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CONNEXIONS BETWEEN HAIR FOLLICLE AFFERENT FIBRES AND SPINOCERVICAL TRACT NEURONES IN THE CAT: THE SYNTHESIS OF RECEPTIVE FIELDS

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SUMMARY

1. Relationships between the terminal arborizations of hair follicle afferent fibres and dendritic trees of spinocervical tract (s.c.t.) neurones were studied using intra-axonal and intracellular injections of horseradish peroxidase in chloralose-anaesthetized, paralysed cats.

2. Seventeen afferent-neurone pairs were successfully stained and their receptive fields determined. Ten of the pairs had s.c.t. neurones with a field containing that of the hair follicle afferent and seven pairs had separate fields on the hind limb.

3. Where the afferent fibre's field was outside the neurone's field there were no indications of synaptic contacts between the two neuronal elements.

4. Synaptic contacts were always observed (at the light microscope level) for the ten pairs with the hair afferent's receptive field contained within the s.c.t. cell's field. Contacts were always made by the branches of only a single collateral from the hair follicle afferent fibre. The numbers and locations of synaptic contacts were related to the relative positions of the receptive field: where the hair follicle afferent's field was centrally placed there were many (forty to sixty) contacts on proximal dendrites; where the hair follicle afferent's field was peripherally placed in the s.c.t. cell's receptive field there were few contacts (two to thirteen) and these were peripherally placed on the dendritic tree. Where the primary afferent fibre had a centrally placed field contacts upon dendritic spines were observed.

5. The results are discussed in terms of the synthesis of receptive fields and the organization of neuronal connexions within the mammalian spinal cord.

INTRODUCTION

The receptive field of a central sensory neurone consists of component parts. Each part is the field of either another neurone (interneurone) or of a primary afferent fibre. At present little is known about the rules governing convergence onto central neurones for the organization of their receptive fields. Yet this sort of organization must reflect fundamental principles of neurobiology. The present paper represents an attempt to demonstrate the operation of some of these principles.

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The system chosen for study was the spinocervical tract (s.c.t.) together with its input from hair follicle afferent fibres. This input is known to be, at least in part, monosynaptic and represents the major excitatory input to s.c.t. cells, and probably the only input from axons conducting faster than Aδ fibres (see Brown, 1973). No obvious subliminal fringe has been demonstrated for s.c.t. cells (Wall, 1960; Brown, 1971) and the question can be asked 'How do connexions made from hair follicle afferents from the centre of the cell's field differ from those made by axons from the periphery?'. There may be differences in the positions and numbers of synapses according to the location of the primary afferent's receptive field. But the absence of a subliminal fringe might be expected to lead to a more or less even distribution of synapses from individual afferent fibres, irrespective of the location of their receptive fields. Hongo & Koike (1975) have suggested, however, on the basis of intracellular recordings from s.c.t. cells, coupled with graded electrical stimulation within the cells' receptive fields, that afferent fibres from the centre of a s.c.t. cell's receptive field have synaptic contacts on the soma and proximal dendrites whereas fibres from the periphery of the field make contact with distal dendrites.

Intracellular ionophoresis of the enzyme horseradish peroxidase (HRP) allows a direct attack on these sorts of problems. Single hair follicle axons may be injected near their entry into the spinal cord and, in the same experiment, single s.c.t. cells may also be filled with the enzyme. Subsequent histochemistry allows the injected pair of elements to be visualized and examined for the location and density of any synaptic contacts between them. At the same time other questions may be answered, e.g. 'Are contacts made only by a single collateral on each central neurone (as appears to be the case with Ia muscle afferent fibres and α-motoneurones (Brown & Fyffe, 1981*a*), or may more than one collateral from a single axon make contacts with a single neurone? Are contacts made on one or two major dendrites or are they spaced out over the dendritic tree? Are contacts made on dendritic spines?' Answers to these sorts of questions are important for setting up hypotheses about the neuronal organizations of the spinal cord and the central nervous system in general.

A preliminary communication of the present work has been published (Brown & Noble, 1979; see also Brown, 1981).

METHODS

The experiments were performed on young adult cats anaesthetized with chloralose (70 mg kg^{-1}), after induction with halothane in an oxygen:nitrous oxide mixture, and paralysed with gallamine triethiodide. Carotid arterial blood pressure, end-tidal CO_2 and rectal temperature were monitored and kept within normal limits; the bladder was catheterized and kept empty. The state of anaesthesia was checked throughout the experiment by examination of the blood pressure record and the degree of constriction of the pupils. The animals were allowed to recover from the effects of gallamine from time to time and checked for the presence of flexion reflexes. Additional doses of chloralose (30 mg kg^{-1}) were given if required.

Glass micro-electrodes filled with a solution of HRP were used to record from and make intracellular injections into both hair follicle afferent fibres and s.c.t. neurones (for details of methods see: Snow, Rose & Brown, 1976; Brown, Rose & Snow, 1977*a*, *b*). Usually the hair follicle axon was injected first and then the lumbosacral spinal cord, close to the site of injection, was searched for a s.c.t. neurone with a receptive field that contained the field of the hair follicle afferent. In some experiments s.c.t neurones with fields adjacent to the primary afferent's field were injected and in a few other experiments s.c.t cells with fields separated from the axon's field were injected.

Sections of spinal cord were cut at 100 μm in either the transverse or parasagittal planes, treated for the histochemical demonstration of HRP (Hanker, Yates, Metz & Rustioni, 1977) and examined with the light microscope. Reconstructions were made with the aid of a camera lucida.

RESULTS

Ten hair follicle afferent fibre-s.c.t neurone pairs, in which the neurone's receptive field contained that of the axon, were stained successfully. Although initially our aim had been to examine pairs of this type we also stained seven pairs in which the primary afferent's field was outside that of the s.c.t. cell. This latter group of stained pairs of elements provided supplementary data to that of the former group and also allowed us to address other problems of spinal cord organization, such as the positional relationships of hair follicle afferent terminal arborizations and s.c.t. dendrites and also the problem of the possible occurrence of 'silent synapses' (see the Discussion). The results for stained pairs with separate receptive fields will be presented first.

