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THE MORPHOLOGY OF GROUP Ib AFFERENT FIBRE COLLATERALS IN THE SPINAL CORD OF THE CAT

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SUMMARY

1. The enzyme horseradish peroxidase (HRP) was injected into single Ib muscle afferent fibres in anaesthetized cats. Subsequently, histochemistry allowed the morphology of the axons and their collaterals in the lumbosacral spinal cord to be determined.

2. Eleven Ib axons were stained, seven from lateral gastrocnemius-soleus, one from medial gastrocnemius and three from muscles innervated by the posterior tibial nerve. Ten of the axons were traced into the dorsal roots and all but one (from the posterior tibial nerve) bifurcated upon entering the cord. Between 5·1 and 9·9 mm of each axon was stained and the fibres gave off eighty-four collaterals at intervals of 100–2300 μm, at an average spacing of about 900 μm. The spacing between collaterals on the (finer) descending axon branches was generally less than the intervals between collaterals on ascending branches.

3. All Ib collaterals had a characteristic morphology. The collaterals coursed cranially on a direct path through the dorsal horn to lamina IV or V before branching. They arborized widely in the intermediate region, mainly in lamina VI and in the dorsal part of lamina VII. Occasionally, less extensive arborizations were seen more dorsally in lamina IV and V. The rostro-caudal extent of individual collateral arborizations was limited to 200–400 μm and there was no overlap between adjacent collaterals. Each terminal arborization gave rise to 56–384 boutons, mainly of the 'en passant' type.

4. The results are discussed in relation to previous anatomical and electrophysiological studies.

INTRODUCTION

The central projections of group Ib afferent fibres from Golgi tendon organs have proved difficult to characterize. Classical anatomical methods are incapable of providing a definite identification of primary afferent fibre collateral arborizations in the spinal cord. Réthelyi & Szentágothai (1973) tentatively identify Ib afferent collaterals as the relatively large diameter collaterals that arborize widely in the intermediary region and do not reach the motor nuclei. The intermediary region corresponds with the area in which focal potentials greater than 20 % of maximum were evoked by electrical stimulation of Ib fibres (Eccles, Fatt, Landgren & Winsbury, 1954). Ib

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afferents are also known to excite, monosynaptically, the cells of origin of the dorsal and ventral spinocerebellar tracts – the d.s.c.t. and v.s.c.t. respectively (Oscarsson, 1965, 1973; Lundberg, 1971; Lundberg & Weight, 1971).

The recent introduction of intra-axonal staining of electrophysiologically identified axons with horseradish peroxidase (HRP) allows the morphology of primary afferent collaterals to be determined (Brown, Rose & Snow, 1977, 1978; Brown & Fyffe 1978*a*). The present paper describes the morphology of collaterals of group I b muscle, afferent fibres. Some preliminary results were demonstrated to the Physiological Society at the Bristol meeting, January 1978 (Brown & Fyffe, 1978*b*). While we were completing this work a preliminary report by Hongo, Ishizuka, Mannen & Sasaki (1978) was published with findings essentially the same as ours.

METHODS

Full details of the methods have been published previously (Snow, Rose & Brown, 1976; Brown *et al.* 1977). The experiments were performed on eleven cats anaesthetized with chloralose (70 mg.kg^{-1}) and paralysed with gallamine triethiodide. For the present experiments on muscle afferents, the nerves to medial gastrocnemius, lateral gastrocnemius-soleus, and the posterior tibial nerve were exposed in both hind limbs and mounted on bipolar platinum or silver-silver chloride electrodes for stimulation in continuity. Ingoing volleys were monitored at the dorsal root entrance zone with a monopolar silver ball electrode. Conduction distances from peripheral nerve to the spinal cord were carefully measured at the end of each experiment. Glass microelectrodes filled with an 8 % solution of HRP were used for recording and injecting axons near their entry into the spinal cord. Frozen, 100 μm thick transverse or longitudinal sections were cut and processed by the method recently developed by Hanker, Yates, Metz & Rustioni (1977). Some sections were counterstained with 0·1 % methylene green.

RESULTS

Eleven I b afferent fibres with their collaterals were stained in the present experiments, seven from lateral gastrocnemius-soleus, one from medial gastrocnemius and three from muscles with axons in the posterior tibial nerve. For each axon the peripheral conduction velocity and the threshold to electrical stimulation of the nerve were measured. All the axons had peripheral conduction velocities between 80 and 98 m.sec^{-1}. None of the axons had ongoing activity when isolated and required noticeable stretch (manual extension or flexion of joints) to excite them. The differentiation of the group I muscle afferent fibres into I a and I b fibres on the basis of these characteristics was always supported by subsequent morphological data. Fibres identified as belonging to group I a had collaterals reaching the motor nuclei (Brown & Fyffe, 1978*a*). Group II fibres were excluded from our sample on the basis of conduction velocity. These fibres conduct at less than 70 m.sec^{-1} (Matthews, 1963) and have recently been shown to have collaterals with a characteristic morphology (Fyffe, 1979).

Successful staining of the I b afferent fibre collaterals, to the level of boutons in the intermediate region, required more than 150 nA.min of current to be passed. At the end of the injection period (up to 30 min) it was usually possible to continue recording the activity of the fibre and then to monitor a change in membrane potential when the electrode was removed.

