PROJECTIONS FROM PACINIAN CORPUSCLES AND RAPIDLY ADAPTING MECHANORECEPTORS OF GLABROUS SKIN TO THE CAT'S SPINAL CORD

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SUMMARY

1. Single axons innervating Pacinian corpuscles and rapidly adapting mechano-receptors of the foot and toe pads were injected with horseradish peroxidase near their entrance to the lumbosacral spinal cord in cats anaesthetized with chloralose and paralysed with gallamine triethiodide. Subsequent histochemistry revealed the morphology of the intra-spinal parts of the axons.

2. All Pacinian corpuscle axons that could be traced into the dorsal root bifurcated upon entering the cord into ascending and descending branches. All Pacinian cor-puscle axons gave rise to collaterals that entered the dorsal horn.

3. The collaterals of Pacinian corpuscle afferent fibres had a distinctive morphology. They provided two regions of termination, a larger dorsal region in laminae III and IV and a smaller ventral region in laminae V and VI. Within the dorsal region the terminal axons ran mainly in the longitudinal axis of the cord and carried many boutons *en passant*. Within the ventral region the axons ran dorso-ventrally in the transverse plane of the cord and although carrying some boutons *en passant* also gave rise to clusters of boutons.

4. The collaterals of rapidly adapting afferent fibres had a distinctive morphology different from that of the Pacinian corpuscle afferent fibre collaterals. The termination region of rapidly adapting afferents was limited almost exclusively to lamina III, with only slight extension into lamina IV. Boutons were mainly of the *en passant* type and terminal axons were generally orientated within the longitudinal axis of the cord.

5. The morphology of the afferent fibre collaterals is discussed in relation to the physiology of the dorsal horn.

INTRODUCTION

There are two kinds of rapidly adapting mechanoreceptors, innervated by large myelinated axons, in the subcutaneous tissue under and near to the glabrous skin of the foot and toe pads of the cat (Jänig, Schmidt & Zimmerman, 1968*a*). It has been known since the work of Adrian & Zotterman (1926) and Maruhashi, Mizuguchi & Tasaki (1952) that there are rapidly adapting receptors in these tissues but Jänig

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et al. (1968*a*) established there are two kinds and that one of them has the properties expected for Pacinian corpuscles.

Typical Pacinian corpuscles are present in the subcutaneous tissue of the cat's foot and toe pads and on the digits between the tendons and the bones (Adrian & Umrath, 1929; Gray & Matthews, 1951; Malinovsky, 1966; Lynn, 1969; Jänig, 1971*a*). Lynn (1971) and Jänig (1971*b*) have confirmed that the Pacinian corpuscle-like responses do in fact arise from Pacinian corpuscles. The other type of encapsulated ending in the foot and toe pads, the Krause corpuscle, gives rise to the other kind of rapidly adapting response (Jänig, 1971*b*; Iggo & Ogawa, 1977).

The central projections of afferent fibres from Pacinian corpuscles are not well understood in spite of their characteristic response properties. In fact Boivie & Perl (1975) have suggested that these afferent fibres may not have major branches at the segmental level, since the axons do not show much, if any, reduction in conduction velocity after entering the spinal cord (Jänig *et al.* 1968*a*; Brown, 1968, 1973; Petit & Burgess, 1968). But it has been shown by Jänig, Schmidt & Zimmermann (1968*b*) that axons from Pacinian corpuscles activate dorsal horn interneurones responsible for producing presynaptic inhibition of (mainly) axons innervating rapidly adapting mechanoreceptors including the Pacinian corpuscles themselves. Furthermore, it seems likely (see Jänig *et al.* 1968*a*) that the interneurones studied by Armett, Gray & Palmer (1961) and Armett, Gray, Hunsperger & Lal (1962) were excited by input from Pacinian corpuscles in the central foot pad. It would be expected, therefore, that axons from Pacinian corpuscles should have collaterals at and near their point of entry into the lumbosacral spinal cord.

Even less is known about the central projections of the rapidly adapting glabrous skin receptors (Krause endings). Jänig *et al.* (1968*b*) demonstrated that activity in these fibres produced presynaptic inhibition of the axons of rapidly adapting mechanoreceptors, including hair follicle receptors, at and near their point of entry into the lumbosacral cord.

In the work reported in the present paper single physiologically identified axons from Pacinian corpuscles and rapidly adapting mechanoreceptors of the foot and toe pads were stained with horseradish peroxidase. It will be shown that these axons have extensive and characteristic collaterals in the spinal cord. A preliminary account of part of the work has appeared (Brown, Fyffe, Heavner & Noble, 1979).

METHODS

The experiments were performed on young adult cats anaesthetized with chloralose (70 mg. kg^{-1}) after induction of anaesthesia with halothane in a nitrous oxide:oxygen mixture. 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 animals were paralysed with gallamine triethiodide and the state of anaesthesia checked throughout the experiments by examination of the state of the pupils and the continuous blood pressure record. Additional doses of chloralose (30 mg kg^{-1}) were given if required.

The medial plantar nerves were exposed in the feet and placed on pairs of silver-silver chloride or platinum electrodes for stimulation. Axons were recorded with glass micro-electrodes near their entrance to the lumbosacral spinal cord. Pacinian corpuscle afferent fibres had conduction velocities of 57–75 $m.s^{-1}$ measured from the medial plantar nerve to the recording point and responded, in a one-to-one fashion, to a vibrating tuning fork (500 Hz) applied to their receptive

fields. Receptive fields were diffuse and often difficult to localize precisely, except that they were always limited to part of the central foot pad or to a single toe pad. Pacinian corpuscle units always responded with one or two action potentials to a tap on the experimental table or the frame supporting the animal. Rapidly adapting mechanoreceptors were innervated by axons conducting at 54–60 m.s^{-1}, did not respond in a one-to-one fashion to the tuning fork and had highly localized receptive fields limited to a spot-like area on part of the central foot pad or a single toe pad.

The glass micro-electrodes were filled with a 4–9 % solution of horseradish peroxidase (Sigma, Type VI) in Tris HCl buffer containing 0·2 mol. l^{-1} KCl, pH 7·6 (Snow, Rose & Brown, 1976). Full details of the methods for intra-axonal injection of the horseradish peroxidase and its subsequent histochemical demonstration have been published previously (Snow *et al.* 1976; Brown, Rose & Snow, 1977; Brown & Fyffe, 1978). The material was examined in serial transverse or sagittal sections of the cord cut at 100 μm. Some sections were counterstained with methylene green. Reconstructions were made with the aid of a *camera lucida*.

