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SPINAL CORD COLLATERALS FROM AXONS OF TYPE II SLOWLY ADAPTING UNITS IN THE CAT

BY A. G. BROWN, R. E. W. FYFFE, P. K. ROSE* AND P. J. SNOW†
From the Department of Veterinary Physiology, University of Edinburgh, Summerhall, Edinburgh EH9 1QH

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SUMMARY

1. The morphology of single axons, and their collaterals, of Type II slowly adapting mechanoreceptors situated at the claw bases was studied. Intra-axonal injections of horseradish peroxidase were made into the axons near their entrance to the lumbosacral spinal cord of anaesthetized cats. The morphology was revealed by subsequent histochemistry.

2. Nine Type II axons were stained. All but one bifurcated into ascending and descending branches upon entering the cord. Eighty-nine collaterals arose from the axons at a mean spacing of about 570 μm.

3. The collaterals formed plate-like arborizations usually about 500–600 μm wide in the transverse plane but only 100–300 μm thick in the longitudinal axis of the cord. The terminal arborizations were in laminae III–VI.

4. Synaptic boutons in laminae III and IV were more numerous than in laminae V and VI. Boutons *en passant* were common in laminae III and IV and arranged in series of three to six, whereas in deeper laminae only two or three boutons formed a series *de passage*.

5. The morphology of the slowly adapting Type II collateral is discussed.

6. Some general principles of the organization of cutaneous afferent fibres in the lumbosacral cord are presented.

INTRODUCTION

In mammalian hairy skin there are two distinct types of slowly adapting mechanoreceptors innervated by myelinated axons. Iggo (1966) first clearly differentiated them and called them Types I and II. The Type I sense organs contain Merkel cells and their electrophysiological response to a maintained displacement is characteristically irregular (Iggo & Muir, 1969). The Type II sense organ is the Ruffini corpuscle (Ruffini, 1894; Dogiel, 1903; Chambers, Andres, von Duering & Iggo, 1972) situated in the dermis. Type II receptors respond to a maintained displacement with a very regular discharge and are also excited by stretching the skin containing the ending (Burgess, Petit & Warren, 1968; Chambers *et al.* 1972).

*† Postdoctoral Fellows of the Canadian M.R.C.
* Present address: Department of Physiology, Queen's University, Kingston, Ontario, Canada.
† Present address: Department of Anatomy, University of Queensland, St Lucia, Queensland, Australia.

There appears to be a group of Type II sense organs situated near the claw bases in cats. In 1964, Gordon & Jukes described neurones in the cat's gracile nucleus that responded with a maintained steady discharge to claw displacement. This observation was confirmed by Brown, Gordon & Kay (1974) and in the meantime one of the present authors had confirmed the presence of Type II responses to claw movement (A. G. Brown, unpublished observations).

Recently Johansson (1978) has shown that Type II endings in human glabrous skin may be divided into three classes and one (Johansson's C type) has a pronounced sensitivity to mechanical stimulation of the nail and often has an identation-sensitive zone close to the proximal or lateral borders of the nail. The 'claw' receptors and Johansson's C type receptors therefore appear to form a special sub-group of the slowly adapting type II category.

In the experiments reported in this paper, axons from Type II receptors at the claw bases were stained by intra-axonal ionophoresis of horseradish peroxidase (HRP) just after they had entered the lumbosacral spinal cord. Subsequent histochemistry provided detailed information about the anatomy of the collaterals entering the dorsal horn. The results demonstrate that Type II slowly adapting units have collaterals in the spinal cord quite different from those of any other cutaneous or muscle afferent unit so far studied (Brown, Rose & Snow, 1977, 1978; Brown & Fyffe, 1978, 1979; Brown, Fyffe & Noble, 1980*a*; Fyffe, 1979; Light & Perl, 1979). Preliminary reports of some of the results have been published (Brown, Rose & Snow, 1976; Brown, 1977).

METHODS

Full details of the methods used in this laboratory have been published (Snow, Rose & Brown, 1976; Brown *et al.* 1977; Brown & Fyffe, 1978). Briefly, the experiments were performed on young adult cats anaesthetized with chloralose (70 $mg.kg^{-1}$) and paralysed with gallamine triethiodide. Anaesthetic level was monitored throughout the experiment by reference to the arterial blood pressure, the state of the pupils of the eyes and by allowing the effects of the gallamine to wear off from time to time.

Single axons innervating Type II receptors at the claw bases were impaled near their entry to the spinal cord in segments L6–L7 and injected with HRP by passing depolarizing currents through the HRP-containing micro-electrode. Type II units were easily recognized by their characteristic regular discharge to steady displacement of a claw or of the spot-like receptive field in the fold of skin at the claw base.

At the end of each experiment the cats were killed with an overdose of barbiturate, perfused through the descending aorta with heparinized saline and buffered formalin (pH 7·6) or modified Karnovsky's fixative (Karnovsky, 1965; Graybiel & Devor, 1974). Serial transverse sections (100 μm, frozen) were cut and processed as described by Graybiel & Devor (1974) or Hanker, Yates, Metz & Rustioni (1977). Collaterals of injected neurones were reconstructed using a Zeiss drawing apparatus (camera lucida) at magnifications of $\times 250$ to $\times 1000$.