Relationships where the hair follicle afferent fibre and the s.c.t cell had receptive fields on separate areas of skin

In all seven afferent-neurone pairs where the two receptive fields were on separate areas of skin there was no evidence of synaptic connexions between them. Fig. 1 shows the relative positions in the transverse plane of hair follicle afferent terminal arborizations and s.c.t. cell dendritic trees for three stained pairs where their receptive fields were well separated from each other along the longitudinal axis of the hind limb. The axon's field was, in each case, distal to the s.c.t. neurone's field and for two pairs in line with it on the limb. In all these pairs the terminal arborization of the afferent fibre was medial to the dendritic tree of the neurone. Between the arborization and the dendritic tree there was a region of dorsal horn grey matter that contained neither element. Where the two receptive fields were much closer to one another, then the hair follicle afferent arborization and the s.c.t. neurone's dendritic tree could be closer together also. Careful examination of the histological material, however, failed to find any suggestions of synaptic contact between them.

Relationships where the receptive field of the hair follicle afferent fibre was contained within that of the s.c.t. cell

We were successful in staining ten afferent-neurone pairs where the receptive field of the s.c.t. cell contained the field of the primary afferent fibre. In each pair synaptic contacts could always be observed between them; criteria for synaptic contact were similar to those used previously (Brown & Fyffe, 1981*a*) and included the presence of a bouton on the terminal axonal arborization and no evidence of a gap (at the level of light microscopy) between the bouton and the neurone's dendrite or soma.

Relative positions of the afferent arborizations and the dendritic trees

Hair follicle afferent fibres form longitudinal columns of terminal arborizations that run in the sagittal plane of the cord. These columns are some 150–400 μm in width (Brown *et al.* 1977*a*). S.c.t. neurones have dendritic trees that are about 200–

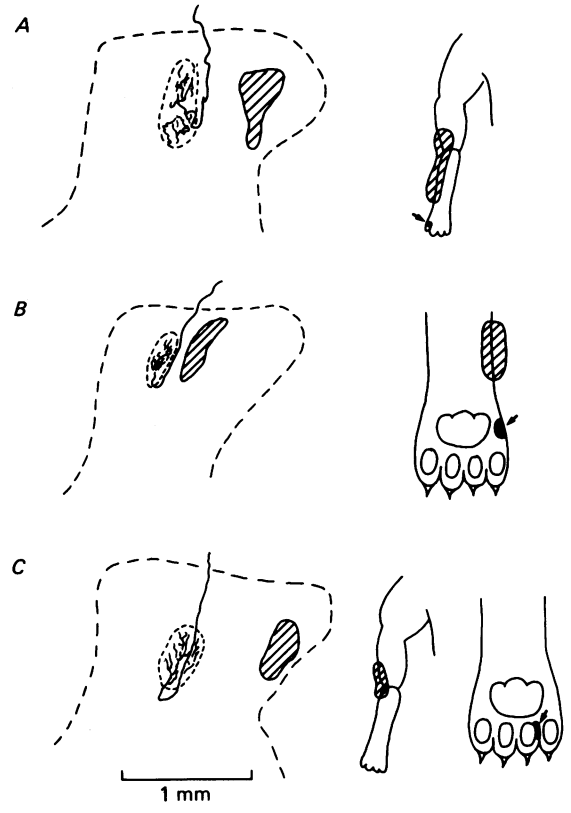

Fig. 1. Relative positions of hair follicle afferent terminal arborizations and s.c.t. neurone dendritic trees where there was no receptive field overlap. Each Figure shows, on the left, the positions of the afferent arborization and the dendritic tree (cross-hatched) as seen in a transverse view of the dorsal horn (medial to the left) and, on the right, the positions of the receptive fields with the afferent's field (filled in black and arrowed) and the s.c.t. neurone's field (cross-hatched). In each pair the hair follicle afferent termination is medial to the s.c.t. neurone and the afferent's receptive field is distal to that of the cell.

550 μm in transverse extent (Brown *et al.* 1977*b*). It is, therefore, pertinent to enquire whether this similarity leads to the two elements always being in register in the transverse plane when the s.c.t. cell's field contains that of the afferent fibre. For none of the ten pairs was there coincidence between the positions of the axons's arborization and the cell's dendritic tree; there was always overlap between the two but part of the bouton-carrying terminal axonal arborization always occupied a region of the dorsal horn free from dendrites of the cell. In some pairs the major part of the axon's arborization was well outside the region where the dendrites ramified (as viewed in transverse sections of the cord; see Fig. 5). In these cases the receptive field of the afferent fibre was at the periphery of the s.c.t. cell's field (see below).

Numbers of collaterals from a single axon distributed to each cell

In each of the ten stained hair follicle afferent fibre–s.c.t. cell pairs in which contacts were observed it was possible to determine how many collaterals from each axon

provided the synaptic boutons making the contact. In all ten examples the contacts were made by boutons carried by a single collateral. Even where more than one collateral had branches interdigitating with the cell's dendritic tree only the branches of one made contact.

Contacts between hair follicle afferent fibres and s.c.t. cells

As mentioned above, presumed contacts were only included if they consisted of a bouton-like swelling on the hair follicle afferent collateral that, under light microscopic examination, appeared to touch the soma or a dendrite of the s.c.t. neurone. Even if the presumed contact was not a true synaptic connexion, and only electron microscopical examination would provide more conclusive information, it is likely that our estimates of contacts under-represent the true numbers. This is because of the difficulties of identifying such contacts due to lack of visual contrast in material where the two elements are stained in the same manner. The problem was particularly acute where stained axonal arborizations ramified over the soma or large proximal dendrites of a neurone. In this situation it was not possible to differentiate the two elements and undoubtedly some contacts will have been missed. This latter situation, however, was only present where the axon's receptive field was centrally placed in the neurone's and, as will be seen below, there were clear-cut differences according to the relative positions of the two fields even without taking into account any possible underestimation due to the difficulties outlined above.

