SOME REMARKS ON THE ULTRASTRUCTURE OF SYMPATHETIC GANGLION SYNAPSES IN MAMMALS

by

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Some difficulties have been met with in the investigation of vegetative *ganglion* synapses by the aid of the electron microscope, due probably mainly to the rather dense packing of the elements — particularly in mammalian *ganglia* — and the rather complex relations between *ganglion* cell processes, preganglionic fiber arborizations and their terminals, as well as the *plasma* of SCHWANN cells that envelops all neural elements of the *ganglia*. It has been suspected already by TAXI (1957) that the majority of mammalian sympathetic *ganglion* synapses might be of axo-dentritic nature rather than axosomatic. The axosomatic synapses of the *sympathicus* in frogs have been described in normal stage and during secondary degeneration in an impressive series of investigations by TAXI (1961, 1962a, 1962b). This is, however, a peculiar situation, due to the fact that most sympathetic ganglion cells of the frogs have no dendrites at all. — One of us (J. Sz., 1962) has given a preliminary report on the ultrastructure of the sympathetic *ganglion* synapse in the turtle *(Emys orbicularis)*, where owing to the relatively less dense packing of elements the structure of the synapse is more easily understood than in mammals. It could readily been observed that the vast majority of the synapses is axo-dendritic, many of them established by parallel or „de passage" contact, and only relatively few of the synapses are established with the cell body surface. A particularly interesting feature of these synapses is that all synaptic regions, in fact all nerve elements are closely enveloped by the *plasma* of satellite elements that forme strange „loose myelin" structures surrounding *ganglion* cell bodies and some of their processes as well as their synapses. — Conclusive proof of the mainly axo-dendritic character of sympathetic *ganglion* synapses in the cat has recently been given in an excellent paper by ELFVIN (1963), using reconstruction of several regions of synaptic contact from ultrathin section series. This exempts us from describing in detail our own observations, gathered since some time on the structure of synapses in the sup. cervical sympathetic *ganglion* of the rat, the findings being essentially the same as those of ELFVIN. It is only with respect to the membraneous structures — or „loose myelin" formations — of the satellite elements that our observations differ considerably from the pictures of ELFVIN, but whether this is from some difference in the material used or the different histological and staining technique, we cannot tell. Our findings on the superior cervical *ganglia* of the turtle and the rat, however, being essentially similar, it is more probably the latter that is to be held responsible for these discrepancies. — The present paper, therefore, gives only a brief account of our observations ot the rat, with some emphasis on the „loose myelin" — like double membrane systems of the satellite elements.

Material and methods

The superior cervical *ganglion* of the sympathetic has been exposed under narcosis in adult albino rats and first fixed in situ by 1% osmic acid solution, according PALADE, buffered to pH 7,5 and cooled. Fixation was continued after removal of the *ganglion* for one hour in the same solution in the refrigerator. After dehydration in graded alcohol the material was embedded into araldite according to LUFT (1961). Ultrathin sections were made with glass knives on the LKB–Ultrotome. Sections were stained with lead-hydroxyde according to KARNOVSKY (1961) and investigated with the aid of the Zeiss (Jena) ElMi–2 electron microscope. Original magnifications used were 3000–8000 and enlarged further by optical means.

Results

Figs. 1 and 2, which are taken from the same visual field, are showing most of the general features of sympathetic *ganglion* synapses. Dendrites (D) are recognisable from their characteristic tubules (Dt), which offer some difficulties if cut in transversal direction, as it occurs on transverse sections of the dendrites and more often in the neighbourhood of synaptic contacts. The cross sections of the tubules could easily be mistaken for vesicles. The upper dendrite of Fig. 1. is approached by an axon terminal filled with synaptic vesicles (Sv); no synaptic contact, however, is established in this plane, as clearly seen from the two separate double membranes separating them, which indicates that a thin statellite *plasma* layer intervenes. The lower dendrite of this figure, cut transversally, has between the two ringed arrows a clear synaptic contact with an *axon* terminal containing synaptic vesicles (Sv). Some of the synaptic with an *axon* are of the usual size of 400–500 Å, whereas larger vesicles of 1000–1500 Å diameter containing a denser body in the center (indicated by black arrows) are seen in most synaptic terminals of the *ganglion*. They are the known „dense-core" or „osmiophilic" vesicles, also called as neurosecretory elementary bodies e. g. in some parts of the *hypothalamus*. In the lower part of the figure two dendrites are closely attached to one another with some thickening of both membranes (Dap). They very much resemble the „dendritic attachement plaques" frequently seen in the CNS and described also by ELFVIN (1963) in the sympathetic *ganglion* of the cat. In the upper part of Fig. 2 a terminal part of an *axon*, with synaptic vesicles is seen to have direct synaptic contact with another dendrite.