RESULTS

Nine axons of Type II slowly adapting units were stained. They were all from receptors at the claw bases. Although axons innervating Type II mechanoreceptors in the hairy skin on the thigh and leg were recorded, and even injected, they were not recovered from the histological material. This report, therefore, is limited to Type II units with receptors at the claw bases. The nine axons described here all had similar

collateral branching patterns and terminal distributions and formed a distinct class quite different from those of the other cutaneous and muscle afferent fibres.

The axons had peripheral conduction velocities (from the medial plantar nerve) of 41–67 m s^{-1}, and central conduction velocities within the dorsal columns (from C2) of 28–51 m s^{-1}.

Entry of axons into the spinal cord and the distribution of collaterals to the dorsal horn

All nine Type II axons could be traced from a dorsal root into the spinal cord and eight of these bifurcated into ascending and descending branches shortly after entering the cord: one axon did not bifurcate but turned and ascended. Ascending branches usually ascended the dorsal columns in a position no deeper than the level of the dorsal border of the dorsal horn and generally 100–200 μm superficial to it. The total lengths (ascending plus descending branches) of axons stained ranged from about 6 to 8·5 mm. The axons could be excited from the second cervical segment so the ascending branches were stained for only about 2% of their total length. Descending branches were usually thinner than ascending ones. The nine axons gave off a total of eighty-nine collaterals, twenty-one from descending branches, sixty-six from ascending branches and two from the main axons before they bifurcated. None of the descending branches terminated as a collateral and presumably further, unstained, collaterals were present in the caudal direction.

The eighty-nine collaterals arose over distances of 5·6–8·3 mm. Intercollateral spacing varied from 100 to 1800 μm (577 $\pm$ 345 μm; mean $\pm$ S.D.) and collaterals were closer together on descending branches (360 $\pm$ 316 μm) than on ascending ones (607 $\pm$ 362 μm). This difference is significant at the 1% level (Student's *t* test). The overall mean spacing (577 μm) is similar to that for other cutaneous axon collaterals that, like the Type II 'claw' units, have their arborizations distributed to the medial part of the dorsal horn.

The morphology of Type II afferent collaterals

The distinctive arborization pattern of Type II collaterals is shown in Figs. 1–4 and the photomontage of Pl. 1. The collaterals followed the usual rostral trajectory after leaving the parent axon and entered the grey matter at its dorsal or dorso-medial border about 100 μm rostral to their origin. A feature of Type II collaterals, however, was that the main collateral frequently divided just before or just after entering the grey matter (Figs. 1*C*, 4*B*). The collaterals pursued a more or less straight course through the most dorsal three laminae, usually dividing once or twice. In lamina IV the collaterals divided profusely; some branches turning and ascending back into lamina III (Figs. 2, 3), others ramifying more or less horizontally and the remainder carrying on in the ventral direction. The collaterals therefore formed a fairly dense arborization that stretched from the most dorsal parts of lamina III through lamina IV and into V or even to the most dorsal part of lamina VI. Not all collaterals had such extensive arborizations; some were limited to laminae III and IV (Fig. 4*B*), and others to laminae IV and V (Fig. 1*A*, *B*), but most occupied parts of laminae III, IV and V.

In the transverse plane the terminal arborizations of Type II collaterals were 300–600 μm in extent, generally 500–600 μm, and occupied the medial third of the

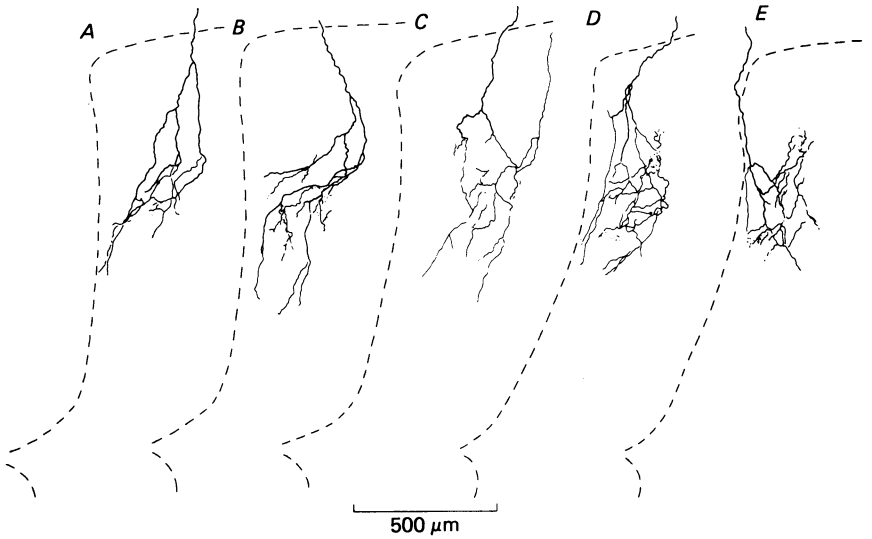

Fig. 1. Reconstructions, from transverse sections, of six adjacent collaterals from a Type II axon. *A* is the most caudal and *E* is the most rostral. In *C* two collaterals whose arborizations partially overlapped are shown. Collaterals enter the dorsal horn through its dorsal (*A–D*) or medial (*E*) border. Most collaterals divide two or three times before breaking up into their terminal arborizations. In *D* and *E* the main axon trifurcates. In this, and all other Figures, the outline of the dorsal horn is indicated by a dashed line.