RESULTS

Afferent fibres from Pacinian corpuscles

A total of nine axons innervating Pacinian corpuscles of the foot or toe pads was stained. Their collaterals had a characteristic morphology quite different from those of any other type of cutaneous or muscle afferent fibre we have studied.

Entry of axons into the spinal cord, branching and collateral distribution

Four of the nine stained axons were traced into the L$_7$ dorsal root. All of these axons bifurcated into ascending and descending branches shortly after entering the spinal cord. The remaining axons were injected at more rostral levels: the stained portions of these axons lay in the dorsal columns. Both branches (ascending and descending) ran medially over the dorsal horn to assume wavy courses in the dorsal columns, close to the medial or dorsomedial border of the dorsal horn. As with all of our afferent fibre material the intra-axonal horseradish peroxidase method allows visualization of up to about 10 mm (6·2 ± 2·6 mm; mean ± S.D.) of the axon (ascending plus descending branches), that is, only a fraction of the total lengths. The descending branches were generally thinner than ascending branches of the main axon. None of the descending branches ended as a collateral and it must be assumed that branches descended further than the maximum visualized (1·6 mm).

The ascending and descending branches of Pacinian corpuscle afferent fibres gave off numerous collaterals (between four and twelve per axon; 7·11 ± 3·55, mean ± S.D.) over lengths of 2·4–8·1 mm of stained axon. A total of sixty-four collaterals arose from the nine axons at intervals of 100–3100 μm (688 ± 469: mean ± S.D.). This mean spacing is similar to that of other cutaneous axons with collaterals distributed to the medial part of the dorsal horn. There were differences, however, between the spacing of collaterals on ascending *versus* descending branches. For six spaces between collaterals arising from descending branches the spacing was 333 ± 163 μm, whereas for fifty-seven collaterals arising from ascending branches the spacing was 882 ± 504 μm. These differences are significant at the 1 % level (Student's *t* test). It was also observed that ascending branches did not show any noticeable reduction in diameter as they gave off successive collaterals.

The morphology of collaterals from afferent fibres innervating Pacinian corpuscles

As mentioned above the collaterals from Pacinian corpuscle afferent fibres had a distinctive morphology quite different from that of other cutaneous and muscle afferent fibre collaterals we have examined. Typical collaterals are shown in Figs. 1–3 as seen in reconstructions from transverse sections and in Fig. 4 as seen in reconstructions from sagittal sections.

The axons from Pacinian corpuscles in the foot and toe pads had collaterals that terminate in the medial half or less of the dorsal horn in keeping with the somatotopic organization of the horn. The collaterals entered the dorsal horn at its dorsal or medial border, in the latter case from a parent axon (ascending or descending branch of the axon) within the dorsal columns. Collaterals entering the dorsal horn through its dorsal border descended through Rexed's (1952) laminae I and II sometimes dividing on the way (Fig. 1A) to enter III where they underwent repeated subdivision. Collaterals entering from the dorsal columns usually proceeded directly to lamina III (Fig. 2). Collaterals may divide in the white matter before entering the dorsal horn. Like all primary afferent fibre collaterals, those from Pacinian corpuscle afferent fibres usually had a rostral trajectory from the parent axon to their entrance into the dorsal horn (Fig. 4).

Collaterals from Pacinian corpuscle afferent fibres terminated in two main areas of the dorsal horn. There was a main termination in laminae III and IV and a lesser area of termination in laminae V and VI. These two areas could usually be clearly seen in the reconstructions and there was generally a gap (in dorsal lamina V or around the IV–V border) between them, connected by two to four branches of the collateral. In a few collaterals the ventral arborization was relatively more extensive than the dorsal one (Fig. 3B). In these instances the dorsal arborization was less well developed and the ventral one was not obviously more extensive than usual.

The complete arborizations from individual collaterals had a dorso-ventral extent of 700—800 μm. Their distribution to four laminae makes the Pacinian corpuscle collaterals, along with collaterals from slowly adapting Type II receptors (Brown, 1977), those with the largest dorso-ventral distribution of any collaterals from large myelinated cutaneous axons. In the transverse plane the medio-lateral extents of the arborizations were usually some 170–350 μm and rarely more than 500 μm. In the rostro-caudal direction the arborizations ranged from about 400 to 750 μm at their longest extent. The dorsal termination area was longer than the ventral one; this led to overlap or continuity between many adjacent collaterals in their dorsal parts but there was only rarely overlap between the ventral aborizations of adjacent collaterals (Fig. 4).