Figs. 3, 4 and 5 show some details of individual synaptic contacts. In Fig. 3 a small *axon* terminal with synaptic vesicles is synaptically attached (between two ringed arrows) to a hooked small *ganglion* cell process (Gcp) of a *ganglion* cell body easily recognizable by its ribosomes. Fig. 4 shows a longitudinally cut axo-dendritic contact with thickened membranes and a row of dense bodies arranged in parallel with the subsynaptic membrane, similar to the subsynaptic apparatus described by TAXI (1962a) in the frog sympathetic *ganglion*. – On the left of Fig. 5 there is synaptic contact between *axon* and dendrite cut transversally, on the right several axons and cell processes are seen without direct contact, separated from one another by several layers of satellite cell double membranes, occasionally forming „loose myelin"-like formations as well as mesaxons and mesodendrites. Fig. 6 gives an impression of the complex relations between nervous and SCHWANN satellite elements, the *plasma* of the latter being seen in the lower part (Sp) of the figure. In our own preparations the *plasma* of satellites is by no means so empty as it might be gathered from the pictures of ELFVIN. Both in the turtle and the rat sympathetic *ganglion* the plasma of the SCHWANN elements was found to contain a relatively dense system of cytomembranes, ribosomes, GOLGI system, and centrosome. This figure is a tangential section of a flat SCHWANN cell *plasma* process, containing several axons and dendrites. An *axon* part (Ax) is cut longitudinally on the lower left, in most part devoid of synaptic vesicles. The synaptic vesicles are generally accumulated in strange bulges of the axons (Ab), one of which is seen cut longitudinally in the lower part of this *axon* and others cut transversally more above and in the center of the figure. No direct attachment of *axon* bulges to the dendrites is seen in this plane, but there can be no doubt that these bulges contact the dendrites (D) embedded in the same SCHWANN cell process in a neighbouring level. Mesaxons (Ma) and probably some mesodendrites (Md) are seen in different parts of the figure, the „loose myelin" — like double membrane systems — particularly in the upper part of the figure — making it, however, rather difficult to trace them in continuity.

As described already in the turtle (SZENTÁGOTHAI, 1962) and the cat (ELFVIN, 1963) the whole sympathetic *ganglion* is pervaded by a lacunar system of connective tissue spaces (Ctp) which is separated from the surface membrane of the satellite elements by a continuous „basement membrane". In the rat sympathetic *ganglion* this membrane is not very well defined and often an ambiguous relatively broad layer, in the turtle, however, it is clear and shows a villous or spiny surface towards the connective tissue space.

Summary and conclusions

The synapses of the superior sympathetic cervical *ganglion* in the rat show essentially the same structural details as already described in sympathetic *ganglia* of the turtle *(Emys orbicularis)* and the cat. Most synapses are established between terminal or „de passage" bulges of preganglionic axons, filled with synaptic vesicles, and dendrites of the *ganglion* cells. Relatively few synapses are established with the body surface of the *ganglion* cells. All nervous elements of the *ganglion* are enveloped by an intricate system of satellite elements, synapses are also effected inside this envelope. Especially axons, but also dendrites and cell bodies are surrounded often by several double layers of satellite surface membranes, which thus establish a formation of loose myelin, the layers of which are by mesaxons connected with the axons or dendrites on one hand and the surface of the satellite elements on the other. A lacunar system of connective tissue spaces pervades the whole *ganglion*. — Besides synaptic vesicles of ordinary size, large, so called „dense core" or „osmiophilic" vesicles are found regularly in the synaptic terminals. With respect to the general occurence of these characteristic organelles in (1) cells of the adrenal *medulla*, (2) peripheric terminal arborizations of postganglionic sympathetic

neurons, (3) the hypothalamic neurosecretory neurons of vertebrates, (4) many neurosecretory neurons of invertebrates, (5) synaptic terminals in some parts of the *hypothalamus,* and (6) their supposed connexion with adrenergic transmitters (WOLFE et al, 1962), it seems rather difficult to attribute any peculiar function to them at the present state of our knowledge.