Numbers and positions of synaptic contacts. The numbers and positions of synaptic contacts between hair follicle afferent fibres and s.c.t. neurones varied according to the relative position of the afferent's field in that of the s.c.t. cell. These extreme examples were where the afferent's field was either at or close to the geometrical centre of the cell's field compared with where it was located in the periphery of the cell's field. These extreme cases will be described in detail.

When the receptive field of the hair follicle afferent fibre was at or near the centre of the s.c.t. cell's field there were many contacts between them and they were located on proximal parts of the dendritic tree. Figs. 2, 3, and 4 and Pls. 1 and 2 show some of these contacts in two axon-neurone pairs of this type. There were at least forty contacts in the pair of Figs. 2 and 3 and at least sixty for that of Fig. 4.

For the pair shown in Figs. 2 and 3 and Pl. 1 *A* and *B* the neurone's receptive field was on the plantar surface of toes 2 and 3 and the hair follicle afferent had its field at the centre of this area between the two toes. This s.c.t. cell had well developed ventrally directed dendrites and it was onto two of these and their branches that the majority of contacts were made (Fig. 3 *B* and Pl. 1). There was also a cluster of ten contacts on a dorsally directed dendrite and its two second order branches (Fig. 3 *A*). All the contacts were located on the proximal parts of the dendritic tree, from between 20 and 30 μm of the soma to about 200 μm from it. Contacts were made on dendrites of the first to fourth order.

The hair follicle afferent-s.c.t. neurone pair shown in Fig. 4 and Pl. 2 *A* and *B* also had the afferent's field centrally located in that of the s.c.t. cell. The cell's field was on the dorsal and ventral surfaces of the lateral two toes and adjacent parts of the foot; the afferent's field was very close to the geometrical centre of this area. The sixty or so contacts observed between these two members of the pair were spread rather

more widely over the dendritic tree than in the previously described pair. The cell had eleven primary dendrites and contacts were made on five of these and their branches; on four dendrites directed dorsally and caudally and on one ventrally directed dendrite. The contacts were located on dendrites of the first to the sixth order at distances from about 30 μm to 500 μm from the soma.

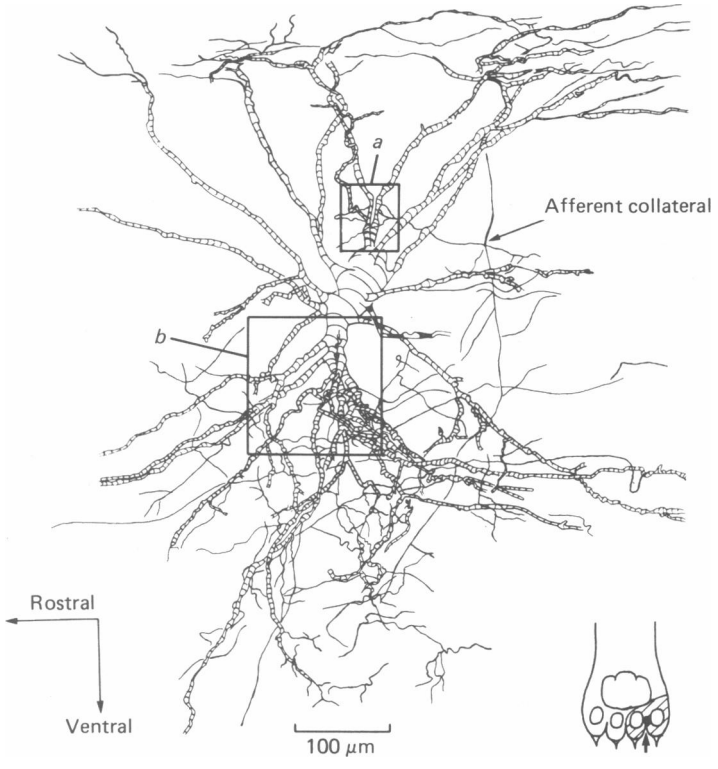

Fig. 2. Reconstruction, from serial sagittal sections, of a s.c.t. neurone and part of a hair follicle afferent fibre collateral from which it received contacts. Most of the contacts (over forty) were made in the regions included in boxes *a* and *b* (see Fig. 3). The receptive fields are shown at the lower right of the figure and it can be seen that the afferent's field (black) was centrally placed in the neurone's field (hatched).

When the hair follicle afferent fibre had its receptive field at the periphery of the s.c.t. cell's field there were far fewer contacts between the pair and these contacts were further out on the dendritic tree. Examples of three pairs are shown in Figs. 5, 6 and 7. For the pair in Fig. 5 the s.c.t. cell had a field on the lateral distal leg and proximal foot and the hair follicle afferent's field was at the most distal part of this area, touching its very perimeter. The terminal arborization of the axon's collaterals was medial and slightly ventral to the dendritic tree of the neurone (the neurone was quite dorsally located). Very few axonal branches intermingled with the cell's dendrites. Five contacts were observed, however, two on the rostral half of the cell and three on its caudal half (arrows in Fig. 5). The contacts were on second to fourth order dendrites, each from a different primary dendrite, at distances of 200–800 μm from the soma.

The pair shown in Fig. 6 had receptive fields on the third and fourth toes and the hair follicle field was at the periphery of the cell's field, again touching its perimeter. Seven contacts were observed between these two neuronal elements. The contacts were on the second to fourth order branches of four primary dendrites at distances of 200 to about 850 μm from the soma.

