# NEURAL UNITS IN THE SUPERIOR CERVICAL GANGLION OF THE GUINEA-PIG

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## SUMMARY

The size and arrangement of the set of neurones innervated by individual preganglionic axons (the neural unit) has been investigated in the superior cervical ganglion of the guinea-pig.

1. Based on the ratio of preganglionic neurones to ganglion cells, and the average number of axons contacting each ganglion cell, we estimated that individual preganglionic axons innervate on the order of 50–200 superior cervical ganglion cells.

2. Of 562 pairs of ganglion cells examined with intracellular recording, forty-seven (8·4 %) were innervated by one or more common axons.

3. Pairs of ganglion cells innervated by the same axon were not necessarily near each other. Although nearby cells were more likely to share innervation than neurones far apart, cells sharing innervation were often found several hundred micrometers apart, and were occasionally separated by the largest dimension of the ganglion (about 1–2 mm).

4. The incidence of cell pairs that shared innervation from *more* than one axon was greater than expected from the frequency of pairs sharing at least one axon.

5. Extracellular recordings from small fascicles of the cervical sympathetic trunk showed that preganglionic axons from different segmental levels intermingle extensively en route to the superior cervical ganglion.

6. Taken together, these findings support the view that sets of ganglion cells are innervated in common not because of any special topographic relationship within the ganglion, but because they share one or more properties that make them especially attractive to particular preganglionic axons.

## INTRODUCTION

Because of its relative simplicity, the mammalian superior cervical ganglion has been studied in detail with the aim of understanding the rules that govern the formation and maintenance of synaptic connexions between nerve cells (see Purves & Lichtman, 1978, for a review).

The adult pattern of superior cervical ganglion cell innervation is selective: neurones which project to particular regions of the post-ganglionic periphery are contacted in a highly organized way by preganglionic axons arising from different

rostro-caudal levels of the spinal cord (Njå & Purves, 1977a; Lichtman, Purves & Yip, 1979; Rubin & Purves, 1980). This arrangement might arise in one of several ways. As in some other parts of the nervous system (the visual system, for example), presynaptic axons might project topographically to post-synaptic cells. The anatomical disposition of pre- and post-synaptic elements would then promote connectivity between appropriate partners. Alternatively, individual post-synaptic cells mixed more or less randomly might have identifying labels that preganglionic axons recognize during synapse formation. A number of experiments support this latter view. First, ganglion cells preferentially innervated by a particular spinal segment are widely distributed within the ganglion (Lichtman et al. 1979); secondly, ganglion cells that project to a particular post-ganglionic target are also distributed (Lichtman et al. 1979); and thirdly, ganglion cells are reinnervated specifically following preganglionic nerve section (Njå & Purves, 1977b, 1978; Purves & Thompson, 1979; Purves, Thompson & Yip, 1981).

In the present work we have examined the size and arrangement of neural units in the guinea-pig superior cervical ganglion, and the arrangement of preganglionic axons in the cervical sympathetic trunk. Our aim in this was to explore further the rules that govern the innervation of mammalian neurones, and, in particular, to examine the arrangement of cells innervated by a single axon. We found no indication within the superior cervical ganglion of a topographical basis of connectivity between synaptic partners; rather our results provide additional support for the recognition of individual ganglion cells by preganglionic axons.

## METHODS

### Anatomical techniques

The preganglionic neurones projecting to the superior cervical ganglion of young adult guinea-pigs (200–350 g) were labelled retrogradely by applying about 0·5 mg of crystalline horseradish peroxidase (HRP, Sigma type VI) to the proximal cut end of the cervical sympathetic trunk of anaesthetized animals (see Rubin & Purves, 1980). Two days later, the animals were re-anaesthetized and perfused through the heart with 0·5 l. oxygenated mammalian Ringer solution, followed by 0·3 l. phosphate-buffered fixative (1 % paraformaldehyde, 2·5 % glutaraldehyde, 4 % sucrose). Spinal segments were identified by the position of dorsal and ventral roots. Frozen blocks of three or four segments were cut horizontally into serial 60 $\mu$m sections; sections were processed using tetramethylbenzidine as the chromagen (De Olmos, Hardy & Heimer, 1978), and counterstained with thionine. Counts of labelled neurones were corrected for split cells (Abercrombie, 1946); the smallest cell fragments counted were approximately 5 $\mu$m in diameter.

