J. Anat. (1987), **153**, pp. 203–215
With 5 figures
Printed in Great Britain

Topographic and quantitative description of rat dorsal column fibres arising from the lumbar dorsal roots*

KENNETH J. SMITH AND B. JAMES BENNETT

Microsurgical Research Center, Eastern Virginia Medical School, Norfolk, Virginia 23501

(*Accepted* 14 *October* 1986)

INTRODUCTION

Growing use of the rat in neuroscience research requires a more detailed knowledge of rat neuroanatomy, particularly that of the central nervous system. The aim of this study is to ascertain the number and course of lumbar dorsal root fibres at different levels of the rat dorsal column, since this tract is frequently the subject of neurophysiological studies. Earlier studies (reviewed in part by Brown, 1973, and Réthelyi & Szentágothai, 1973) have explored the neuroanatomy of the dorsal column of the frog (Chambers, Sprague & Liu, 1960; Antal, Tornai, & Székely, 1980); clawed toad (Nikundiwe, de Boer-van-Huizen & ten Donkelaar, 1982); frog and toad (Joseph & Whitlock, 1968*a*); lizard (Goldby & Robinson, 1962); crocodile, iguana and lizard (Joseph & Whitlock, 1968*b*); turtle (Kusuma & ten Donkelaar, 1979); snake, lizard and turtle (Kusuma & ten Donkelaar, 1980); pigeon (Leonard & Cohen, 1975); opossum (Culberson & Kimmel, 1975); North American opossum, brush-tailed possum, cat and bushbaby (Culberson, Haines, Kimmel & Brown, 1979); cat (Glees & Soler, 1951; Liu, 1956; Sprague, 1958; Sprague & Ha, 1964; Petras, 1966; Imai & Kusama, 1969; Brown, Rose & Snow, 1976; Wall & Werman, 1976; Brown & Fyffe, 1978; Umetani, Hasegawa, Yoshida & Takeda, 1981; Culberson & Brown, 1984); lesser bushbaby (Albright, 1978); monkey (Walker & Weaver, 1942; Petras, 1966; Carpenter, Stein & Shriver, 1968; Shriver, Stein & Carpenter, 1968; Whitsel, Petrucelli & Sapiro, 1969; Whitsel, Petrucelli, Sapiro & Ha, 1970); and human (e.g., Barker, 1899; Winkler, 1918; Foerster, 1936; Smith & Deacon, 1984). There is, however, a conspicuous absence of knowledge about the central projections of dorsal root fibres in the rat.

While we anticipated that the anatomy of the rat dorsal column would conform in general to that present in the other species, it was not possible to predict either the proportion of dorsal root fibres projecting to the different spinal levels, the precise topographic distribution of the fibres at those levels, or the effect on this anatomy of the corticospinal tract which in the rat is contained within the dorsal columns (Zimmerman, Chambers & Liu, 1964). The present study was undertaken to answer these questions.

METHODS

Six rats (male, Sprague–Dawley; 250 to 430 g, Taconic Farms) were anaesthetised with sodium pentobarbital and hemilaminectomies performed with aseptic precautions

* Reprint requests to Dr K. J. Smith, Department of Anatomy, Eastern Virginia Medical School, P.O. Box 1980, 700 Olney Road, Norfolk, Virginia 23501, U.S.A.

at either L_1 and L_2; L_3 and L_4; L_5 and L_6; L_5 and S_2; S_3 and L_6; S_4 and L_4, in order to expose the dorsal root ganglia and associated dorsal roots. A small slit was made in the dura at the caudal end of each hemilaminectomy, and either the left or right dorsal root entering beneath that lamina was identified, elevated and severed. In each rat the two rhizotomies were performed on opposite sides to avoid complications arising from the presence of ipsilateral degenerating fibres from two roots. Care was taken to avoid trauma to any of the other roots, except that in some cases the related ventral root was also severed. The severed ends of the roots were replaced within the dural sac and the wound closed in layers. The animals were allowed to recover from the anaesthetic and then assessed daily for any unexpected clinical signs resulting from the surgery (none were found). Two age-matched rats served as unoperated controls. All the rats were deeply re-anaesthetised (sodium pentobarbital) on the 21st to 34th days after the operation and perfused via the left ventricle with warmed (28–32 °C) glutaraldehyde (4% in 0·15 M cacodylate; pH 7·4). A complete laminectomy was performed from C_1 to Co_3 and the identity of each vertebra determined, labelled, and re-checked. A portion of the right lateral white column was excised longitudinally, *in situ*, to permit the correct orientation of subsequent histological sections. The spinal cord was then cut transversely, *in situ*, into blocks equal in length with the associated vertebral segments (i.e. 3–6 mm), and each block was removed to allow the middle 1 mm length of tissue to be cut transversely and saved for subsequent processing. The L_1 to Co_3 dorsal roots were also identified, labelled and blocked for tissue processing. The blocks were left in buffered glutaraldehyde (4%) for several hours, prior to being washed in cacodylate buffer (0·15 M) and postfixed in osmium tetroxide (1% in 0·15 M cacodylate buffer; pH 7·4). The blocks were subsequently dehydrated in ascending ethanols, passed through propylene oxide and embedded in Epon. Selected blocks (see Results) were cut transversely for examination at light microscopy in 1 μm, toluidine blue-stained sections. A low power drawing of each section was made for orientation purposes (with the aid of a drawing tube; Nikon), and then either a general map was made at × 750 of the areas containing numbers of easily identified degenerating fibres, or a detailed map was drawn at × 1875 showing the location of each degenerating fibre. Since at × 1875 only a 110 μm diameter field could be seen through the microscope at any one time, certain blood vessels or other recognisable structures were drawn as landmarks to ensure the accurate alignment of successive fields. Our criteria for designating a fibre as undergoing degeneration included: (1) the presence of myelin debris in any form, and (2) the absence of a recognisable axon. Thus occasional fibres where the myelin was disorganised, but where an axon could be identified were considered non-degenerating, and were not drawn. Such fibres could be found in small numbers scattered throughout the whole white matter of the spinal cord. In common with other methods based on the presence of degenerating myelin it was not possible to identify degenerating unmyelinated axons with this technique.