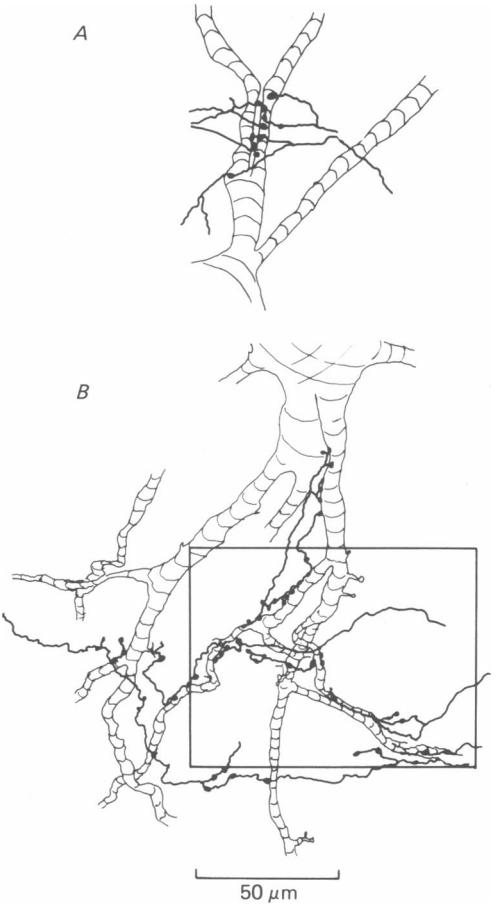

Fig. 3. Detailed reconstruction of the arrangement of synaptic contacts from a hair follicle afferent fibre upon the dendrites of a s.c.t. neurone. This Figure shows drawings made at high power (× 1000 under oil) of the two boxed areas indicated in Fig. 2. Contacts are made on proximal dendrites and many are of the 'en passant' variety. The boxed area in *B* is shown in Pl. 1*A*.

Fig. 7 shows a third pair where the hair follicle afferent fibre had its receptive field peripherally located in the s.c.t. cell's field. Again there were few contacts (thirteen; box and arrows in Fig. 7) which were clustered at three sites on different dendritic systems at about 300–600 μm from the soma.

Types and arrangements of synaptic contacts between hair follicle afferents and s.c.t. cells. Both 'climbing' and 'crossing over' types of synaptic contacts were observed. The 'climbing' type of contact, where a series of boutons *en passant* makes contact along the length of a segment of dendrite, was the most common. It was extremely

common in pairs where the hair follicle afferent's field was centrally placed in the s.c.t. cell's field. As many as seven boutons on a single fine branch of collateral terminal arborization could be arranged along as little as 25 μm of dendritic segment with other runs of boutons *en passant* in close proximity (Fig. 3*B*, and Pl. 1*A*). 'Crossing over' type contacts were much less common.

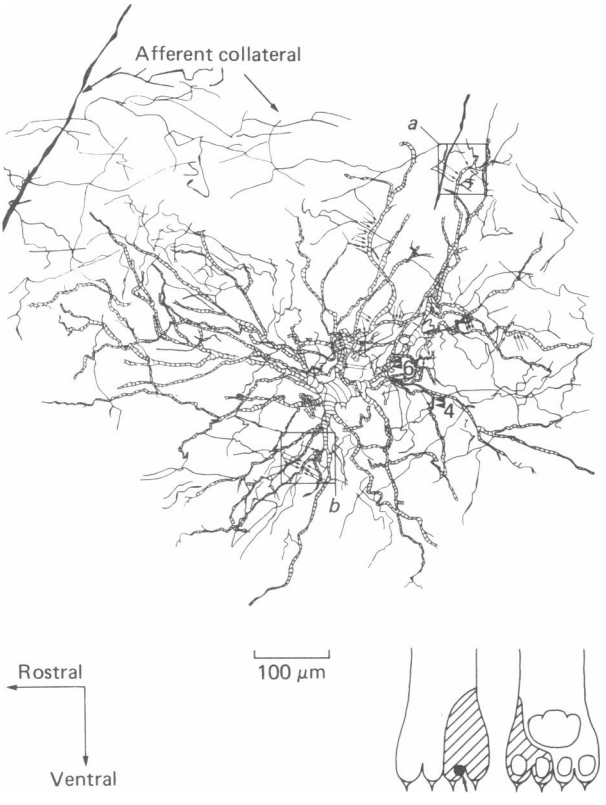

Fig. 4. Reconstruction, from serial sagittal sections, of another hair follicle afferent – s.c.t. neurone pair where the afferent's receptive field was centrally located in the neurone's field. Only part of the hair follicle afferent collateral has been drawn. Over sixty contacts were observed; the positions of many have been arrowed in the Figure (large arrow heads indicate a cluster of boutons; the number of contacts are indicated). The boxed areas *a* and *b* are shown in Pl. 2. The receptive fields are shown at the bottom right; conventions as in Fig. 2.

An unusual, but not infrequent, type of 'climbing' contact series is shown in Pl. 2*C*. Here, although a single axon branch gave rise to a series of boutons running along the length of a dendritic segment in true 'climbing' fashion, the boutons were not arranged *en passant* along the axon. Instead, each bouton was of the terminal type and was borne on a short branch or stalk given off from the axon, producing a 'ladder-like' effect.

Where the hair follicle afferent's receptive field was peripherally located in that of the s.c.t. cell, synaptic contacts were often single and isolated from other contacts between the members of the pair (Figs. 5 and 6). But also in this situation, there were small groups of two to four boutons close together on a dendrite (Fig. 7).