### Electrophysiological techniques

The innervation of the guinea-pig superior cervical ganglion was examined in vitro using electrophysiological methods described previously (Purves, 1975; Njå & Purves, 1977a). Briefly, the right superior cervical ganglion was dissected in continuity with the cervical sympathetic trunk and the sympathetic chain attached to the communicating rami and ventral roots (Fig. 1). This isolated preparation was placed in a bath continuously superfused with oxygenated mammalian Ringer fluid at room temperature. The ventral roots of spinal segments C8–T7 were drawn into suction electrodes for individual stimulation and simultaneous intracellular recordings were made from pairs of ganglion cells using two independent micro-electrodes. The separation of the micro-electrodes was measured with an eye-piece graticule. Since these ganglion cells receive synapses on dendrites which radiate from the cell body (McLachlan, 1974; Purves, 1975), this measurement provides only an approximate index of the distance between two cells. Neurones were considered to be innervated by the same axon if: (1) a synaptic response appeared in both cells

at exactly the same stimulus strength, (2) the latency of the response in both cells was the same, and (3) the responses in both cells failed or occurred together when a stimulus just at threshold was presented in at least ten consecutive trials (see Lichtman, 1980). Not every axon innervating one or the other of the impaled cells could be tested in this way. Once one cell of a pair reached threshold, the ensuing action potential could obscure additional synaptic potentials that might have been correlated with inputs to the other cell. Thus we could test only about two thirds of the axons
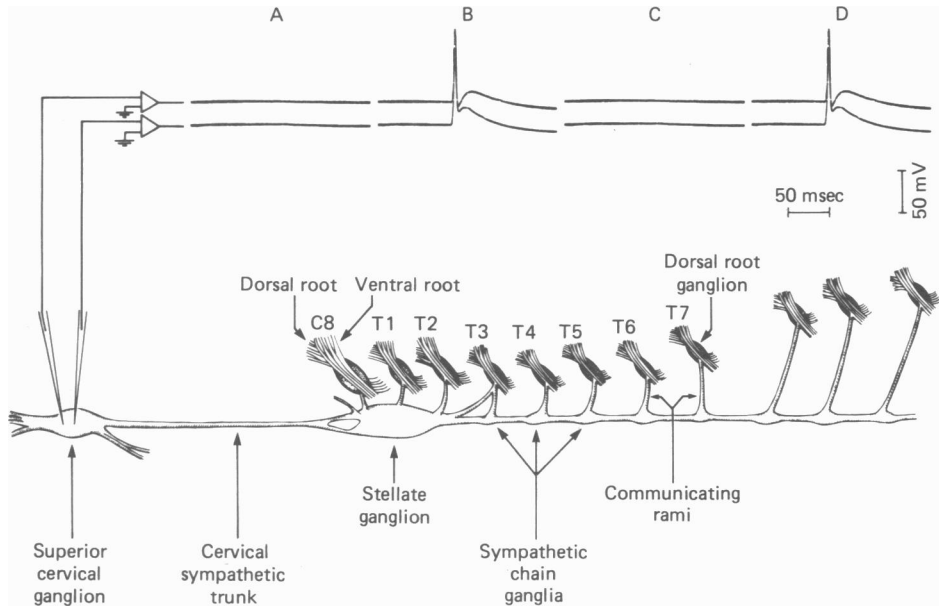


Fig. 1. Diagram of the preparation and the method of recording. The ventral roots of segments C8–T7 were drawn into suction electrodes for individual stimulation whilst pairs of superior cervical ganglion cells were monitored simultaneously with intracellular micro-electrodes. Oscillographic records show responses typical of a cell pair with shared innervation (in this case the shared axon arose from T3). At a stimulus strength just below threshold no synaptic response occurred in either ganglion cell (A). With a slight increase in stimulus intensity, a response with the same latency appeared in both cells (B). When the stimulus was held at threshold levels on repeated trials ($\sim 50 \%$ failures), the responses always failed (C) or appeared (D) together. The same result was obtained when the stimulus polarity was reversed.

that innervated each neurone. All neurone pairs were also examined for synaptic and electrical coupling by alternately depolarizing and hyperpolarizing one of the cells by 50–100 mV while observing the membrane potential of the other.

