considerable distance from the body of the neurone. From their position and morphological features they should be classed as sensory terminations. The termination of Fig. 2, B differs from the previous type in the greater length of the terminal fibers, the high degree of scatter of the branches and in their position in the connective tissue; here we have yet further evidence of the sensory nature of the termination and consequently of the presence of sensory neurones, because in ganglia deprived of entrant fibers there are no other sources from which such sensory fibers could arise other than the ganglion cells themselves. This form of neurone is shown in Fig. 2, C where

a broad flattened outgrowth, scarcely separated from the body, branches out, and, giving off side branches, forms the characteristic structure of a sensory ending with a large number of terminal portions of various sizes. Not all the fibers terminate near the cell body, but some leave it and become merged in with other fibers. The bushy form of a typical sensory ending is shown in Fig. 2, D: a quite thick fiber branches dichotomously a number of times, breaks up into a large number of very fine fibers which run out in various directions, and so enclose a large area of glia and connective tissue. This kind of termination is found in the capsule of the ganglion (Fig. 2, E), and between nerve cells. This fact is also evidence of the presence of sensory neurones in the extramural ganglia.

Our own and published results show that in addition to central preganglionic connections there are also others which are intraganglionic and which differ from the former in many respects. On this account the arrangement described by Langley must not be accepted as the only kind of connection in the autonomic nervous system, but as only one of a number of variants. We have also demonstrated the presence of sensory neurones in extramural ganglia.

#### SUMMARY

The ganglia of the solar plexus were freed from preganglionic fibers, and it was found that in addition to simple synapses there were also complex intraganglionic connections. The branches of an intraganglionic fiber might include two or three neurones in the chain. Just as in the CNS, two endings from two different neurones may lie on a single ganglion cell. Intraganglionic and preganglionic endings may be distributed on the body of a single neurone. The processes of some of the neurones of the ganglion form typical sensory endings in the glia and in the connective tissue of the ganglion.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.

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