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CUTANEOUS RECEPTIVE FIELD AND MORPHOLOGICAL PROPERTIES OF HAMSTRING FLEXOR α-MOTONEURONES IN THE RAT

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SUMMARY

1. Intracellular recordings have been made from twenty antidromically identified posterior biceps femoris/semitendinosus (p.b.s.t.) hamstring flexor α-motoneurones in the decerebrate-spinal rat.

2. The hamstring motoneurones had either low or no spontaneous background activity. In nineteen of the twenty cells high-frequency phasic responses could be elicited by stimulation of the ipsilateral hind paw with firm pressure or pinch. There was no response to light touch or brush. Contralateral cutaneous mechanoreceptive fields with higher thresholds and weaker responses were present in 70% of the motoneurones.

3. Noxious heating of the ipsilateral hind paw produced excitatory responses in six of eight cells tested and two of these cells also responded to heating of the contralateral hind paw.

4. Stimulation of the ipsilateral sural nerve at graded strengths that successively activated Aβ, Aδ and C afferents produced excitatory post-synaptic potentials (e.p.s.p.s) at progressively longer latencies in the motoneurones. The C-fibre induced e.p.s.p. lasted up to 200 ms.

5. Horseradish peroxidase was injected into ten motoneurones and in seven cases full reconstructions of dendritic field, cell body and axon could be made. In agreement with previous reports from studies in the cat, the dendritic fields of rat motoneurones are very extensive in the rostrocaudal, mediolateral and dorsoventral planes.

6. The general pattern of dendritic branching for each motoneurone in this functionally homogeneous population was uniformly organized. Three major spatial orientations were always present: a rostrocaudally restricted series of dendrites emerging from the cell body and directed dorsolaterally towards the dorsolateral funiculus with branches in the lateral dorsal horn, a laterally, and a ventromedially directed series of branches arranged obliquely in the ventral horn, both of which were distributed rostrocaudally for equal distances from the cell body. Many of these dendritic branches terminated within the lateral and ventral white columns.

7. Although the sizes of the rat flexor motoneurones' somas ($51 \pm 4{\cdot}9$ μm, S.E., $n = 10$) were similar to those of cat lumbosacral α-motoneurones, the tip-to-tip

rostrocaudal extent of their dendritic fields (1130 ± 34 μm, S.E., $n = 7$) was half that reported in the cat.

8. These results are discussed in terms of the organization of the cutaneous flexor withdrawal reflex in the rat.

INTRODUCTION

A combination of electrophysiological and anatomical techniques has recently greatly extended our understanding of the structural and functional basis of the monosynaptic reflex arc in the cat spinal cord (Brown & Fyffe, 1981; Jack, Redman & Wong, 1981; Redman & Walmsly, 1983). Equivalent experiments are much more difficult to perform for polysynaptic reflexes but progress has been made in studying the organization of some of these reflexes (Lundberg, Malmgren & Schomburg, 1977; Egger, Freeman & Proshansky, 1980; Brink, Harrison, Jankowska, McCrea & Skoog, 1983). However, surprisingly little work has been performed on the morphological basis of the flexor withdrawal reflex (Willis, 1982). This reflex represents a segmental link between nociceptive afferents which terminate primarily within the superficial laminae of the dorsal horn (Light & Perl, 1979) and the flexor motoneurones which lie deep within the ventral horn (Romanes, 1951).

Sherrington was the first to recognize that flexor α-motoneurones have distinct high threshold cutaneous receptive fields (Sherrington, 1910), although this particular aspect of their input tended to be overlooked by subsequent studies that emphasized the convergence of a wide range of afferent inputs onto these cells (Eccles & Lundberg, 1959). A recent study in our laboratory has found that in the decerebrate-spinal rat posterior biceps femoris/semitendinosus (p.b.s.t.) flexor α-motoneurones are characterized by: absent spontaneous activity, polymodal high threshold cutaneous receptive fields and a short-duration high-frequency discharge to suprathreshold cutaneous stimuli (Woolf & Swett, 1984).

We have now examined the cutaneous receptive field properties of identified p.b.s.t. flexor α-motoneurones in the decerebrate-spinal rat using intracellular recordings and have injected horseradish peroxidase (HRP) into functionally characterized cells, enabling their morphology to be established. Preliminary results have been presented to the Physiology Society (Cook & Woolf, 1984).

METHODS

Experiments were performed on ten Sprague–Dawley rats (200–300 g). Under ether anaesthesia the trachea and one carotid artery were cannulated. The rats were then maintained under Althesin anaesthesia (Alphaxalone/Alphadalone; Glaxo) until decerebration was performed when the anaesthetic was discontinued. The rats were then paralysed with gallamine and artificially ventilated. Rectal temperature, heart rate and end-expiratory p_{CO_2} were monitored and maintained within normal physiological limits. The spinal cord was transected at T8–T10 and the lumbar enlargement (L3–L6) exposed. The preparation was stabilized by application of a plaster cast to the hips and a thoracic vertebral clamp. The nerves to the posterior biceps femoris and the principal head of the semitendinosus and the sural nerve were exposed in the popliteal fossa and placed on stimulating electrodes. Warmed mineral oil was used to cover both the spinal cord and the exposed nerves.