In a second series of experiments individual fascicles of the cervical sympathetic trunk were teased apart with fine forceps and drawn one at a time into a tightly fitting suction electrode made from a broken glass micro-electrode (tip diameter approximately 50–100 $\mu$m). Extracellular compound action potentials from each fascicle were then recorded whilst stimulating ventral roots C8–T7, and compared with recordings made previously from the major post-ganglionic nerve.

*Ganglion cell number*

The reported number of cells in the superior cervical ganglion of a single species varies widely. In the rat, for example, estimates range from about 13,000 (Hendry & Campbell, 1976; Brooks-

Fournier & Coggeshall, 1981) to more than 50,000 (Gabella, 1976). In the guinea-pig, one study estimated that the superior cervical ganglion contains about 16,000 cells (Purves, 1975) while another estimated a value of about 57,000 cells (Johnson, Gorin, Brandeis & Pearson, 1980). The reason for these discrepancies is primarily that large correction factors based on uncertain assumptions must be applied to raw counts. The actual number of neurones in the ganglion is not especially important in the present work; it is, however, convenient to discuss the neural unit in terms of particular numbers. The smaller values estimated by Purves (1975) seem to us more realistic and will be used here, but it should be noted that the neural unit size may be larger than the value we give.

TABLE 1. Total number of preganglionic neurones labelled in the lower cervical and upper thoracic spinal cord by HRP application to the cervical sympathetic trunk. Values have been corrected for double counting of split cells. (A correction factor of 0·78 was based on a mean cell diameter of 17·3 $\mu$m; $n = 100$).

| | Experiment | | | | | | | | Mean ± S.E. of mean |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Total number of labelled neurones in the spinal cord | 1979 | 1467 | 1550 | 1819 | 1471 | 1284 | 1502 | 1776 | 1606 ± 81 |

<center>RESULTS</center>

<center>*The size of neural units in the superior cervical ganglion*</center>

*(a) Size of the preganglionic cell population*

We estimated the number of preganglionic neurones that project to the superior cervical ganglion by counting retrogradely labelled cells in the spinal cord following HRP application to the cut cervical sympathetic trunk. In agreement with previous work, virtually all the labelled neurones were found ipsilaterally in spinal segments C8–T7 (Dalsgaard & Elfvin, 1979; Rubin & Purves, 1980). Rarely, one or two labelled cells were present in segment T8; none were contralateral to the treated cervical trunk. The corrected number of labelled cells in the spinal cord was about 1600 (Table 1).

This estimate of the preganglionic population is larger and shows less variation than that obtained after injection of HRP solution into the superior cervical ganglion (Dalsgaard & Elfvin, 1979), a method which may rely primarily on uptake by nerve terminals (see Oldfield & McLachlan, 1977). Indeed, one might have expected an even larger population since the cervical sympathetic trunk of the guinea-pig contains two or three times this number of axons (Purves, 1976). The probable explanation of this apparent discrepancy is that the cervical trunk contains sensory and post-ganglionic axons as well as preganglionic fibres (see Lichtman, Purves & Yip, 1980; Brooks-Fournier & Coggeshall, 1981; Bowers & Zigmond, 1981); furthermore, some preganglionic axons probably branch in the cervical trunk before reaching the superior cervical ganglion (Lichtman *et al.* 1980). None the less, it is conceivable that some axons may not have taken up or transported HRP; if so, our cell counts may underestimate the true size of the preganglionic cell population.

*(b) Estimate of neural unit size*

The superior cervical ganglion of the guinea-pig has been estimated to contain about 16,000 neurones (see Methods). The ratio of the number of preganglionic neurones to the number of superior cervical ganglion cells is therefore on the order of 1/10. If each ganglion cell were innervated by a single axon, then each preganglionic axon would contact an average of ten cells. However, superior cervical ganglion cells are, on average, innervated by about twelve separate axons (Njå & Purves, 1977 *a*, *b*). Therefore a preganglionic neurone on average innervates $10 \times 12$ or about 120 ganglion cells in the superior cervical ganglion. By analogy with the motor unit of muscle innervation, we refer to this group of cells as the neural unit, even though the relationship between an axon and the cells comprising the neural unit is not exclusive; in contrast to adult mammalian skeletal muscle fibres, each superior cervical ganglion cell belongs to a number of different neural units (see below).