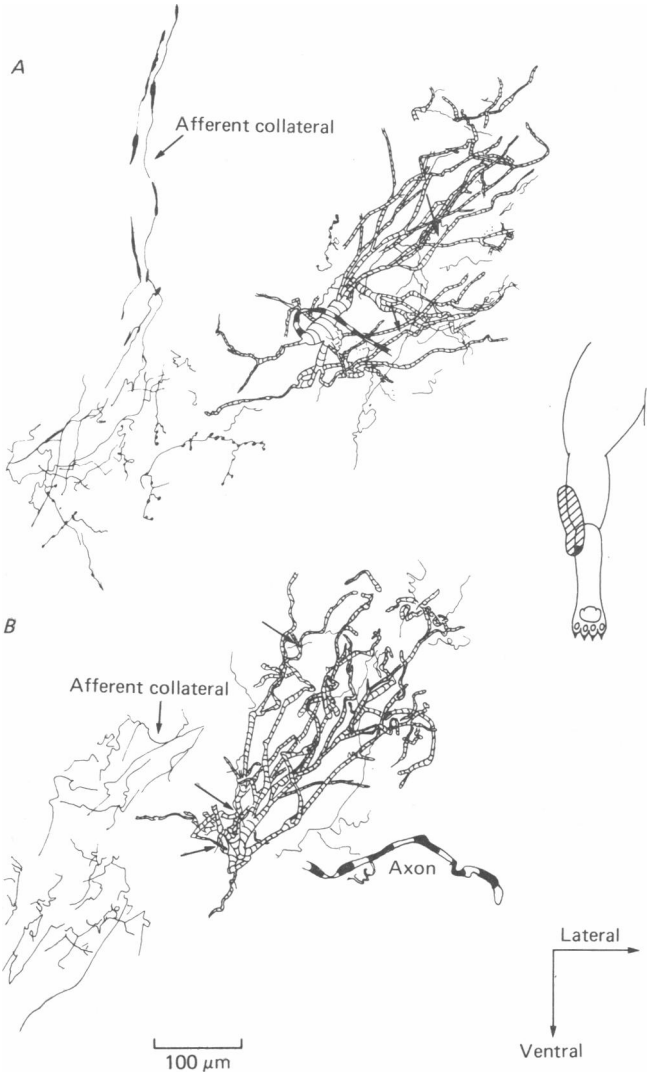

Fig. 5. Reconstruction, from serial transverse sections, of a s.c.t. neurone and hair follicle afferent fibre collateral where the afferent's field was located peripherally in the neurone's field. One half of the cell, and its associated collateral arborization, is shown in each of *A* and *B*. Only five contacts were observed and their positions are indicated by arrows. The receptive fields are shown on the right hand side; conventions as in Fig. 2.

S.c.t. neurones are often well endowed with dendritic spines (Brown *et al.* 1977*a*) and it is pertinent to ask whether hair follicle afferent fibres have synaptic contacts with spines. Spine contacts were, indeed, observed and the synaptic bouton formed a cap over the spine head in some instances (Pl. 1*A*). Contacts upon spines formed, however, a small minority of the total number of contacts between hair follicle afferent fibres and s.c.t. neurones; they made up about 5 % of contacts where the hair follicle afferent's field was central and were not observed in pairs where the hair follicle afferent's field was peripheral in the s.c.t. cell's field.

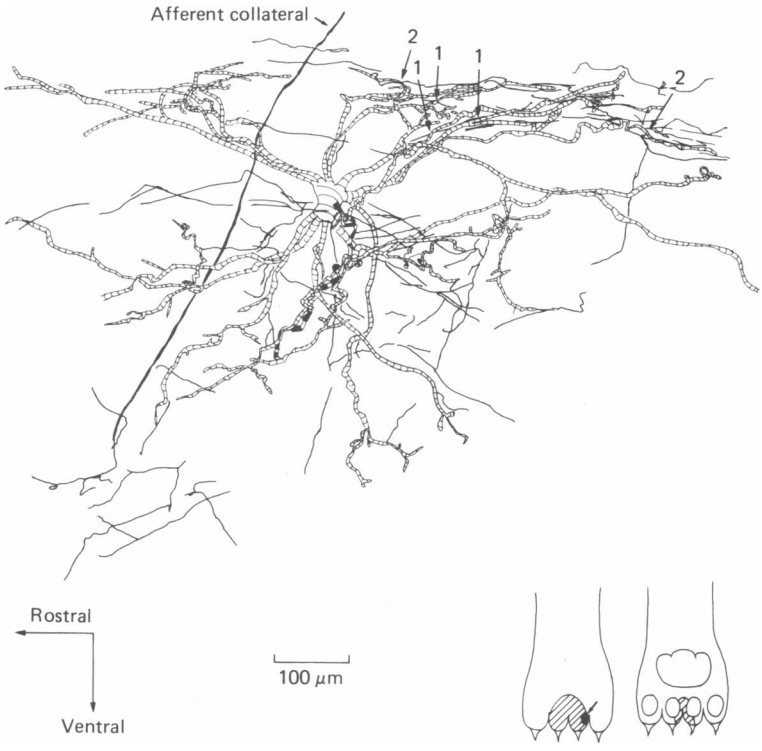

Fig. 6. Reconstruction, from serial sagittal sections, of a s.c.t. neurone and part of a hair follicle afferent collateral where the afferent's receptive field was peripherally located in the neurone's field. Seven contacts were observed (arrows and numbers) on second to fourth order dendrites. The receptive fields are shown at the bottom right; conventions as in Fig. 2.

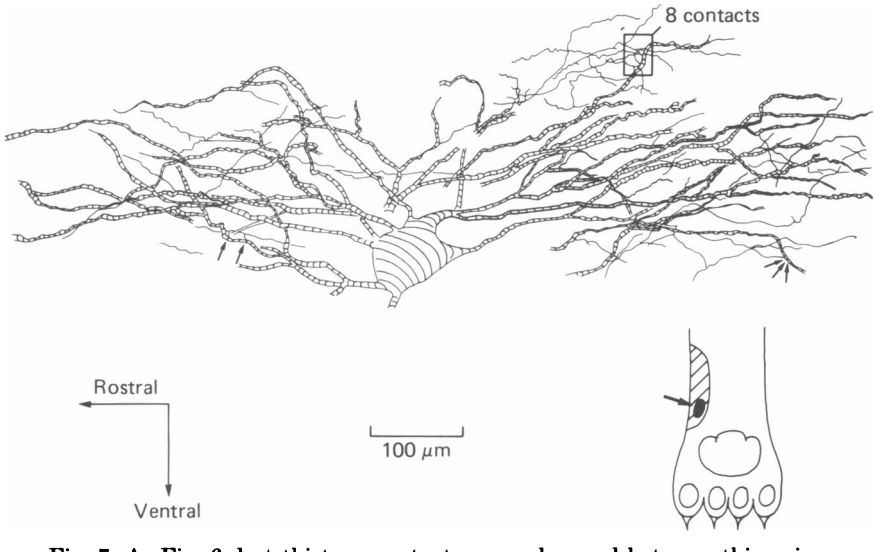

Fig. 7. As Fig. 6, but thirteen contacts were observed between this pair on widely divergent dendritic systems.