Glass recording electrodes with broken tips (1 μm) were filled with 3 M-KCl (15 MΩ) or 4% HRP

in a 0·1 M-KCl, 0·1 M-Tris HCl buffer (pH 8·0) solution (60 MΩ). The recording electrodes were directed at the p.b.s.t. motoneurone pool, the position of which had been found previously in other animals by retrograde labelling with HRP. Intracellular recordings were made from motoneurones, identified by antidromic invasion, following stimulation of their periperal axons.

The cell's response to sural stimulation was tested with graded stimuli (50 μA, 50 μs; 500 μA, 50 μs and 5 mA, 500 μs) to activate successively Aβ, Aδ and C afferent fibres (Woolf & Wall, 1982). The cell's response to noxious cutaneous stimuli was measured by applying controlled mechanical and thermal stimuli to the hind paws.

Following functional characterization, ten motoneurones were injected with HRP as described previously (Woolf & Fitzgerald, 1983). The experiment was terminated 1 h post-injection and the animal perfused with normal saline followed by a mixture of 1% glutaraldehyde and 2% paraformaldehyde. Serial transverse sections (50 μm) were made from the cord using a freezing microtome and processed to display the HRP (Hanker, Yates, Metz & Rustioni, 1977). The sections were mounted serially and reconstructions of motoneurones drawn with a camera lucida attachment to the microscope. No correction for shrinkage during fixation has been made, although a shrinkage factor of up to 12–16% can be expected (Lux, Shubert & Kreutzberg, 1970).

RESULTS

Intracellular recordings were made from twenty p.b.s.t. motoneurones, which were identified as α-motoneurones by the latency of their antidromic responses to stimulation of the nerves to the posterior head of biceps femoris and the principal head of semimembranosus in the popliteal fossa. Antidromic responses were characterized by their origin from a flat membrane potential and their ability to follow high frequencies without latency shift (Fig. 1*A*). Suprathreshold stimulation of the peripheral nerves did not always result in full somadendritic antidromic invasion even in cells with membrane potentials of $\leqslant -70$ mV. Depolarization of the motoneurones, either orthodromically or by the intracellular current injection, did however ultimately result in somadendritic spikes in all the motoneurones. Many of the motoneurones showed a delayed depolarization following the somadendritic spike (Fig. 1*A*) which is a feature of rat motoneurones (Granit, Kernell & Smith, 1963).

In the absence of peripheral stimuli most of the motoneurones showed no spontaneous background activity. When spontaneous firing was present, it was intermittent and never exceeded 1 Hz. The presence of cutaneous receptive fields was tested by applying a range of mechanical and thermal stimuli to the ipsilateral and contralateral hind paws. Nineteen of the twenty motoneurones had high threshold mechanoreceptive fields on the ipsilateral hind paw including the toes and the dorsal and plantar footpads. These cells responded to firm pressure ($>$ 20 g tested with von Frey hairs) and pinch but not to light touch or brush. The greatest response could be elicited by stimulation of the plantar surface of the toes followed in declining order by the dorsal surface of the toes, the plantar surface of the foot and the dorsum of the foot. The response to a standard (150 g) sustained pinch consisted of an initial high-frequency burst of activity (Fig. 2*A*) which lasted for 1–2 s but which rapidly diminished so that there was no response to the sustained stimulation beyond 3 s. The short-duration phasic response occurred in all the motoneurones. Repeated pinches to the ipsilateral foot at a frequency of 0·5 Hz resulted in a progressive habituation of the response which was spatially restricted. Stimulation of the contralateral hind paw elicited action potentials in fourteen of the motoneurones but the response was weaker (Fig. 2*B*) and required a more intense stimulus. In only one

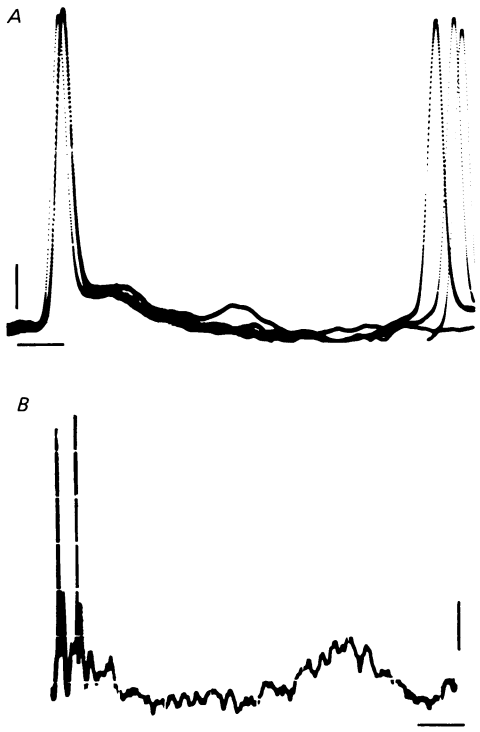

Fig. 1. *A*, An intracellular recording obtained from a p.b.s.t. flexor α-motoneurone showing the response to antidromic stimulation of the p.b.s.t. nerve at a frequency of 1 Hz (3 stimuli). The record shows the antidromic impulse followed by a delayed depolarization and the variable latency of the orthodromic impulses. Calibration: horizontal, 5 ms; vertical, 10 mV. *B*, an intracellular recording obtained from a p.b.s.t. flexor α-motoneurone showing the response to stimulation of the sural nerve at a strength sufficient to activate C afferent fibres (500 μs, 5 mA). The short latency e.p.s.p.s and action potentials were evoked by stimulation of A fibres and were followed by a wave with a latency of 225 ms, lasting 190 ms, which only appeared when the stimulus strength activated C fibres. Calibration: horizontal, 100 ms; vertical, 15 mV.

