J. Physiol. (1976), **255**, *pp.* 321–334
With 1 plate and 4 text-figures
Printed in Great Britain

THE PHYSIOLOGY AND ANATOMY OF LONG RANGING AFFERENT FIBRES WITHIN THE SPINAL CORD

BY P. D. WALL AND R. WERMAN

From the Cerebral Functions Research Group, Department of Anatomy, University College London, London WC1E 6BT, England, and Neurobiology Unit, Institute of Life Sciences, Hebrew University, Jerusalem, Israel

(*Received 10 January 1975*)

SUMMARY

1. The caudal extent of the terminal arborizations of dorsal root afferents was determined in adult cats. The method used micro-electrode stimulation within the dorsal horn and the recording on a distant dorsal root filament of the antidromic action potentials evoked by the stimulation of axons within the spinal cord.

2. It was found that all filaments examined in the L2, 3 and 4 dorsal roots contained axons which projected at least as far as the S1 segment. The axons descended in or near the dorsal columns and from there penetrated into the grey matter.

3. The course of single fibres was followed to their apparent terminals. Thresholds, latencies and relative and absolute refractory periods were measured for single axons. These measurements confirmed that continuous axons ran from dorsal roots to distant segments and that the action potentials recorded were not dorsal root reflexes.

4. The majority of fibres with long range central arborizations were shown to have normal receptive fields in the dermatome of their parent dorsal root. They were not aberrant fibres leaving the spinal cord.

5. The long range afferents exist in substantial numbers since fifteen of eighty axons isolated by micro-electrode recording in the L2 dorsal root sent their axons as far as the S1 segment. The presence of these afferents from five segments away does not fit the data published on the inhibitory and excitatory receptive fields of dorsal horn cells which appear adequately explained by afferents arriving over nearby dorsal roots up to two segments away.

INTRODUCTION

For good reasons, both anatomists and physiologists have concentrated on the morphology and effectiveness of primary afferent fibres in the segment of entry and in the immediately neighbouring segments. There are two well known distant targets of entering lumbar afferent fibres, nucleus gracilis and Clarke's column. However, some anatomists have also mentioned that there is a diffuse innervation of dorsal horn for many segments rostral to the entry point (Liu, 1956; Sprague, 1958; Szentagothai, 1964; Imai & Kusama, 1968). Szentagothai (1964) writes, 'When a whole dorsal root is cut, a high density of degeneration fragments around large posterior horn neurons occurs in the immediately adjacent rostral segment but not in any other neighbouring segments. Degeneration fragments in these latter sites are encountered only as thin rows here and there.' Imai & Kusama (1968) showed that section of the L4 dorsal root results in degeneration in dorsal horn extending from T11 to at least S1. The bulk of the distant degeneration is in the intermediate region between dorsal and ventral horns but they also show clear degeneration in dorsal horn. Physiologists have not reported dorsal horn monosynaptic responses to dorsal root stimulation with recordings made more than one to two segments away from the entry zone except for the well studied example of Clarke's column.

We have studied here the far reaches of the caudal extent of primary afferent terminal arborizations. We chose to examine the descending limbs of the afferents to avoid confusion with the dense rostral projection of afferents to dorsal column nuclei and Clarke's column. The nature of the distant terminals is more than a curiosity for two reasons. Wall (1960) had shown that the afferents responsible for generating the receptive field of a lamina 4 cell ran in a small bundle within the nearest dorsal root. However, Merrill & Wall (1972) showed that neighbouring dorsal roots contained afferents which would excite the cell monosynaptically if they were electrically stimulated but which would fail to influence the cell when asynchronous 'natural' stimuli were applied. The observation of these relatively ineffective terminals obviously raised the possibility that there might be terminals at an even greater distance. In the present paper, we describe the results of a search in distant segments in intact adult cat dorsal horn for the presence of afferent terminals. The technique used to detect the terminal arborizations of afferent axons was micro-electrode stimulation.

METHODS

Experiments were completed on twenty-nine adult cats weighing 2·5–4 K anaesthetized with sufficient I.V. Nembutal or I.P. Dial to abolish the flexor reflex. Flaxedil and artificial respiration were used when necessary to control movement produced by stimulation within the cord. Temperature and blood pressure were monitored throughout. An extensive laminectomy was carried out to expose all lumbar segments and the cauda equina which were then covered with paraffin oil.

Recording methods

(*a*) *Dorsal root filaments.* Filaments of rostral lumbar dorsal roots fan out on entering the subarachnoid space and enter the cord separately. Filaments were freed by cutting the overlying arachnoid membrane. A fine coloured glass hook, which is visible under oil, was used to separate the filaments from their accompanying blood vessels. The rootlets were then cut peripherally and mounted on fine silver wire hooks for recording.