We have stained one axon that probably innervated Pacinian corpuscles in the interosseous region: the unit could be excited by tapping anywhere on the hind limb and on the supporting frame. Its collaterals were similar in morphology to those described above except that one of them sent a branch via the dorsal commissure to the contralateral dorsal horn. Unfortunately this branch was not stained well enough for us to see any morphological details of its terminal arborization on the contralateral side.
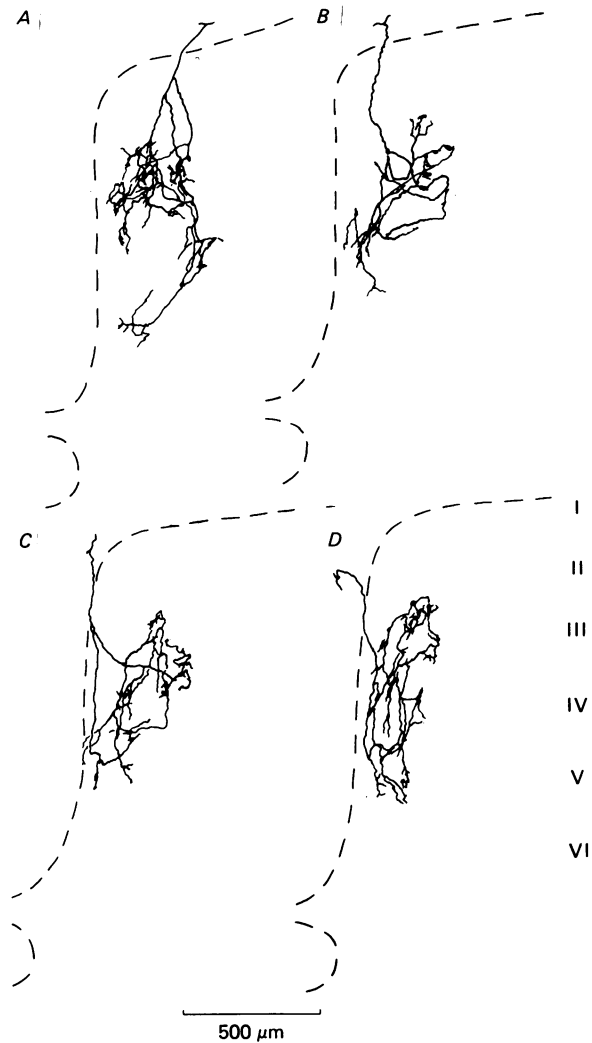
Fig. 1. Reconstructions from serial transverse sections of the spinal cord of four adjacent collaterals from an axon innervating a Pacinian corpuscle in the cat. Collateral *A* is most caudal and arises as the main axon crosses the top of the dorsal horn to ascend the spinal cord. The axon assumes a course close to the dorso-medial border of the dorsal horn as it ascends and gives off further collaterals *B*, *C* and *D*. Collaterals *C* and *D* enter directly into lamina III from the dorsal columns. All collaterals arborized in the medial third of the dorsal horn, with terminals located in lamina III, IV, V and the dorsal part of lamina VI. The dashed lines indicate the grey-white border and position of the central canal. In *D* the approximate locations of Rexed's (1952) laminae are indicated by Roman numerals.

Terminal axons and synaptic boutons

Photomicrographs of the terminal parts of axons carrying synaptic boutons are shown in Pls. 1 and 2. There were distinct differences in the arrangement of the boutons in the two termination regions. In the dorsal region, especially in its lamina
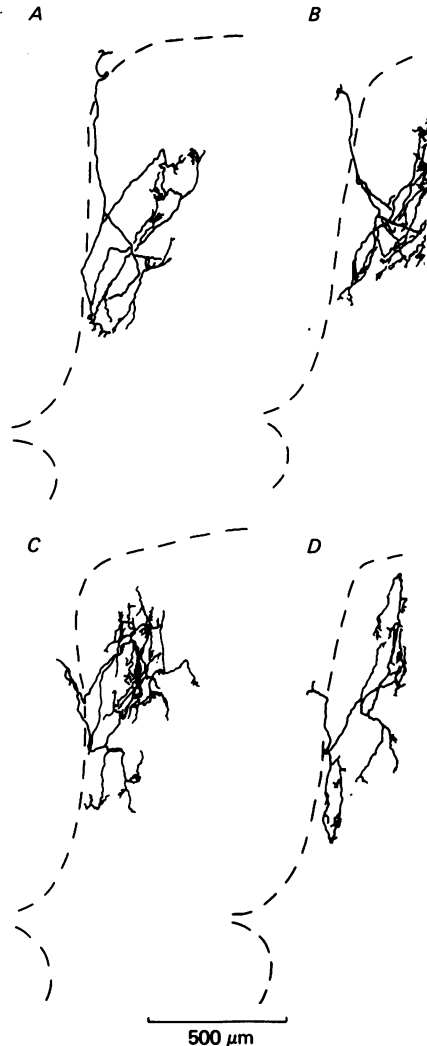

Fig. 2. Reconstructions, in the transverse plane, of four adjacent collaterals from a Pacinian corpuscle axon which ascended the cord in the dorsal columns. Between the caudal collateral *A* and the most rostral one, *D*, the main axon takes up a deeper position. Again the collaterals arborize in the medial third of laminae III–VI. Although collateral *D* loops. through lamina II, there were no terminals in that region. Collateral *C* divides into two branches before entering the dorsal horn.

III part, the terminal axons usually ran in the longitudinal axis of the cord (Pl. 1) and carried boutons *de passage* (Pl. 1). As many as 12–14 boutons were strung out along the terminal 50 μm of the axon although the more usual number was 6–10. In the ventral region the terminal axons ran dorso-ventrally in the transverse plane

(Pl. 2) and although boutons *de passage* were present they were fewer in number and the usual arrangement was for terminal axons to branch several (2–4) times and each branch to terminate in a bouton so that small clusters of boutons were formed (e.g.

Fig. 3. Reconstructions, in the transverse plane, of collaterals from Pacinian corpuscle and rapidly adapting afferent axons. *A*, two adjacent Pacinian corpuscle axon collaterals generating extensive arborizations in laminae III–VI. *B*, a single Pacinian corpuscle axon collateral which has a sparse dorsal termination zone but is still well developed ventrally in laminae V and VI. *C*, a single Pacinian corpuscle axon collateral. This collateral gives two branches, one arborizing in lamina III and the other producing a distinct second terminal zone ventrally in lamina V. *D*, a collateral from an axon innervating a rapidly adapting mechanoreceptor. A dense zone of termination is formed mainly in lamina III, with only a few boutons ventral to this.

Pl. 2*E*). This clustering of boutons was not seen in lamina III and only rarely in the dorsal part of lamina IV.

The numbers of boutons carried by individual collaterals were counted for collaterals that were well and evenly stained. The numbers ranged from forty-seven to

367 per collateral (170 ± 94; mean ± S.D., $n = 3235$; nineteen collaterals from six axons). Because of the greater development of terminal arborizations in the dorsal region there were many more boutons in laminae III and IV than in V and VI.

