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EFFECTS OF HIND LIMB NERVE SECTION ON LUMBOSACRAL DORSAL HORN NEURONES IN THE CAT

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SUMMARY

1. The sciatic and saphenous nerves of one hind limb were sectioned in young adult cats anaesthetized with halothane. Between 19 and 55 days later, under chloralose anaesthesia, dorsal horn neurones in the L6 and L7 segments were recorded and their receptive field properties examined.

2. In seven animals recordings were made from identified spinocervical tract, post-synaptic dorsal column and dorsolateral funicular neurones as well as from neurones that did not project through these pathways. Thirty-one neurones were intracellularly stained with horseradish peroxidase, and fifty-three were recorded extracellularly and located by reference to stained cells. In two animals (both 31 days after nerve section) no attempt was made to identify axonal projections of the dorsal horn neurones in order to avoid any effects of cervical cord search stimuli on the cells' properties, but all isolated extracellularly recorded units were examined. On the side ipsilateral to the nerve sections 143 units were recorded.

3. In all experiments, neurones in the medial three-quarters of the dorsal horn had no discernible cutaneous, mechanosensitive receptive fields between 19 and 55 days after nerve section. There were only two exceptions to this generalization, one neurone being one of the most rostral cells in the sample (in caudal L5) and the other being one of the most caudal cells (in caudal L7). We present evidence to show that neither of these two neurones had inappropriate receptive fields in terms of the somatotopic organization of the dorsal horn. All other neurones with receptive fields on the skin were appropriately located in the somatotopic map laid out in the dorsal horn.

4. There was no evidence for gross anatomical changes in the dendritic trees of dorsal horn neurones following sciatic and saphenous nerve sections.

5. We have been unable to confirm that, following loss of cutaneous receptive fields by peripheral nerve section, dorsal horn neurones in adult cats acquire 'inappropriate' receptive fields. Possible reasons for this are discussed.

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INTRODUCTION

In the dorsal horn of the lumbosacral spinal cord, neurones of Rexed's (1952, 1954) laminae III, IV and V (the latter at least in its dorsal part) have receptive fields that form a somatotopic map of the hind limbs, tail and caudal part of the trunk. This map has been described in most detail by Brown & Fuchs (1975) for an indiscriminate sample of dorsal horn neurones and by Brown, Fyffe, Noble, Rose & Snow (1980) for an identified sample of neurones: spinocervical tract neurones in laminae III, IV and dorsal V. The receptive fields of dorsal horn neurones indicate that the mapping is of an area-to-area rather than a point-to-point type. Thus, although in the most medial half to two-thirds of the L6 and L7 segments the skin of the toes is represented, there is considerable variability in receptive field size (presumably indicative of different degrees of excitatory convergence) and adjacent neurones may have quite different receptive fields. In spite of this, however, when the centres of the receptive fields are considered the mapping is quite precise (see Figs. 5–8 in Brown *et al.* 1980).

The somatotopic map in the dorsal horn of the lumbosacral cord has been used as a base on which to examine the effects of altering the primary afferent input, by sectioning either the dorsal roots or peripheral nerves. Essentially two diametrically opposed sets of results have been generated by such experiments. On the one hand, Basbaum & Wall (1976), Mendell, Sassoon & Wall (1978), Devor & Wall (1978, 1981*a*, *b*) and Lisney (1982, 1983) concluded that within a month after such lesions many dorsal horn neurones respond to input that would be classed as inappropriate in the intact animal. On the other hand, Pubols & Goldberger (1980), Pubols & Brenowitz (1981, 1982) and Brown, Brown, Fyffe & Pubols (1983*a*) concluded that cutting dorsal roots does not lead to any rearrangement of the lumbosacral somatotopic map.

In the experiments of Brown *et al.* (1983*a*) a limited sample of dorsal horn neurones was studied: neurones of the spinocervical tract. The spinocervical tract transmits information from cutaneous receptors with a high degree of fidelity, i.e. there is a high degree of synaptic security in the system (Brown & Franz, 1969; Brown, Koerber, Noble, Rose & Snow, 1984). It is possible that the spinocervical system is 'hard wired' and that other dorsal horn neurones might show unmasking of previously ineffective input more easily. Furthermore, it seems that peripheral nerve section is more efficacious in revealing inappropriate connexions than dorsal rhizotomy (Devor & Wall, 1978). For these reasons we carried out the present experiments in which peripheral nerves were sectioned and a variety of dorsal horn neurones sampled. A preliminary account of some of the experiments has been published (Brown, Fyffe & Rowe, 1983*b*).

METHODS

Experiments were performed on nine young, adult cats (1·9–2·3 kg body weight). The cats were anaesthetized with halothane, the left sciatic and saphenous nerves were transected, between ligatures, and a few (3–5) millimetres of the nerves removed at mid-thigh level using strict aseptic precautions. At the end of surgery, 100000 u. benzyl penicillin were given I.M. All animals made and uneventful recovery.

An acute electrophysiological experiment was performed between 19 and 55 days after the nerve transections had been carried out. The cats were anaesthetized with chloralose (70 mg kg^{-1}) after induction with halothane in a $N_2O:O_2$ mixture and paralysed with gallamine triethiodide.

During electrophysiological experiments the state of anaesthesia was assessed by examination of a continuous blood pressure record and the degree of constriction of the pupils of the eyes. End-tidal

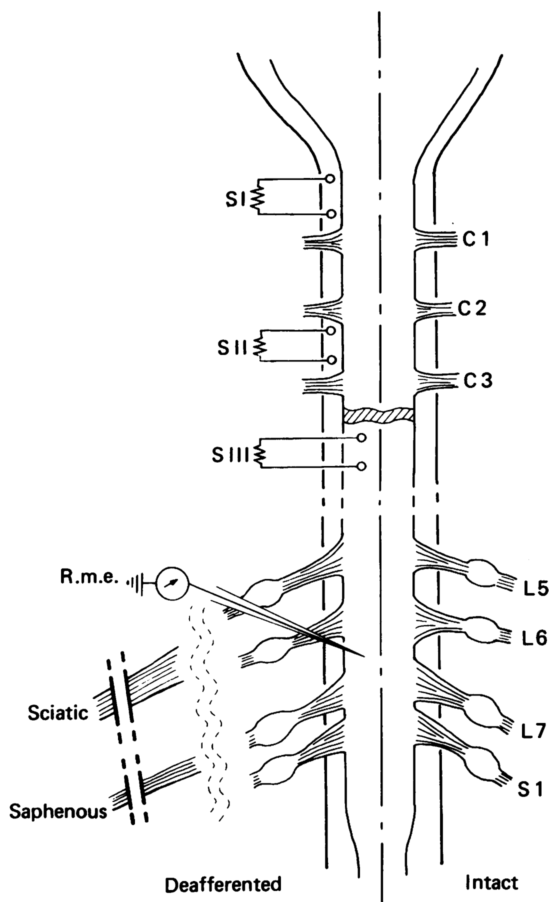

Fig. 1. Diagrammatic representation of the experimental arrangement. The Figure shows a dorsal view of the spinal cord with the levels of dorsal roots C1–C3 and L5–S1 indicated on the right-hand side. SI, SII and SIII are bipolar stimulating electrodes, r.m.e. is the recording micro-electrode. For further details see the text.