RESULTS

Clinical signs

None of the rats developed any clinical signs beyond those that could be directly attributed to the loss of the particular dorsal roots.

Unoperated controls

Detailed maps were prepared (at × 1875) showing the location of degenerating fibres in the dorsal column at the C_3 and T_{13} levels. Although some fibres were found to

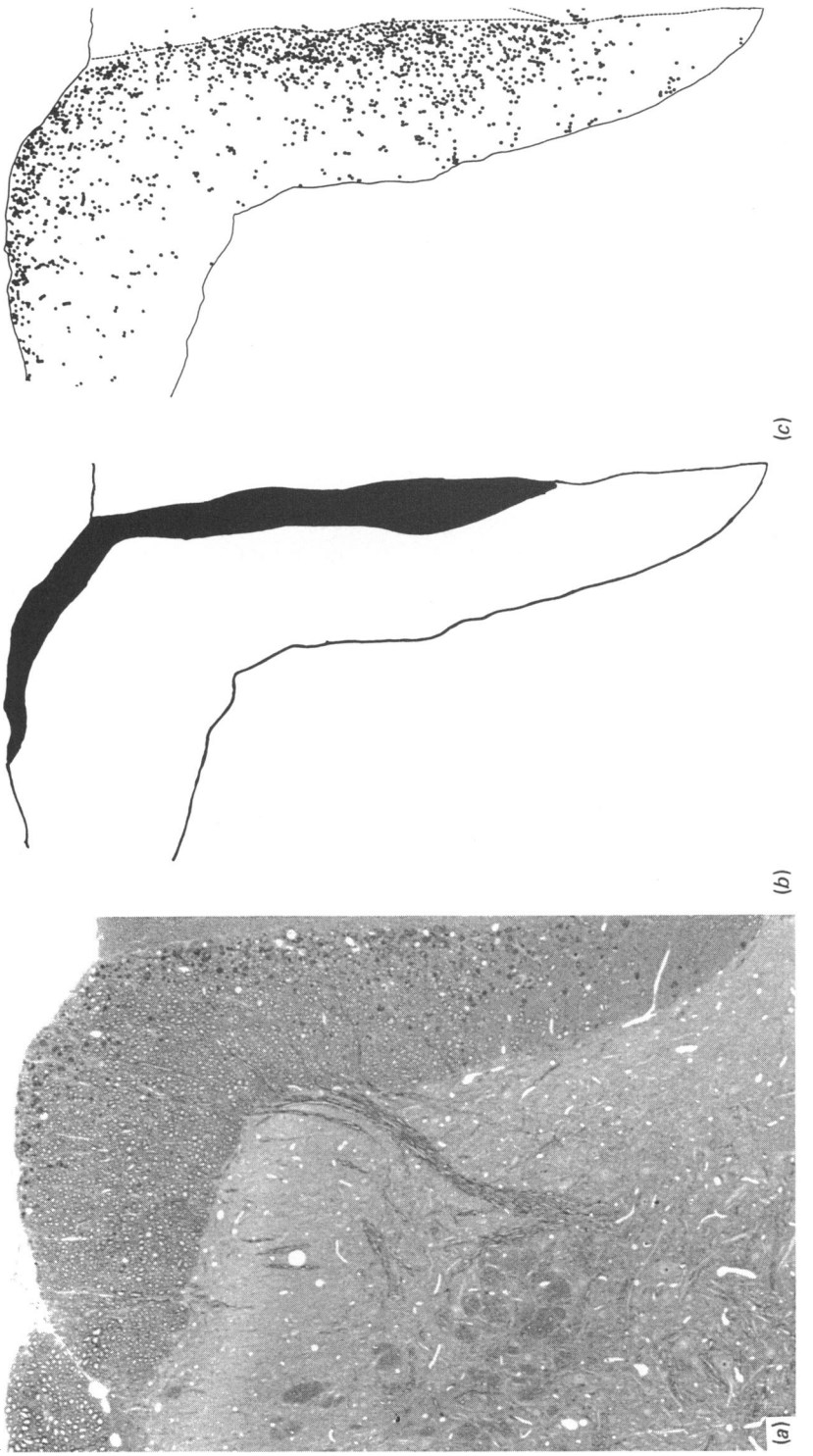

Fig. 1(*a–c*). (*a*) Light micrograph showing a transverse section of the dorsal column beneath lamina T_{13} in a rat in which the L_5 dorsal root was severed 21 days previously. A thin band of degenerating fibres can be easily distinguished extending along the dorsal surface and down the midline. (*b*) Map drawn at × 750 showing the outline of the distinct band of degenerating fibres seen in (*a*). (*c*) Map showing the location of each degenerating fibre detected in the dorsal column illustrated in (*a*), when examined at × 1875. A dot of uniform size is used to represent each degenerating fibre. Subdivisions of the dorsal column are shown by dashed lines.