(*b*) *Single fibres.* Single units were also recorded in dorsal roots by using fine high impedance (more than 30 MΩ) KCl filled micro-electrodes. Here it was possible to examine single units individually without the danger of confusion between individual spikes which can occur with recordings from entire filaments on recording hook electrodes. Furthermore this method allowed the roots to be left intact so that the peripheral receptive field of single fibres could be examined as well as the extent of their central terminal arborizations. Since these dorsal root filaments are thin (often less than 100 μm) there was a danger that the recording electrode might slip through the root and enter fibres in the underlying dorsolateral white matter. To avoid this danger, the intact dorsal rootlet was dissected free of arachnoid in some animals and gently raised away from the surface of the cord with a fine silver hook. In other preparations, the rootlet to be examined was dissected free but not cut, and a sheet of parafilm was slipped under the rootlet to raise it above the cord surface.

Stimulation methods

(*a*) *Micro-electrodes.* Glass covered tungsten micro-electrodes with 30 μm of exposed tip (Merrill & Ainsworth, 1972) were used for stimulation within the spinal cord. The electrodes were held in a three dimensional micromanipulator. The stimulus was delivered with the micro-electrode tip negative from a constant current source (Devices, NeuroLog). For each electrode penetration, the tip of the electrode was brought to the cord surface and rapidly advanced for a trial penetration to the maximum intended depth to check for dimpling, bending or failure of penetration. The electrode was withdrawn to the surface and the experimental penetration was then commenced. In some trials NaCl filled electrodes with impedance of 3–5 MΩ were used for stimulation.

(*b*) *Surface stimulation.* In some experiments, the intraspinal course of fibres was checked by placing pairs of stimulating electrodes on the surface of the cord. Silver wires with fused rounded tips were placed so that the cathode was on the root entry zone of a particular segment and the anode was on the mid line of the same segment.

Electrode location

To locate the track of the stimulating electrode, a glass marker electrode of the type used for recording was cut off and left in position having been inserted along the same track as the metal electrode. Glass micro-electrodes can be cut with fine scissors on the thin part of the electrodes with remarkably little displacement. The

reason is that the glass tube shatters under the blades rather than twisting. The proof of the small distortion is that immediately after section the two cut ends, the piece free in the cord and the piece still held in the micromanipulator, can be seen under the microscope to be closely approximated, often touching. Further proof of the lack of distortion comes from the subsequent histological examination where the known depth of penetration of the electrode and the known separation of electrodes can be compared with the position of the electrodes after processing. In almost all tracks the final dimensions match the original measurements within $\pm 5\%$ and were considered acceptable. However, on occasions, presumably due to faulty penetration, the experimental and histological readings matched poorly and these tracks were rejected. At the end of the experiment, the exposed cord was soaked for some hours in 10% formol-saline. Then a large piece of cord containing the cut off electrodes was carefully dissected free and left in formol–saline for a further 12 hr. A free hand section of cord, about 1 mm thick, containing the electrodes is cut under a microscope with a razor blade. This section is dehydrated with 70, 90 and 100% ethyl alcohol, 2 hr in each solution. The section is then transferred to methyl salicylate and becomes transparent (Pl. 1). In this photograph, oblique lighting and the use of filters exaggerate the differences of transparency of the grey and white matter. With normal lighting, the course of the electrodes through the white matter can be observed. This method of electrode location is obviously convenient where localization of a recording or stimulating point within 50 μm is adequate for the experimenter's purposes, since results can be obtained within 24 hr without the use of skilled histologists.