motoneurone did contralateral stimulation produce distinct inhibitory post-synaptic potentials. Only one of the twenty motoneurones showed no response to cutaneous mechanical stimulation.

Eight cells were tested for responses to thermal stimuli. None responded to innocuous levels of stimulation (< 45 °C), but six fired in response to heating the ipsilateral hind paw to a temperature greater than 50 °C. In two of these a response could also be elicited by heating the contralateral hind paw to > 50 °C. One cell responded to contralateral noxious thermal stimulation while showing no response to ipsilateral thermal stimulation.

Stimulation of the sural nerve elicited excitatory responses in all motoneurones tested. When only Aβ afferents were stimulated a short latency (5–8 ms) response occurred, recruitment of Aδ afferents resulted in further e.p.s.p.s at longer latencies (15–100 ms) while stimulation at a strength that also stimulated the non-myelinated C fibres produced a long-latency (150–300 ms), slowly rising, prolonged (200 ms) depolarization (Fig. 1 *B*).

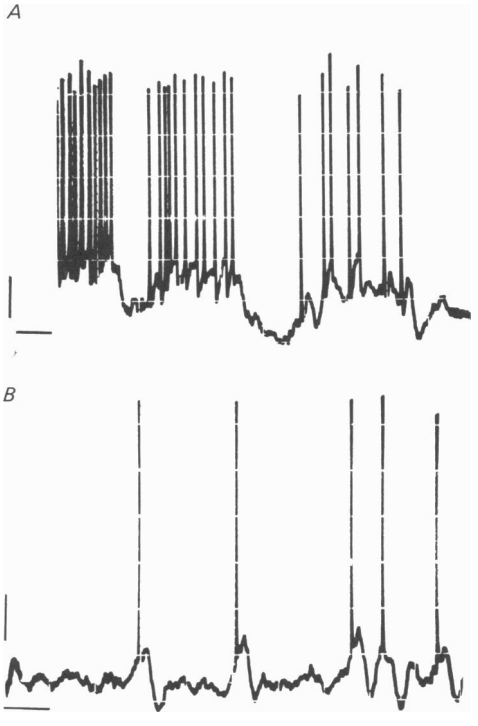

Fig. 2. Two intracellular recordings obtained from one p.b.s.t. flexor α-motoneurone. *A*, shows the response to sustained noxious mechanical stimulation of the ipsilateral hind paw. The record shows three waves of e.p.s.p.s generated by the stimulus, which give rise to action potentials of decreasing frequency. *B*, shows the response to sustained noxious mechanical stimulation of the contralateral hind paw. Note the relatively small number of action potentials evoked by this stimulus. Calibration: horizontal, 50 ms; vertical, 10 mV.

Ten p.b.s.t. flexor α-motoneurones were injected with HRP in ten different animals following characterization of their cutaneous receptive fields. All ten cells were recovered following histological processing. Examination of transverse sections of the cord showed that, with one exception, the cell bodies of all the filled α-motoneurones lay within the limits of the posterior biceps femoris/semitendinosus motor pool in lamina IX (Fig. 3). The mean size of the ten cell bodies, measured in two directions at right angles in the transverse plane was 51 μm $\pm$ 4·9 (S.E. of mean).

Seven of the ten motoneurones filled with HRP could be fully reconstructed (Fig. 4). Three cells were either damaged or were obscured by leakage of HRP, but the position and size of the cell bodies were still visible. The seven motoneurones reconstructed were judged to have been adequately filled by the large extent of their dendritic trees, the high order of dendritic branching and the presence of axon collaterals (Fig. 8). The numbers of primary dendrites ranged from five to ten with a mean of eight. The general pattern of orientation of the dendrites was similar in all cells, extending in three main directions: one dorsal set of dendrites, having branches in the lateral dorsal horn and the dorsolateral funiculus, a lateral set extending directly into the lateral white columns, and a medial set directed ventromedially down into the ventral white matter (Fig. 4).