CO_2 was maintained at 3·5–4·0 % by adjusting the rate and stroke volume of the respiratory pump. The effects of the gallamine were allowed to wear off from time to time. Additional chloralose was given if required.

In seven animals (19, 24, 25, 32, 42 and 55 days' survival) micro-electrode recordings were made from identified spinocervical tract, post-synaptic dorsal column and dorsolateral funicular neurones as well as from neurones that did not project through these pathways (Fig. 1), on both sides of the L6 and L7 segments of the cord. The spinocervical and post-synaptic dorsal column neurones were identified by methods previously described (Brown, House, Rose & Snow, 1976; Brown, Rose & Snow, 1977; Brown & Fyffe, 1981). Dorsolateral funicular neurones were identified by antidromic activation from the ipsilateral dorsolateral funiculus at both C3 and C1 with no conduction velocity

reduction between these two sites. Glass micro-electrodes were filled with a 4–9% solution of horseradish peroxidase (HRP) in Tris–HCl buffer (pH 8·6) containing KCl (0·2 mol l^{-1}) and bevelled to give initial resistances of 25–40 MΩ. Neurones recorded intracellularly were injected with HRP for subsequent histological examination. Neurones recorded extracellularly were carefully located in terms of the depths from the cord dorsum (measured from the digital read-out of the stepping motor micro-electrode drive) and also with reference to the locations of injected cells. All micro-electrode entry points were carefully located on photographs of the dorsal surface of the lumbosacral enlargements.

In two cats (both 31 days survival) the axonal projections of dorsal horn neurones were not tested. Instead, systematic rows of electrode tracks were made across the cord at rostral or mid-L7 levels and all recorded units were examined for receptive fields. The micro-electrode tracks were spaced 100–250 μm apart, depending on the arrangement of surface blood vessels, and the tracks were taken down to depths of between 2500 and 3000 μm with examination for unit responses every 50 μm. The micro-electrodes were similar to those used in the other experiments except that they had been broken or bevelled back to give lower impedances (between about 10 and 20 MΩ). In one of these experiments a neurone was penetrated and injected with HRP. In both experiments blank marker electrodes were inserted to known depths and left in the cord until after fixation.

In all experiments peripheral receptive fields were defined by manual exploration of the skin of the hind limbs, tail and caudal back and abdomen. Receptive field examination was carried out with hand-held brushes, probes and toothed clips. The sciatic neuroma was very sensitive to mechanical stimuli, applied either to the neuroma or to overlying tissue, and during some experiments it was exposed and occasionally removed (in both experiments where axonal projections were not tested).

At the end of an experiment 5000 u. heparin were given I.V. and the animal perfused with normal saline followed by a mixture of 1–3% paraformaldehyde and 2–3% glutaraldehyde (pH 7·6). The lumbosacral cord with its dorsal roots was removed and kept in fixative overnight. The next day the positions of lumbosacral cord segments were confirmed and the segmental lengths carefully measured. Serial transverse sections of cord were cut on a Vibratome or a freezing microtome at 100 μm and reacted with the method of Hanker, Yates, Metz & Rustioni (1977) with cobalt intensification (Adams, 1977) to demonstrate HRP reaction product. Neurones were reconstructed with the aid of a camera lucida attachment to the microscope. The positions of stained neurones were located within their segments (cross-checked with drawings and photographs of the cord during the experiments) and the locations of extracellularly recorded units determined with reference to stained cells, electrode tracks and the positions of marker electrodes.

RESULTS

Neuronal recognition and identification

Section of the sciatic and saphenous nerves at mid-thigh level in the cat leads to anaesthesia of the foot and toes, i.e. of the whole of the limb distal to the ankle (Devor & Wall, 1978, 1981*a*, *b*). Many neurones in the dorsal horn of the L6 and L7 segments lose their peripheral receptive fields following such sections and do not have receptive fields for at least several months afterwards. A problem that immediately arises is how such neurones, with no receptive field, can be recognized during an electrophysiological experiment. In the seven experiments where attempts were made to identify the axonal projections of neurones, this problem did not present any difficulties: as the micro-electrode was advanced through the dorsal horn, the upper cervical cord, either the dorsal columns below a transection at C3–4 or the dorsolateral funiculus at C2–3 (Fig. 1), was stimulated electrically. Such stimuli elicited either antidromic or orthodromic impulses in neurones even when they had no discernible cutaneous or deep receptive fields. Furthermore, the vast majority of neurones with no peripheral receptive fields could be excited by tapping over the

position of the sciatic neuroma or, where the neuroma had been removed, by more vigorous tapping over the cut end of the nerve directly (after exposure). Excitation from the neuroma, or freshly cut sciatic nerve, also allowed recognition of units in the remaining two experiments in which there was no cervical stimulation. Further-

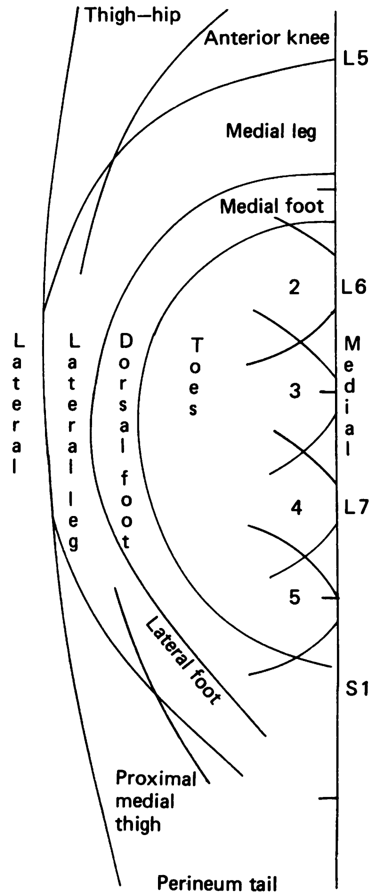

Fig. 2. The somatotopic organization of the dorsal horn of the spinal cord. The Figure is a schematic diagram of the organization as represented in a dorsal plan view of the lumbosacral spinal cord with the appropriate spinal segments indicated on the right-hand side. The areas representing the toes, foot, leg, etc. are indicated but it should be realized that the boundaries between the areas are not as clear-cut as shown: rather there is a degree of overlap between the areas (Modified from Brown *et al.* 1980).

more, in all of the experiments, many units with no receptive field did have some background activity.