The entire set of neurones innervated by any one preganglionic axon must often be larger than the neural unit size estimated *within* the superior cervical ganglion. Many of the preganglionic axons that reach the superior cervical ganglion have branches that also innervate cells in more caudal ganglia of the sympathetic chain (Lichtman *et al.* 1980). Furthermore, some preganglionic axons traverse the ganglion and continue in the post-ganglionic nerve, presumably to innervate neurones along the post-ganglionic route (Perri, Sacchi & Casella, 1970; Purves, 1975).

*(c) The size of neural units innervated by preganglionic axons arising from different spinal levels*

Different thoracic segments contribute characteristically different numbers of preganglionic axons to the superior cervical ganglion (Njå & Purves, 1977 *a*; Dalsgaard & Elfvin, 1979; Rubin & Purves, 1980; see also Rando, Bowers & Zigmond, 1981). We therefore wished to know whether preganglionic axons arising from different levels of the spinal cord innervate different numbers of cells in the superior cervical ganglion. Accordingly, we estimated the size of the preganglionic cell population within each segment (Table 2) and used these numbers to calculate, for each segment, the average number of ganglion cells innervated by individual axons. To make this estimate, the approximate number of ganglion cells innervated by various segments was determined from the proportion of ganglion cells innervated by each ventral root (Njå & Purves, 1977 *a*, *b*) and a total ganglion cell number of 16,000. This value was then multiplied by the mean number of axons from each segment contacting individual ganglion cells (Njå & Purves, 1977 *a*, *b*) and divided by the values in Table 2 to give the estimated neural unit size (Table 3). By this calculation the neural units associated with axons arising from the most caudal segments that innervate the ganglion (T5–T7) were 2–4 times larger on average than the neural units of axons arising from the most rostral segments (C8–T2).

*The arrangement of ganglion cells innervated by the same preganglionic axon*

To assess the disposition of neurones innervated by the same axon we impaled 562 pairs of neurones in sixty-six ganglia. For each of these cell pairs, we first elicited action potentials in one cell whilst observing the membrane potential of the other.

In no case was a synaptic response observed; neither was there any evidence of electrical coupling between neurones (see Methods). In confirmation of an earlier study which examined this question in a different way (Purves, 1976), we conclude that there are few connexions between these ganglion cells under normal circumstances. Thus the vast majority of synaptic responses observed were elicited directly by preganglionic axons.

TABLE 2. Mean number of HRP-labelled preganglionic neurones in each of the spinal segments projecting to the guinea-pig superior cervical ganglion. Values have been corrected for double counts of split cells and are given $\pm$ the s.e. of the means ($n = 8$)

| | Spinal segment | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | C7 | C8 | T1 | T2 | T3 | T4 | T5 | T6 | T7 | T8 |
| Number of | 0 | 24 | 268 | 466 | 438 | 246 | 110 | 43 | 12 | < 1 |
| preganglionic | — | ±8 | ±39 | ±23 | ±39 | ±33 | ±24 | ±10 | ±3 | — |
| neurones | | | | | | | | | | |

TABLE 3. Calculated neural unit size in the superior cervical ganglion for preganglionic axons arising from different spinal cord segments

| | Segment of origin | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | C8 | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
| Average number of superior cervical ganglion cells innervated by individual preganglionic axons | 44 | 89 | 90 | 98 | 139 | 188 | 212 | 184 |

Synaptic responses to preganglionic stimulation showed that forty-seven of these pairs of ganglion cells (8·4 %) were innervated by at least one common axon. The cell bodies of the pairs of neurones that shared innervation were not necessarily close to one another, and were often widely separated (Fig. 2). Indeed, nearby neurones generally were not innervated by a common axon (see also Lichtman, 1980; Hume & Purves, 1982). However, the probability of finding two cells that shared one or more axons did increase somewhat with smaller electrode separations. For example, thirty-one of 275 (11·3 %) pairs of cells separated by less than 500 $\mu$m shared one or more axons, while sixteen of 287 (5·6 %) pairs separated by more than 500 $\mu$m had detectable innervation in common (Fig. 2). Thus although the cells that make up a neural unit are widely distributed, they are probably not evenly dispersed throughout the ganglion (see also Hume & Purves, 1982).