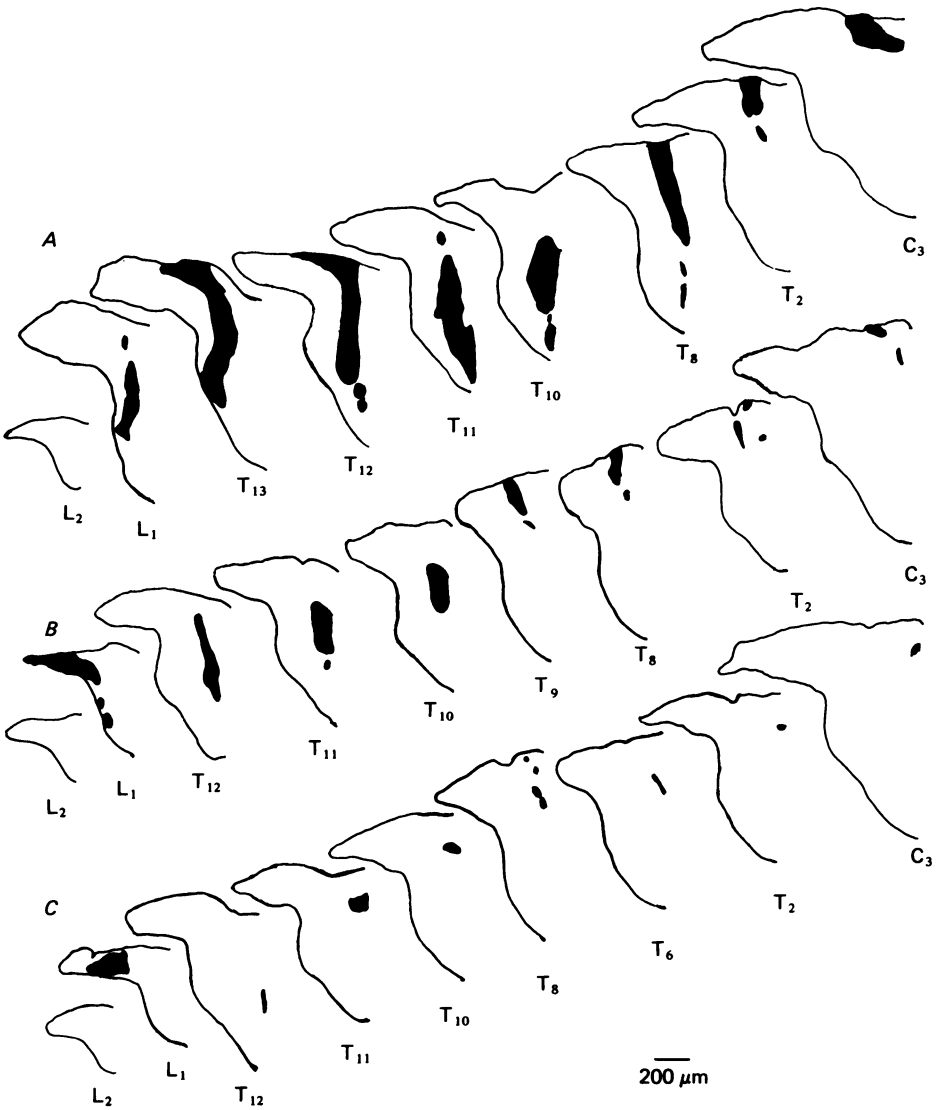

Fig. 2. Outlines of the dorsal columns at the spinal levels indicated, showing the general area(s) containing the majority of degenerating fibres (determined at × 750) three to four weeks after section of the L_4 (A), L_5 (B) and L_6 (C) dorsal roots.

be undergoing degeneration, the number was small (only 12–23 at T_{13}, and 14–15 at C_3) in comparison with the numbers present in the operated groups (see e.g. Fig. 5).

Dorsal roots

Examination at autopsy of the identity of the severed roots confirmed that the intended roots had been severed in all cases except one: in this instance (root S_3) the identity of the root severed was ambiguous and the results have therefore been omitted from the study. In the case of another root (S_4), histological examination revealed that it had been only incompletely severed, and this preparation was also therefore excluded from the study. In the remaining ten cases the correct identities of the roots were