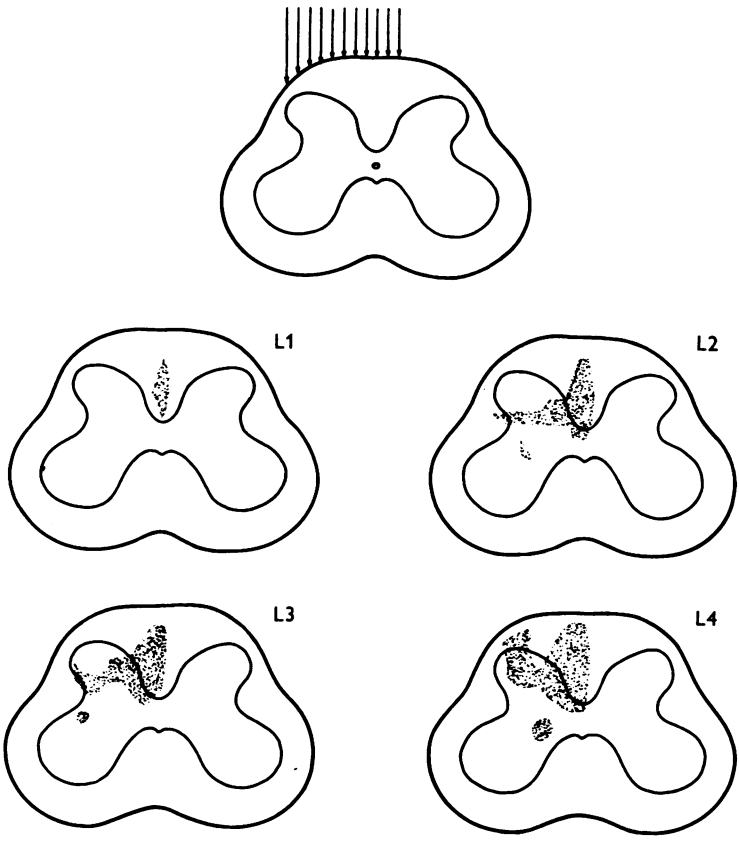
RESULTS

(1) *Over-all pattern of distant terminations*

In order to determine the general pattern of long ranging afferents, recordings were made on filaments of dorsal roots and antidromic impulses in the afferent fibres were generated by micro-electrode stimulation in segments L7 or S1. In every one of eighty filaments tested, there was evidence that afferent axons ran from the filament into the dorsal grey matter at least six segments caudal to the entry point.

In nineteen animals, a complete map of a single cross-section in one segment was completed using the following search procedure. One to four dorsal root filaments were placed on pairs of recording hooks so that for each stimulus point within the cord, each filament could be checked separately to see if the stimulus produced antidromic unit spikes running from the cord to the rootlet. Metal micro-electrodes were then inserted to produce a regular grid of stimulus points separated by 100 μm in the vertical direction and 200 μm in the medio-lateral direction. The first electrode track was placed on the opposite side of the cord from the recording root and then the search proceeded until the entire ipsilateral side of the cord had been covered in one plane. At each point on the grid, square wave stimuli with 0·05 msec duration at a frequency of 10 Hz were delivered and the intensity was raised from 0 to a maximum of 50 μA. The rootlet recording was examined for spikes which maintained a fixed latency after

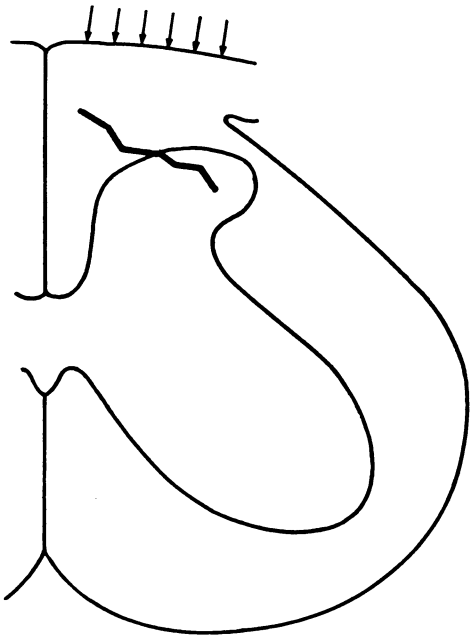
the stimulus and which followed the stimulus regularly. Threshold, latency and location of the stimulus point were recorded. Of seventy-five filaments of the L1 dorsal root, sixty-six contained fibres projecting as far as the junction of segments L7–S1. All filaments of dorsal roots L2, 3 and 4 which we examined sent axons as far as the L7–S1 region.



Text-fig. 1. The region of termination of afferents from filaments of the L1, 2, 3 and 4 dorsal roots in dorsal horn grey matter of the junction of the L7 and S1 segments. The arrows indicate the direction of the penetrating stimulating micro-electrode tracks separated by 200 μm. The dotted areas indicate the region from which the stimulating electrodes evoked antidromic spikes on the distant roots when pulses of 25 μA strength and 50 μsec duration were applied.

An example of one search is shown in Text-fig. 1. Recordings were made from the most rostral filaments of roots L1, 2, 3 and 4 at distances of 72, 58, 41 and 33 mm from the stimulus plane which was in caudal L7. Eleven stimulus tracks were explored in this plane with a total of 230 stimulus

points. Antidromic impulses appeared on all of the roots when stimulus intensities of less than 25 μA were applied. The location of the stimulus points which generated the antidromic potentials is shown in the figure for each of the four rootlets (Text-fig. 1). It will be seen that the L1 rootlet sent axons into a small zone of the dorsal columns. In this experiment, there was no evidence that these axons penetrated the grey matter, however in the majority of the other maps, L1 axons not only ran in white matter but also in the grey. In all of the maps fibres from L2, 3 and 4 penetrated the grey matter but the distribution varied from rootlet to