Since most of the axons innervating a pair of ganglion cells were *not* shared, the members of a typical neural unit also participate in a large number of other units (recall that each ganglion cell is innervated by about twelve axons on average: Njå & Purves, 1977a, b). Finally, the degree of sharing we observed is consistent with our anatomical estimate of neural unit size.

*Ganglion cells that shared innervation from more than one axon*

Some pairs of ganglion cells shared innervation from more than one axon. Based on the incidence of pairs that shared at least one axon (forty-seven pairs or 8·4 %), by chance one would expect about four instances of double sharing in our sample (8·4 % × 47). However, we found that seventeen pairs had at least two axons in common, or greater than four times that expected by chance. Moreover, one pair of
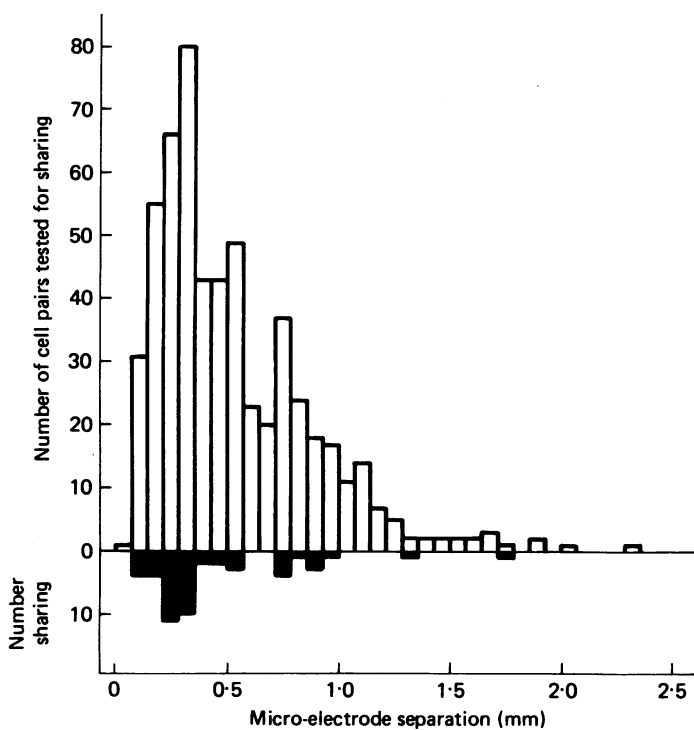


Fig. 2. Incidence of ganglion cell innervation by a common axon as a function of the separation between 562 pairs of superior cervical ganglion cells monitored simultaneously during preganglionic stimulation. The numbers of pairs that shared one or more inputs have been redrawn below the horizontal axis and shaded.

ganglion cells shared three axons, and another pair four. If sharing were random, the probability of finding a pair of cells in this sample that shared three axons would be on the order of 0·0006 (about one in 1600 pairs), and that of finding four shared axons would be about 0·00005 (about one in 20,000 pairs). Thus ganglion cell pairs that share one axon have an increased probability of sharing others.

*The arrangement of preganglionic axons within the cervical sympathetic trunk*

The guinea-pig cervical sympathetic trunk is made up of a number of discrete fascicles, five to ten of which can usually be teased apart under the dissecting microscope. To determine the segmental origin of the axons comprising each fascicle