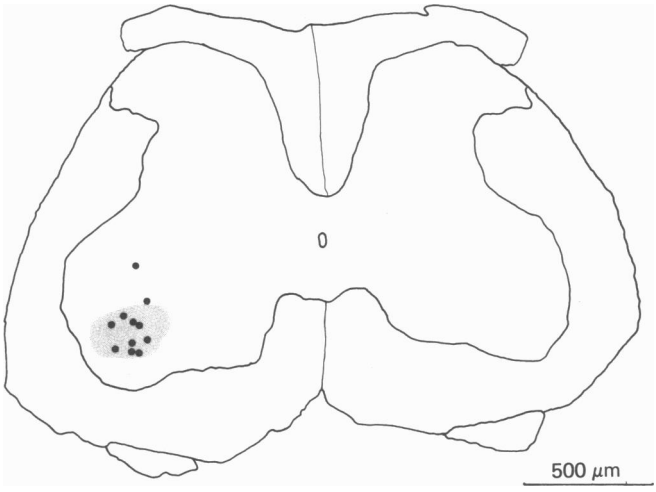

Fig. 3. A transverse section of the spinal cord illustrating the extent of the p.b.s.t. motoneurone pool established by retrograde labelling with HRP (shaded area). ●, relative positions of the cell bodies of the p.b.s.t. flexor α-motoneurones injected with HRP and recovered in this experiment. The actual position of the motoneurone pool varies in its rostrocaudal extent and not all the motoneurone cell bodies studies were situated at the same lumbar level.

The three main divisions of this dendritic field form a recognizable spatial pattern if reconstructed in the longitudinal plane (Fig. 5). It can be seen that the ventrally and laterally directed arms are essentially present throughout the entire rostrocaudal extent of the dendritic spread. The dorsally directed arm, however, appears at the level of the cell body and only extends in the rostrocaudal plane for 100 μm either rostrally or caudally of the cell body. This spatial restriction of the dorsolaterally directed extension was present in all seven motoneurones. Fig. 6 also shows that with respect to the cell body the extent of the dendritic spread is approximately the same

Fig. 4. Camera lucida reconstructions of four p.b.s.t. flexor α-motoneurones. The dashed lines indicate the boundaries between the grey and white matter. The arrows indicate the axons. The outline of the spinal cord for each reconstruction is taken from that at the level of the cell body. Because there is a considerable change in the size and shape of the spinal cord throughout the lumbar enlargement, the actual position of the dendrites relative to the white/grey boundaries or dorsal/ventral horns is not necessarily as depicted here. *A*, reconstruction from twenty-five, 50 μm transverse sections. This motoneurone was activated by noxious mechanical stimulation of both the ipsilateral and contralateral hind paw and by noxious thermal stimulation of the ipsilateral hind paw. *B*, reconstruction from twenty-three, 50 μm, transverse sections. This motoneurone was activated by noxious mechanical stimulation of both the ipsilateral and contralateral hind paws. *C*, reconstruction from seventeen, 50 μm, transverse sections. This motoneurone was activated by noxious mechanical stimulation of both the ipsilateral and contralateral hind paw and by noxious thermal stimulation of the contralateral hind paw. *D*, reconstruction from twenty-three, 50 μm, transverse sections. This motoneurone was activated by noxious mechanical stimulation of both the ipsilateral and contralateral hind paw and by noxious thermal stimulation of the ipsilateral hind paw. Calibration: 500 μm.