Density and distribution of Ib collaterals

Fig. 1 shows, in diagrammatic form, the main features of the Ib axons and their collaterals. For each axon the following information is shown: the total rostro-caudal length of axon stained, whether or not it could be traced into the dorsal root, whether it bifurcated into ascending and descending branches upon entering the cord, and the number and spacing of the collaterals. Ten of the axons could be seen entering the cord through the dorsal roots and nine of these bifurcated into ascending and descending branches. The axon that did not appear to bifurcate ran in the posterior tibial nerve. In general the ascending branch was thicker than the descending branch of the axon. The total lengths of axon stained ranged from 5·1 to 9·9 mm (7·64 ± 1·8 mm; mean ± S.D.). The ascending branches were stained for distances of 5·0–9·6 mm whilst the descending branches ranged from 0 to 3·8 mm. These values are similar to those for cutaneous and other muscle afferent fibres we have stained. None of the main branches in the present sample terminated in a collateral; presumably the axons were longer than the stained material indicated, and gave off further collaterals.

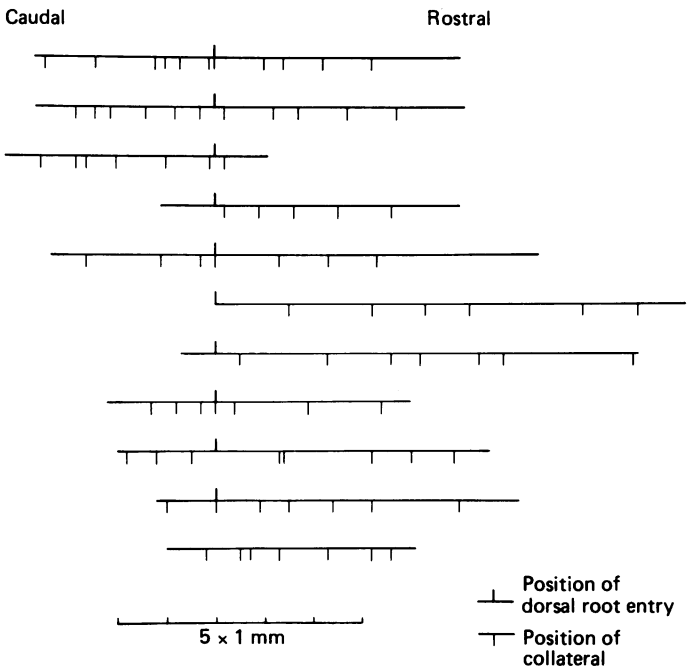

Fig. 1. Diagrammatic representation of the branching pattern of Ia afferent fibres in the spinal cord. The total stained length of each axon is shown, together with (where possible) the position of its entry to the cord through the dorsal root and the origin of stained collaterals. All but one of the axons that could be traced into the dorsal root can be seen to bifurcate upon entering the cord. For further description see the text.

We have no evidence that the HRP fails to stain collaterals between the most rostral and caudal ones, and therefore we obtain some useful data on the spacing of collaterals. Typically a few collaterals close to the injection site were well stained and

demonstrated extensive branching and filling of fine terminal branches and boutons. Collaterals arising further away were more lightly stained; few if any terminal branches or boutons could be observed.

The main rostral and caudal branches moved medially from their entry into the cord and bifurcation, to assume wavy courses in the dorsal column. A total of eighty-four collaterals arose from the eleven Ib axons, with a range of five to eleven from each axon (7·4 ± 2·0; mean ± S.D.). Fifty collaterals arose from the ascending branches, twenty-seven from the descending branches and seven from the axon which could not be traced into a dorsal root. The latter axon was probably part of the ascending branch of the Ib afferent – as it was traced rostrally its course assumed a deeper position in the dorsal columns.

The distance between the most rostral and most caudal collaterals of a stained axon ranged from 3·4 to 8·0 mm, and the collaterals were spaced at intervals of 100–2600 μm (890 ± 506 μm; mean ± S.D.). There is no significant difference between this value and that obtained for Ia afferents, which have a mean spacing between collaterals of about 1 mm (Brown & Fyffe, 1978*a*). However in the present sample of Ib axons it was apparent that collaterals arising from the descending branches of the axons were more closely spaced than collaterals arising from the ascending branches. Intervals on descending branches ranged from 200 to 1500 μm (690 ± 331 μm; mean ± S.D.) whilst spaces between collaterals on ascending branches ranged from 100 to 2600 μm (1080 ± 524 μm; mean ± S.D.). The difference between collateral spacing on the ascending and descending branches is highly significant ($P < 0·001$). There was no significant increase in the spacing of collaterals arising further from the root entrance of the parent axon. This was so even on ascending branches stained for up to 9·6 mm from the entrance.

Morphology of Ib collaterals

The main morphological features of a variety of Ib afferent fibre collaterals from triceps surae and muscles innervated by the posterior tibial nerve are shown in Figs. 2–5 and Pl. 1. The characteristic branching patterns are strikingly similar for all Ib collaterals stained in this sample.

Collaterals usually entered the dorsal horn at the dorsomedial or dorsal edge and ran ventrally in a direct course to lamina IV or V before branching. As can be seen most clearly from the sagittal reconstructions of Fig. 4, collaterals ran slightly rostrally and approximately in parallel with each other for this initial part of their course through the dorsal horn. Branching, which started in lamina V, gave rise to an extensive fan shaped arborization, 400–800 μm wide in the transverse plane, in which the terminal collateral branches were mainly located in the medial and central parts of lamina VI and in the dorsal part of lamina VII.