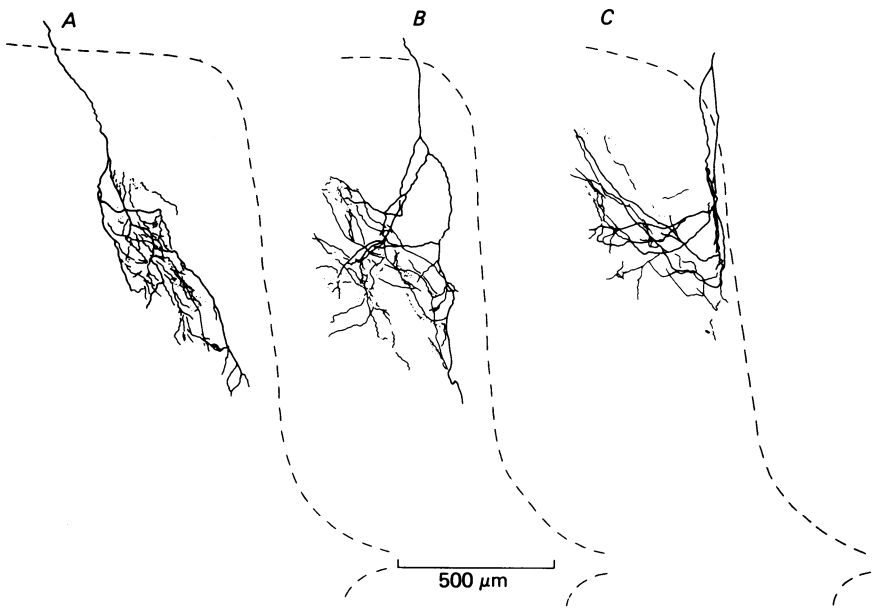

Fig. 2. Three adjacent collaterals from a Type II axon. In *C* the collateral divides before entering the grey matter.

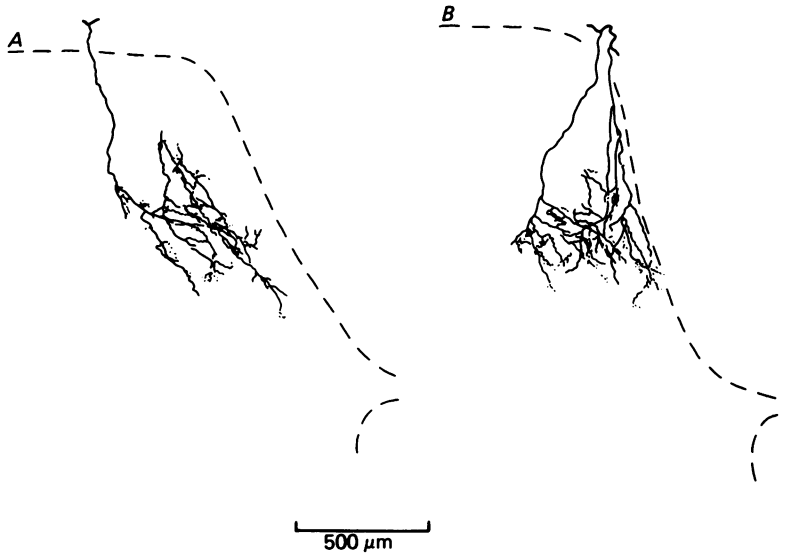

Fig. 3. Three adjacent collaterals from a Type II axon. In *B* the two collaterals were given off about 100 μm apart and their arborizations overlapped slightly.

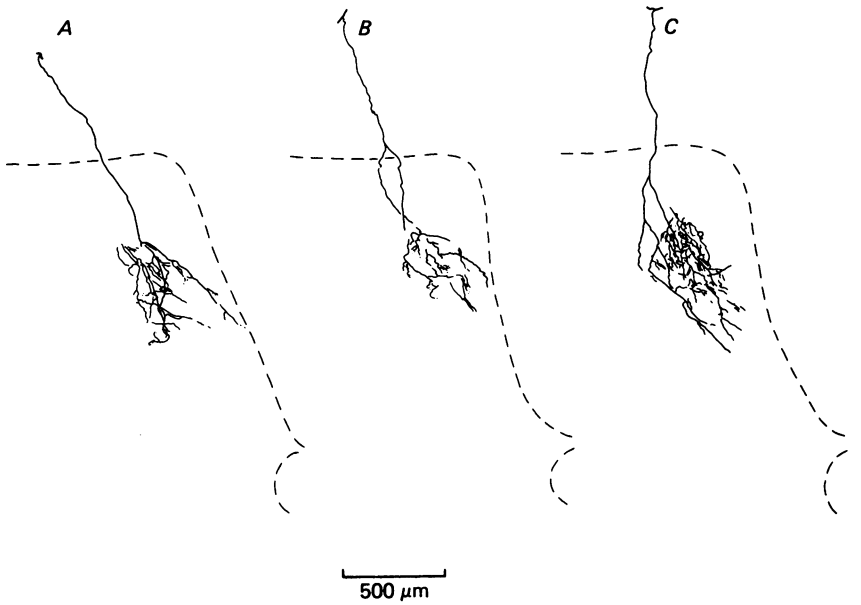

Fig. 4. Three adjacent collaterals from a Type II axon. In *B* the collateral divides before entering the grey matter and the arborization is limited to laminae III and IV, as it is in *A*. Part of the terminal arborization of collateral *C* is shown in the photomicrograph of Pl. 1*A*.