The somatotopic organization of the lumbosacral dorsal horn after peripheral nerve section

In the intact cat the representation of the toes and foot occupies the medial parts of the dorsal horn in segments L5 to S1. As shown in Fig. 2, when viewed from above, the toe representation includes most of the medial half to two-thirds of segments L6,

L 7 and the rostral parts of S 1. The lateral boundary of the toe area is convex laterally, such that the widest part of the toe representation is at about the level of the L 6–L 7 junction (in cats with no obvious pre- or post-fixation of the lumbosacral plexus). Surrounding the toe representation is the representation of the foot, with the medial

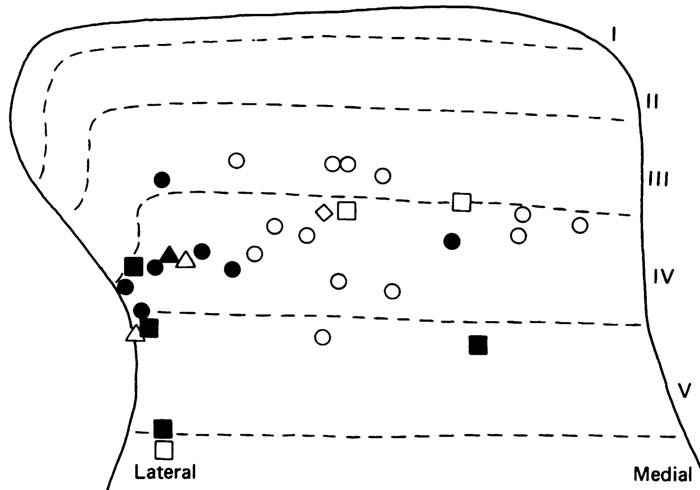

Fig. 3. The locations of intracellularly stained neurones ipsilateral to sciatic and saphenous nerve sections. The Figure represents a standard transverse section of the dorsal horn at the level of the L 6–L 7 junction and neurones have been placed according to their relative positions in the dorso-ventral and medio-lateral axes. The boundaries between Rexed's laminae are indicated by dashed lines. The locations of the cell bodies of neurones with receptive fields are shown as filled symbols, those with no discernible receptive field are shown as open symbols. ○ ●, spinocervical tract; △ ▲, post-synaptic dorsal column; ◇, dorsolateral funicular; □ ■, unidentified.

foot rostrally located next to the most medial toe (toe 2), and the lateral foot caudally located next to the most lateral toe (toe 5). The foot representation forms a crescent-shaped shell around the toe representation. Surrounding the foot representation are shells for more proximal parts of the hind limb and caudal body parts, including the tail. Section of the sciatic and saphenous nerves, as in the present experiments, will remove primary afferent input to the toe and foot areas in the dorsal horn. We therefore made our micro-electrode recordings from segments L 6 and L 7 and sampled the whole width of the dorsal horn, although concentrating on the lateral *half* where the borders between the leg and foot and the foot and toe representations are found, and where any changes might be expected.

Stained neurones. Thirty-one neurones were stained by intracellular injection of HRP. This sample consisted of twenty spinocervical, three post-synaptic dorsal column, one dorsolateral funicular and seven unidentified neurones. Their locations on a standard dorsal horn outline are shown in Fig. 3. (For an explanation of how they were placed on the outline see Brown *et al.* (1976); neurones were placed according to their relative positions from the medial, lateral and dorsal borders of the grey matter and the dorsal border of the central canal and checked against their

locations in their own dorsal horns to ensure that no obvious laminar displacement had occurred due to this procedure.)

As shown in Fig. 3, the stained neurones were located in laminae III, IV and V, with one in lamina VI. The complete width of the dorsal horn was sampled, although the lateral half received more attention and more neurones were stained there (twenty-three, 74 %, compared to eight, 26 %, in the medial half). Twelve of the thirty-one stained neurones (39 %) had receptive fields (all on skin proximal to the ankle), and nineteen (61 %) had no discernible receptive field. All but two of the neurones with receptive fields were located in the lateral half of the dorsal horn and, indeed, all but three were in the most lateral quarter of the horn. Of the cells with no receptive field, all but three were in the medial three-quarters of the dorsal horn.

The two cells in the medial half of the dorsal horn which had cutaneous receptive fields are candidates for having inappropriate fields, that is, fields inappropriate in terms of the somatotopic map. Obviously, presenting their locations on a standard transverse section of the dorsal horn leads to loss of important information, namely their rostro-caudal locations within the lumbosacral segments. This information is vitally important and is presented in Fig. 4 for the sample of thirty-one stained neurones. It is immediately apparent from Fig. 4 that the two neurones which were located in the medial half of the dorsal horn and had receptive fields were the most rostral and one of the most caudal cells in the sample. The most rostral cell was situated just rostral to the L5–L6 junction. Its receptive field was on and around the knee and cannot be considered inappropriate (see Fig. 2). The caudally located cell had a receptive field near the root of the tail and might be thought inappropriate; this point will be taken up in the Discussion. As shown in Fig. 4, all the cells in the lateral part of the dorsal horn that had receptive fields were appropriately located in the somatotopic map (see Fig. 2).

Neurones located with reference to stained cells. In addition to the thirty-one stained neurones a further fifty-three units were recorded extracellularly (ten spinocervical, four post-synaptic dorsal column, two dorsolateral funicular and thirty-seven unidentified neurones). We are reasonably confident that these were cellular as opposed to axonal recordings: many were killed by the micro-electrode and some were briefly recorded intracellularly. We were able to locate them with reference to stained cells in the same or adjacent micro-electrode tracks. The positions of these cells, which were similar to those of the stained cells, are shown in Fig. 5, where they have been added to the stained ones shown in Fig. 4. Of these fifty-three cells, thirteen (24 %) had receptive fields and forty (76 %) did not. The thirteen cells with receptive fields were all situated in the lateral quarter of the dorsal horn and all had fields appropriate for their position, that is, they were on the leg, thigh or caudal trunk.