A feature of the boutons of Pacinian corpuscle axon collaterals was their wide variation in size. The smallest were about $1·0 \times 1·0$ μm while the largest were up to
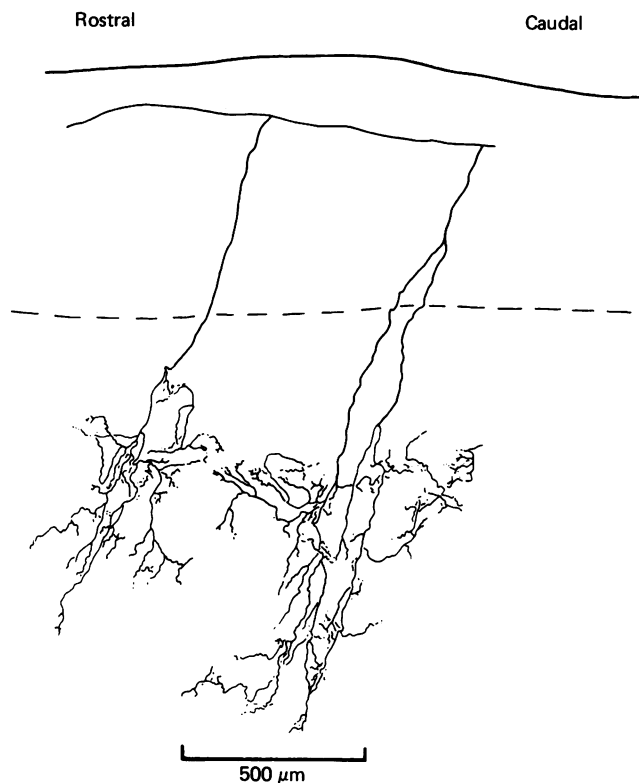
Rostral   Caudal

500 μm

Fig. 4. Reconstruction, from sagittal sections, of two adjacent collaterals from the ascending branch of a Pacinian corpuscle axon. The caudal collateral divides before it enters the grey matter, and generates terminal arborizations in two regions: dorsally in laminae III and IV and ventrally in laminae V and VI. There is some continuity between the dorsal parts of the two collaterals.

$5·5 \times 2·5$ μm (mean about 3×2 μm). This variation was apparent in both the dorsal and the ventral areas, and there was no tendency for boutons of any particular size to be distributed to one or other area.

For twenty-six boutons measured in each area from sagittal sections and eighty (ventral area) and sixty-seven (dorsal area) measured from transverse sections, there were no statistical differences in size between the samples (Student's t test).

In sections counterstained with methylene green boutons could be seen to contact neuronal cell bodies in the medial part of the dorsal horn. Somal contacts from clusters of boutons were frequently observed in the ventral parts of the arborization, on small to medium sized neurones (Pl. 2). In the dorsal region somal contacts were rare suggesting that most of the *en passant* boutons contact dendrites.

Afferent fibres from rapidly adapting mechanoreceptors

Only three axons innervating rapidly adapting mechanoreceptors in the foot and toe pads have been stained. Their collaterals had a distinctive morphology very different from that of the Pacinian corpuscle afferent fibres. We are confident, although the sample size is small, that the following description is representative of collaterals from rapidly adapting pad receptors.
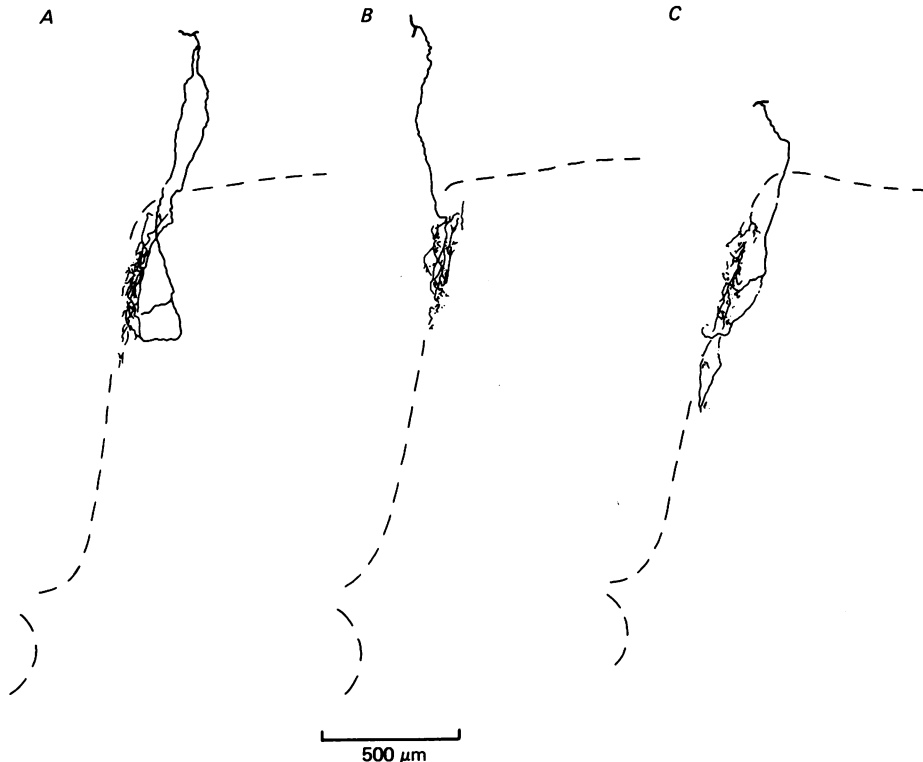

Fig. 5. Reconstructions, in the transverse plane, of three adjacent collaterals from an axon innervating rapidly adapting mechanoreceptors in the glabrous skin of the cat hind limb. The collaterals are from the ascending branch of the axon; *C* is at the most rostral level. Most of the boutons of these collaterals are distributed to lamina III, close to its medial edge. The main collateral branches tend to re-enter lamina III from deeper levels before terminating there. Collateral *A* divides soon after leaving the main axon. Both branches terminate in lamina III.

Entry of axons into the spinal cord, branching and collateral distribution

Each of the three stained axons could be traced into a dorsal root. Two axons bifurcated shortly after entering the spinal cord; one did not. The intraspinal parts of the axons ran medially over the dorsal horn in the dorsal columns to take up their position dorsomedial or medial to the dorsal horn. Fifteen collaterals arose from the stained axons at an average spacing of $783 \pm 338 \, \mu$m (s.d.) with a range of 400–1500 μm. These values for intercollateral spacing of rapidly adapting pad afferent fibres are not statistically different from those for Pacinian corpuscle afferent fibres (Students' *t* test).