dorsal horn. In contrast to their extensive dorso-ventral and medio-lateral development their rostro-caudal development was severely restricted. Each Type II collateral formed a plate of terminal arborizations only some 100–300 μm thick in the longitudinal axis of the cord. Terminal arborizations of adjacent collaterals from the same parent axon were therefore nearly always separated from one another by cord containing no terminals from the axon. Even where collaterals arose at intervals of 100–200 μm there was usually a clear gap between the adjacent arborizations. Collaterals from a single Type II axon therefore formed a series of plates or sheets oriented transversely across the medial third of the dorsal horn in laminae III to V or VI; the sheets were in line in the longitudinal axis of the cord.

Terminal arborizations and synaptic boutons of Type II afferent fibre collaterals

Within the 100–300 μm thick sheets of collateral arborizations the terminal, bouton-carrying axons ran in the plane of the sheets. That is, they ran in the transverse plane of the spinal cord. Their general orientation was dorso-ventral, usually at an angle of up to 45° from the vertical, running from a more lateral to a more medial position (see Pls. 1*B*, *C*, 2). Some terminal axons were observed that ran more or less horizontally across the cord (Pl. 2*D*, *E*).

The distribution of terminal axons and synaptic boutons to different laminae of the dorsal horn varied. There were more axons and more boutons in laminae III and IV than in V and VI and the arrangement of the boutons on the axons also differed.

Lamina III and dorsal lamina IV. In these laminae (Pls. 1*B*, *C*, 2*A*, *B*, *C*) the boutons were usually arranged in the *en passant* way with up to ten boutons strung out along the last 50–60 μm of an axon. Sometimes groups of three to six boutons *en passant* were intercalated along an axon whose termination was not within the section under observation and at least 50–100 μm away from the intercalated group. Occasional boutons were offset from the axon on short stalks. The density of boutons in these laminae (III and dorsal half of IV) was about 40–50 per 100 μm^3.

Ventral lamina IV. The ventral half to one third of lamina IV was intermediate in organization between the more superficial and the deeper areas of termination. It contained fewer axons and boutons than the superficial area and boutons *en passant* were less well developed.

Lamina V and dorsal lamina VI. There was a marked difference between the terminal arborizations in this area in comparison with lamina III and dorsal lamina IV. As mentioned above, in ventral lamina IV there was a region of transition between the two areas. In lamina V and dorsal lamina VI (when the arborization penetrated as far as this) there were fewer terminal axons than in the more dorsal regions and they carried fewer boutons. Boutons were grouped together in twos and threes in *en passant* arrangements, often 100 μm or more away from the final bouton *terminal* (Pl. 2*E*, *F*); occasionally single boutons *en passant* were intercalated along the terminal 100–200 μm of axon. In this region too, the number of single boutons offset from the axon on short stalks was relatively more common than in the dorsal regions of termination, but the absolute number of such occurrences was about the same as in the dorsal regions. The density of boutons in lamina V was about 10–20 per 100 μm^3, that is, usually less than half that in laminae III–IV.

DISCUSSION

The gross organization of the axons from Type II slowly adapting (claw) receptors is summarized in Fig. 5. This figure represents the organization within about 1 cm of their entry into the lumbosacral spinal cord. Upon entering the cord the axons usually bifurcate and collaterals are given off both ascending and descending branches at a frequency of about two every millimetre.

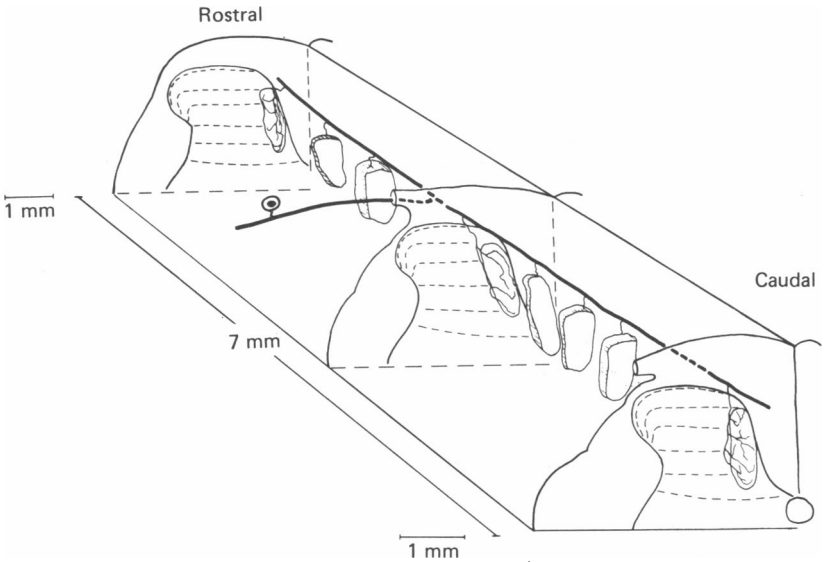

Fig. 5. Summary diagram of the organization of collaterals from an axon innervating slowly adapting Type II receptors. For further discussion see the text.