In contrast to the wide transverse distribution of Ib terminal arborizations in the intermediate region, the rostro-caudal extent of any collateral was usually restricted to 200–400 μm. There was no overlap between adjacent collaterals so that in effect each collateral from a Ib axon occupied a discrete volume of the spinal cord. Even when the origins of adjacent collaterals were as close as 100 μm, the courses taken by the collaterals and the restricted rostro-caudal extent of the aborizations, resulted in the aborizations being separated by as much as 300–400 μm (see Fig. 4).

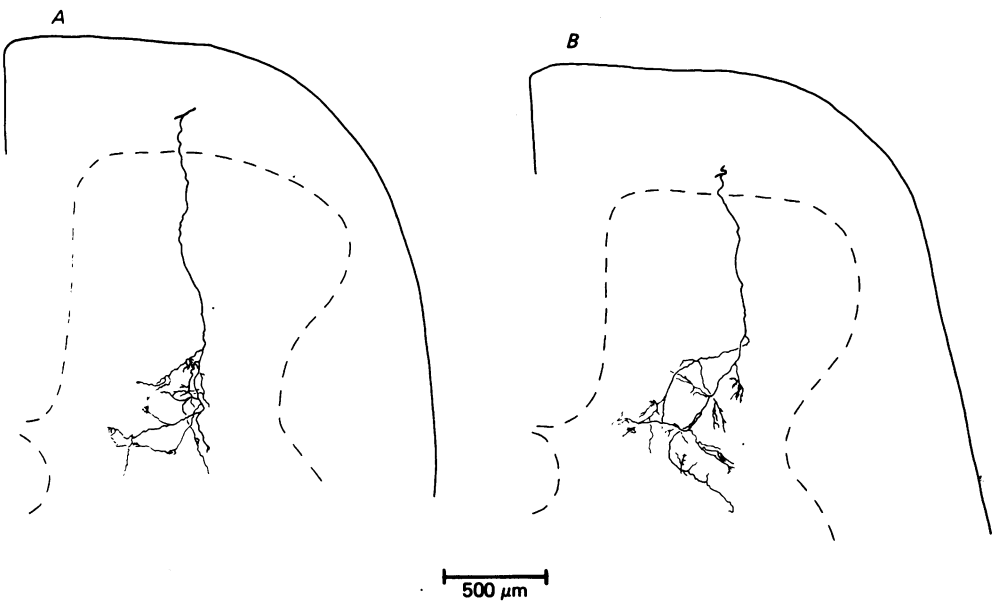

Fig. 2. Reconstructions, in the transverse plane, of two adjacent collaterals from the descending branch of a medial gastrocnemius Ib afferent. Collateral *A* was caudal to collateral *B*. The collaterals enter the dorsal horn at its dorsal edge and run ventrally to lamina V before branching into the characteristic fan shaped arborizations in lamina VI and the dorsal part of lamina VII. The outline of the grey matter is indicated by the dashed line.

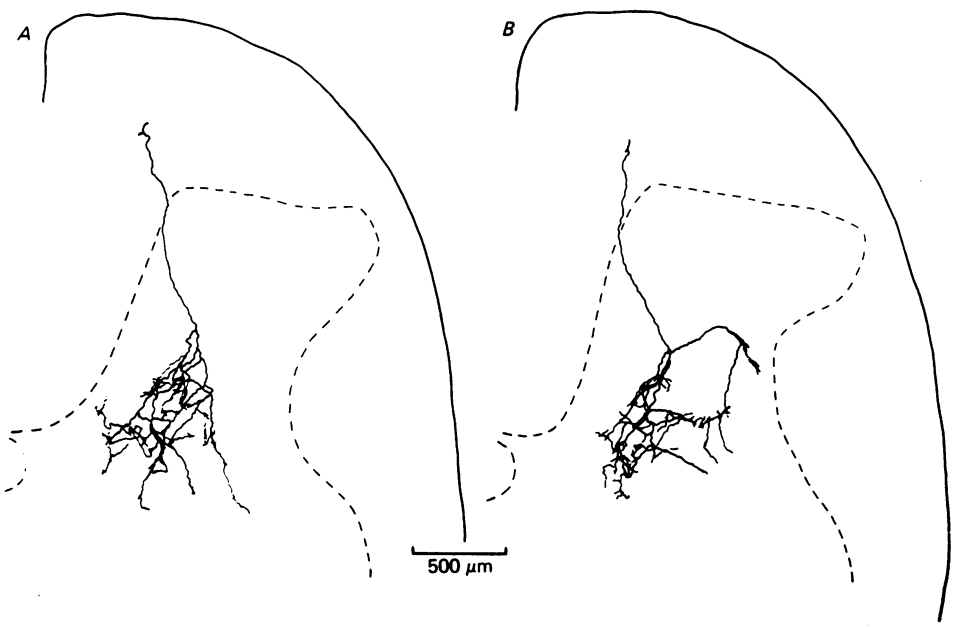

Fig. 3. Reconstructions, in the transverse plane, of two adjacent collaterals from the ascending branch of a lateral gastrocnemius-soleus Ib afferent. The main arborizations in medial and central lamina VI are similar to those in Fig. 2. The more rostral collateral (*B*) also projects to the lateral parts of laminae V and VI.