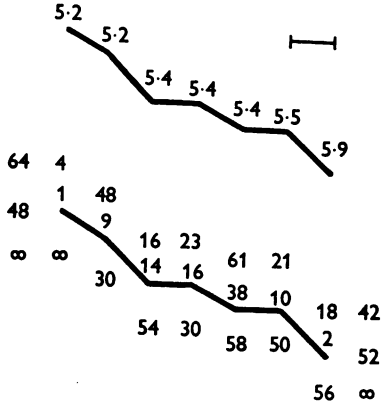
Text-fig. 2. The course of a single axon from dorsal columns to its apparent termination. The axon originated from the L1 dorsal root and terminated in the S1 segment. Its course was determined by micro-electrode stimulation and antidromic single unit recording. The direction of the stimulating micro-electrode tracks is shown by the arrows which are separated by 200 μm. As the micro-electrode approached the fibre, the threshold was continually tested and the point of lowest stimulus intensity was recorded. The line joins the seven points of lowest threshold.

rootlet and from animal to animal. For two rootlets of L2, fibres penetrated only into the medial region of lamina 6 but, in the other nine maps they extended across the entire width of the dorsal horn. In all maps of the distribution of L3 and 4, fibres were found in all parts of laminae 4, 5 and 6 as well as in the dorsal columns. Isolated islands of fibres originating from

L2, 3 and 4 were located in the ventral horn. In three maps these ventral horn regions were found to be connected by thin strands running from the dorsal columns.

(2) *Properties of single axons and their terminations*

(*a*) *Location*. Single units were identified in a dorsal root filament by their spike height, shape and latency. The cord was then searched with the stimulating micro-electrode to identify the points at which the axon could be stimulated with the lowest intensity stimulus. An example of the course



Text-fig. 3. Latency of antidromic conduction and threshold for the fibre shown in Text-fig. 2. Upper line: numbers on the line show the time in msec from the stimulus in S1 to the arrival of the evoked impulse in the L1 dorsal root 95 mm rostral. Lower line: numbers on the line show the threshold (μA) for firing the axon at the lowest threshold point along the electrode track. The numbers above and below the line show the threshold when the electrode was 200 μm dorsal or ventral to the lowest threshold point.

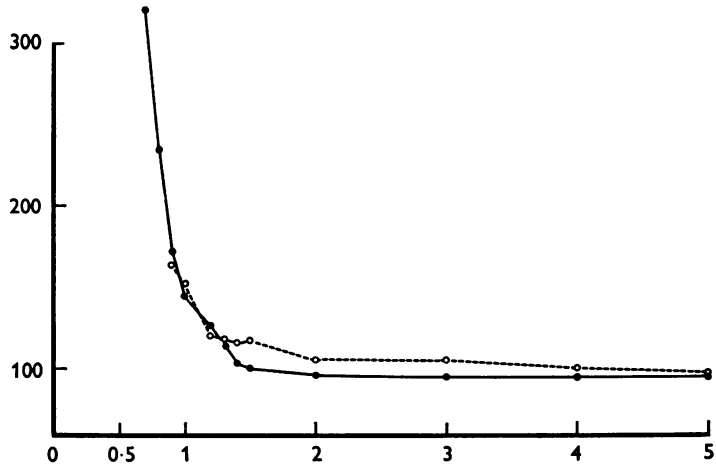
of a single axon is shown in Text-fig. 2. This fibre could be antidromically stimulated at a low intensity from seven parallel tracks separated by 200 μm. The line joins the location of the lowest intensity stimulus points. Its course was followed for approximately 1·2 mm running from dorsal columns in a ventrolateral direction to end in lamina 4 having passed through substantia gelatinosa. The axon appeared to terminate at the most lateral point of the line since stimulation at rostral or caudal or lateral locations to this point required a marked increase of stimulus strength before the axon would respond. Stimulation rostral to the medial end of the line showed that the axon originated from a fibre running in the dorsal columns. Six such fibres were traced. Many followed a meandering course usually slanting in a rostro-caudal direction.