The collaterals are organized in a characteristic way. Each collateral forms a wide and deep transversely oriented sheet of arborizations that occupies the medial third of the dorsal horn. Synaptic boutons are given to laminae III to V and dorsal VI, although not all collaterals distribute their endings to all the laminae. The sheets of terminals are 100–300 μm thick in the sagittal plane and are separated from each other by cord free from endings. This sheet-like distribution is similar to that of axons of the rapidly adapting mechanoreceptors in glabrous skin, but they have arborizations limited to lamina III and the dorsal parts of lamina IV.

The distribution of synaptic boutons to as many as four laminae (III–VI) is similar to the distribution of collaterals from axons of Pacinian corpuscles (Brown *et al.* 1980*a*), but Pacinian corpuscle collaterals form continuous sagittal columns of terminal arborizations in laminae III and IV.

Although there is no clear division of Type II collateral arborizations into a superficial and deep area (as there is with collaterals from Pacinian corpuscle units) there are marked differences between terminal arborizations in lamina III and dorsal lamina IV on the one hand and lamina V and dorsal lamina VI on the other, with ventral lamina IV acting as a transition zone. In the superficial region there is a high density of boutons and most are of the *en passant* variety with up to ten boutons

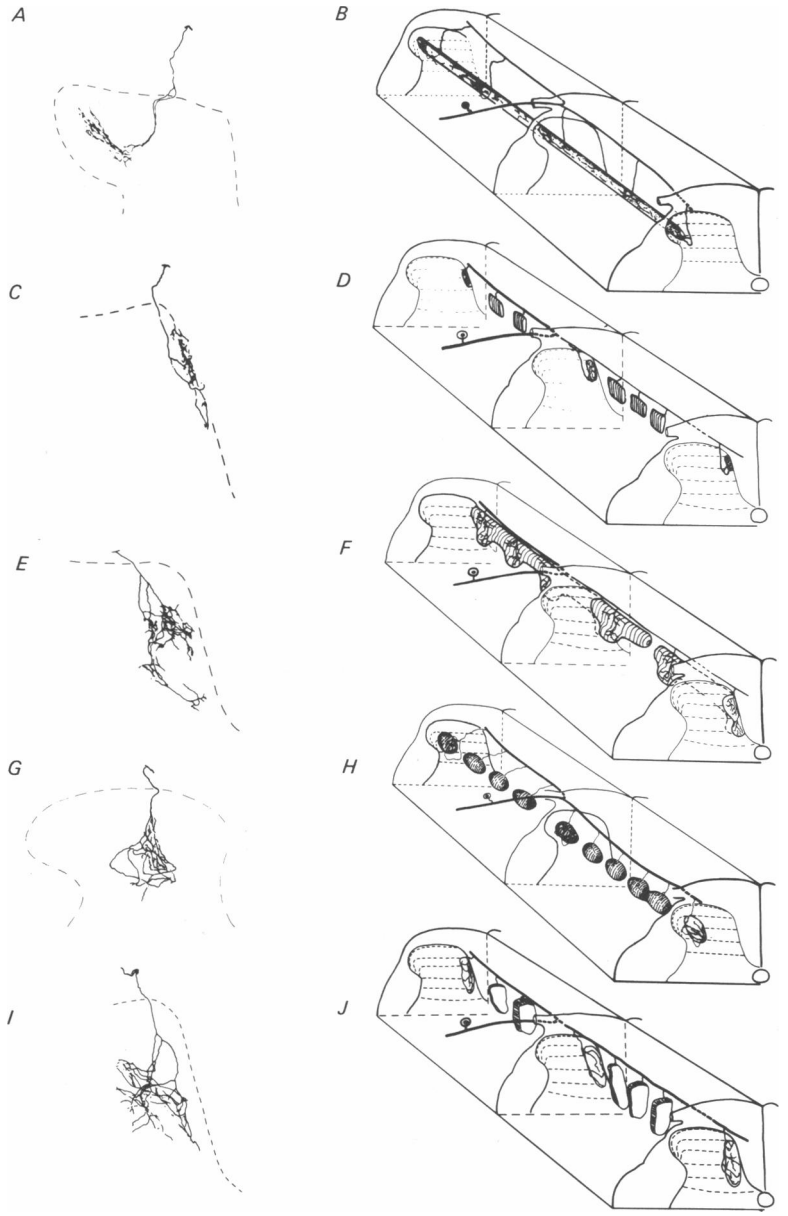

Fig. 6. Summary diagrams of the organization of axon collaterals from cutaneous afferent fibres in the cat's lumbosacral cord. The column of figures on the left shows reconstructions of representative single collaterals; the column of figures on the right shows three-dimensional representations of the different types. *A*, *B*, hair follicle afferent; *C*, *D*, rapidly adapting (Krause) mechanoreceptive afferent; *E*, *F*, Pacinian corpuscle afferent; *G*, *H*, slowly adapting Type I afferent; *I*, *J*, slowly adapting Type II afferent.

arranged on the terminal 50–60 μm of axon. In the deep region the density of boutons is much less and clusters of only two to five is the usual arrangement. There were no differences of orientation, however, throughout the terminal regions; terminal axons all ran in the transverse plane of the cord.