Extracellularly recorded neurones whose axonal projections were not tested. In the seven cats in which attempts were made to identify dorsal horn neurones (as spinocervical, post-synaptic dorsal column, dorsolateral funicular) repeated stimulation of the upper cervical spinal cord was carried out during the course of the experiments. Experiments lasted up to about 18 h and, although stimulation was not carried out during all of that time, there was certainly considerable excitation of cervical cord for the periods during which neurones were being looked for. It was

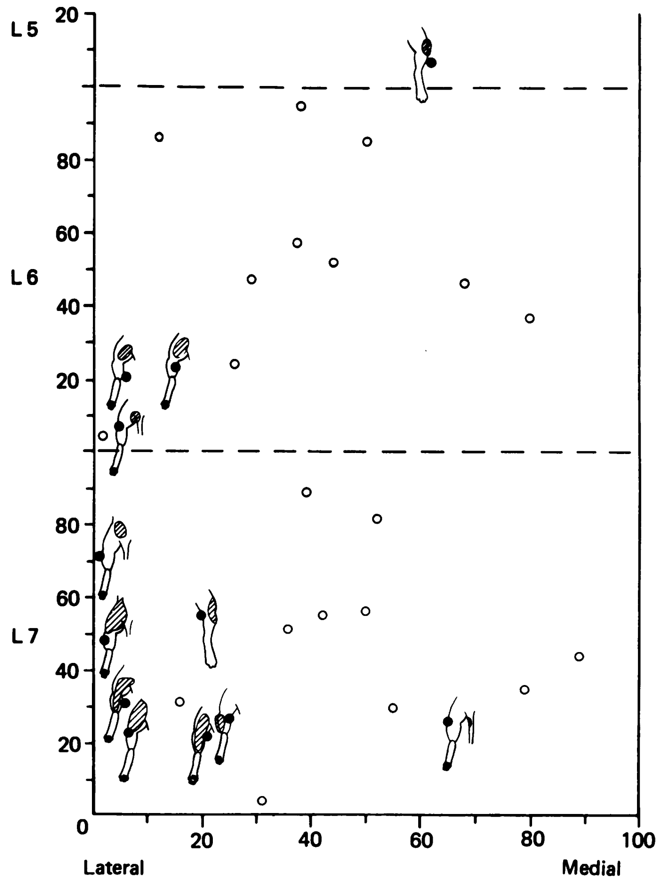

Fig. 4. The locations of intracellularly stained neurones ipsilateral to sciatic and saphenous nerve sections. The Figure is a plan view of the dorsal horn segments L5–L7 to demonstrate the rostro-caudal and medio-lateral locations of the cells shown in Fig. 3. Note the rostral and caudal positions of the two medially located cells with receptive fields. The rostro-caudal lengths of the segments have been normalized.

pointed out to us (by P. D. Wall) that such stimulation might conceivably lead to the build-up of some sort of long-term inhibitory phenomenon that might prevent the uncovering of rather ineffective synaptic excitation. Such long-term inhibition has been described in the spinal cord by Abrahams (1974).

In order to avoid any possibility that the cervical cord stimulation was masking the appearance of inappropriate receptive fields of dorsal horn neurones we prepared two animals in which the approach of Devor & Wall (1981 *a*) was followed. Thirty-one days after nerve section systematic rows of micro-electrode tracks were made in the L7 segment and all recorded units (extracellular recording) were examined for the presence of a receptive field. The results are shown in Figs. 6 and 7, where the locations of recording sites are assessed in terms of the distance from the cord dorsum at which units were recorded, the locations of micro-electrode tracks (including marker

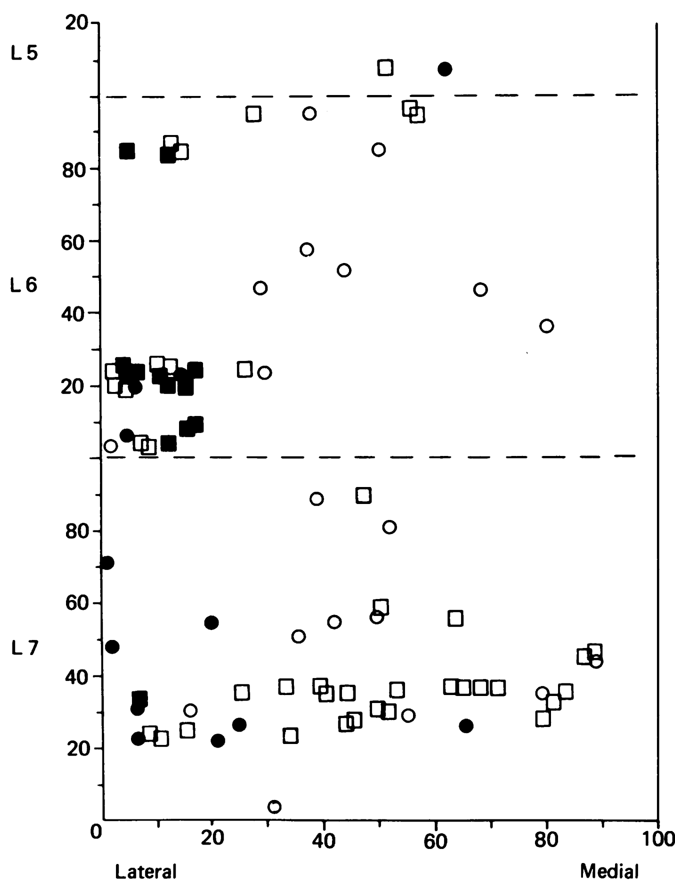

Fig. 5. The positions of both intracellularly stained and extracellularly located neurones. This Figure is similar to Fig. 4, showing both labelled neurones (○, ●) and extracellularly located cells (□, ■). Neurones with receptive fields are indicated with filled symbols and those with no discernible receptive field with open symbols.

electrodes) in the histological material and, in Fig. 6, the position of a neurone that was stained by the intracellular injection of HRP. No systematic attempt was made to differentiate axonal from cellular recordings, although the electrodes were certainly capable of recording from some of the larger axons; for example, muscle afferent fibres could be identified by their ongoing activity and by manipulation of muscles in the proximal limb and the tail, and we have indicated such axonal recordings in Figs. 6 and 7. Some of the other units recorded may well have been axons, but these would have been very few in our opinion. It is very rare in our experience to record from axons other than muscle spindle or tendon organ afferents within the spinal grey matter with micro-electrodes of the type used in these experiments. This view is supported by consideration of the receptive fields from these experiments: units with cutaneous receptive fields were located exclusively in the lateral quarters of the deafferented dorsal horns. If many axons had been recorded from then some, at least,