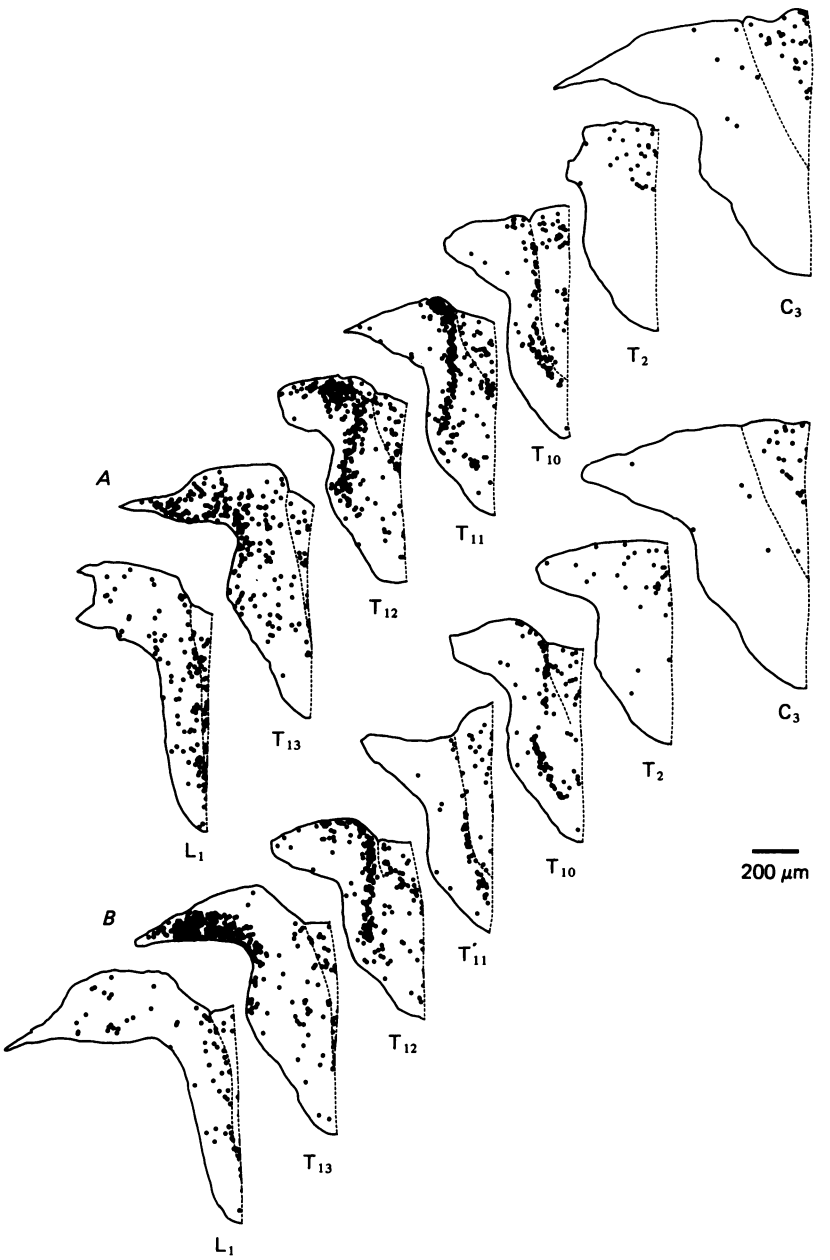

Fig. 3(*A–B*). For legend see p. 209.

confirmed, and each root was found upon histological examination to have been completely severed. In eight of these cases histological examination of the remaining roots established that none had sustained any accidental damage, and in the remaining two cases (L_3 and L_5) one other adjacent root (i.e. L_4 and L_6 respectively) exhibited only a few ($< 4\%$) degenerating fibres; these were judged to have probably arisen by intersegmental cross-over (Lugaro, 1906; Jacob & Weddell, 1975) and the data from these preparations have been included in the study. Several of the severed dorsal roots exhibited substantial numbers of nerve fibres presumed to be regenerating (since they

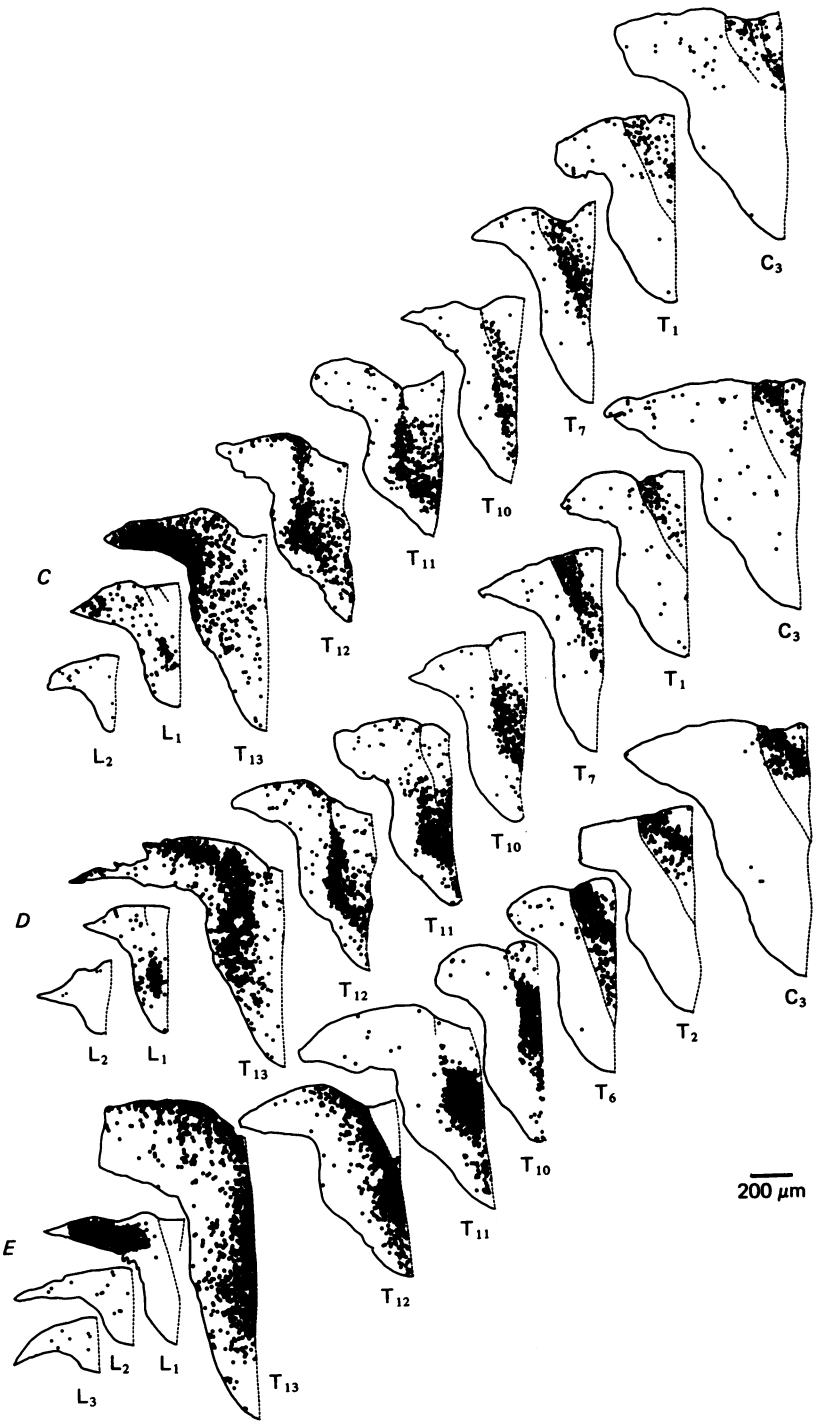

Fig. 3(*C–E*). For legend see p. 209.