There is, unfortunately, no physiological evidence available on the central connexions of Type II units at spinal cord level. Obviously, on the basis of the present results, neurones receiving a monosynaptic Type II input from the claw base should be looked for in the medial parts of laminae III–VI. There is no evidence that any such neurones project into the spinocervical tract and the function of Type II input at spinal level remains unknown.

The present report completes our initial survey of the anatomy of the central organization of the large myelinated axons innervating cutaneous mechanoreceptors. We have described axons innervating hair follicle receptors (Brown *et al.* 1977), Type I slowly adapting receptors (Brown *et al.* 1978), Pacinian corpuscles and rapidly adapting mechanoreceptors in glabrous skin (Brown *et al.* 1980*a*) and now Type II slowly adapting receptors. Light & Perl (1979) have described collaterals from cutaneous Aδ axons. On the basis of these observations it is possible to extract some general principles of the organization of cutaneous axon collaterals:

(1) Each type of afferent unit has its own characteristic axon collaterals. The anatomy of the collateral arborizations is such that examination of the histological material alone allows an accurate identification of the type of afferent unit to which the collaterals belong. At and near the entrance of the dorsal root fibres into the cord this morphological specificity is (*a*) the same for each collateral from a single axon, (*b*) the same for all collaterals innervating the same type of receptor, and (*c*) characteristic of the afferent unit type. The specificity extends to the branching pattern of the collaterals, the arrangement of the terminal arborizations, the laminar distribution of their synaptic boutons and the orientation of the terminal axons and the bouton arrangements on them. Summary diagrams of the anatomy of the different types are shown in Fig. 6.

Hair follicle afferent fibres (fig. 6*A*, *B*) have collaterals of the 'flame-shaped arbor' type (Scheibel & Scheibel, 1968) and form long uninterrupted columns of sagittally running terminal arborizations limited almost exclusively to lamina III with some slight extension into lamina IV (Brown *et al.* 1977; Light & Perl, 1979). Rapidly adapting units with receptors in glabrous skin (Fig. 6*C*, *D*) have collaterals with some similarities to hair follicle axons in that the arborizations are limited to laminae III and dorsal IV and some collaterals have a 'flame-shaped' appearance. However, collaterals of axons from rapidly adapting mechanoreceptors in glabrous skin do not form long uninterrupted columns in the long axis of the cord but narrow plates of arborizations only some 400–600 μm thick and there are well-developed gaps between adjacent arborizations (Brown *et al.* 1980*a*). The other type of rapidly adapting sensitive mechanoreceptor, the Pacinian corpuscle, has axons with collaterals that have very well-developed arborizations giving terminals to laminae III–VI (Fig. 6*E*, *F*). In laminae III and IV long uninterrupted columns of sagittally running terminals are formed but in laminae V and VI the terminals run dorso-ventrally and there are usually gaps between those from adjacent collaterals (Brown *et al.* 1980*a*). Slowly adapting Type I units (Fig. 6*G*, *H*) have axons with collaterals that form arborizations

terminating in laminae III, IV and V in a spheroidal volume of cord with gaps between adjacent collaterals (Brown *et al.* 1978). High-threshold mechanoreceptors have axons with collaterals ending in either or both the marginal zone (lamina I) and lamina V (Light & Perl, 1979). Slowly adapting Type II units have, as described in the present paper, axons with collaterals forming transversely oriented slabs of terminal arborizations in laminae III–VI, each slab being only some 100–300 μm thick (Fig. 6*I*, *J*).

The differences in laminar distribution and terminal arborization seen in the collaterals from the different types of cutaneous afferent unit show that there must be a high degree of selectivity in the organization of connexions between the primary afferent fibres and spinal cord neurones. There is no reason to doubt, nowadays, that cutaneous receptors are highly specific. The demonstration of such individual differences between their central collateral arborizations emphasizes that the specificity extends to the complete afferent unit.

(2) Each primary afferent fibre distributes its central connexions via collaterals that are given off over at least 1 cm as the axon runs in the dorsal columns. The collaterals form arborizations in line with one another in the longitudinal axis of the cord. The arborizations may or may not form a continuous column (see above) but the end result is the formation of a column of endings in the longitudinal axis of the cord. The spot-like or round to oval cutaneous receptive field that is essentially two-dimensional is transformed into a three-dimensional column (continuous or interrupted) enormously elongated in comparison with its width – by a factor of at least 20. This arrangement of the cutaneous input forms the basis of the somatotopic organization of dorsal horn neurones, which also show a sagittal columnar distribution of their receptive fields (Brown, Fyffe, Noble, Rose & Snow, 1980*b*).