Although the branching pattern of the Ib collaterals usually generated a single extensive arborization in the medial half of lamina VI some Ib collaterals projected to other regions. One lateral gastrocnemius Ib afferent injected close to the dorsal root entrance had three well stained collaterals with minor branches given off more dorsally, in lamina IV. These gave rise to small arborizations in the centre of lamina IV. All of these collaterals arose from the descending branch of the Ib axon, about 2–3 mm caudal to the dorsal root entrance. The most caudal of these collaterals is shown in Fig. 5*A*. Apart from this minor arborization the general pattern of this collateral was similar to collaterals from other Ib axons; further branching produced the main fan-shaped terminal arborization in lamina VI.

The other region to which some of the present sample of Ib collaterals projected was the lateral part of laminae V and VI. Projections to this area were observed more commonly than the projections dorsally in lamina IV, especially on collaterals located

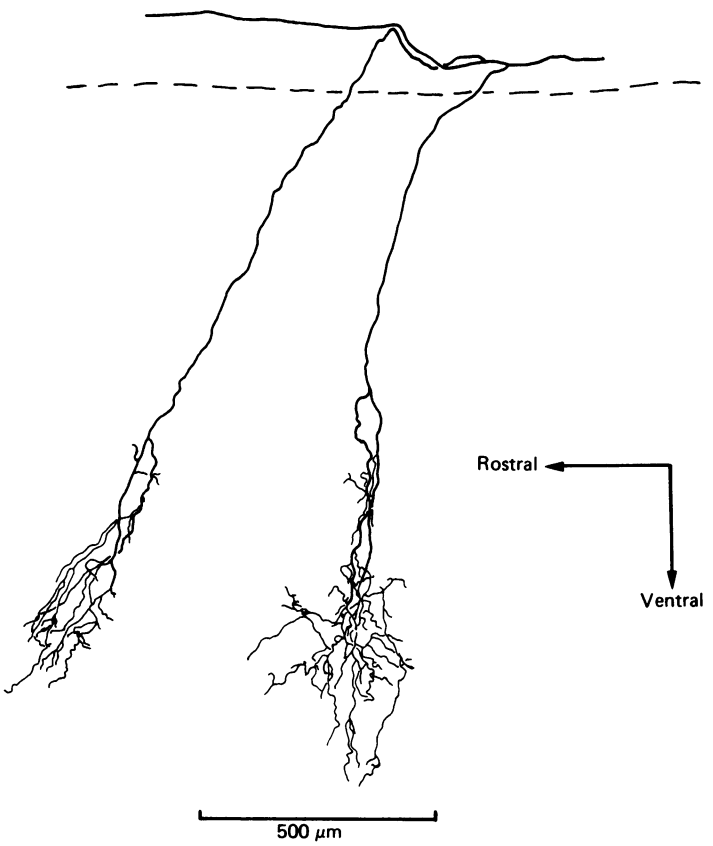

Fig. 4. Reconstructions, in the sagittal plane, of two adjacent collaterals from the ascending branch of a lateral gastrocnemius-soleus Ib afferent. This view shows the cranial trajectory of the collaterals towards their terminal arborizations. Although the collaterals arise close to each other on the parent axon there is no overlap between the two arborizations. The rostro-caudal extent of each arborization is restricted to less than 400 μm in contrast to the wide transverse spread seen in Figs 2, 3 and 5. The dashed line indicates the dorsal border of the dorsal horn.

in the upper L7 segment. Two examples, from different Ib axons are shown in Figs. 3*B* and 5*B*. The collaterals shown in these reconstructions were located 6–8 mm rostral to the entry of their respective parent axons into the spinal cord. In both cases the ascending branch of the Ib axon had been injected 3–4 mm rostral to the dorsal root entry. In Fig. 3 the collaterals are from the same Ib axon. Both arborize characteristically in medial and central lamina VI but additionally the more rostral collateral (3*B*) sends branches to terminate within 100 μm of the lateral border of lamina V and also in the lateral part of lamina VI. Fig. 5*B* is a reconstruction of a rostral collateral from a different Ib axon. This collateral branched soon after entering the medial part of the dorsal horn and sent branches ventrolaterally to terminate in lateral lamina VI and in dorso-lateral lamina VII. Other branches of the collateral arborized extensively in the medial half of laminae V and VI.