The morphology of collaterals from afferent fibres innervating rapidly adapting mechanoreceptors

The distinctive morphology or collaterals from rapidly adapting glabrous skin receptors, as seen in reconstructions from serial transverse sections, is shown in Figs. 5 and 6 and Pl. 3*D*. The collaterals were distributed to the most medial parts of the dorsal horn in line with the somatotopic organization of the horn. In fact because
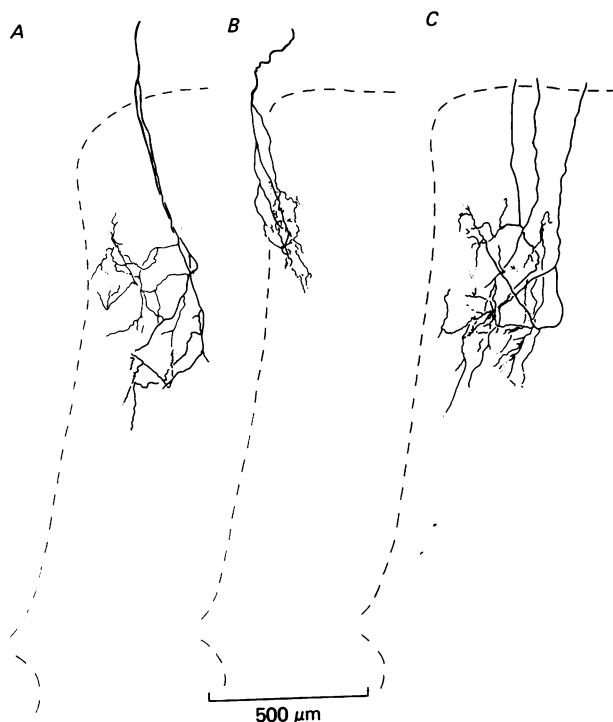

Fig. 6. Reconstructions, in the transverse plane, of five adjacent collaterals from an axon innervating rapidly adapting mechanoreceptors in the glabrous skin of the cat hind limb. These five adjacent collaterals have similar morphologies although they do send more terminal branches into lamina IV than the example in Fig. 5. Again, many of the main collateral branches assume a C-shaped or re-curving trajectory to enter and terminate in lamina III.

of the narrowness of the terminal arborization in the transverse plane (see below) they were distributed to the medial quarter or less of the horn (Figs. 5 and 6).

In reconstructions from the transverse sections (Figs. 5 and 6*B* and Pl. 3*D*) some collateral arborizations bore a resemblance to the 'flame-shaped arbours' typical of hair follicle afferent fibre collaterals (Brown *et al.* 1977). This resemblance extended not only to the over-all branching of the collaterals and their recurving nature, but also to the location of the terminal parts of the arborization which were situated almost exclusively in Rexed's lamina III. Other collaterals (Fig. 6*A* and *C*) did not resemble hair follicle collaterals. When the arborizations were examined for their longitudinal extent, however, it was apparent that they differed from those of hair follicle afferent fibres. In the rostro-caudal direction collateral arborizations of

rapidly adapting mechanoreceptive afferents from glabrous foot pad skin did not form long uninterrupted columns of terminal arborizations with overlap between the arborizations of adjacent collaterals. In our material there have always been gaps between the arborizations of adjacent collaterals. The gaps ranged from 100 to 700 μm in length and the arborizations themselves occupied some 400–600 μm in the longitudinal direction. In the transverse plane the arborizations were 50–300 μm wide, considerably narrower, on the average, than the arborizations of most hair-follicle afferent fibre collaterals (Brown *et al.* 1977).

The terminal axons of the collaterals from rapidly adapting glabrous skin mechano-receptors tended to run in the longitudinal direction in lamina III, although their orientation was not as strictly confined to this direction as those of hair follicle or Pacinian corpuscle units in the same part of the cord. Occasional terminal axons, carrying synaptic boutons, were also seen in lamina IV, but most of the terminal arborization, by far, was in lamina III.

The terminal axons carried synaptic boutons. Many of these were of the *en passant* variety but small groups or clusters of boutons were also observed, arising from two or three short axonal branches. The boutons were of similar sizes to those carried by other primary afferent fibre collaterals.

DISCUSSION

The diagram of Fig. 7*A* summarizes the gross morphology of Pacinian corpuscle afferent fibres at and near their entrance to the spinal cord. Like most cutaneous and muscle afferent axons (Brown, 1977; Brown *et al.* 1977; Brown, Rose & Snow, 1978; Brown & Fyffe, 1978, 1979), those innervating Pacinian corpuscles associated with the foot and toe pads usually bifurcate into an ascending and a descending branch shortly after entering the cord. Both branches move medially over the dorsal horn and come to lie in the dorsal columns. From both ascending and descending branches of the parent axon numerous collaterals arise. The suggestion made by Boivie & Perl (1975) that axons from Pacinian corpuscles might not have major branches at the segmental level is therefore refuted.

Boivie's & Perl's (1975) suggestion was always unlikely to be correct. There is no *a priori* reason why axons that have little or no conduction velocity reduction over a given distance should not give off branches. Furthermore, it was known that selective activation of Pacinian corpuscles could lead to primary afferent depolarization at the segmental level (Jänig *et al.* 1968*a*) and it is generally accepted that this depolarization (responsible for presynaptic inhibition) is mediated via local inter-neurones (see Schmidt, 1973). These interneurones, located in the dorsal horn, would necessarily receive excitation from collaterals of Pacinian corpuscle afferent fibres. In addition, according to Jänig *et al.* (1968*a*) the receptors activated in the studies of Gray and his collaborators (Armett & Hunsperger, 1961; Armett *et al.* 1962) may be positively identified as Pacinian corpuscles. It may be concluded, therefore, that the population of interneurones in the medial part of the dorsal horn studied by Armett *et al.* (1961, 1962) received monosynaptic input from axons innervating Pacinian corpuscles.