(3) The somatotopic organization of the dorsal horn is such that information from different types of cutaneous afferent unit, that have receptors in the same skin area, is brought together in the same dorso-ventral axis. The precision of this organization is probably greatest in lamina III where the transverse extents of the collateral arborizations, especially from axons of hair follicle endings and rapidly adapting mechanoreceptors, are least. In deeper layers there will undoubtedly be more overlap (between collaterals from Pacinian corpuscles and slowly adapting Type I and II receptors) and smearing of the somatotopic organization of the input. The overlap between collateral arborizations will at all levels, in addition to causing smearing, provide continuity across adjacent skin areas, for example at junctions between hairy and glabrous skin.

(4) The spacing of collaterals along a cutaneous axon depends more on the medio-lateral position of its arborization in the dorsal horn than on the type of afferent unit to which it belongs. Axons with terminal arborizations in the medial part of the dorsal horn have collaterals spaced at about 550 μm whereas those with arborizations in the most lateral parts of the horn have collaterals spaced at intervals of about 1500 μm; collaterals providing arborizations to the middle region of the horn have intercollateral spacings intermediate in value. These data have been obtained by examining the complete sample of cutaneous afferent fibres so far studied (fifty to sixty). Independent electrophysiological results on Ia muscle afferent fibres (Munson & Sypert, 1979) have confirmed that determination of intercollateral

spacing by horseradish peroxidase injection gives an accurate result and that all collaterals between the most rostral and most caudal cones revealed are stained.

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EXPLANATION OF PLATES

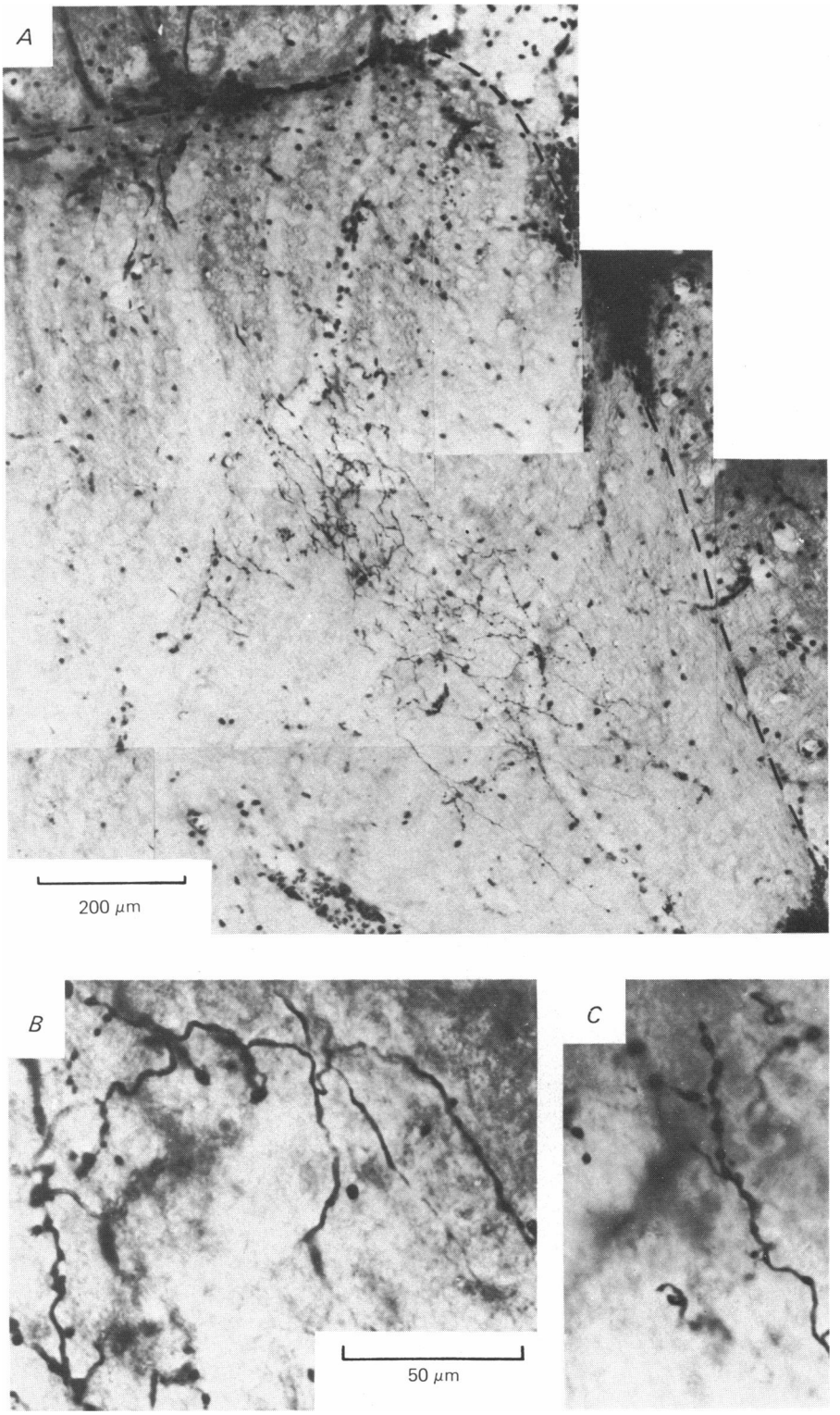
All photomicrographs are from single 100 μm thick transverse sections of lumbosacral spinal cord.