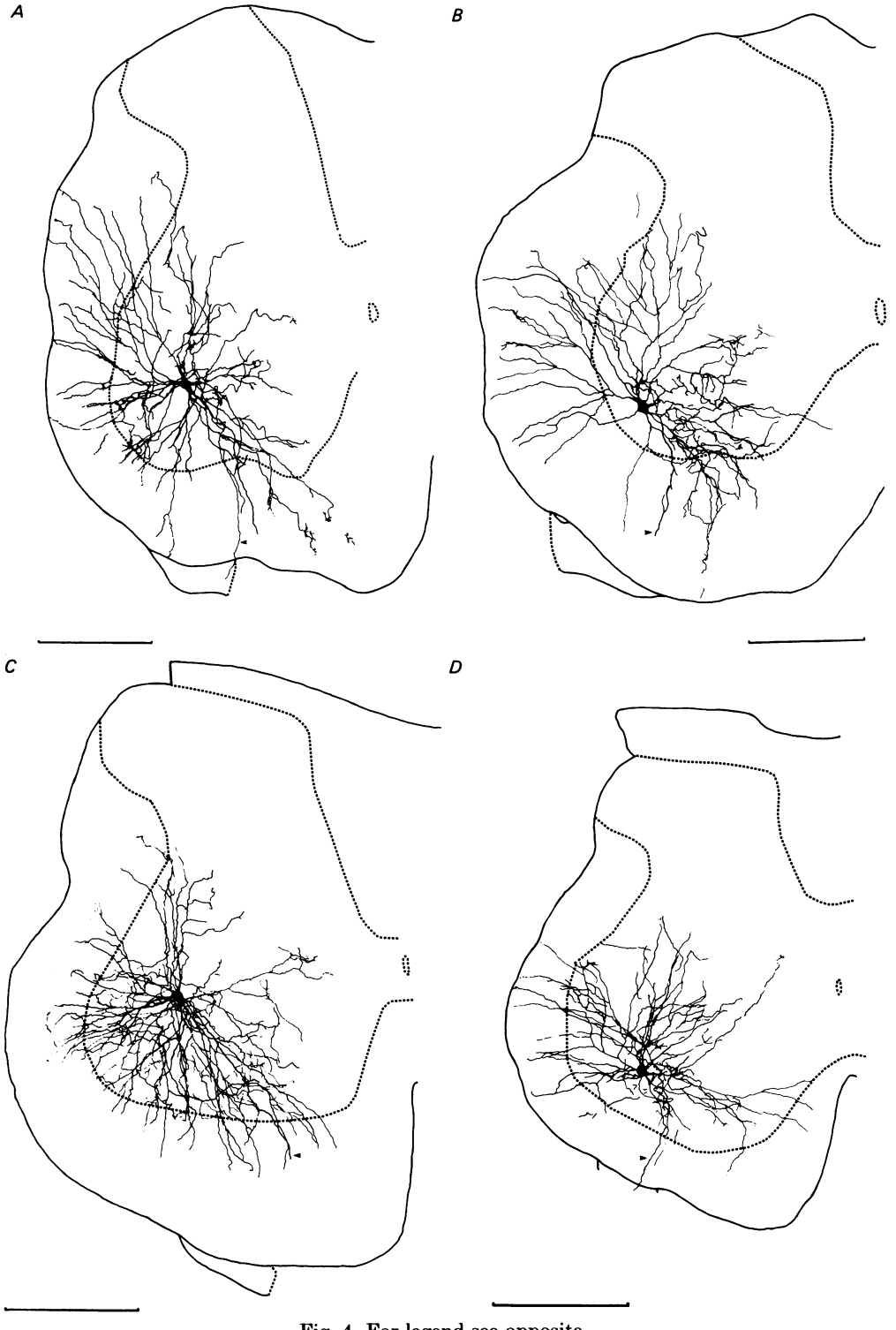

Fig. 4. For legend see opposite.

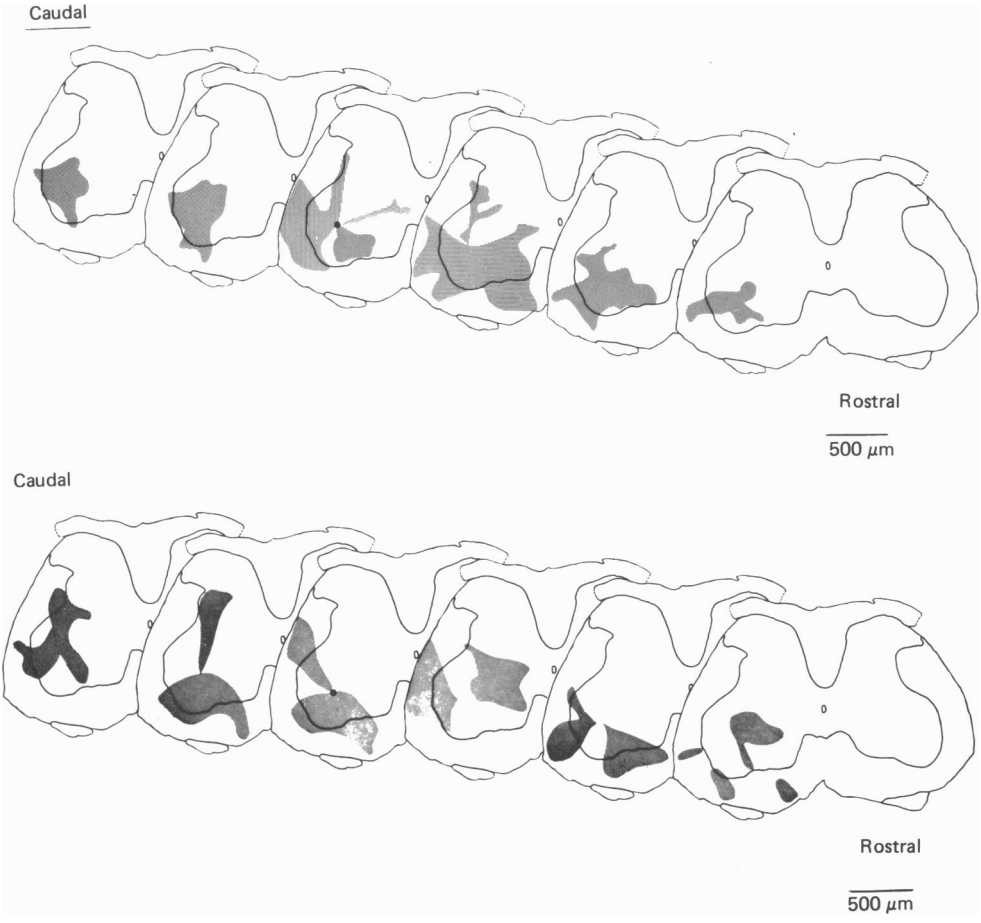

Fig. 5. Diagrammatic reconstruction of the dendritic envelopes of two p.b.s.t. α-motoneurones along the rostrocaudal axis. Each individual spinal cord outline shows the dendritic field reconstructed from four successive transverse sections (each of 50 μm). The cell body is represented by ●. The upper diagram illustrates the same motoneurone as shown in Fig. 4*C*, the lower diagram, the same as in Fig. 4*A*.