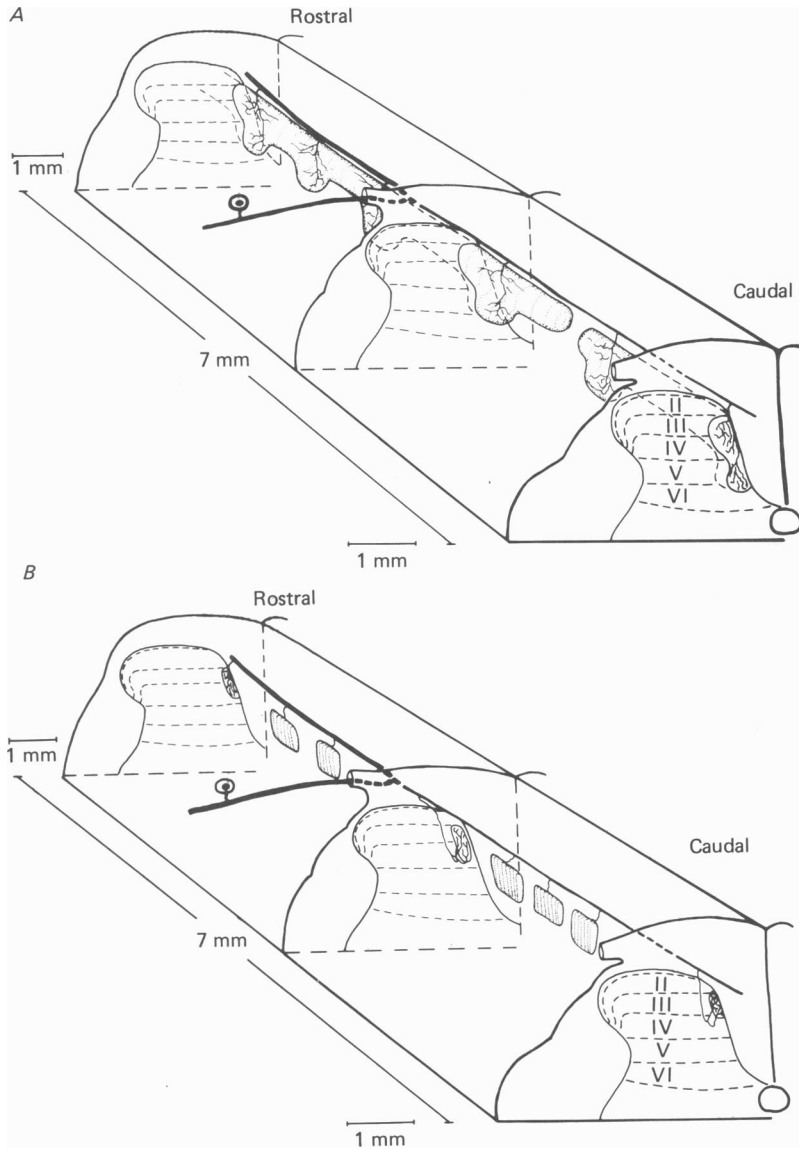The present results showing that axons from Pacinian corpuscles give off collaterals

Fig. 7. Schematic representation of terminal arborizations of A, Pacinian corpuscle, and B, rapidly adapting afferent fibres in the lumbosacral dorsal horn. The Figure is drawn to scale except that collateral spacings are somewhat wider than the average to provide a clearer diagram. The terminals from Pacinian corpuscle afferent fibres (A) are distributed to laminae III–VI with the more dorsal part (laminae III–IV) having greater rostro-caudal development and often being contiguous, or overlapping, with that of adjacent collaterals. The terminal arborizations of the rapidly adapting afferent fibres are limited mainly to lamina III and adjacent arborizations rarely overlap.

near their point of entry to the cord establish that the degree of branching of an axon is not necessarily reflected in condution velocity, and therefore diameter, reduction. Axons from Pacinian corpuscles give off about the same numbers of collaterals at about the same spacing as other cutaneous axons distributing their input to the medial dorsal horn (Brown *et al.* 1977, 1978). But Pacinian corpuscle afferent fibres have little, if any, change in conduction velocity after entering the cord (Jänig *et al.* 1968*a*; Brown, 1968, 1973, and A. G. Brown, unpublished observations; Petit & Burgess, 1968), whereas hair follicle afferent fibres exhibit drastic conduction velocity reductions (Brown, 1968; Petit & Burgess, 1968; Horch, Burgess & Whitehorn, 1976). Conduction velocity changes are therefore not reliable guides to the degree of branching of an axon.

The axons innervating Pacinian corpuscles of the foot and toe pads have collaterals with a characteristic morphology. The collaterals appear not to have been described previously in the anatomical literature. The collaterals distribute their terminal arborizations to Rexed's (1952) laminae III to VI of the dorsal horn. They do not send terminals to laminae I or II and in this respect are similar to those of other large myelinated cutaneous and muscle afferent fibres. Within laminae III–VI there are two distinct regions of termination (Fig. 7), a larger dorsal region in laminae III and IV and a smaller ventral region in laminae V and VI. There is nearly always a clear gap between the two regions of termination and within them the orientation of the terminal, bouton carrying, axons differs. In the dorsal region, especially in its lamina III part, the terminal axons are aligned within the plane of parasagittal sections and run more or less parallel with the long axis of the cord. This orientation is similar to that of other primary afferent collateral terminals in lamina III, for example those from hair-follicle afferent fibres (Brown *et al.* 1977) and also of many of the dendrites that are contained in this part of the cord (Scheibel & Scheibel, 1968). In the ventral region the terminal axons of Pacinian corpuscle axon collaterals are orientated mainly within the transverse plane and run dorso-ventrally, either perpendicularly near the medial edge of the horn or, more often, at up to 45° from the perpendicular. This orientation reflects that of many dendrites in this region (Scheibel & Scheibel, 1968; Proshansky & Egger, 1977). These observations suggest that input from Pacinian corpuscles of the foot and toe pads is distributed to at least two separate populations of neurones in the dorsal horn. At present it is not possible to identify these populations of neurones with respect either to their morphology or their function.

Of the three sets of somaesthetic pathway arising in the dorsal horn (the spino-cervical, the spinothalamic and the post-synaptic pathways to the dorsal column nuclei running in both the dorsal columns and the dorsolateral funiculus; see Brown, 1973; Brown & Gordon, 1977; Gordon & Grant, 1972; Rustioni & Molenaar, 1975; Rustioni & Kaufman, 1977) none has been shown to carry information from Pacinian corpuscles. Sensitive mechanoreceptors in the foot and toe pads do not excite spino-cervical tract neurones (Brown & Franz, 1969; Brown, 1973). Cells of the spinothalamic tract in primate species may respond at the onset and termination of a mechanical stimulus to the glabrous skin (Willis, Trevino, Coulter & Maunz, 1974). They might, therefore, receive excitation from Pacinian corpuscles but the matter has not been examined rigorously. A similar position exists for the post-synaptic dorsal column path in the cat. Angaut-Petit (1975) described neurones of the system with receptive

fields including glabrous skin and which responded with a rapidly adapting discharge to 'light tactile stimulation'.