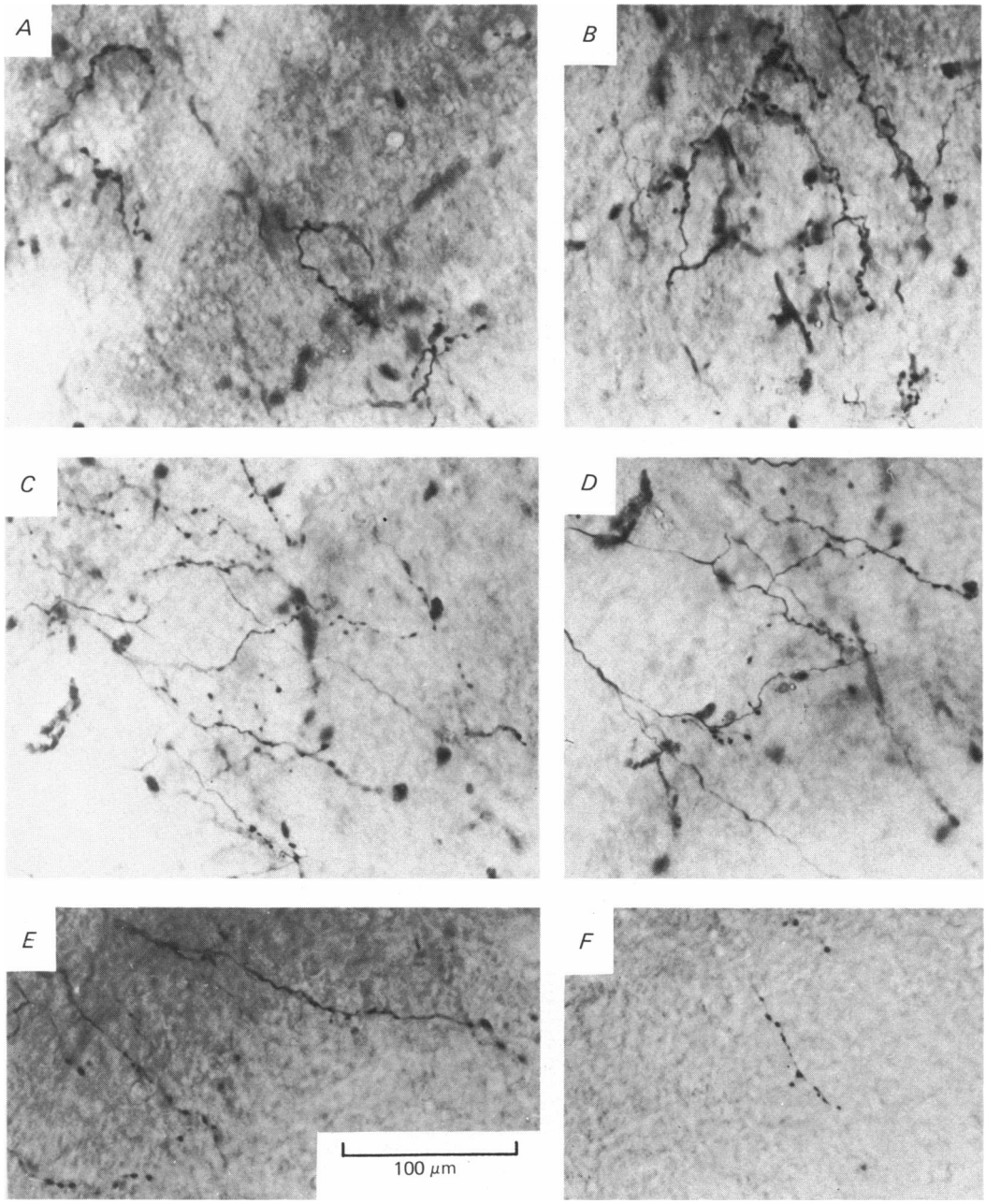
PLATE 1

A, part of the extensive arborization, in laminae III and IV, of the Type II collateral reconstructed in Fig. 4*C*. The dashed line indicates the border of the dorsal horn; dorsal columns are to the right. *B*, *C*; bouton-carrying terminal axons in lamina III. In *B* there is profuse branching within the transverse plane and in *C* a terminal axon carrying many boutons *en passant* is shown.

PLATE 2

A, *B*: Terminal axons within lamina III. *C*, *D*: Terminal axons in lamina IV. These are, as shown, usually oriented at about 45° to the dorso-ventral axis, within the transverse plane. *E*, *F*: terminal axons within laminae V (*E*) and VI (*F*). Again many boutons *en passant* are present but they are much less numerous than in more superficial regions. Note the single bouton offset from the terminal branch in *F*.


A
200 μm
B
50 μm
C


A
B
C
D
E
F
100 μm