Fig. 3(*A–G*). Maps showing the locations of individual degenerating nerve fibres (determined at × 1875) at different spinal levels, three to four weeks after section of the specified dorsal root. Specimens are different from those illustrated in Fig. 2. The different series of illustrations (*A–G*) depict the results from section of dorsal roots L_1, L_2, L_3, L_4, L_5, L_6 and S_2 respectively. The vertebral levels at which the drawings were made is indicated.

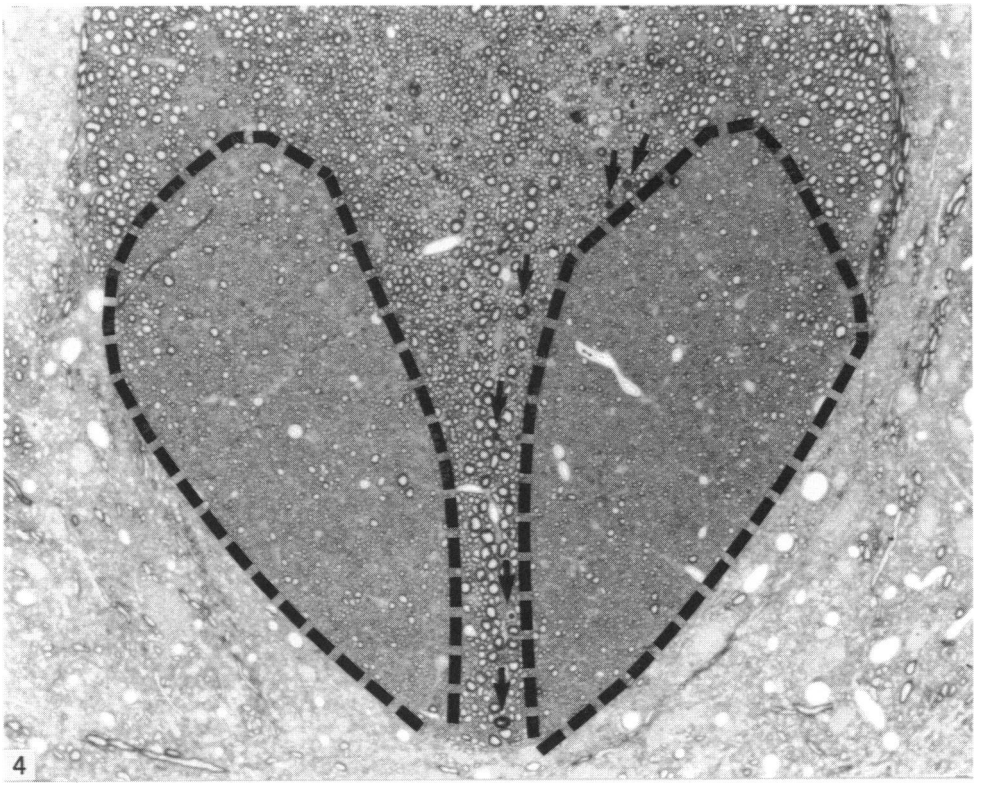

Fig. 4. Light micrograph of the ventral portion of the dorsal column showing the region of small diameter fibres (outlined) which constitute the corticospinal tract. Note (*a*) the virtual absence of degenerating fibres within the region outlined, (*b*) the presence of a population of large diameter axons near the midline, and (*c*) the presence of some degenerating fibres (arrowed) among this population.

had relatively small axons and inappropriately thin myelin sheaths), but such fibres would not be expected either to enter the spinal cord, or to affect the interpretation of the results if they did so.

Dorsal columns

The immediate impression gained from examination (× 750) of the dorsal column at most spinal levels was that of a well circumscribed, orderly pattern of degenerating fibres (Fig. 1 *a*), and the outline of this region could be readily transferred to paper using the drawing tube (Fig. 1 *b*). However, closer examination at high power (× 1875) routinely revealed the presence of many other degenerating fibres both within the well circumscribed region, and outside it (Fig. 1 *c*). Myelin debris remaining from those easily identified degenerating fibres within the circumscribed region was generally greater in quantity (and therefore more conspicuous) than debris from the degenerating fibres situated elsewhere in the dorsal column, and this gave the impression of the loss of large and small diameter fibres respectively. However, in this study no attempt was made to interpret the likely former diameter of degenerating fibres, and the location of each degenerating fibre has simply been represented by a dot of uniform size (as in Fig. 1 *c*). Where there was a clear subdivision of the dorsal column into distinct tracts (e.g. fasciculus cuneatus and fasciculus gracilis), this has been noted with dashed lines.