Individual collaterals from axons of Pacinian corpuscles have, in the present material carried up to about 370 synaptic boutons. Most (two-thirds) of these are within the dorsal termination region. This dorsal arborization contains a greater density of axons (and boutons) than the ventral region as well as being wider medio-laterally and longer rostro-caudally – the dorsal arborizations of adjacent collaterals often overlap in the long axis of the cord whereas the ventral arborizations only rarely overlap. A feature of the synaptic boutons of collaterals from Pacinian corpuscle afferent fibres is their heterogeneous appearance. They have widely varying sizes and show different arrangements in the two termination areas. Boutons *en passant* are found in both areas, and in the dorsal area this type predominates. In the ventral area boutons are often arranged in clusters on neuronal somata. It is reasonable to speculate that synaptic transmission between the synaptic boutons and dorsal horn neurones might be very secure but study of the synapses at the ultrastructural level will be necessary for any firm conclusions to be drawn.

The present results have also established that rapidly adapting mechanoreceptors in glabrous skin (the Krause corpuscles) are innervated by axons whose collaterals in the spinal cord have a distinct morphology. This morphology, summarized in Fig. 7B, is different from that of the axons innervating Pacinian corpuscles deep to the glabrous skin and from that of axons innervating other cutaneous and muscle receptors. The specific morphology and distinctive distribution to different parts of the dorsal horn grey matter imply specific connectivity of the afferent fibres.

At first sight some collaterals of the rapidly adapting mechanoreceptive afferent fibres bear a resemblance to those from hair-follical units (Brown *et al.* 1977). Both types of collaterals have recurving branches that descend into lamina IV and sometimes to lamina V before turning to ascend and break up into their terminal arborizations in lamina III. The terminal arborizations are both of the 'flame-shaped arbour' type. There are, however, marked differences between the two. Hair-follicle afferent fibre collaterals form continuous columns of terminal arborization running for many millimetres and supplied by several (at least ten) collaterals. In contrast, the collaterals of axons innervating rapidly adapting glabrous skin receptors each terminate in their own private volume of cord with (in our sample) no overlap between adjacent collaterals. A further difference between the two types is that synaptic boutons of hair follicle axons are nearly all of the *en passant* type whereas axons from rapidly adapting mechanoreceptors also show clusters of boutons in addition to boutons *en passant*.

Information from rapidly adapting mechanoreceptors is distributed to lamina III and (weakly) to lamina IV. Neurones receiving monosynaptic excitation from these receptors will have their dendrites and somata in laminae III and IV. Little is known, however, about the possible identity of such neurones. The position is similar to that with regard to input from Pacinian corpuscles; they should excite neurones on presynaptic inhibitory pathways (Jänig *et al.* 1968*b*), and possibly cells of the spinothalamic tract (Willis *et al.* 1974) and the post-synaptic dorsal column path (Angaut-Petit, 1975). But much neurophysiological work is required before conclusions can be drawn regarding the function of input from the Krause corpuscles.

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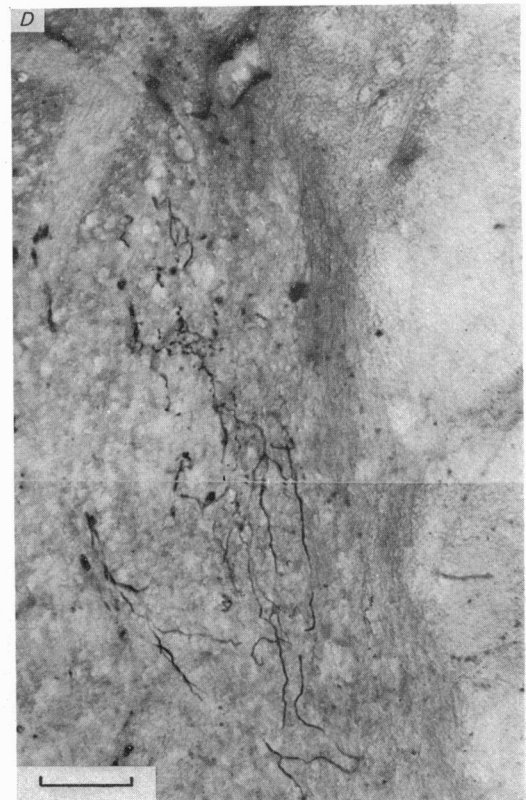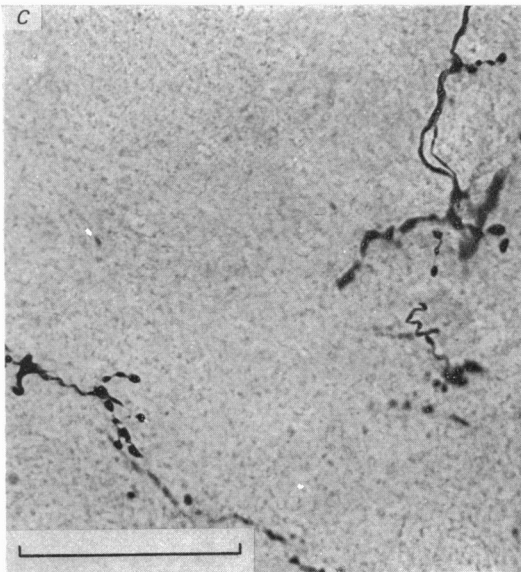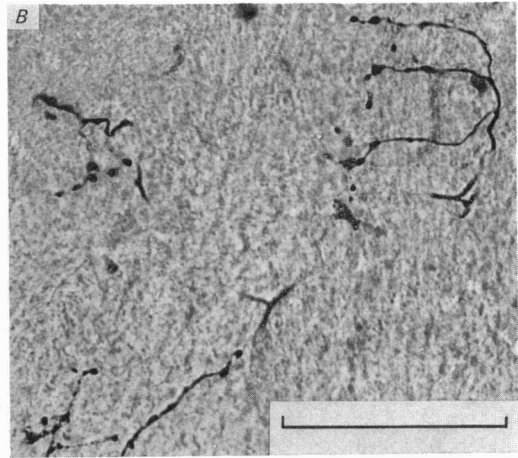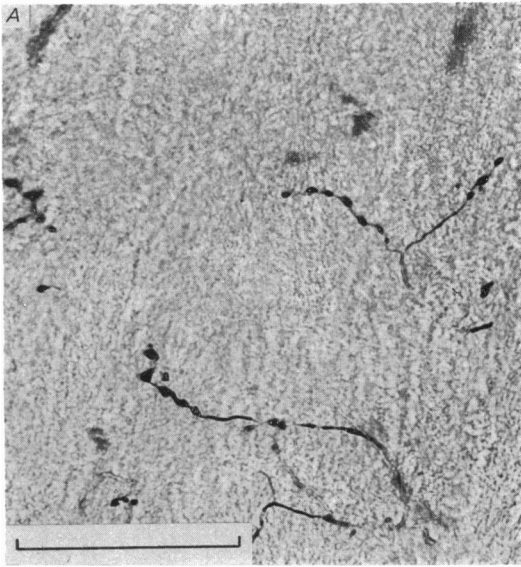
EXPLANATION OF PLATES