in both the rostral and caudal directions. For all motoneurones studied the entire dendritic tree had a mean rostrocaudal distribution of 1130 ± 34 μm (S.E. of mean) and a mediolateral spread of 907 ± 62 μm (S.E.), (Fig. 6). Plan views of the motoneurones (Fig. 6) reveal another aspect of their morphological homogeneity, the dendritic envelope is maximal in the mediolateral direction at its most rostral and caudal extents and narrows to a waist at the level of the cell body. Although all the cells had dendritic branches which extended dorsomedially towards the mid line, these were the least numerous of all the dendrites and the mid line was not reached in any of the cells. The over-all pattern of the cells seen in the transverse plane is one of an oblique orientation from dorsolateral to ventromedial with the cell body in the middle. Many of the dendrites had extensive arborizations in the white matter of the lateral and ventral funiculi. An unusual feature of some of the dendritic branches in

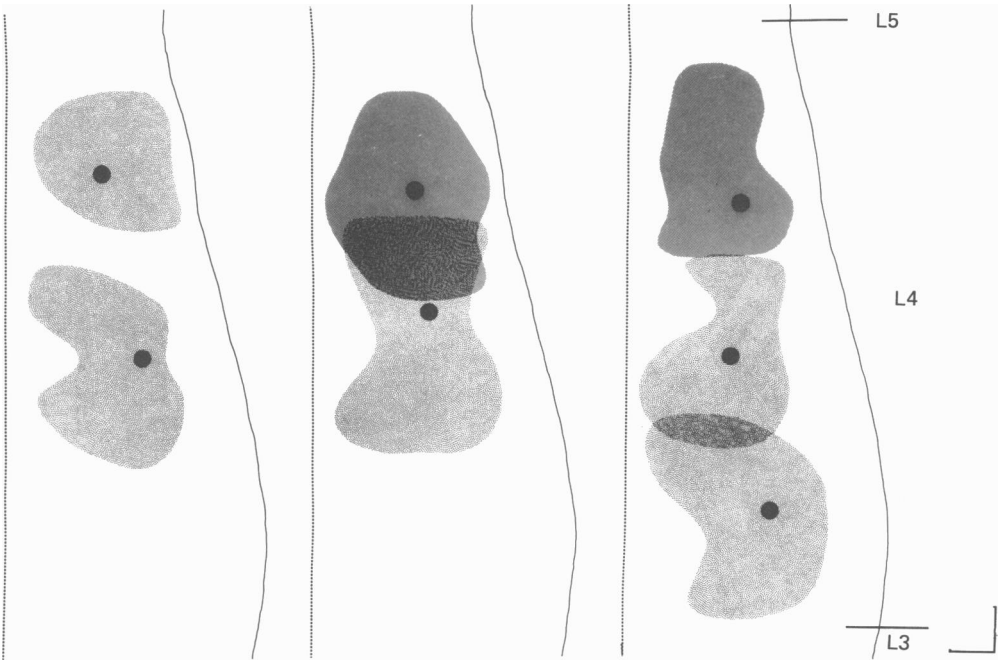

Fig. 6. Plan view of the spinal cord from the rostral region of the 3rd lumbar segment to the caudal region of the 5th lumbar segment, illustrating the dendritic envelope of seven flexor α-motoneurones (shaded areas). The cell body of each motoneurone is represented by a ●. The dotted lines represent the mid line of the spinal cord and the continuous lines represent the most lateral edge of the white matter. Calibration: horizontal and vertical, 250 μm.

the white matter was an abrupt change in their direction on approaching the edge of the spinal cord in the lateral funiculus.

The general spatial orientation of the dendritic fields of the p.b.s.t. flexor α-motoneurones is not shared by all motoneurones in the rat. This is illustrated by the motoneurone shown in Fig. 7. This cell, although possessing a cutaneous receptive field was not antidromically activated by stimulation of the p.b.s.t. nerve and its cell body lies within the tibial motor pool. The dendritic field is organized radially around the cell body and has a prominent medial projection towards the central canal. Note the prominent dendritic distribution in the dorsal horn including the most superficial laminae.

All the p.b.s.t. flexor motoneurones reconstructed had axons that were clearly seen to leave the spinal cord via the ventral root. In some cases a dendritic branch and the axon lay close together in the same fibre tract leaving the ventral grey matter. Fig. 8 shows an axon collateral typical of these motoneurones. The collateral leaves the axon in the white matter and runs back towards the grey matter, with up to 4th order branching in the vicinity of the motor pool. The appearance and complexity of these axon collaterals is very similar to that reported in the cat (Cullheim & Kellerth, 1978).