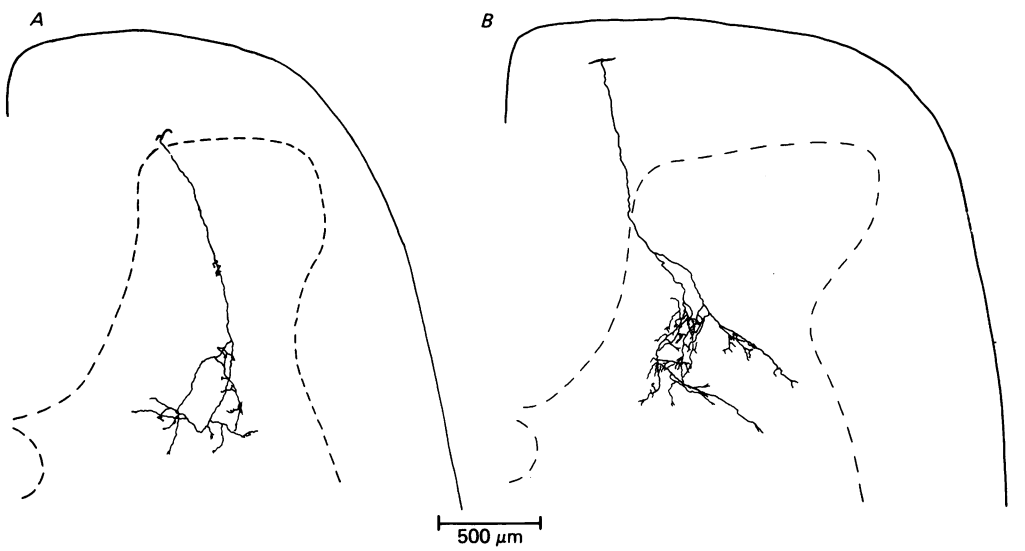

Fig. 5. Reconstructions, in the transverse plane, of two collaterals from different Ib axons. Collateral *A* is from the descending branch of a lateral gastrocnemius-soleus afferent and has a small arborization in lamina IV as well as the major zone of termination in central lamina VI and the dorsal part of lamina VII. Collateral *B* is from a lateral gastrocnemius-soleus afferent ascending the cord. The collateral arises about 7 mm from the dorsal root entry. The main arborization is in the medial half of laminae V and VI. There are also prominent projections to the lateral part of lamina VI, and to dorso-lateral lamina VII.

Terminal arborizations and synaptic boutons of Ib collaterals

Successive branching of the pre-terminal axons gave rise to fine terminal branches usually located in lamina VI and in dorsal lamina VII. Most of the terminal branches were oriented more or less in the dorso-ventral or medio-lateral directions, with very few instances of terminal axons running longitudinally up or down the cord. This fine branching pattern expressed itself in the gross morphology described in the previous section, as wide transverse arborizations with restricted rostro-caudal spread. Branch-

ing in and around lamina VI did not always occur at simple bifurcations; often an axonal branch would divide into three daughter branches as illustrated in Pl. 2*A*.

Fig. 6 and Pl. 2 illustrate some of the terminal patterns and bouton arrange-

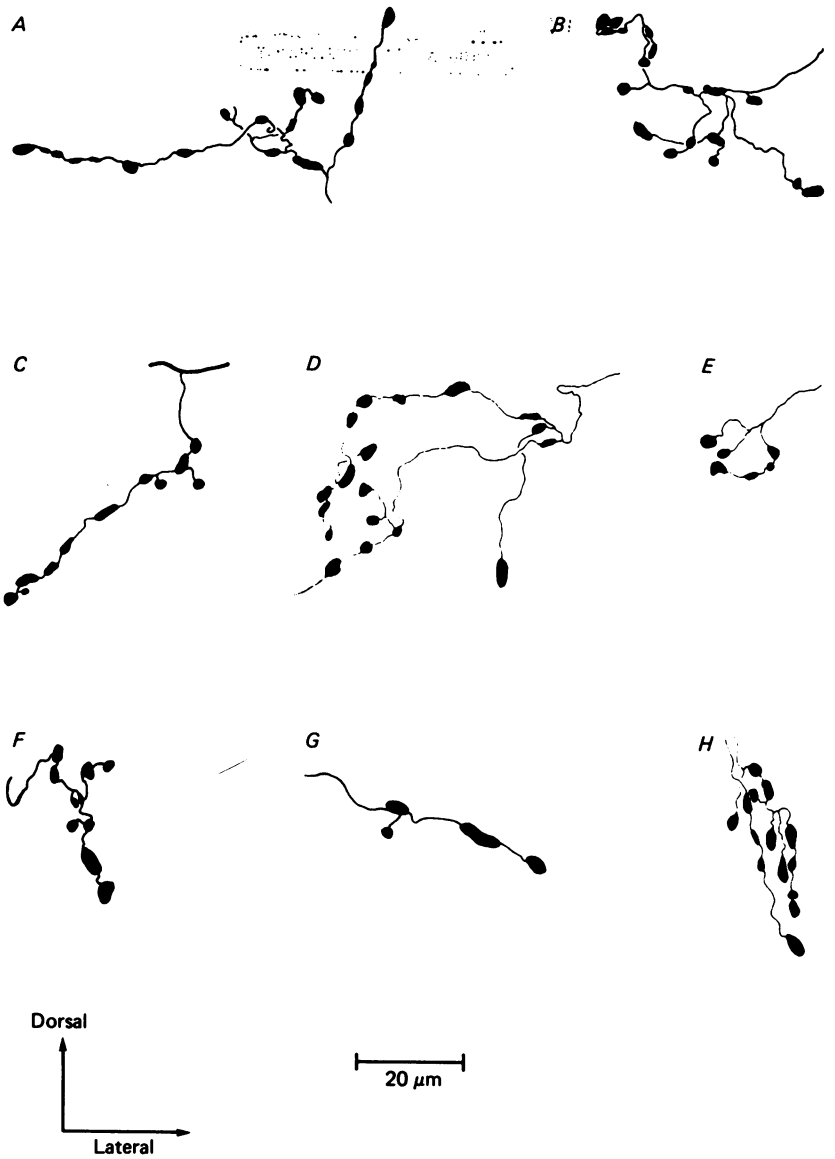

Fig. 6. Reconstructions, in the transverse plane, of some terminal patterns from HRP-labelled Ib afferents. The terminals in *A–E* were located in the medial and central parts of lamina VI and illustrate examples of boutons 'en passant' along the fine terminal branches. More complex branching and clustering of boutons is also evident. Single boutons are often offset from the terminal branch on short fine stalks. In *F–H* are reconstructed some terminals in lateral parts of lamina VI. Boutons were fewer in this region, but even close to the lateral border of the neck of the dorsal horn (e.g. in *H*) complex arrangements could be seen.