(*b*) *Latency*. The latencies of the particular fibre whose location is shown

in Fig. 3 are shown in the upper part of Text-fig. 3. The latency was measured from the time when a threshold stimulus was delivered at the indicated point to the time of arrival of the identified single unit spike on the dorsal root filament. The lowest latency, 5·2 msec, will be seen to occur when the stimulus point was at the medial end of the line in the dorsal columns. Since the conduction distance was 95 mm, this means an overall conduction velocity of 18 m/sec. As the stimulus point was moved laterally toward the presumed terminal point, it will be seen that the latency increases. Over a distance of 1·2 mm, the latency rises 0·7 msec, giving an over-all conduction velocity of 1·7 m/sec. However, it will be noticed that 0·4 of the 0·7 msec rise of latency occurs between the two most lateral stimulus points. It seems likely that the axon was sharply tapering or dividing in its most lateral course. The same general pattern of shorter latency in the medial part of axons was seen in all examples and suggests that the axons located in the dorsal grey originated from axons running in dorsal columns. The over-all conduction velocity, 18 m/sec, of the fibre shown in Fig. 4 measured from its location in dorsal columns was slower than that recorded in many fibres. Of all rootlets and single fibres recorded, the over-all conduction velocity for L1 fibres projecting to L7–S1 varied between 1·6 and 40 m/sec: for L2, 4·0–36 m/sec: for L3, 2·7–27 m/sec and for L4, 3·6–36 m/sec. The conduction velocities of the parent fibres in the dorsal root filament were not known but judging by the height of the single unit spikes which were more than 300 μV, one must assume that their conduction velocities would be considerably faster than that measured over the entire length of the descending limb of the axon running in the dorsal columns. The shift of latency of 0·7 msec between the dorsal columns and the apparent terminal was less than that observed for many fibres. The meaning in terms of conduction velocity of these latency shifts was difficult to assess because the meandering course and branching of fibres made it difficult to determine the exact conduction distance. Furthermore, as the threshold rose toward the termination of many fibres, it became progressively more difficult to determine if the action potential was being generated in a nearby fine fibre or in a distant thicker one. A common finding, where the stimulating electrode was in the grey matter and the stimulus strength was held at threshold, was to observe latencies shifting between two fixed points as much as 0·4 msec apart without any apparent movement of the electrode or the stimulus parameters. Here presumably the stimulus was sometimes affecting the distal side of a branch point and on other occasions was stimulating more proximally.

(*c*) *Thresholds.* The lower line of Text-fig. 3 shows the spatial distribution of thresholds on a 200 μm grid about the single fibre described in Text-fig. 2. The figures are the threshold in μA for evoking an action potential with

a 100 μsec square wave pulse. It will be seen that the threshold rises quite steeply as the stimulating electrode moved away from the lowest threshold point. As the stimulus point moves laterally from dorsal columns into grey matter the threshold rises from 1 to 38 μA but then, as the lateral progress is continued, the threshold again drops to 2 μA. The presumed explanation for this is that the axon had meandered away from the search plane in the substantia gelatinosa but then swung back into the plane by the time it



Text-fig. 4. Refractory period and relative refractory period for a single axon terminating in L7 from the L1 dorsal root. The continuous line shows the results for stimulation of the axon within the dorsal columns and the interrupted line shows the results on the terminal end of the fibre in the grey matter. Two pulses were given through the stimulating micro-electrode. The pulses were separated by the time shown in msec on the horizontal axis. The stimulus strength needed to evoke a second shock is expressed on the vertical axis as a percentage of the strength needed to evoke a single impulse at 1 sec intervals. The absolute refractory period of the axon in the dorsal columns was 0·7 msec while at the termination of the same axon it was 0·9 msec. The relative refractory period lasted for 1·5 msec when the axon was stimulated in the dorsal columns and for 4–5 msec when the terminal was stimulated.

entered lamina 4. The rise of threshold observed by moving the stimulus point in the vertical plane suggests that the extent of this swerve of the axon out of the search plane would have been less than 200 μm.

(*d*) *Refractory periods.* It was obviously important to establish that the element being stimulated in the distant segment was in fact an axon continuous with the parent axon in the dorsal root. Therefore we measured the refractory period of eight of the distant axons in the dorsal columns and in the grey matter. Text-fig. 4 shows the result for one axon tested in

the two locations. A single suprathreshold pulse was delivered through the micro-electrode followed at various times by a second pulse. The threshold to evoke a second action potential was measured. For the axon illustrated the absolute refractory period was 0·9 msec for the terminal region in the grey matter and 0·7 msec for the axon in the dorsal column. All axons tested had absolute refractory periods of 1 msec or less. In all examples where we compared the absolute refractory period of an axon in dorsal columns and in grey matter, the absolute refractory period was shorter in the dorsal columns. It will be seen from the graph that the relative refractory period was very much longer when the terminal region was stimulated than when the axon in the dorsal column was stimulated. In this example the threshold for the terminal remains raised for 4–5 msec after its stimulation while that of the dorsal column part of the axon has returned to normal by 1·5 msec. This difference was also a consistent finding. Although the axons were capable of responding to two stimuli separated by 1 msec or less, the conduction velocity of the second impulse was considerably slowed when the interval between the two stimuli was short.