DISCUSSION

The results presented in this paper allow some discussion of the synthesis of receptive fields of s.c.t. neurones and also of some general problems of the organization of neuronal connexions within the mammalian spinal cord. The latter will be considered first.

In recent years some interest has been generated by the concept of 'non-functioning' or 'silent' synapses (Mark, 1970, 1974*a*, *b*), the terms referring to the electrophysiological signs of synaptic function. Experiments on the dorsal horn of the mammalian spinal cord (Merrill & Wall, 1972; Basbaum & Wall, 1976; Wall, 1977; Devor, Merrill & Wall, 1977; Devor & Wall, 1978; Mendell, Sassoon & Wall, 1978) have described phenomena attributed to 'long-ranging' or 'relatively ineffective' afferent fibres which seem similar to those of the 'silent' synapses. The effects of 'long-ranging' afferent fibres may be revealed under certain circumstances such as after the removal of more powerful synaptic inputs by dorsal root section or peripheral nerve division. The evidence is equivocal, however, with regard to whether previously silent synapses are revealed or whether new connexions are made following the loss of normal input. Certainly, evidence based on extracellular recordings from dorsal horn neurones (Pubols & Goldberger, 1980; Pubols & Brenowitz, 1981) provides no strong support for the presence of inappropriate connexions following such disturbances, as the somatotopic organization of the de-afferented horns can be considered normal. Only the preliminary report by Devor & Wall (1978) seems to require a conclusion for the appearance of inappropriate connexions.

Unfortunately the use of extracellular recording methods, together with the indiscriminate pooling of all dorsal horn neurones, makes interpretation of the data extremely difficult. Thus, even within laminae III, IV and V, there are many different subsets of neurones and great variation in receptive field sizes even though the somatotopic map is quite precise *if the centres of the receptive fields* are considered. For example, within lamina III it is possible to record, from the same electrode position, a neurone belonging to the s.c.t. with quite a small receptive field and a neurone sending its axon into the dorsal columns (post-synaptic dorsal column neurone) with a receptive field containing that of the s.c.t. cell but extending beyond it (A. G. Brown, R. E. W. Fyffe & L. M. Pubols, unpublished observations). Furthermore, only intracellular recording will reveal subliminal fringes to receptive fields under many conditions in the normal animal and only intracellular recordings will allow determination of the presence of monosynaptic connexions that fail to fire the cell unless the cell's excitability can be raised in some way.

Only Mendell *et al.* (1978) have used intracellular recording methods in studying 'long-ranging' afferent connexions. They did, in fact, provide evidence that some of the effects, such as the occurrence of excitatory post-synaptic potentials upon electrical stimulation of skin well away from the receptive area defined by natural stimulation, did have latencies within the likely monosynaptic range.

In the present study both elements of the neuronal pairs examined were identified – as the larger diameter hair follicle afferent fibres (types G and T of Brown & Iggo, 1967) and spinocervical tract cells. When the hair follicle afferent's receptive field was outside that of the s.c.t. cell there were no contacts between them. This result was

observed irrespective of whether the afferent's field was just outside the cell's field or was separated from it by several centimetres. For this system, comprising the hair follicle afferent fibres and neurones of the s.c.t., we could find no evidence of 'silent' synapses. Mendell *et al.* (1978) demonstrated 'long-ranging' connexions in 14–78% of dorsal horn neurones with 'lamina IV and V' characteristics. S.c.t. cells are supposed to have such characteristics and yet show no inappropriate connexions. The importance of working with identified neurones is thus emphasized. It is, of course, possible that the s.c.t. is not a good choice for a system to show such 'long-ranging' actions; perhaps a system with well developed subliminal fringes to its excitatory receptive fields, such as the post-synaptive dorsal column system (Brown & Fyffe, 1981*b*) would be a better choice.

Where the receptive field of a s.c.t. cell contained that of the hair follicle afferent fibre we always observed synaptic contacts between the two. Obviously, only ultrastructural examination of putative contacts seen with the light microscope would allow such an assertion to be made unequivocally. But one of our criteria for a synaptic contact – the presence of a bouton-like swelling on the axon – has been shown to hold at the electronmicroscope level (Brown, Fyffe & Maxwell, 1981). It would seen reasonable for the time being to conclude that presumed contacts seen at the light microscope level are in fact synaptic contacts, and that for the s.c.t. all hair follicle afferent fibres with receptive fields contained within the perimeter of a s.c.t. cell's field make excitatory contacts onto the soma-dendritic membrane of the neurone. This conclusion is for the larger axons innervating hair follicles; the contribution of the type D hair follicle afferents with diameters in the Aδ range is unknown.

The results described in this paper provide direct anatomical support for the electrophysiological observations and the conclusions of Hongo & Koike (1975). These authors stimulated single cutaneous axons, by careful electrical stimulation in the receptive field, while making intracellular recordings from s.c.t. neurones. They observed that when the primary afferent fibre had its field centrally located in the s.c.t. cell's field the excitatory post-synaptic potentials were larger and had faster rise times than when the fibre's field was peripherally located. They suggested that the former result was due to a larger number of synapses more proximally located on the neurone in comparison with the situation in the latter instance. This is indeed the case.