ments observed on the Ib collaterals. The predominance of boutons 'en passant' along the terminal branches was characteristic of the Ib collateral arborizations. In transverse sections the boutons 'en passant' lay in the plane of the section. In lamina VI, where most of the Ib boutons were observed, another feature was that single boutons were often offset from terminal branches on short, fine stalks (e.g. Fig. 6 *C*). Some terminal branches divided several times in their final 20–30 μm to give rise to quite complex clustering of boutons 'en passant' and 'terminaux' (e.g. Fig. 6 *B*, *D*). Branches which terminated in dorsal lamina VII generally had rather simpler arrangements, consisting of only a few boutons 'en passant' along the terminal branches. Boutons were also observed on those collateral branches projecting more laterally in laminae V, VI and dorso-lateral VII. Again, the terminal branches carried a few 'en passant' boutons with single boutons offset from the main terminal branch. The few collaterals from the Ib axon which projected to lamina IV, as well as lamina VI, generated quite complex arborizations in the centre of lamina IV. Pl. 2 *B* illustrates the arrangement of one of these minor arborizations.

Boutons in the main terminal arborization in lamina VI were sometimes seen in close association with cell body profiles in sections counterstained with 0·1 % methylene green. The most commonly observed pattern was where a fine branch divided to deliver two to six boutons, on two to three terminal branches, to the stained cell body. Pl. 2 *E* shows four boutons in relation with a medium sized lamina VI neurone. Pl. 2 *D* shows an example of 'en passant' boutons near or on a cell in lamina VI – this arrangement was quite rarely seen. In lateral lamina VI apparent contacts were also observed on some cell bodies (Pl. 2 *F*). In fact only a small proportion of the boutons from the Ib collaterals seemed to be involved in possible contacts on cell bodies. The predominant boutons 'en passant' along the final 20–50 μm of the terminal branches may then be expected to be involved in forming 'climbing' contacts along the dendrites of interneurones in this area.

The total number of boutons from a single Ib collateral ranged from 56 to 384 (179 ± 114; mean $\pm$ S.D.). This number is much larger than the number of boutons in the lamina VI arborization of Ia collaterals (up to ninety-seven, A. G. Brown & R. E. W. Fyffe, unpublished) and reflects the more extensive arborization of Ib collaterals and predominance of boutons 'en passant'. The size of Ib boutons ranged from $1{\cdot}0 \times 1{\cdot}0$ μm to $5{\cdot}0 \times 3{\cdot}0$ μm ($3{\cdot}1 \pm 0{\cdot}97 \times 1{\cdot}7 \pm 0{\cdot}53$ μm; mean $\pm$ S.D., $n = 170$).

DISCUSSION

The technique of intra-axonal staining of electro-physiological identified axons has recently been applied to demonstrate the morphology and central connexions of primary afferent fibres in several systems including the monosynaptic Ia pathway to motoneurones (Brown & Fyffe, 1978*a*, *c*), hair follicle afferent fibre collaterals (Brown, 1977; Brown *et al.* 1977), collaterals from afferent fibres of slowly adapting type I units (Brown *et al.* 1978) and the collaterals of other types of cutaneous and muscle afferent fibres (A. G. Brown, R. E. W. Fyffe, P. K. Rose & P. J. Snow, unpublished results). The present paper extends the sample of stained, identified primary afferent fibres to include the group Ib afferents from Golgi tendon organs of the cat.

The identification of muscle afferent fibres into groups Ia, Ib and II (see Matthews,

1972) was based during each experiment on the conduction velocity of the peripheral nerve fibre and a subjective assessment of its response to passive stretch of the muscle. The group II muscle afferents from muscle spindle secondary endings conduct impulses at less than 70 $m.sec^{-1}$ and are excluded from the present sample of axons which all had conduction velocities greater than 80 $m.sec^{-1}$. This is important since some of the group II muscle afferents have recently been shown to have monosynaptic excitatory connexions to motoneurones (Kirkwood & Sears, 1974; Stauffer, Watt, Taylor, Reinking & Stuart, 1976) and also to project to the intermediate region and the dorsal horn (Fu & Schomburg, 1974; Fu, Santini & Schomburg, 1974). These findings have been supported by intra-axonal injection of HRP into identified group II fibres which show a characteristic branching pattern vastly different from the Ia and Ib collaterals (Fyffe, 1979). The tentative classification of the group I fibres into Ia and Ib carried out during recording was always correlated with the subsequent demonstration of a collateral morphology characteristic of receptor type. The Ia fibres had a regular ongoing discharge when isolated and could be excited by weak stretch or tapping the muscle. All the Ia fibres projected to the appropriate motor nuclei (Brown & Fyffe, 1978*a*). The Ib fibres were silent when isolated and required noticeable stretch of the muscle to excite them. Ib collaterals only projected as far ventrally as dorsal lamina VII.

Successful staining of Ib axons and their collaterals required more than 150 nA.min of current to be passed. The extent of labelling observed was similar to that from previous injections of primary afferent fibres. All but one of the stained Ib fibres was seen to bifurcate on entering the cord and to ascend or descend the cord in the dorsal columns. Generally the rostral branch of the stem axon was thicker than the caudal branch.