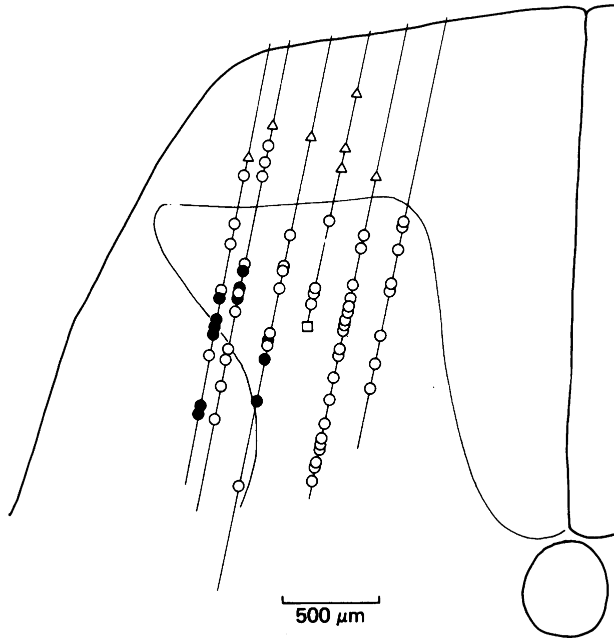

Fig. 6. Locations of extracellularly recorded units in L7 in one experiment where no cervical cord search stimuli were used. Identified muscle afferent fibres are indicated by △, units with cutaneous receptive fields by ●, and those with no receptive fields by ○. □ shows the location of a cell intracellularly stained with HRP.

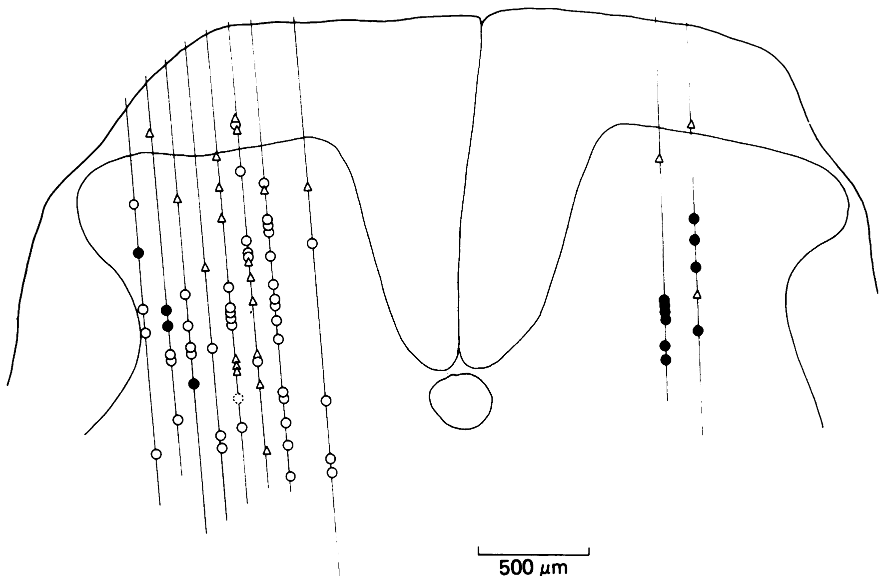

Fig. 7. This Figure is similar to Fig. 6 but shows results from the second experiment in which no cervical cord search stimuli were used. In this experiment two tracks were taken down the side of the cord contralateral to the side where the sciatic and saphenous nerves had been cut 31 days previously. On this (right) side the tracks through the middle of the horn resulted in the recording of units with cutaneous receptive fields in contrast to the other side, where units with cutaneous receptive fields were restricted to the most lateral third of the dorsal horn. ●, cutaneous receptive field; ○, no receptive field; △, muscle afferent fibre (◌ indicates a unit for which there was some doubt: see text).

should have had cutaneous receptive fields and their recording sites should have been in the medial half of the dorsal horn, since the trajectories of axons in the dorsal horn cut across the somatotopic organization of the dorsal horn neurones. Finally, as a further check on the micro-electrode recording capabilities and on the state of the animal preparation, in one cat two electrode tracks were taken down the mid-region

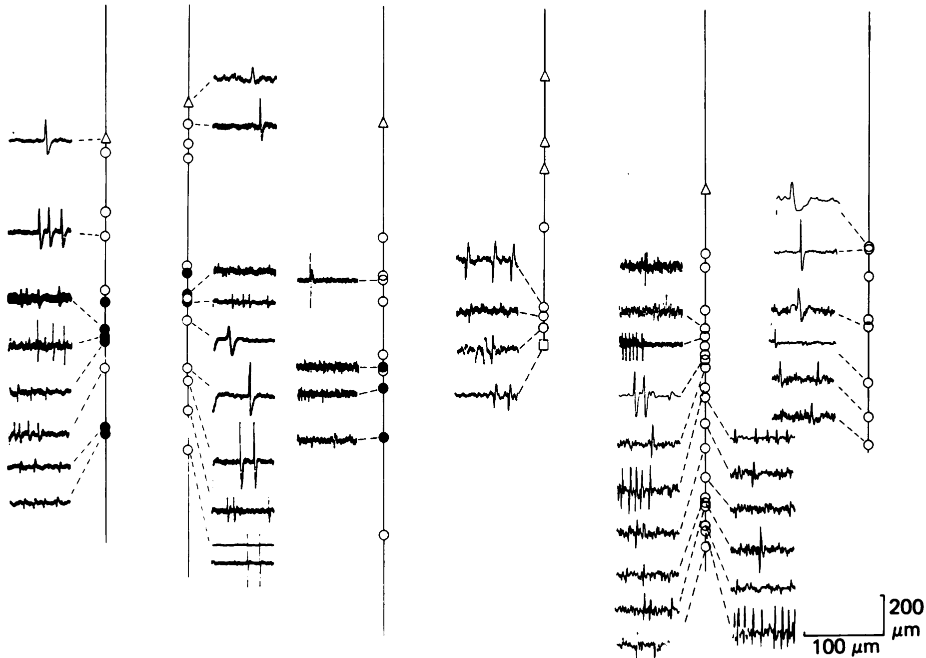

Fig. 8. Examples of extracellularly recorded unit activity from the experiment of Fig. 6. The calibration refers to distances within and between micro-electrode tracks. All records have positivity upwards but vary in time calibration (length of sweep 8–40 ms) and amplitude calibration (action potentials ranged from 0·2 to 20 mV peak to peak). For further details see the text. ●, cutaneous receptive field; ○, no receptive field; △, muscle afferent fibre.

of the dorsal horn on the side where the sciatic and saphenous nerves were intact. All recorded units had receptive fields and they were all appropriate in terms of the somatotopic map (Fig. 7).

In these two animals, 143 units were recorded on the side of the cord ipsilateral to the nerve sections. Twenty-five units were identified as muscle afferent fibres. Of the remaining 118 units only sixteen (14 %) had cutaneous receptive fields (for one other unit there was doubt as to whether there was a field or whether the response was to mechanical stimulation of the neuroma). Between four and twenty-one units were recorded in each micro-electrode track with an average of 10·2 units a track (if the muscle afferent fibres are excluded the average becomes 8·9 units a track).