PLATE 1

A, *B* and *C*, photomicrographs, from 100 μm thick sagittal sections, of terminal branches of Pacinian corpuscle afferent fibre collaterals. Each example shows boutons from the laminae III–IV arborizations of these collaterals. Note how clearly the terminal branches, with their *en passant* boutons, are oriented within the plane of these sections. Dorsal is at the top, rostral to the left of the Figure. *D*, photomicrograph, from a single 100 μm thick transverse section of cord, showing part of a collateral from an axon innervating rapidly adapting mechanoreceptors. The medial and dorsal borders of the dorsal horn can be seen. Although collateral branches penetrate deep into lamina IV, they then change direction and recurve dorsally again to terminate mainly in lamina III. Scale bars: 100 μm.
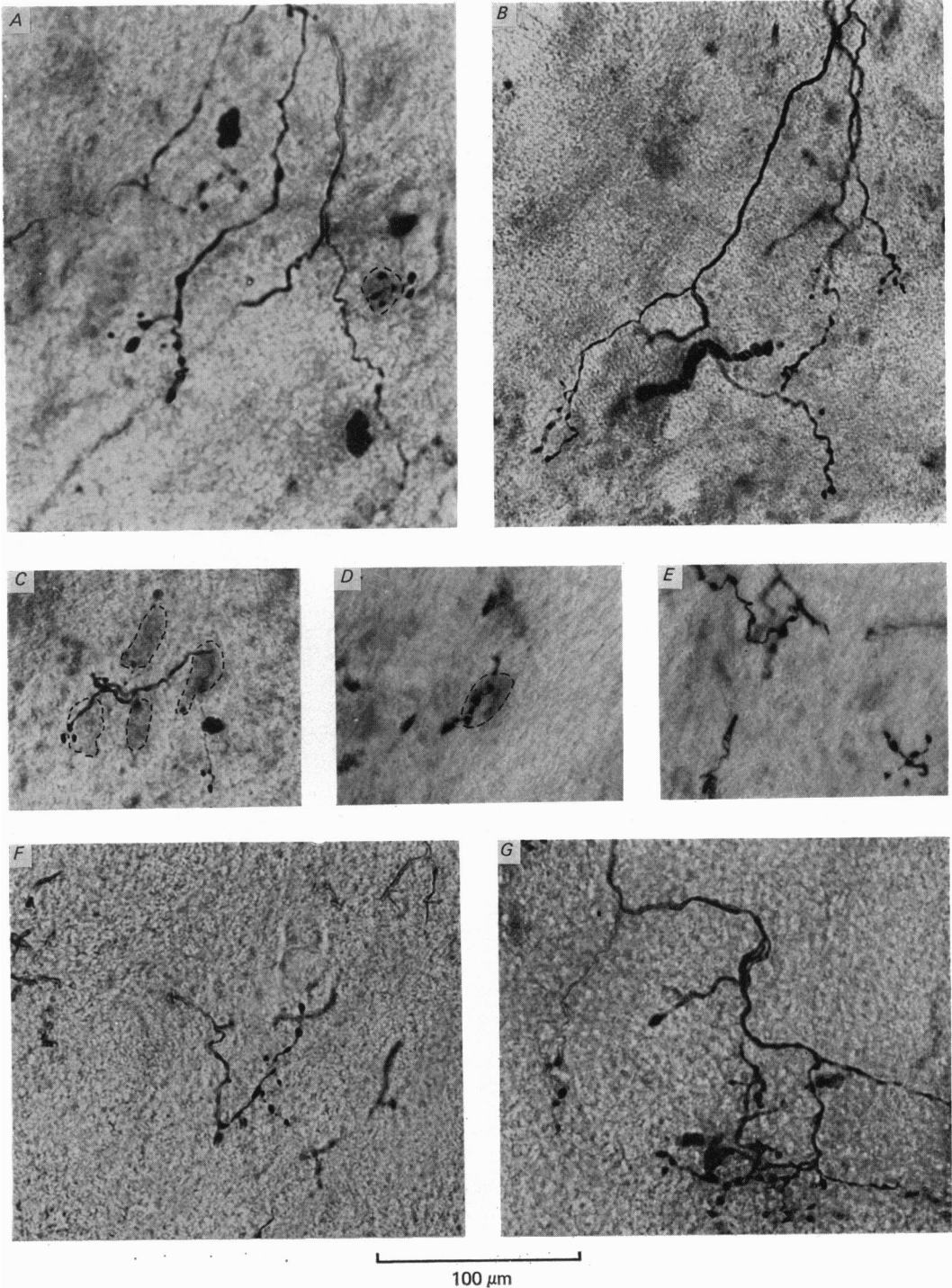
PLATE 2

All micrographs are from 100 μm thick sections through parts of Pacinian corpuscle axon collateral branches in laminae V and VI; *A*, *B* and *C* from transverse sections, *D–G* from sagittal sections. In counterstained sections (*A*, *C* and *D*) neurones contacted by boutons are outlined by dashed lines. Many of the fine terminal branches carry only one or two boutons and distribute these boutons in small clusters. There was no significant difference in size between these boutons and the *en passant* boutons predominant in more dorsal laminae (Pl. 1).

100 μm

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