Assuming that all the collaterals between the most rostral and most caudal ones were stained, the average distance between adjacent collaterals was about 890 μm. This is similar to the value obtained for the inter-collateral distances on Ia fibres (Brown & Fyffe, 1978*a*) and considerably longer than values obtained from Golgi studies of primary afferent fibres in young animals (Scheibel & Scheibel, 1969). However it was apparent that collaterals arising from the descending branch were more closely spaced, with a mean distance between adjacent collaterals of 690 μm, than collaterals on the ascending branch of the axon, which had average intervals of 1080 μm. Although the ascending branches were always stained for greater distanees than the descending branches, there was no significant increase in the collateral spacing further away from the dorsal root entry. In the 3 mm either side of the dorsal root entry collaterals were, as stated, more closely spaced on the descending branches. In a recent preliminary report, Hongo *et al.* (1978) also observed longer inter-collateral distances on the ascending branches of a small pooled sample of stained Ia and Ib axons. The significance, if any, of this observation is obscure.

Ib collaterals had a characteristic gross morphology which agreed with expectations from many previous anatomical and electrophysiological experiments. In the transverse plane the general pattern is strikingly similar to the collaterals shown in Fig. 5*A* of Réthelyi & Szentágothai (1973). The collaterals run directly through the dorsal horn to lamina V before branching extensively and arborizing in laminae V, VI and dorsal lamina VII, mainly in the medial half of lamina VI. None of the Ib collaterals

in the present sample projected more ventrally than dorsal lamina VII. Only one Ib axon had (three) collaterals which projected dorsal to lamina V. These collaterals, which projected to the centre of lamina IV, all arose from the descending branch of that axon.

Ib collaterals pursue a cranial trajectory towards their terminal arborizations. This is similar to the path taken by Ia collaterals and this feature has not been observed in anatomical investigations of primary afferent fibre projections using Golgi staining methods in young animals (see for example Fig. 9 in Scheibel & Scheibel, 1969). Presumably the cranial trajectory of the collaterals develops as the kitten grows.

The wide fan-shaped arborization seen in lamina VI and dorsal VII in transverse sections contrasts with the sagittal view of the Ib arborizations. Each collateral has a restricted rostro-caudal spread, with most of the terminal branches oriented transversely or in the dorso-ventral direction. There was never any overlap between adjacent collaterals; each arborization occupied a discrete zone of the spinal cord. In the previous study of Ia fibres, some collaterals gave rise to an almost uninterrupted sagittal column of terminals in the intermediate region, although the lamina VI arborizations of Ia collaterals are much less complex in transverse spread and bouton density than the Ib arborizations.

The zone of termination of Ib collaterals corresponds very closely with the localization of focal synaptic potentials greater than 20 % of maximum evoked by electrical stimulation of Ib afferents from hind limb muscles (Eccles, Fatt, Landgren & Winsbury, 1954). The effects of tendon organ activation must be mediated by interneurones located in, or with dendritic arborizations in, this part of the intermediate region. The mechanism of autogenetic inhibition of homonymous and synergic muscles has been intensively studied. Laporte & Lloyd (1952) associated this inhibition, and the reflex facilitation of antagonistic motoneurones, with activity in tendon organ afferents. They also postulated a disynaptic linkage mediating these effects. Since these early experiments a wealth of data on the segmental reflex response patterns to the Ib impulses has been provided by intracellular recording from interneurones and motoneurones (see, for example, Eccles, Eccles & Lundberg, 1957; Eccles & Lundberg, 1959; Jankowska & Lindström, 1972). Recently Lucas & Willis (1974), using adequate stimulation of tendon organs, demonstrated monosynaptic excitation by Ib afferents of interneurones in the medial parts of laminae VI and VII.

Studies using either electrical or adequate stimulation of Ib afferents (Eccles, 1965; Jankowska & Lindström, 1972; Lucas & Willis, 1974) have indicated that most of the interneurones in the intermediate region activated by group I afferents belong to the Ib pathway from Golgi tendon organs. The projection of Ib afferent fibre collaterals described in this paper provides an anatomical basis for such excitation of interneurones in the intermediate region. Where counterstained sections were examined, two to six boutons could occasionally be seen in close apposition to stained cell bodies. Furthermore, Ib collateral terminal branches in and around the medial half of lamina VI commonly carried five to ten boutons 'en passant'. Such arrangements may indicate 'climbing' bouton connexion along dendrites, and provide a powerful synaptic input.

Detailed electrophysiological work has also been carried out on the distribution of Ib effects to pathways ascending from the spinal cord to the cerebellum, especially

through the d.s.c.t. and v.s.c.t. (for review see Oscarsson, 1973). The d.s.c.t. takes its origin in the cells of the nucleus dorsalis or column of Clarke (Clarke, 1859; see Rexed, 1954) an anatomically well defined column of cells extending from thoracic segments down into the fourth lumbar segment. Thus primary afferents entering the cord at lower lumbar levels have to ascend for at least two segments before giving collaterals to these cells. It would clearly be of interest to stain Ib collaterals at the level of Clarke's column in the upper lumbar segments. None of the present sample of Ib axons was stained for that distance. However, the most rostrally located collaterals described in this paper had indeed marked arborizations in the medial parts of the intermediate region and if this pattern is also characteristic of Ib collaterals in upper lumbar segments then it would provide an anatomical basis for Ib excitation of d.s.c.t. cells in these locations.