The numbers and locations of synapses between a hair follicle afferent fibre and a s.c.t. neurone depend upon the relative positions of their receptive fields. On the one hand, when the afferent's field is centrally placed in the neurone's field there are many contacts (forty to sixty) on the proximal geometrical half of the dendritic tree. On the other hand, when the afferent's field is located peripherally in the neurone's field there are few contacts (two to thirteen) on the more distal parts of the dendritic tree, on the middle and distal thirds of the dendrites.

In general, only a fraction of the primary dendrites and their branches receive contacts from a single hair follicle afferent fibre. Even when there were many contacts between the two it was unusual for contacts to be made upon more than two or three primary dendrites and their branches. The most widely spread sets of contacts in the present sample were situated on four and five primary dendrites and their branches

and these two s.c.t. neurones had twelve and eleven primary dendrites respectively. Obviously there is a degree of grouping of the contacts made by a single hair follicle afferent fibre upon a single s.c.t. cell. Strategically placed inhibitory synapses, at the bases of appropriate dendrites, could be most effective in inhibiting the excitatory actions of the input from single hair follicle axons. However, there is no electrophysiological evidence for such a mechanism. The monosynaptic excitatory action of hair follicle afferent fibres upon s.c.t. cells is very resistant to interference from both segmental and descending inhibitory systems (Brown, 1971; Brown, Kirk & Martin, 1973; Brown & Martin, 1973).

The results raise a number of questions of which two seem worth discussing at present. First, afferents from the periphery of a s.c.t. cell's receptive field make fewer and more distal contacts than those from near the centre and yet there is no obvious subliminal fringe to a s.c.t. neurone's field nor is there in most s.c.t. cells any obvious gradient of sensitivity across the field to movement of hairs. In addition, Hongo & Koike (1975) have shown that single fibre excitatory post-synaptic potentials evoked from the periphery are smaller and have longer rise times than those from the centre. If this observation is substantiated it seems unlikely that all synaptic excitatory inputs are equally efficacious, as seems to be the case for dendritic inputs to CA1 pyramidal cells of the hippocampus (Andersen, Silfvenius, Sundberg & Sveen, 1980). A complication for the hair follicle afferent s.c.t. system is the likely occurrence of disynaptic excitatory linkages made by the same hair follicle afferents that excite the cell monosynaptically (Hongo & Koike, 1975). This disynaptic linkage appears to be particularly effective in firing the s.c.t. cell when only single afferents are excited. Obviously, further combined anatomical and electrophysiological experiments are required to throw light on these problems. Secondly, the present results indicate a highly ordered organization of the synaptic contacts between hair follicle afferent fibres and s.c.t. cells dependent on relative field positons. It has been calculated (Brown, Rose & Snow, 1980) that a single hair follicle afferent fibre might make contact with between 100 and 150 s.c.t. neurones, that is, with between 12 and 20% of the total population receiving input from the hind limb. How such an ordered organization combined with considerable divergence comes about is unknown, but the hair follicle afferent-s.c.t. system should provide a useful model with which to study the formation and maintenance of synaptic connexions.