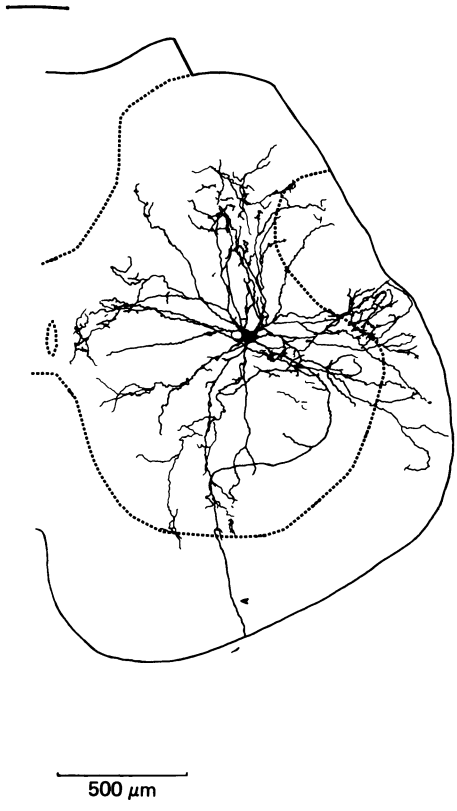

Fig. 7. Reconstruction from eighteen, 50 μm transverse sections of a tibial motoneurone. Note the over-all radial shape of the dendritic field and its extent in the dorsal horn. The dashed lines indicate the boundary between the grey and the white matter. An arrowhead indicates the axon.

DISCUSSION

In comparison with the cat, only very few studies have used intracellular recordings to investigate rat α-motoneurones *in vivo* (Bradley & Somjen, 1961; Granit *et al.* 1963) and *in vitro* (Fulton & Walton, 1981) and none have used injection of HRP into the neurones to assess their morphology. The present study shows both that rat p.b.s.t. flexor α-motoneurones are suitable for investigating electrophysiologically the organization of the flexor reflex and that the morphology of the rat motoneurones resembles in many respects that previously reported for the cat (Cullheim & Kellerth, 1978; Burke, Walmsley & Hodgson, 1979; Egger *et al.* 1980; Brown & Fyffe, 1981; Ulfhake & Kellerth, 1981; Westbury, 1982).

The cutaneous receptive field properties of the p.b.s.t. flexor α-motoneurones reported here from intracellular recordings of antidromically identified motoneurones in the decerebrate-spinal preparation, agree completely with those previously found in this laboratory during a study of single units isolated from the peripheral nerve (Woolf & Swett, 1984). These motoneurones respond characteristically with a limited burst of activity following suprathreshold stimulation of their cutaneous receptive

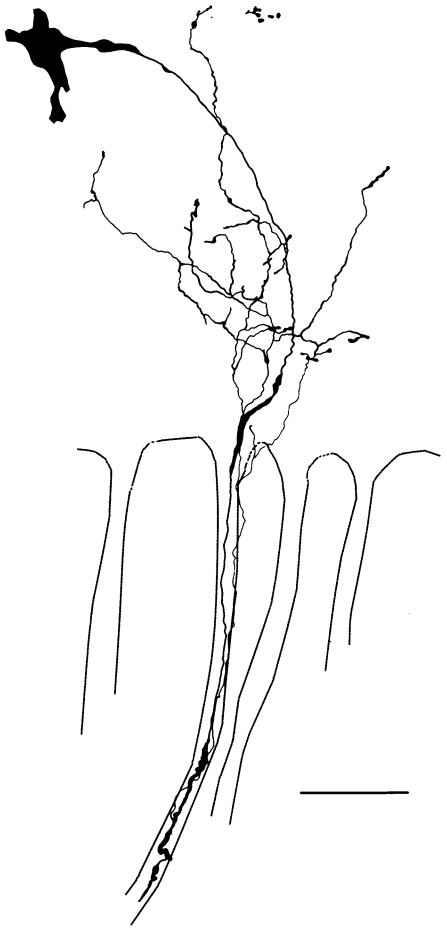

Fig. 8. Reconstruction from three, 50 μm transverse sections of the cell body and axonal system of a p.b.s.t. flexor α-motoneurone showing the distribution of axon collaterals. The dashed lines represent the border between the grey and white matter. Calibration: 60 μm.

fields, generating the output of the phasic flexion withdrawal reflex arc. In the rat the type of primary afferents likely to be specifically activated by firm pressure and pinch of the skin will be a mixture of Aδ and C afferent fibres (Lynn & Carpenter, 1982) while noxious heat is likely to activate predominantly C afferent fibres (Lynn & Carpenter, 1982). Neither light touch nor brush activated the flexor motoneurones, even though stimulation of the sural nerve at a strength that only activates Aβ low threshold mechanoreceptive afferents did evoke e.p.s.p.s in the motoneurone. This response to electrical stimulation may be dependent on the synchronization of activity in many afferents during such an input, which never occurs as a result of natural stimulation. The response of the motoneurone to stimulation of Aδ and C cutaneous afferents agreed with both previous extracellular findings (Woolf & Swett, 1984) and with intracellular recordings in cat flexor motoneurones (Endo, Hori & Willis, 1984). The relatively low rate of rise of the C-evoked e.p.s.p.s and their

prolonged duration are likely to mean that small changes in the membrane potential may make large differences in the number of action potentials evoked.

The general pattern of cutaneous receptive field organization found in the flexor motoneurones is one of maximum responsiveness to ipsilateral noxious stimuli, although a substantial number of motoneurones also respond to contralateral inputs; this means that for this population of flexor motoneurones in this preparation the 'rule' of crossed inhibition does not hold. The differences in the size of the mechanical and thermal receptive fields in individual motoneurones indicates that there are different organizational principles for different classes of cutaneous flexor reflex afferents and that the spatial pattern of the motoneurone's cutaneous receptive field is not one of convergence only.