Ib input to the v.s.c.t. has also been studied by various workers (e.g. Oscarsson, 1957; Burke, Lundberg & Weight, 1971). Hubbard & Oscarsson (1962) described cells of origin of the v.s.c.t. in a widespread region dorsomedial to the ventral horn. In later studies, Lundberg and coworkers (Burke *et al.* 1971; Lundberg & Weight, 1971; Lundberg, 1971) described the spinal border cells of Cooper & Sherrington (1940) as being the major source of the v.s.c.t. Many of the dorsomedial cells receive monosynaptic Ib input (Eccles, Hubbard & Oscarsson, 1961; Hubbard & Oscarsson, 1962) whilst the spinal border cells receive predominantly monosynaptic Ia input. However since some of these also receive monosynaptic Ib input, the two sources of the v.s.c.t. may complement each other. Spinal border cells giving rise to the v.s.c.t. have been found as far caudally as the sixth lumbar segment. It is interesting to note that the most rostrally stained collaterals in our present sample project towards the lateral border of lamina VI and the dorso-lateral part of lamina VII.

Thus the present report describes projections of single Ib afferent fibres in the lower lumbar segments of the spinal cord. The extensive collateral arborizations in lamina VI and the dorsal part of lamina VII correlate with previous electrophysiological studies of group Ib projections.

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EXPLANATION OF PLATES

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

PLATE 1

Photomontage showing part of the extensive branching and terminations in lamina VI of a Ib afferent fibre collateral. This collateral is reconstructed in Fig. 3*A*.

PLATE 2

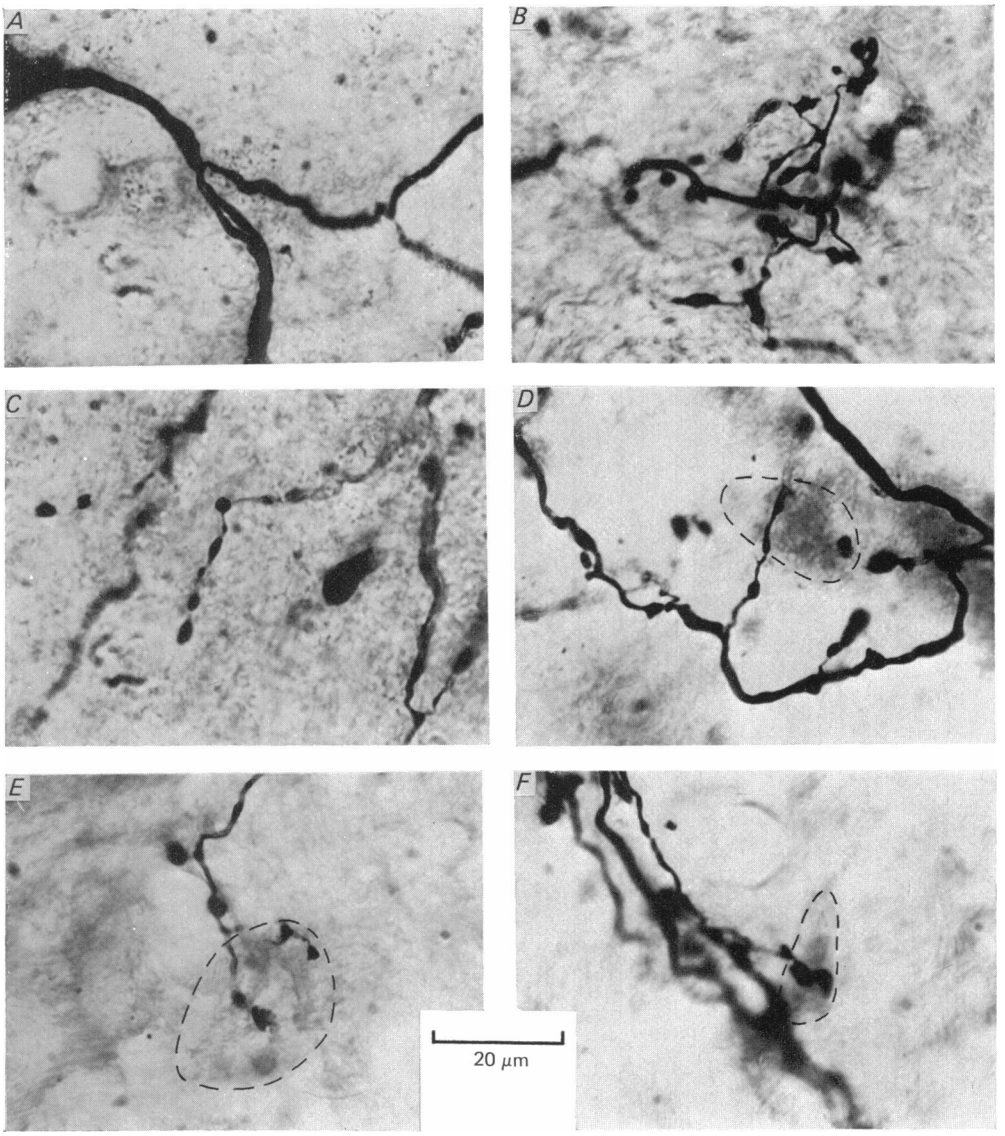
Photomicrographs showing details of Ib terminal arborizations.

A, example of a fibre dividing into three daughter branches in lamina VI.

B, complex clustering of boutons observed in the central part of lamina IV, dorsal to the main arborization.

C–F, boutons in lamina VI. *D–F* are from counterstained sections. Soma profiles are outlined. *C*, branch carrying several 'en passant' boutons. *D*, 2 boutons 'en passant' contacting a stained cell body. *E*, four contacts on a medium sized lamina VI neurone. *F*, two to three contacts on a cell near the lateral border of lamina VI.


500 μm


A
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C
D
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20 μm