we recorded extracellular compound action potentials from individual fascicles whilst stimulating ventral roots C8–T7 in turn (see Methods). In each of the fascicles studied (a total of fifteen fascicles in three animals) a compound action potential could be recorded in response to stimulation of ventral roots T1–T6. The relative sizes of the potentials recorded from individual fascicles for the most part mirrored the over-all
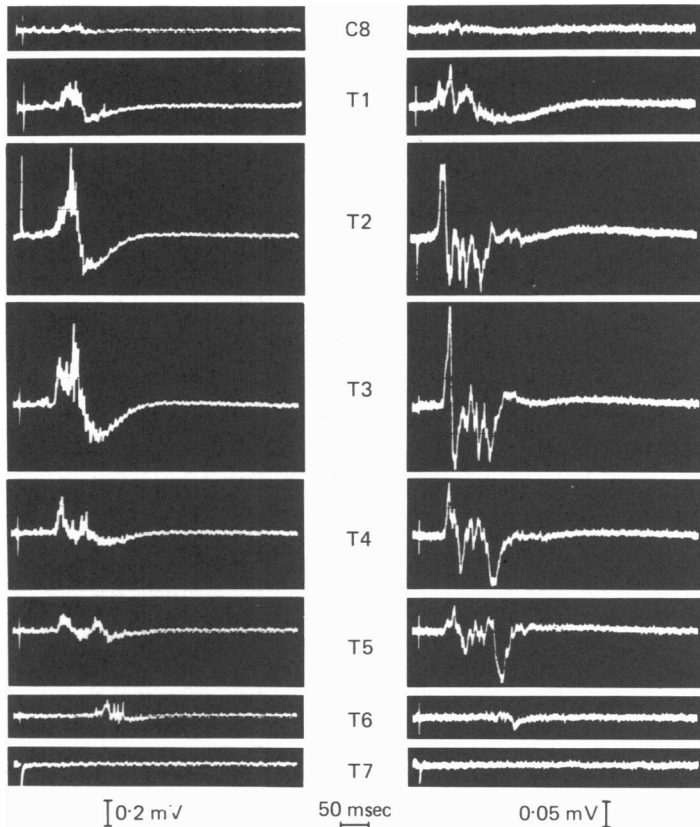


Fig. 3. Extracellular recordings from a small fascicle of the cervical sympathetic trunk (left) compared with recordings made earlier from the major post-ganglionic nerve in the same preparation (right). The ventral root stimulated is indicated between the two columns. The fact that small bundles of preganglionic fibres show responses proportional to those elicited in the post-ganglionic nerve indicates that axons arising from different segments intermingle extensively in the cervical sympathetic trunk.

pattern of segmental innervation to the ganglion (Fig. 3). Thus axons from all the spinal segments that contribute innervation to the superior cervical ganglion intermingle extensively within the preganglionic trunk (see also Maehlen & Njå, 1981).

### DISCUSSION

Previous studies of the superior cervical ganglion have suggested that the selective innervation of ganglion cells by preganglionic axons is based largely on cell

recognition rather than anatomical (topographical) considerations (see Introduction). In the present work we have addressed this issue from the vantage point of neural unit organization in the superior cervical ganglion, and the arrangement of axons arising from different spinal segments in the preganglionic trunk.

Three results reported here provide further evidence of cell–cell recognition in this system. First, axons arising from different spinal segments intermingle extensively within the cervical sympathetic trunk, indicating that they do not retain any particular order en route to the ganglion. Secondly, the many ganglion cells innervated by a preganglionic axon are widely distributed in the ganglion. The arrangement of the cells comprising these neural units is thus similar to the arrangement of motor units in mammalian skeletal muscle (Burke & Tsairis, 1973; Burke, Levine, Salcman & Tsairis, 1974) and of neural units in parasympathetic ganglia (Lichtman, 1980; Hume & Purves, 1982). As we measured only the separation of ganglion cell bodies we have not ruled out the possibility that the dendrites of the cells comprising a neural unit converge upon a region of the ganglion to which a particular axon confines its terminal arborization. We consider this unlikely as the dendrites of these ganglion cells radiate from the cell soma and are not very long (usually less than 200 $\mu$m) (McLachlan, 1974; see also Purves, 1975). Thirdly, a pair of cells holding at least one axon in common showed an increased probability of sharing additional axons. The simplest interpretation of the degree of multiple sharing we observed is that the members of a neural unit have properties in common that make them particularly attractive to the same set of preganglionic axons. Taken together with the outcome of previous experiments on the superior cervical ganglion (see Introduction), these results argue for individual cell recognition as the basis of the selective innervation evident in this part of the nervous system.

It is important to point out that these findings do not rule out some form of topographical ordering in the peripheral autonomic system. On the contrary, from a broader perspective, the systematic innervation of different sympathetic chain ganglia by preganglionic axons arising from various spinal segments (Lichtman *et al.* 1980) seems a straightforward example of the topographic mapping of a set of presynaptic axons onto a post-synaptic set. However, at a finer level of resolution (i.e., within a particular ganglion), innervation appears to be biased by the individual qualities of the available synaptic partners rather than their anatomical arrangement. Perhaps this is a general feature of neuronal innervation.

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