The properties of the micro-electrodes we used for the extracellular recordings are relevant here, and some examples of data are presented in Fig. 8. The data are taken from the experiment illustrated in Fig. 6 and show recordings from forty-seven of

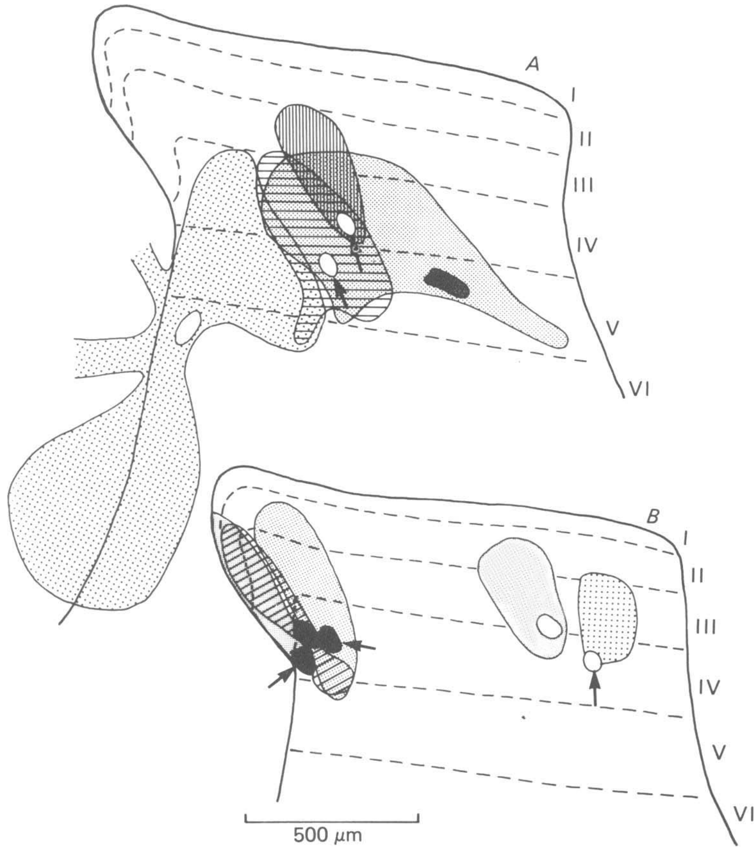

Fig. 9. Dendritic envelopes of stained neurones in the L6 segment on the side of the cord ipsilateral to the peripheral nerve sections. *A* is rostral L6 and *B*, caudal L6. Spinocervical tract neurones are indicated by arrows, and neurones with cutaneous receptive fields have their cell bodies filled in, whereas those with no receptive field have their cell bodies left clear. For further discussion see the text.

the seventy-four units observed in that experiment, that is, 63·5 % of the total. Examples from muscle afferent units as well as units with cutaneous receptive fields and with no discernible field are shown. Note the wide range of action potential shapes and signal-to-noise ratios. It is our experience that it is often impossible to assign particular shapes of extracellularly recorded impulses to either axons or cells (that is, to either axonal or soma–dendritic membrane). Positive–negative, as well as negative–positive, potentials are often recorded from cells, as shown by subsequent penetration, and biphasic potentials are frequently recorded from axons. Pure monophasic positive potentials are, in our experience, axonal in origin. Soma–dendritic impulses recorded extracellularly do not necessarily have an inflexion on their rising phase. Although the signal-to-noise ratio was low for some units studied extracellularly (Fig. 8), all observations were made on units with responses discernible against the background noise and any associated multi-unit activity. For many units the signal-to-noise ratio was large and extended beyond 20 to 1.

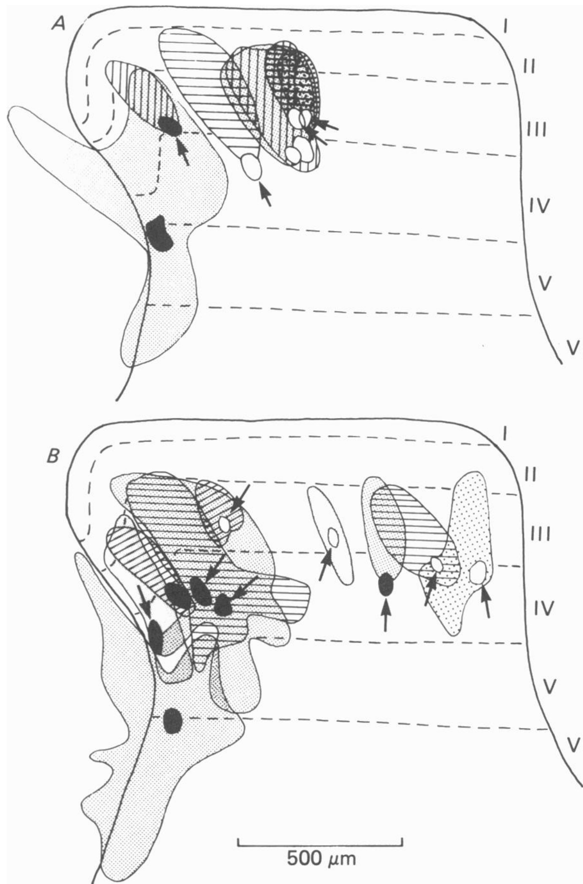

Fig. 10. This Figure is similar to Fig. 9 but is for the L7 segment.

The dendritic envelopes of intracellularly stained dorsal horn neurones

The dendritic trees of neurones injected with HRP were reconstructed. For the sample of spinocervical tract neurones (these are the only neurones where a sufficiently large population of cells in intact cats is available for comparison), the dendritic trees were, as far as could be ascertained by visual inspection, similar to those in intact animals. Figs. 9 and 10 show the dendritic envelopes of all reconstructed neurones as seen in transverse sections, with spinocervical tract neurones identified by arrows, and cells with receptive fields by filled symbols and those without receptive fields by open symbols.