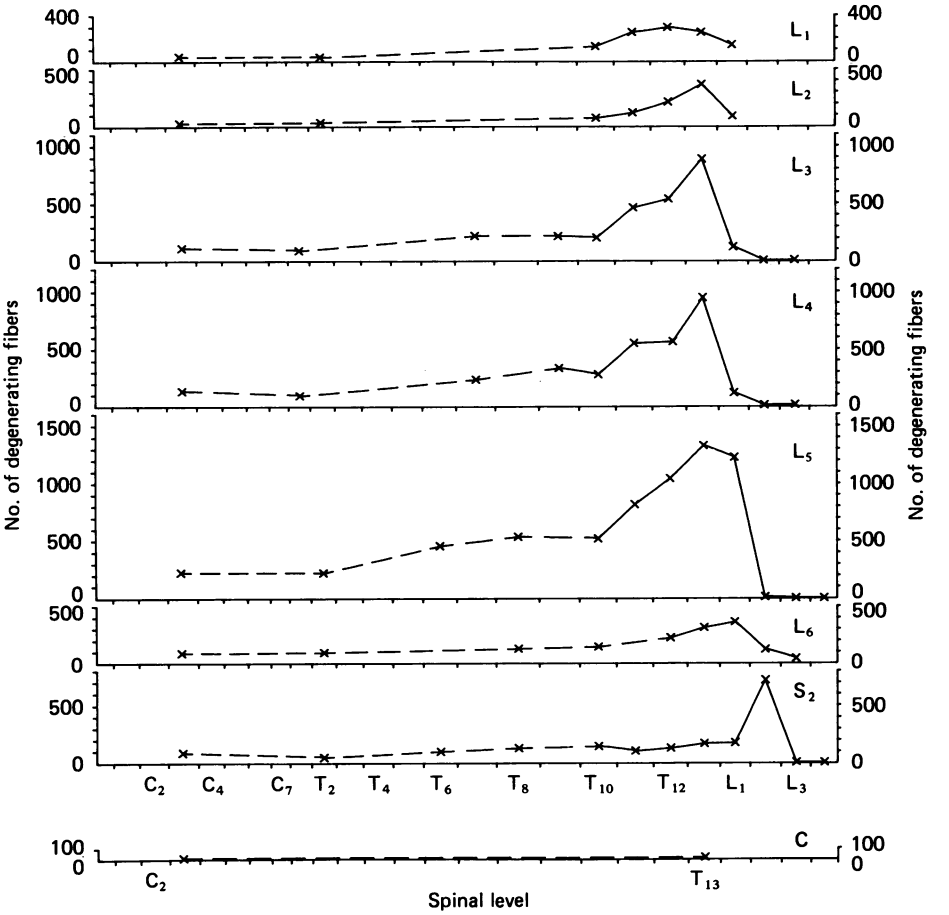

Fig. 5. Graphs showing the numbers of degenerating nerve fibres found (at × 1875) in 1 μm sections taken from the dorsal column at the different spinal levels in response to section of the L_1, L_2, L_3, L_4, L_5, L_6 and S_2 dorsal roots. Graduations on the abscissa indicate the relative lengths of the individual vertebrae. The bottom graph shows the mean number of degenerating fibres detected at the C_3 and T_{13} levels in 3 unoperated controls (C).

Examination of the dorsal columns of each operated rat typically revealed the presence at one level of a cluster of degenerating fibres towards the lateral margin of the dorsal column (Figs. 2, 3), and in each case this cluster coincided with a location a little rostral to the level at which the cut root entered the spinal cord. Rostral to this cluster, the pattern of degenerating fibres followed an orderly progression so that within one or two segments they came to occupy a position near the centre of the dorsal column, and then, at high thoracic and cervical levels, to occupy positions within the fasciculus gracilis, i.e. near the midline, in the superficial parts of the dorsal column. Whereas it appeared that close to the root entry zone the degenerating fibres from the different roots ascended in separate bands with successively more rostral roots occupying more lateral positions, this organisation was not noticeable at high thoracic and cervical levels. Caudal to the dorsal root entry zone most fibres were lost from the dorsal column within only two segments, and the few remaining degenerating fibres appeared to be almost randomly distributed across the particular dorsal column.

The ventral portion of the dorsal column was composed of a relatively homogeneous

population of small diameter fibres (Fig. 4) which were routinely spared by the dorsal root lesions: these fibres are known to constitute the corticospinal tracts (Zimmerman *et al.* 1964). At the medial margins of the tracts, however, there were typically a few fibres of large diameter, and in operated rats there was occasional evidence (i.e. the presence of large units of myelin debris) that some such fibres had undergone degeneration (Fig. 4), suggesting that the large fibres are in fact part of the ascending dorsal column system.

The number of degenerating fibres found in the 1 μm sections taken at the different levels of the spinal cord in each rat is represented graphically in Figure 5. In each graph there is a peak in the number of degenerating fibres near the dorsal root entry zone, and as successively more rostral roots are considered the peak shows a progressive shift in the rostral direction, commensurate with the orderly sequence of insertion of roots into the dorsal column. (Note that in the rat the spinal cord ends beneath the L_4 lamina, and thus the root entry zones of the six lumbar, four sacral and three coccygeal roots are displaced rostrally and all enter the cord within only 5 or 6 vertebral segments. This observation accounts for the peaks in the number of degenerating fibres between the T_{12}–L_2 spinal levels.) Although degenerating fibres were found both rostral and caudal to the root entry zone, only the rostral projections typically extended for more than two segments, so that the number at high thoracic levels was only $13 \pm 6{\cdot}3\%$ of the peak number. In high cervical regions a small increase (to $15 \pm 4{\cdot}7\%$) in the number of degenerating fibres was observed, implying that some dorsal column fibres may branch near this level. Most (97%) of the caudal projections terminated within two segments of root entry.

DISCUSSION

The data demonstrate that the topographic organisation of the dorsal columns in the rat has some similarities with the organisation established in other species (see above). Thus, near the entry zone of a dorsal root the associated fibres are aggregated near the lateral margin of the dorsal column, becoming displaced medially at progressively more rostral levels by the entry of additional dorsal roots. While 56 to 82% of the ascending fibres are lost from the dorsal column within 3 vertebral segments, between 8 and 24% of fibres ascend to high cervical levels and may therefore enter the dorsal column nucleus. The number of descending projections is small and seemingly quite randomly distributed within the dorsal column.