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Figs. 1 and 2 Two parts of the same visual field of the superior cervical sympathetic *ganglion* of the rat, showing axo-dendritic synapses and interdendritic contacts.
Magn. 32 000 ×
Abbreviations:
Cts = connective tissue space
D = dendrite
Dap = interdendritic desmosome
Dt = dendritic tubules
M = *mitochondria*
Ma = *mesaxon*
Sv = synaptic vesicles

Figs. 3, 4, 5 Details of synaptic contacts in the superior cervical sympathetic *ganglia* of the rat.
Magn. Fig. 3, 5 = 32 000 × Fig 4 = 21 000 ×
Abbreviations:
Cts = connective tissue space
D = dendrite
Gcb = *ganglion* cell body
Gcp = *ganglion* cell protrusion
Sv = synaptic vesicles

Fig. 6 *Axon* terminal branches and dendrites invaginated into the *plasma* of SCHWANN element with „loose myelin"-like membrane systems
Magn. 22 000 ×
Abbreviations:
Ab = *axon* bulges
Ax = *axon*
Cts = connective tissue space
D = dendrite
Ma = *mesaxon*
Md = mesodendrite
Sp = satellite cell *plasma*

Fig. 1.

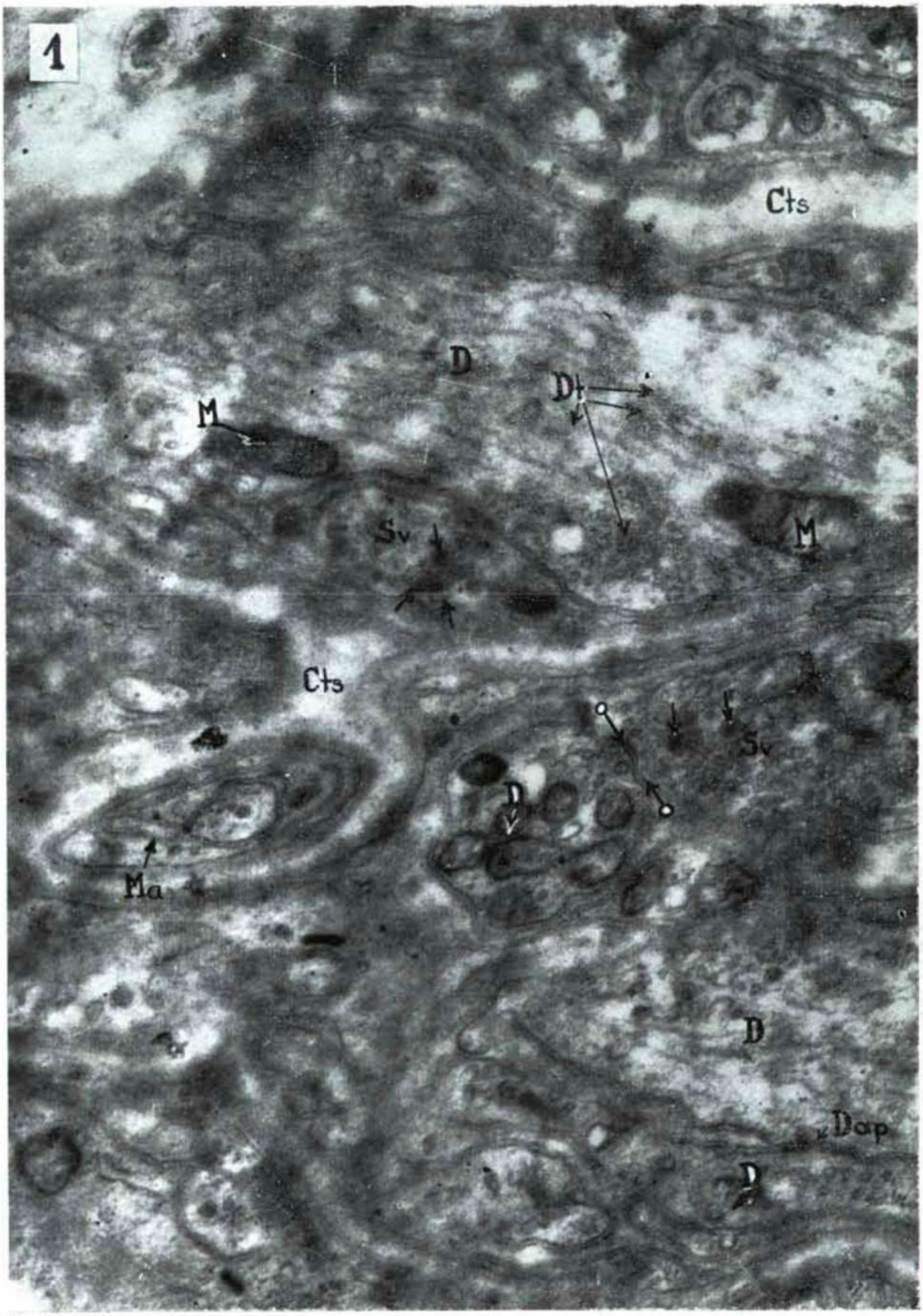

Fig. 2.

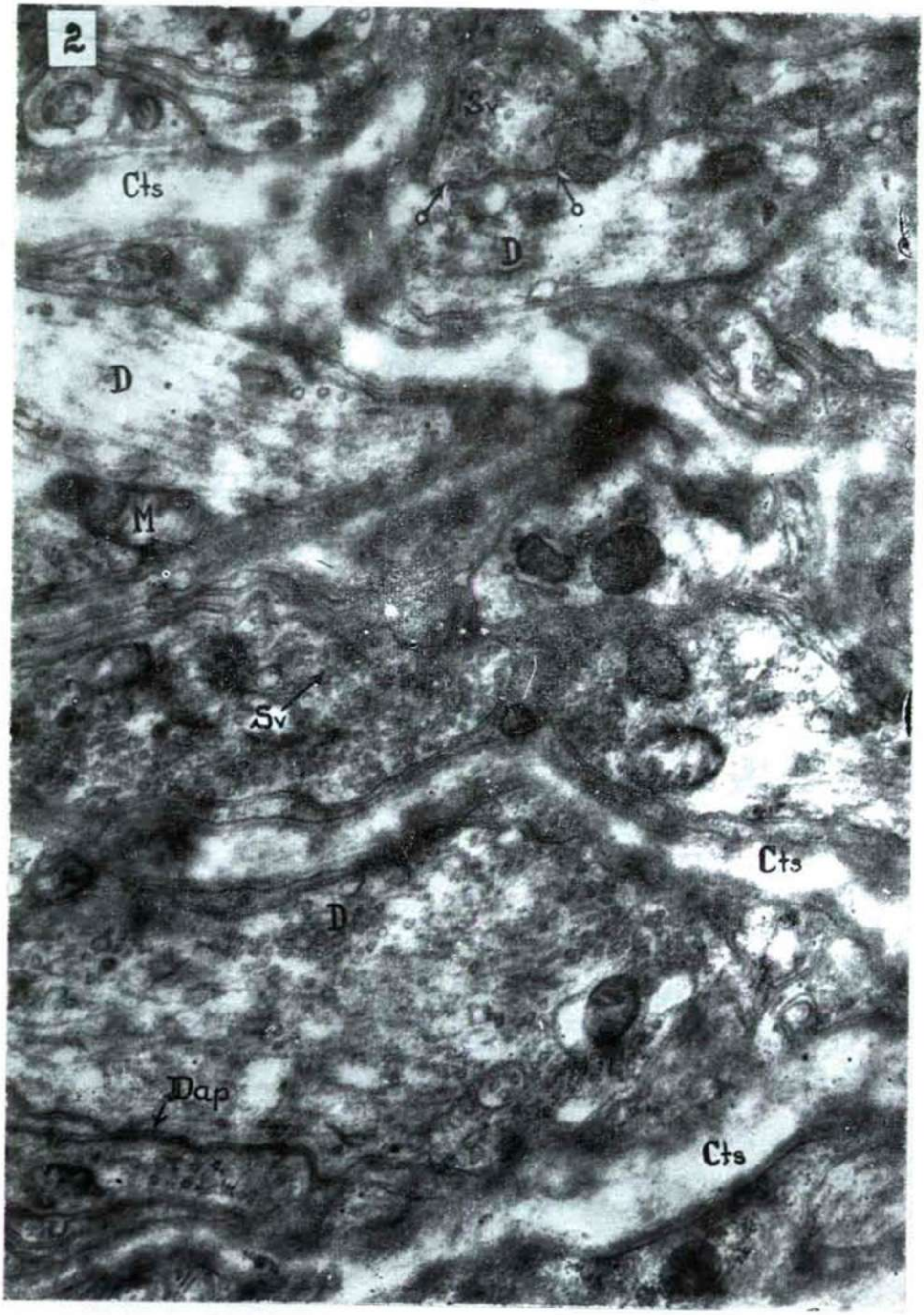

Fig. 3, 4, 5.