The dendritic envelopes of two of the cells call for comment. In rostral L6 (Fig. 9*A*) the most medial cell had a receptive field on and around the knee (see Fig. 4). This neurone, in fact located very near the L5–L6 border in the most caudal part of L5, had a very extensive dendritic tree that extended laterally across the middle two quarters of the dorsal horn, mainly in laminae IV and V, as well as

TABLE 1. Dendritic extents of spinocervical tract cells in lumbosacral cord ipsilateral to sciatic and saphenous nerve sections

Neurones with cutaneous receptive fields

Location in dorsal horn	In lateral third						In medial third
Cell no.	1	2	3	4	5	6	7
Rostro-caudal extent (μm)	1200	1600	1700	1100	1300	1000	900
Medio-lateral extent (μm)	265	250	280	620	630	225	140
Rostro-caudal : medio-lateral ratio	4·5	6·4	6·1	1·8	2·1	4·4	6·4

Neurones with no discernible cutaneous receptive field

Location in dorsal horn	In lateral third		In middle third					In medial third		
Cell no.	1	2	3	4	5	6	7	8	9	10
Rostro-caudal extent (μm)	1300	700	1000	800	1400	1600	1100	1300	1000	700
Medio-lateral extent (μm)	290	145	175	130	165	250	370	165	220	265
Rostro-caudal : medio-lateral ratio	4·5	4·8	5·7	6·2	8·5	6·4	3·0	7·9	4·5	2·6

extending medially in lamina V almost to its medial border. The lateral extension of the dendritic tree may have been the receptive surface for input from intact peripheral nerves. However, as mentioned above, the receptive field of this neurone is not considered inappropriate in the somatotopic map and the cell's dendritic extent

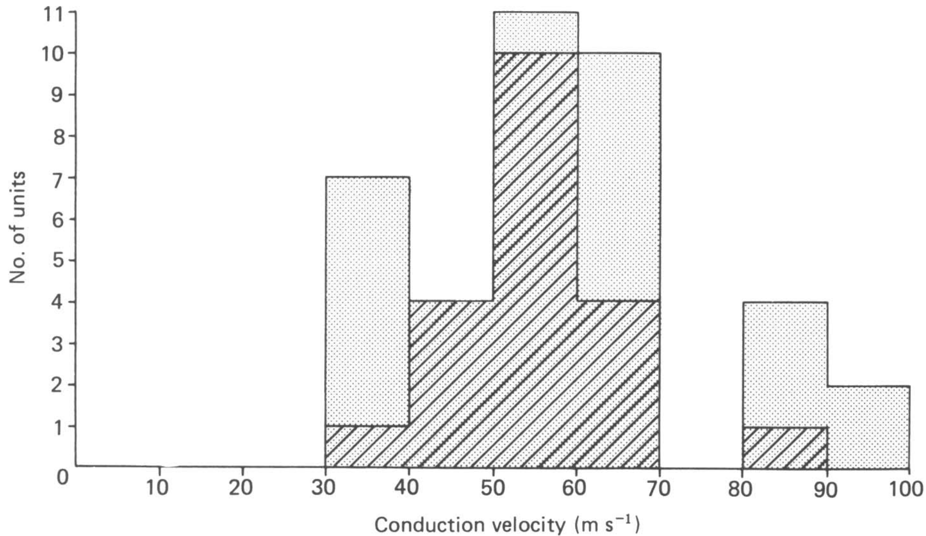

Fig. 11. Conduction velocities of the axons of spinocervical tract neurones. There is no obvious difference between those neurones with (▨) and those without (▩) cutaneous receptive fields, and they all fall within the range recorded for spinocervical tract neurones in intact cats.

may not be of overriding importance in this respect. In caudal L 7 (Fig. 10*B*) the most medial cell with a receptive field (a spinocervical tract neurone) had a very restricted dendritic tree envelope in both the transverse (140 μm) and also the sagittal (900 μm) planes (cell 7 in upper part of Table 1). The presence of a receptive field for this cell cannot be due to a lateral extension of the tree into the lateral dorsal horn. As mentioned above, the field of this cell might be considered inappropriate (see the Discussion).

Dendritic extents of spinocervical tract neurones. Table 1 presents data on the rostro-caudal and medio-lateral extents of the dendritic trees of spinocervical tract neurones, and on the rostro-caudal to medio-lateral dendritic extent ratios. These values may be compared with those for a population of similar neurones in intact cats (Brown *et al.* 1977). With the exception of one neurone (cell 2 in lower part of Table 1) located in the lateral third of the dorsal horn and which had no discernible field, all cells had dendritic extents similar to those in intact cats. The exceptional cell had a very limited dendritic tree of 700 μm rostro-caudally and 145 μm medio-laterally compared to the more usual values of about 1000–2000 μm and 200–450 μm respectively for laterally located neurones. However, the total numbers of spinocervical tract neurones examined are still a very small proportion of the total population and it seems unwise to make too much of this isolated example. In con-

clusion, it may be stated that no obvious signs of dendritic shrinkage or extension were found after 19–55 days of peripheral nerve section.

Conduction velocities of spinocervical tract neurones

The conduction velocities of the axons of the sample of spinocervical tract neurones ranged from 32 to 92 m s^{-1} (Fig. 11), the complete range being covered by cells with and without receptive fields. The conduction velocity values fall within the range previously observed for spinocervical tract neurones in intact cats (Brown & Franz, 1969; Brown *et al.* 1976, and unpublished observations).

DISCUSSION

The results presented in the present paper are clear: section of the sciatic and saphenous nerves in one hind limb of the cat (which denervates the limb distal to the ankle) leads to loss of all, or part, of the cutaneous receptive fields of neurones in laminae III, IV and V (and also dorsal lamina VI at least) in the medial two-thirds of dorsal horn in segments L6 and L7; this loss is maintained for at least 55 days after the nerve sections. These results are at variance with those reported by Devor & Wall (1978, 1981 *a*) and Lisney (1982, 1983) for the cat and by Devor & Wall (1981 *b*) for the rat. It is obvious that the possible reasons for these discrepancies must be discussed in detail.

The samples of recorded neurones

In most of the present experiments attempts were made to identify the recorded neurones in terms of their axonal projection as well as to locate them precisely by intracellular injection of HRP or by relating the positions of their recording sites to those of stained neurones. Eighty-four neurones were located in this way, thirty-one by staining and fifty-three by recording site, and of these thirty were spinocervical, seven were post-synaptic dorsal column and three were dorsolateral funicular in their projections. The remaining forty-four neurones were not identified by their axonal projections except that their axons did not project through the spinocervical tract, the dorsal columns or the ipsilateral dorsolateral funiculus. The neurones were located in laminae III, IV, V and the dorsal parts of lamina VI. The complete width of the dorsal horn was sampled, although we concentrated on the lateral half (fifty-nine of the eighty-four neurones) because we expected that if any signs of inappropriate receptive fields were to appear then they were more likely to appear at the border between the leg and foot representations.