The variation in receptive field properties found between individual motoneurones is likely to represent both the balance between excitatory and inhibitory influences operating on the motoneurones and the anatomical constraints imposed by the relative distribution of primary afferent terminals, the dendritic fields of the interneurones and their pattern of convergence onto the motoneurones. In the present study we did not separate the posterior biceps femoris and semitendinosus motoneurones, which may differ slightly in the size of their cutaneous receptive fields (Woolf & Swett, 1984), precisely for such reasons.

The major morphological feature of the p.b.s.t. motoneurones studied here was the homogeneity of their dendritic spatial organization. The similarities of the shapes of motoneurones innervating a similar group of muscles is in contrast to the heterogeneous appearance of interneurones in the superficial laminae of the rat dorsal horn where cells with very similar cutaneous receptive field properties often have quite different appearances (Woolf & Fitzgerald, 1983). A previous study of the cat sacral motoneurones which produce plantar flexion (physiological extension) as part of the plantar cushion reflex has also shown a similarity of morphology between functionally homogeneous motoneurones (Egger *et al.* 1980). Most other studies of cat lumbar sacral α-motoneurones have surveyed a mixture of different groups of motoneurones, so that it is not yet possible to say whether all motoneurones in a single motoneurone pool always have a similar appearance, nor whether such appearances are species specific.

In general there are many similarities but some differences between the morphology of cat α-motoneurones and the rat motoneurones described here. The size of the cell body of these two groups of α-motoneurones is very similar (Cullheim & Kellerth, 1978; Egger *et al.* 1980; Brown & Fyffe, 1981). Previous estimates of rat α-motoneuronal soma siza with Nissl stain (Granit *et al.* 1963) are significantly less than that found here with intracellular labelling. The complexity of the dendritic branching of rat α-motoneurones is equivalent to that of the cat (Westbury, 1982) and is much greater than γ-motoneurones. The rat motoneurones possessed five to ten primary dendrites, with a mean of eight which is less than the cat (Egger *et al.* 1980; Ulfhake & Kellerth, 1981; Brown & Fyffe, 1981) but the degree of dendritic branching (up to 6th order) is similar. One major difference is the total size of the dendritic field tip-to-tip, in the rostrocaudal, dorsoventral and mediolateral planes where the rat motoneurone dendrites are about half the size of the cat (Egger *et al.* 1980; Brown & Fyffe, 1981). Because the lumbar sacral cord of the cat is considerably larger than

that of the rat this may merely represent an appropriate scaling factor. Cat motoneurones have been found to give dendritic branches into the dorsal horn (e.g. Egger *et al.* 1980) but these are limited to the deepest laminae. Some of the rat motoneurones which we filled with HRP have dendrites extending into laminae III and IV (Fig. 7).

The p.b.s.t. motoneurone pool in the rat extends from the 3rd to the 5th lumbar segment (Woolf & Swett, 1984; Nicopoulos-Stouros & Iles, 1983). The present study has shown that it is likely that at least 95 % of all the α-motoneurones have cutaneous mechanoreceptive fields, each of which, while slightly different, characteristically responds maximally to stimulation of the ipsilateral toes. The plantar surface of the toes are innervated by the tibial nerve, the dorsal, lateral and medial surfaces by the sural, superficial peroneal and saphenous nerves. The primary C afferent terminals of these nerves are arranged somatotopically in lamina II of the dorsal horn in longitudinal columns which overlie the motoneurone pool (Swett & Woolf, 1985). The tibial terminal afferent field occupies the most medial third of the dorsal horn of the lumbar enlargement. This clearly is a considerable distance from the p.b.s.t. dendrites. Because the dorsally directed p.b.s.t. dendrites only occupy the most lateral portion of the deep dorsal horn and because they are rostrocaudally restricted to 200 μm it is unlikely that these dendrites contribute directly to the cutaneous receptive field properties of the motoneurones. Motoneurones spatially separated such that their dendritic envelopes do not overlap at all in the rostrocaudal plane (Fig. 6), have very similar or even identical cutaneous receptive fields. This indicates that it is also not the absolute rostrocaudal position of the p.b.s.t. motoneurones' dendrites that determines their cutaneous receptive field. The spatial organization, modality responsiveness and temporal properties of the cutaneous receptive fields of p.b.s.t. motoneurones must therefore largely reflect the location, number, distribution and efficacy of the chain of intervening interneurones that link the motoneurones with the primary afferents which innervate their cutaneous receptive fields. These interneurones must be organized longitudinally within the spinal cord such that the most rostral motoneurones in the p.b.s.t. motor pool will receive from the last of the interneurones in the chain practically the same cutaneous input as the most caudal motoneurone. The dendrites of the first of the interneurones in the polysynaptic chain must be positioned dorsoventrally and mediolaterally such that only somatotopically appropriate high threshold cutaneous afferent input will be transferred to the motoneurones. Nothing is known about the location of any of these interneurones at present, nor is it known whether their output is directed solely to the ventral horn. Unravelling the flexor reflex with its major cutaneous input may therefore contribute significantly to the understanding of the organization of the dorsal horn.

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