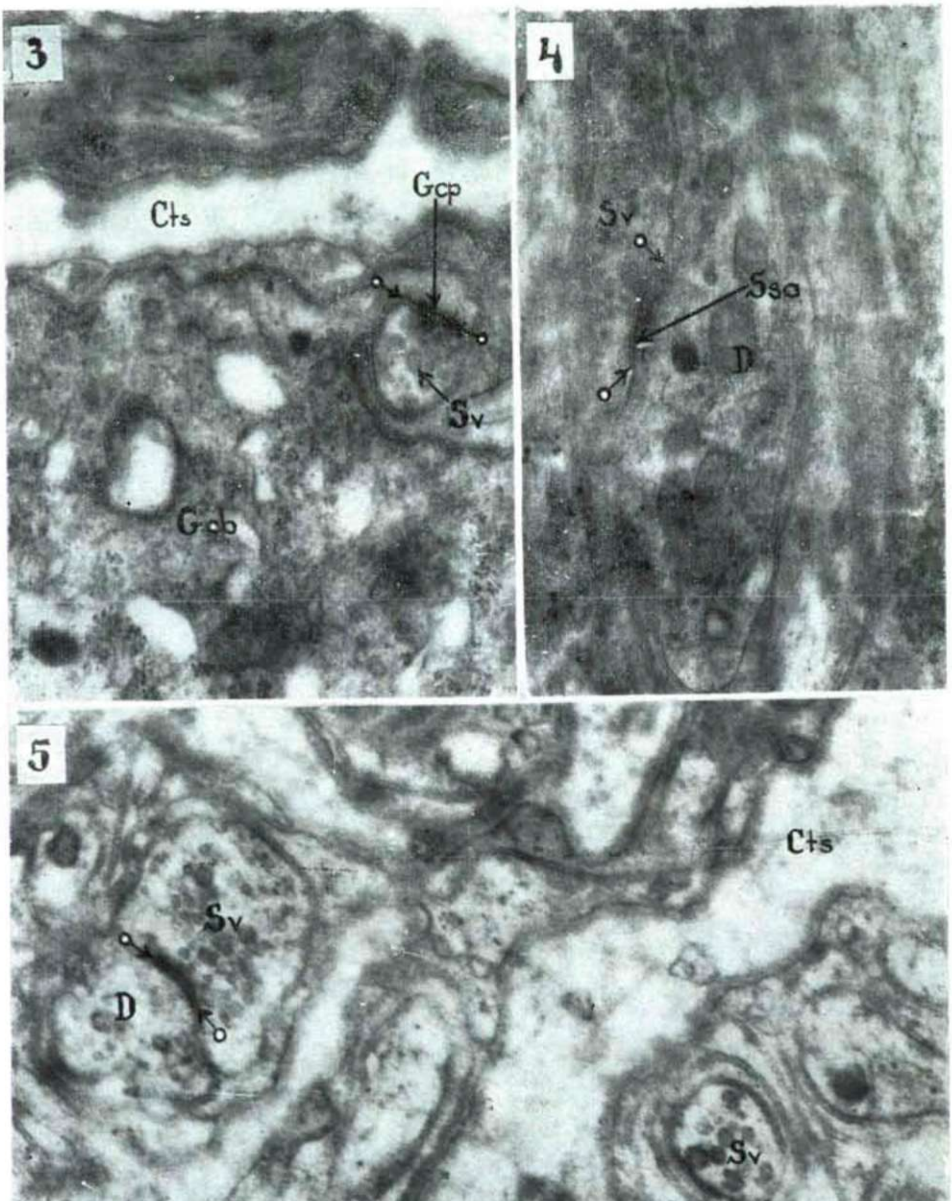

Fig. 6.