In those experiments where neurones were identified, a search stimulus to the upper cervical cord (either the dorsolateral funiculus or the dorsal columns) was used. It might be thought that the use of such a stimulus might reveal samples of cells not seen in experiments where no such search was used. This is not likely to be the case, however, as the vast majority of neurones in these preparations had some background activity and could be isolated without the search stimulus. The presence of a background discharge in neurones which had no discernible receptive field after peripheral nerve section represents a difference between this preparation and that in which dorsal roots have been sectioned. After dorsal rhizotomies there are many

dorsal horn neurones with either no background activity or with a very low rate of ongoing discharge (Brown *et al.* 1983*a*).

Devor & Wall (1978, 1981*a*, *b*) and Lisney (1982, 1983) recorded all isolated units they could find in the dorsal horn without the use of a search stimulus to the central nervous system. It is possible that their samples of units differed from ours. For this reason, and also because of the possibility that stimulating the upper cervical cord might have produced some long-lasting inhibitory phenomenon that masked weak excitatory effects (see Results), we performed two experiments in which the cervical cord stimulation was omitted. In these experiments, also, we could find no evidence for the appearance of inappropriate receptive fields (see below) and other possibilities that might lead to differences in the various samples need to be examined. Two such possibilities present themselves: differences in the micro-electrodes or in the animal preparations used. Devor & Wall used pipettes filled with KCl (3 mol l^{-1}) of 1–5 MΩ impedance and Lisney used pipettes filled with NaCl (2·5 mol l^{-1}) of 8–20 MΩ. We used micro-electrodes containing 4–9 % HRP in Tris–HCl buffer and KCl 0·2 mol l^{-1} with impedances of 15–20 MΩ. Filling electrodes with the HRP mixture increases their impedances by 2–3 times. The recording characteristics of our electrodes do seem different from those used by Devor & Wall and by Lisney. Thus we recorded about ten units in each micro-electrode track through the dorsal horn (about nine units per track if muscle spindle afferents are excluded) whereas Devor & Wall (1981*a*) recorded 5·5 units per track and Lisney (1983) recorded only 1·1 units per track. Even if some of our recordings were from axons (and we have given reasons in the Results why we do not think this can be a major problem) it seems obvious that we were able to record from many more cells in each track. This is likely to have increased the variety of cell types recorded, not reduced them. An unknown factor in all experiments is the distance from the micro-electrode tip that unitary activity may be recorded. It is possible that a very low impedance electrode, such as one at the lower end of the range used by Devor & Wall, might record cells from some distance away, especially as the noise level of the electrode should be very low. Spinocervical tract neurones may be recorded a considerable distance away from the positions of their somata (certainly up to at least 150 μm away from the soma in all directions; Brown *et al.* 1976) even with fairly high impedance electrodes equivalent to about 10–25 MΩ if filled with NaCl, as may some other interneurones in the dorsal horn (unpublished observations). There will always be problems of localization if extracellular recording is used, even with the most careful attempts to localize the position of the electrode tip. All we can say is that in our hands the extracellular data agree remarkably well with the intracellular data, where the locations of recorded neurones are known precisely.

With regard to differences between the animal preparations used by the different sets of authors, Lisney (1983) used chloralose in the same dosage that we used: Devor & Wall (1981*a*) used either pentobarbitone (85 mg kg^{-1} followed by 40 mg kg^{-1} h^{-1}) or a mixture of diallybarbituric acid plus monoethyl urea plus urethane at doses of 70 + 250 + 280 mg kg^{-1} respectively. It is conceivable that these different anaesthetic regimes may have allowed Devor & Wall to record from neurones not observed in the present experiments, or reduced inhibitory effects and so allowed weak excitatory effects to produce neuronal firing. Finally, Devor & Wall (1981*a*) apparently applied

pinching with rat-toothed forceps to the whole hind limb, lower back and perineum throughout each micro-electrode penetration as they were searching for units. Such stimuli may well have raised the excitability of neurones and allowed weak inputs to cause them to fire. In conclusion, we find it difficult to believe that our sample of neurones was deficient in any important way but, it must be admitted, there are differences in the various experimental protocols used by Devor & Wall (1981*a*), Lisney (1983) and ourselves, and these differences might be sufficient to lead to the differences in reported results.

Effects of peripheral nerve lesions on dorsal horn somatotopy

The results presented show that after section of the sciatic and saphenous nerves in one hind limb of the cat those dorsal horn neurones expected to have cutaneous receptive fields on the foot and toes, that is, those neurones in the medial two-thirds of laminae III, IV and V in segments L6 and L7 lose their receptive fields, and between 19 and 55 days after the nerve section show no sign of having inappropriate fields. Of a total of 202 intra- and extracellularly recorded units only forty-one (20 %) had a cutaneous receptive field and in all but one of these the field was appropriately placed in the map. The one exceptional neurone was located in caudal L7 at the junction of the middle and medial thirds of the horn; it had a receptive field near the base of the tail. This field might be considered inappropriate to neurones in the L7 segment. Since the neurone was stained by intracellular HRP injection there can be no doubt about its location or that it was a somatic rather than an axonal recording. It remains a matter of conjecture as to whether this particular neurone was displaying the acquistion of a new inappropriate field or whether the field was already present before the nerve sections. It is, perhaps, relevant that in a previous study (Brown *et al.* 1980) two spinocervical tract neurones with receptive fields on the tail appear to be misplaced in the map in L7. However, the presence of one cell, from a total sample of 202, with an apparently inappropriate receptive field seems insufficient to allow the conclusion that such a phenomenon is of general occurrence.

Anatomy of dorsal horn neurones following peripheral nerve section

In this study there was no evidence for gross anatomical changes in the dendritic trees of dorsal horn neurones following sciatic and saphenous nerve sections. This is similar to the absence of changes after dorsal rhizotomies (Brown *et al.* 1983*a*). It is really only possible to compare the spinocervical tract neurones in the present sample with similar neurones in intact cats, since only for this group of neurones is there a sufficiently detailed data base. Spinocervical tract cells in the present sample had dendritic trees which fell within the morphological range of such cells in intact animals, irrespective of whether or not they had cutaneous receptive fields.

Conclusions

After section of the sciatic and saphenous nerves in the hind limb, dorsal horn neurones in the L6 and L7 segments of the spinal cord, ipsilateral to the sections, lose their cutaneous receptive fields, if those fields were on the foot, and within the next 55 days do not acquire new fields inappropriate to the normal somatotopic

organization. In other words, we have been unable to confirm the results of Devor & Wall (1978, 1981*a*, *b*) and Lisney (1982, 1983). The reasons for our failure are not immediately apparent.

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Note added in proof. In a similar series of experiments to ours, L. M. Pubols (The boundary of proximal hindlimb representation in the dorsal horn following peripheral nerve lesions in cats. *Somatosensory Research*, in the Press) has also failed to find evidence for inappropriate fields following sciatic and saphenous nerve section.

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