In this study, the locations of degenerating myelinated nerve fibres were identified in one micron sections of Epon-embedded tissue, rather than by selectively staining them by methods such as those introduced by Fink & Heimer (1967). A particular advantage of the method used is the high resolution attainable with one micron Epon sections, so that it is usually possible (in well-fixed tissue 3 weeks after operation) to determine quite accurately whether each individual fibre is undergoing degeneration or not: thus it is also possible to quantify the number of degenerating fibres at any particular spinal level. Such a level of confidence is rarely possible in tissue embedded in paraffin. However, since by 3–4 weeks after rhizotomy the myelin sheaths of some degenerating fibres may retract to form ovoids, all degenerating fibres may not be present in all histological sections and this can result in an underestimate of the number of degenerating fibres present at any one level. This underestimate is unlikely to be very significant since the occurrence of Marchi-positive bodies in a study of Wallerian degeneration in the cat dorsal column (Franson & Ronnevi, 1984) was found to be

relatively constant during the 20 to 57 days after dorsal rhizotomy, and the prevalence of 'degenerating myelin' was found to be relatively constant between 4 and 50 days. Furthermore, in the rat spinal cord, most myelin sheaths are collapsed but still intact 52 days after axon section (Lampert & Cressman, 1966).

The slight increase in the number of degenerating fibres identified at high cervical levels compared with the number at high thoracic levels, implies that some branching of fibres may have occurred within the dorsal column. However, it is also possible that high in the dorsal column the formation of myelin ovoids is delayed, thus resulting in the higher count of degenerating fibres.

The number of degenerating fibres found in the dorsal column after section of particular roots is much smaller than the number of fibres normally present in those roots; for example, the results show a peak of 370 degenerating fibres in the dorsal column after section of L_6, whereas this root normally contains 3141 ± 310 myelinated and 10577 ± 1529 unmyelinated fibres (Langford & Coggeshall, 1979 and C. B. Jenq & R. E. Coggeshall, personal communication). It therefore seems likely that most dorsal root fibres either do not enter the dorsal column, or that they travel for only a very limited distance within it.

SUMMARY

The number and topographic distribution of the profiles of degenerating primary afferent fibres were determined within the rat dorsal column 3–4 weeks after division of the lumbar and S_2 dorsal roots. The degenerating fibres were identified in toluidine blue-stained 1 μm transverse sections taken at different spinal levels, and their positions were marked with the aid of a drawing tube. Fibres entered the dorsal column at its lateral margin and sent projections rostrally and caudally. Fibres ascending the column were displaced medially in an orderly progression as the fibres of more rostral roots entered the cord. Most ascending fibres were lost from the dorsal columns within 2–3 segments of their site of entry, with only 15%, on average, reaching cervical levels. The descending fibres maintained a less organised topographic distribution, and typically only 3% of fibres entering the dorsal column descended two segments from their site of entry.

This work was supported by grants from the National Multiple Sclerosis Society (RG 1699-A-2 to K.J.S.) and the National Institutes of Health (1 RO1 NS 21670-01 to K.J.S.). We would like to thank Dr S. M. Hall for her helpful comments during the preparation of this manuscript.

REFERENCES

ALBRIGHT, B. C. (1978). Dorsal column nuclei in a prosimian primate (*Galago senegalensis*). *Brain Behavior and Evolution* **15**, 63–84.

ANTAL, M., TORNAI, I. & SZÉKELY, G. (1980). Longitudinal extent of dorsal root fibres in the spinal cord and brain stem of the frog. *Neuroscience* **5**, 1311–1322.

BARKER, L. F. (1899). *The Nervous System and its Constituent Neurones*, Ch. 32–34. New York: Appleton.

BROWN, A. G. (1973). Ascending and long spinal pathways: dorsal columns, spinocervical tract and spinothalamic tract. In *Handbook of Sensory Physiology* (ed. A. Iggo), Vol. II, *Somatosensory System*, pp. 315–338. Berlin: Springer-Verlag.

BROWN, A. G., ROSE, P. K. & SNOW, P. J. (1976). The morphology of identified cutaneous afferent fibre collaterals in the spinal cord. *Journal of Physiology* **122**, 653–662.

BROWN, A. G. & FYFFE, R. E. W. (1978). The morphology of group Ia afferent fibre collaterals in the spinal cord of the cat. *Journal of Physiology* **274**, 11–127.

CARPENTER, M. B., STEIN, B. M. & SHRIVER, J. E. (1968). Central projections of spinal dorsal roots in the monkey. *American Journal of Anatomy* **123**, 75–118.

CHAMBERS, W. W., SPRAGUE, J. M. & LIU, C. N. (1960). Anatomical organization of the frog and cat spinal cord, dorsal root and propriospinal pathways. *American Journal of Medical Science* **240**, 122–124.

CULBERSON, J. L. & KIMMEL, D. L. (1975). Primary afferent fibre distribution at brachial and lumbosacral spinal cord levels in the opossum (*Didelphis marsupialis virginiana*). *Brain Behavior and Evolution* **12**, 229–246.

CULBERSON, J. L. & BROWN, P. B. (1984). Projections of hindlimb dorsal roots to lumbosacral spinal cord of cat. *Journal of Neurophysiology* **51**, 516–528.

CULBERSON, J. L., HAINES, D. E., KIMMEL, D. L. & BROWN, P. B. (1979). Contralateral projections of primary afferent fibres to mammalian spinal cord. *Experimental Neurology* **64**, 83–97.

FINK, R. P. & HEIMER, L. (1967). Two methods for selective silver impregnation of degenerative axons and their synaptic endings in the central nervous system. *Brain Research* **4**, 369–374.

FOERSTER, O. (1936). In *Handbuch der Neurologie*, Vol. V (ed. O. Bumke & O. Foerster), pp. 79–85; 349–359. Berlin: Julius Springer.

FRANSON, P. & RONNEVI, L.-O. (1984). Myelin breakdown and elimination in the posterior funiculus of the adult cat after dorsal rhizotomy: a light and electron microscopic qualitative and quantitative study. *Journal of Comparative Neurology* **223**, 138–151.