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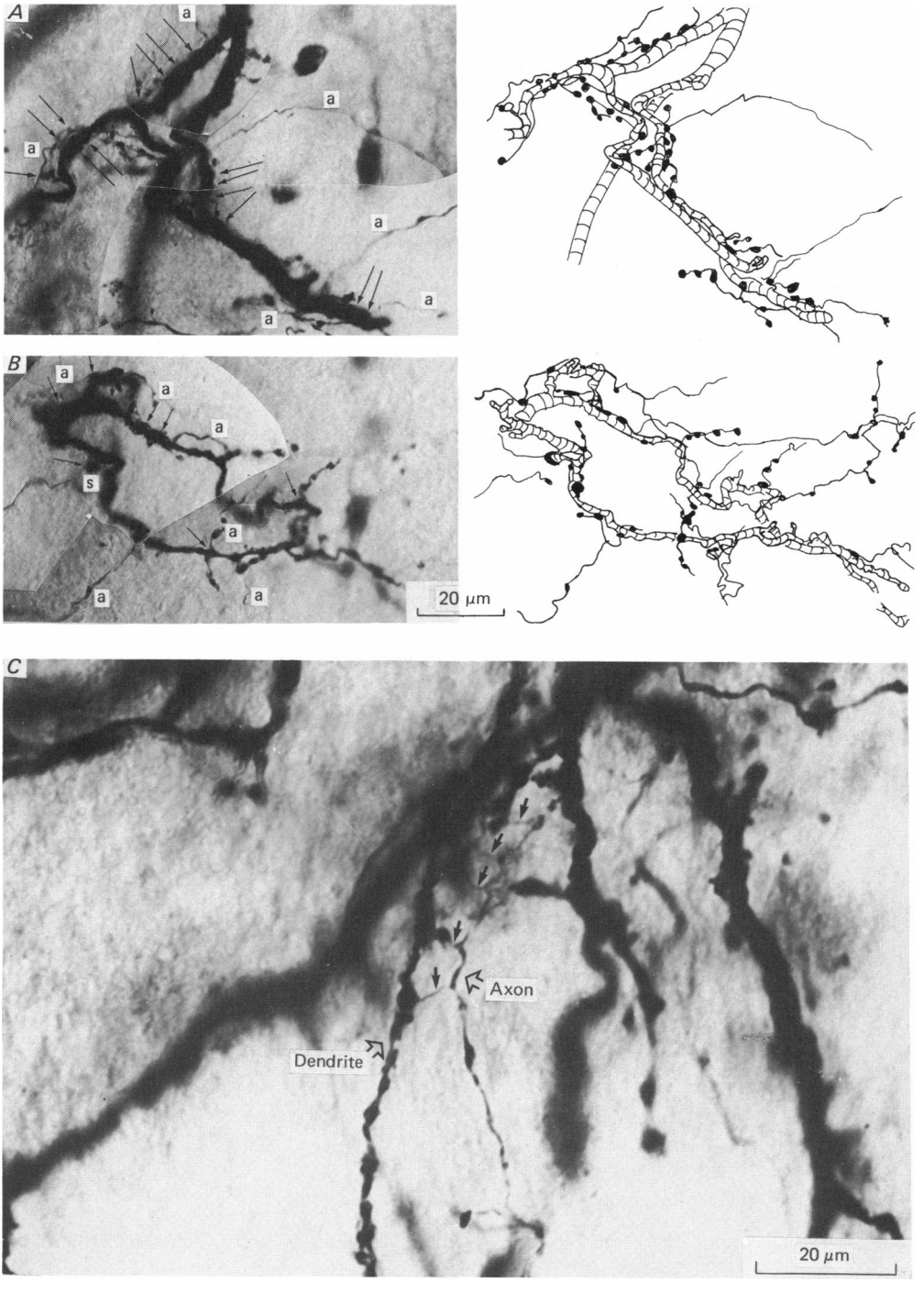
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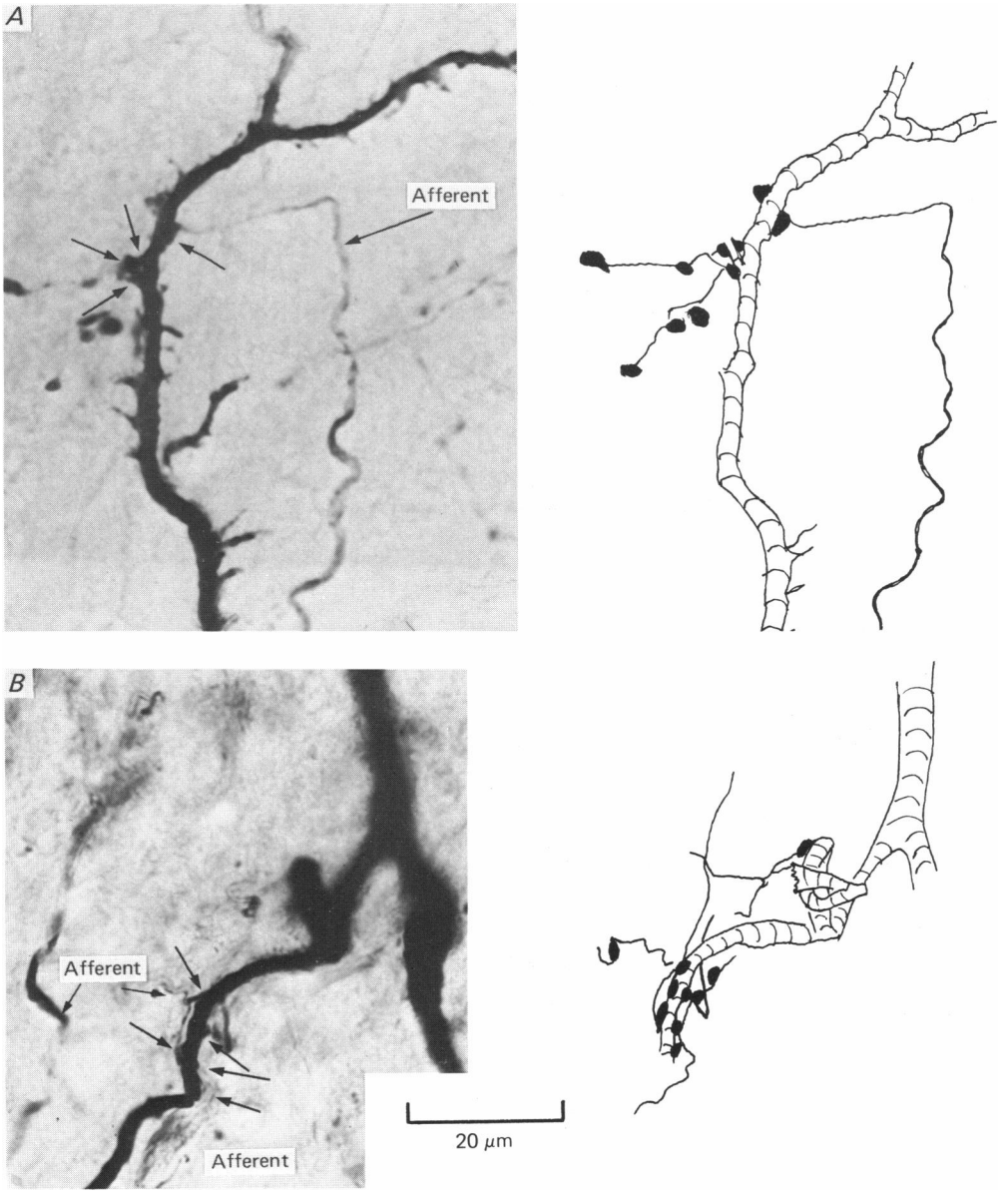
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Afferent
Afferent
20 μm

EXPLANATION OF PLATES

PLATE 1

A and *B* show, on the left, photomicrographs of synaptic contacts made between the hair follicle afferent–s.c.t. neurone pair shown in Figs. 2 and 3, Pl. 1 *A* being the boxed area in Fig. 3. On the right are shown camera lucida drawings of the same fields of view. In the photomicrographs axon collateral branches are indicated by 'a' and, in *B*, 's' denotes a contact on a dendritic spine. Some contacts are indicated by arrows. *C*, shows a photomicrograph of a 'ladder-like' type of synaptic contact. The terminal axonal branch (axon) and the s.c.t. neurone's dendrite (dendrite) run side by side. Fine branches are given off the axon (arrows) and run to the dendrite where they end in synaptic boutons.

PLATE 2

A and *B*. Photomicrographs, on the left, and camera lucida drawings, on the right, of synaptic contacts between hair follicle afferent fibres and s.c.t. dendrites. Some of the contacts are indicated by arrows. *A* and *B* are the boxed areas *a* and *b* in Fig. 4.