(3) *Number of axons*

It was difficult to estimate numbers of fibres projecting from a whole dorsal root filament to distal segments since, if large numbers of axons projected, the individual spikes fused to form a compound action potential and, if small numbers projected so that individual spikes were recorded, each spike would have had to be identified by its shape since latency varied with the particular stimulus point. It was apparent on gross inspection of the records that filaments of the L1 dorsal root sent less than ten axons to the S1 segment while more caudal roots sent more and more axons. To solve this problem, we turned to single axon recording with fine micro-electrodes in the dorsal root. Stimulating electrodes were mounted on the surface of the cord at various segments caudal to the recording root and stimuli were delivered at 10 Hz with 0·05 msec duration. The stimulus strength was raised until the evoked compound action potential on a nearby dorsal root was maximal. Using this technique, eighty axons in the L2 dorsal root were isolated. Of these eighty, seventy-five could be stimulated from the L3 segment 10 mm caudal, forty-four responded to stimuli at the L6 segment 52 mm caudal and fifteen responded to stimuli on the S1 segment 73 mm caudal. Of twenty-eight fibres isolated in the L1 dorsal root, 27 sent axons as far as the L2 segment but only one sent an axon as far as the S1 segment.

(4) *Nature of the fibres*

It was obviously important to establish that the axons which sent long range branches into the cord were in fact normal dorsal root axons. One origin of antidromic impulses in afferent fibres is the dorsal root reflex. None of the antidromic impulses reported here could have been dorsal root reflexes since they all followed stimulation at 10 Hz or more with a fixed latency. It is true that at some stimulus points, we observed the latency of a single unit jumping from one point to another but these jumps occurred between two fixed points in time and did not show the continuous variation characteristic of the dorsal root reflex. Raymond (1969) has reported a type of close coupling between afferent fibres which they termed 'ectodromic' where an afferent volley in one rootlet results in antidromic impulses emerging from another rootlet.

The impulses we observed could not be of this type because they are mainly limited to the same root, they fail to follow reliably at high frequencies, there is a variation of latency and they are influenced by other stimuli. We encountered one example of an aberrant single fibre which entered the cord over a dorsal root two segments caudal to the recorded root and appeared to send a branch out of the root from which recordings were taken. To establish receptive fields of fibres which sent axons caudally in the cord a distance of at least 65 mm, we recorded from thirty-five consecutive single fibres in intact L2 dorsal roots. Having established that the axon sent a long range axon down the cord, the entire thorax, abdomen and leg were gently brushed and probed. Of the thirty-five axons, twelve responded to hair brushing in the dermatome of the root, thirteen responded to probing muscle and for ten, no receptive field could be located. The rather high rate of failure is not surprising since the bulk of the proprioceptive afferents originated from back muscle and it was not possible to probe this muscle close to the recorded dorsal root without displacing the electrode. For similar reasons, deep probing of the abdomen was not possible. Furthermore, the initial exposure and laminectomy of the recorded segment is likely to have denervated some dorsomedial muscle. When a receptive field was located, orthodromic impulses collided with the antidromic ones.

(5) *Course of the fibres*

The axons discussed here did not follow an aberrant course in the periphery since the antidromic impulses evoked by central stimulation disappeared if the root was crushed central to the recording point. The fibres had no peripheral receptive field if the root was cut distal to the recording point. The central course of the descending axons was probably

in or near the dorsal columns. As judged by the progressive latency shift, the individual fibres whose terminal arborization were mapped all appeared to run from dorsal columns into grey matter. In four animals, progressive cord sections were made in the L5 segment while observing the antidromic volley generated in the S1 segment and recorded on the L2 dorsal root. One blade of fine jewellers forceps was inserted at 45° into the Lissauer tract and repeated crushes of the dorsal columns and dorsomedial grey matter were made. When the cord section advanced sufficiently medially to cut all of the dorsal columns, the antidromic impulses disappeared.

DISCUSSION

We have presented evidence that substantial numbers of dorsal root afferents penetrate into the cord many segments in a caudal direction. The fibres discussed here are presumably relatively large myelinated afferents since both of the recording methods which were used fail to detect single fibres of the small myelinated or unmyelinated type. This must be taken into account in any consideration of numbers of axons which send long range branches. 19% of the single units in L2 projected at least 73 mm caudally but there is no doubt that the sample of axons would be heavily biased in favour of large diameter (more than 10 μm) afferents. We can therefore say nothing of the smaller fibres which make up the majority of a dorsal root. We can be reasonably confident that the long range extensions were continuous axons originating in dorsal root for six reasons. The latency of response from a distant stimulus point was fixed with a variation of less than 0·1 msec at threshold. Where latency jumps occurred, they were between two fixed points and can reasonably be explained by stimulation in the region of branch points as has been observed by others who have used the antidromic micro-electrode stimulation technique for the location of axons (Wall, McCulloch, Lettvin & Pitts, 1955; Jankowska & Roberts, 1972; Merrill, 1974). The short absolute refractory period eliminates the possibility that the impulses passed over a normal synaptic region. The elimination of the antidromic impulses by impulses of orthodromic origin has been commonly used as a test of axonal continuity. The presence of a normal receptive field for at least some of the fibres helps discount the possibility that the impulses were dorsal root reflexes. The relatively high percentage of fibres without a detectable peripheral receptive field can be explained by the limitation of permissible stimuli which could be applied without mechanical displacement of the recording electrode and by the partial deafferentation produced by the initial exposure of the cord. Finally the absence of repetitive responses at low frequencies of stimulation and the accurate following at high frequencies

further help to reduce the possibility that the antidromic responses might be either trans-synaptic or examples of the 'ectodromic' impulses described by Raymond (1969).