GLEES, P. & SOLER, J. (1951). Fibre content of the posterior column and synaptic connections of nucleus gracilis. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **36**, 381–400.

GOLDBY, F. & ROBINSON, L. R. (1962). The central connexions of dorsal spinal nerve roots and the ascending tracts in the spinal cord of *Lacerta viridis*. *Journal of Anatomy* **96**, 153–170.

IMAI, Y. & KUSAMA, T. (1969). Distribution of the dorsal root fibres in the cat. An experimental study with the Nauta method. *Brain Research* **13**, 338–359.

JACOB, M. & WEDDELL, G. (1975). Neural intersegmental connection in the spinal root and ganglion region of the rat. *Journal of Comparative Neurology* **161**, 115–124.

JOSEPH, B. S. & WHITLOCK, D. G. (1968*a*). Central projections of selected spinal dorsal roots in anuran amphibians. *Anatomical Record* **160**, 279–288.

JOSEPH, B. S. & WHITLOCK, D. G. (1968*b*). Central projections of brachial and lumbar dorsal roots in reptiles. *Journal of Comparative Neurology* **132**, 469–484.

KUSUMA, A. & TEN DONKELAAR, H. J. (1979). Staining of the dorsal root primary afferent fibres by anterograde movement of horseradish peroxidase and retrograde labelling of motorneurons and preganglionic autonomic cells in the turtle spinal cord. *Neuroscience Letters* **14**, 141–146.

KUSUMA, A. & TEN DONKELAAR, H. J. (1980). Dorsal root projections in various types of reptiles. *Brain Behavior and Evolution* **17**, 291–309.

LAMPERT, P. W. & CRESSMAN, M. R. (1966). Fine-structural changes of myelin sheaths after axonal degeneration in the spinal cord of rats. *American Journal of Pathology* **49**, 1139–1155.

LANGFORD, L. A. & COGGESHALL, R. E. (1979). Branching of sensory axons in the dorsal root and evidence for the absence of dorsal root efferent fibres. *Journal of Comparative Neurology* **184**, 193–204.

LEONARD, R. B. & COHEN, D. H. (1975). Spinal terminal fields of dorsal root fibres in the pigeon (*Columba livia*). *Journal of Comparative Neurology* **163**, 181–192.

LIU, C. N. (1956). Afferent nerves to Clarke's and lateral cuneate nuclei in the cat. *Archives of Neurology and Psychiatry (Chicago)* **75**, 67–77.

LUGARO, E. (1906). Fibre aberranti, fibre centrifughe, e fibre recorrenti nelle radici posteriori. *Monitore zoologico italiano* **17**, 217–220.

NIKUNDIWE, A. M., DE BOER-VAN-HUIZEN, R. & TEN DONKELAAR, H. J. (1982). Dorsal root projections in the clawed toad (*Xenopus laevis*) as demonstrated by anterograde labeling with horseradish peroxidase. *Neuroscience* **7**, 2089–2103.

PETRAS, J. M. (1966). Afferent fibres to the spinal cord. The terminal distribution of dorsal root and encephalospinal axons. *Medical Services Journal of Canada* **22**, 668–694.

RÉTHELYI, M. & SZENTÁGOTHAI, J. (1973). Distribution and connections of afferent fibres in the spinal cord. In *Handbook of Sensory Physiology* (ed. A. Iggo), Vol. II, *Somatosensory System*, pp. 208–252. Berlin: Springer-Verlag.

SHRIVER, J. E., STEIN, B. M. & CARPENTER, M. B. (1968). Central projections of spinal dorsal roots in the monkey. *American Journal of Anatomy* **123**, 27–74.

SMITH, M. C. & DEACON, P. (1984). Topographical anatomy of the posterior columns of the spinal cord in man. *Brain* **107**, 671–698.

SPRAGUE, J. M. (1958). The distribution of dorsal root fibres on motor cells in the lumbosacral spinal cord of the cat, and the site of excitatory and inhibitory terminals in monosynaptic pathways. *Proceedings of the Royal Society of London, B* **149**, 534–556.

SPRAGUE, J. M. & HA, H. (1964). The terminal fields of dorsal root fibres in the lumbosacral spinal cord of the cat, and the dendritic organization of the motor nuclei. *Progress in Brain Research* **11**, 120–154.

UMETANI, T., HASEGAWA, M., YOSHIDA, S. & TAKEDA, H. (1981). Spinal projections of the dorsal root fibres in the cat. *Kobe Journal of Medical Science* **27**, 173–188.

WALKER, A. E. & WEAVER, T. A. JR. (1942). The topical organization and termination of the fibres of the posterior columns in *Macaca mulatta*. *Journal of Comparative Neurology* **76**, 145–158.

WALL, P. D. & WERMAN, R. (1976). The physiology and anatomy of long ranging afferent fibres within the spinal cord. *Journal of Physiology* **255**, 321–334.

WHITSEL, B. L., PETRUCELLI, L. M. & SAPIRO, G. (1969). Modality representation in the lumbar and cervical fasciculus gracilis of squirrel monkeys. *Brain Research* **15**, 67–78.

WHITSEL, B. L., PETRUCELLI, L. M., SAPIRO, G. & HA, H. (1970). Fibre sorting in the fasciculus gracilis of squirrel monkey. *Experimental Neurology* **29**, 227–242.

WINKLER, C. (1918). *Manuel de Neurologie*, Vol. I, *Anatomie du Système Nerveux*, pp. 178–198. Haarlem: F. Bohn.

ZIMMERMAN, E. A., CHAMBERS, W. W. & LIU, C. N. (1964). An experimental study of the anatomical organization of the cortico-bulbar system in the albino rat. *Journal of Comparative Neurology* **123**, 301–323.