If there is acceptable physiological evidence for the existence of these fibres, what of the anatomical evidence? The only recent paper to examine the extent of terminal arborizations is that of Imai & Kusama (1968). They used the Fink–Heimer technique and showed long range axons. Of the older papers using the Nauta technique, Liu (1956) shows very extensive rostral projections of roots but does not discuss their caudal counterpart. Other papers (reviewed in Brown & Fuchs, 1975) do not discuss terminations more than one or two segments from the root entry point. It is not clear if these authors had not examined the far reaches of the terminal arborizations or if the techniques failed to show the extremes of the arborization or if the stain used failed to show a sufficient density of degeneration or transport for the authors to identify terminal arborizations with certainty. All staining techniques produce a certain amount of background stain which ultimately defeats the definite identification of fine diameter thinly scattered axons. The use of micro-electrode stimulation for the localization of axons has a double advantage over anatomical methods. Single fibres may be located with ease. Furthermore it is possible to follow single fibres over very long distances. Clearly the technique has the disadvantage of being limited to those axons or cells from which recordings can be obtained over long periods of time so that the technique may produce information about only a fraction of existing axons. In the experiments reported here, we did not examine in detail the course of the axons between the dorsal root and the distant terminations beyond showing that they were cut by lesions in the mediodorsal segment of cord. Sterling & Kuypers (1967) study of branches of cervical roots descending at least three segments shows that some of the fibres run in longitudinal bundles in the medio-dorsal grey matter. In the lumbar cord the descending axons may run either in dorsal columns or in such longitudinal bundles.

We will not discuss here the post-synaptic effect of impulses in the long range afferents but it is apparent that there is a mismatch between the anatomy which shows a wide extent of terminal arborizations and the physiology of dorsal horn cells which shows relatively restricted and specific receptive fields. The inhibitory and excitatory receptive fields of these cells is adequately explained by assuming that they are affected by the nearest root and at most by two roots rostral and caudal to the main segment (Brown & Fuchs, 1975). In spite of this physiology, we present here evidence that fibres are terminating in the region of the cells from as much as five segments away.

The authors thank Mr A. Ainsworth, Dr E. G. Merrill, Dr M. Devor and Mrs Dinah Schonfeld for their help. The work was supported by the Medical Research Council, the U.S. Public Health Service and the Thyssen Foundation.

REFERENCES

BROWN, P. B. & FUCHS, J. L. (1975). Somatotopic representation of hind limb skin in cat dorsal horn. *J. Neurophysiol.* **38**, 1–9.

CHUNG, S. H., RAYMOND, S. A. & LETTVIN, J. (1970). Multiple meaning of single visual inputs. *Brain, Behav. & Evol.* **3**, 72–101.

IMAI, Y. & KUSAMA, T. (1968). Distribution of the dorsal root fibres in the cat. *Brain Res.* **13**, 338–359.

JANKOWSKA, E. & ROBERTS, N. J. (1972). Electrophysiological demonstration of the axonal projections of single spinal interneurones. *J. Physiol.* **222**, 597–622.

LIU, C. N. (1956). Afferent nerves to Clarke's column and the lateral cuneate nuclei in the cat. *Archs Neurol. Psychiat., Chicago* **75**, 66–77.

MERRILL, E. G. (1974). Finding a respiratory function for the medullary respiratory neurones. In *A Festschrift for J. Z. Young*, ed. BELLAIRS, R. & GRAY, E. G. Oxford: Clarendon Press.

MERRILL, E. G. & AINSWORTH, A. (1972). Glass coated platinum plated tungsten micro-electrodes. *Med. Electron. & biol. Engng* **10**, 662–672.

MERRILL, E. G. & WALL, P. D. (1972). Factors forming the edge of a receptive field. The presence of relatively ineffective afferents. *J. Physiol.* **226**, 825–846.

RAYMOND, S. A. (1969). Physiological influence on axonal conduction and distribution of nerve impulses. M.I.T., Ph.D. Thesis.

SPRAGUE, J. M. (1958). The distribution of dorsal root fibres on motor cells in the lumbosacral spinal cord of the cat. *Proc. R. Soc.* B **149**, 534–556.

STERLING, P. & KUYPERS, H. G. J. M. (1967). Anatomical organization of the brachial spinal cord. 1. Distribution of dorsal root fibres. *Brain Res.* **4**, 1–15.

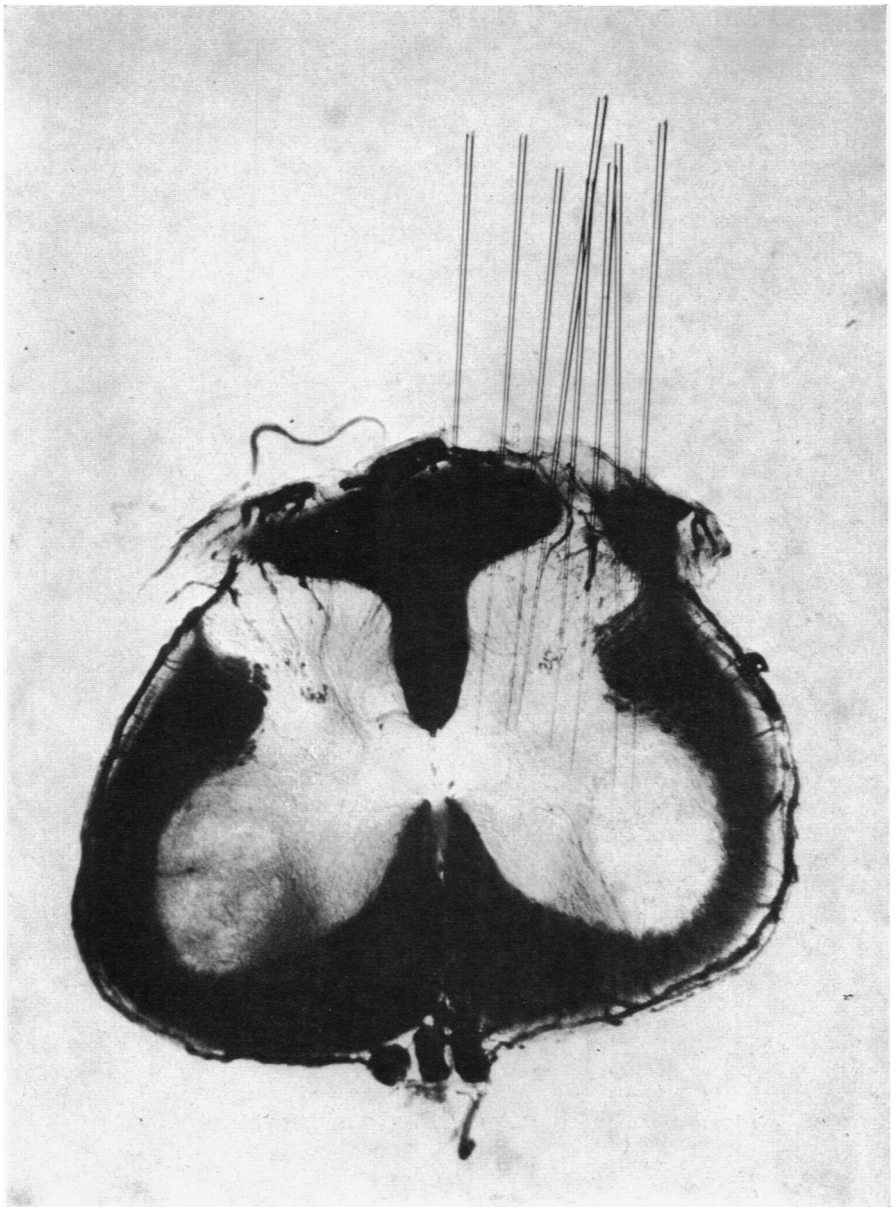
SZENTAGOTHAI, J. (1964). Propriospinal pathways and their synapses. *Prog. Brain Res.* **11**, 155–177.

WALL, P. D. (1960). Cord cells responding to touch, damage and temperature of skin. *J. Neurophysiol.* **23**, 197–210.

WALL, P. D., MCCULLOCH, W. S., LETTVIN, J. Y. & PITTS, W. H. (1955). Terminal arborisations of the cat's pyramidal tract determined by a new technique. *Yale J. Biol. Med.* **28**, 457–464.

EXPLANATION OF PLATE

Section of spinal cord containing micro-electrodes which were cut off and left *in situ* during an experiment. The cord was fixed in formalin and a free hand section containing the electrodes was cut. This thick section was then dehydrated with ethyl alcohol, cleared in methyl salicylate and photographed with oblique lighting.



P. D. WALL AND R. WERMAN

(*Facing p.* 334)