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THE MORPHOLOGY AND PROJECTIONS OF DORSAL HORN SPINOCEREBELLAR TRACT NEURONES IN THE CAT

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SUMMARY

1. The morphology of dorsal horn neurones located in the mid-lumbar segments of the spinal cord and which have an axonal projection to the cerebellum has been investigated. The neurones were identified by antidromic activation from the cerebellum and by their characteristic input from group II afferents as described in the preceding paper (Edgley & Jankowska, 1988).

2. The cell bodies of the neurones were distributed across the width of the spinal cord in laminae IV and V, but particularly at the border between these laminae. Most were in the caudal half of the fourth lumbar segment (L4), caudal to Clarke's column. However, neurones of this type were encountered as far caudal as the middle of the fifth lumbar segment (L5) and as far rostral as the middle of the third lumbar segment (L3).

3. The morphology of the neurones was investigated following intracellular staining with horseradish peroxidase (HRP). Fourteen well-filled cells were recovered. They had large somata and extensive dendritic arborizations within the dorsal horn which could extend more than 2 mm rostro-caudally. The most dense arborization was in laminae III and IV, just dorsal to the cell bodies.

4. The axons of all fourteen cells could be followed well into the white matter. All of them passed into the dorsal part of the ipsilateral lateral funiculus where they ascended. All followed a similar indirect course through the grey matter. Despite careful inspection, initial axon collaterals were never found.

5. All of the neurones were antidromically activated by low-intensity electrical stimulation of the dorsolateral part of the ipsilateral lateral funiculus in the thoracic region and from the cerebellum. The conduction velocities of the axons ranged from 62 to 112 m s^{-1} (mean 84·2 (S.D. $\pm$ 10·1) m s^{-1}).

6. The axonal terminations of some neurones were investigated by mapping the most effective locations for antidromic activation from the cerebellar cortex. Most neurones were activated with lowest stimulus intensities from the rostral part of the anterior lobe. A second effective area was found in the posterior lobe, deep to the paramedian lobule. The majority of neurones were activated from both locations, suggesting that their axons branched to terminate in both areas.

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7. On the basis of their projection and termination, it is proposed that the axons of these dorsal horn spinocerebellar tract neurones contribute to the dorsal spinocerebellar tract (DSCT).

INTRODUCTION

In the preceding paper (Edgley & Jankowska, 1988) the functional properties of a group of spinocerebellar tract neurones located outside of Clarke's column were described. Like the spinocerebellar tract neurones in Clarke's column, these neurones have axons which ascend in the ipsilateral lateral funiculus of the spinal cord, so they could be considered to contribute to the dorsal spinocerebellar tract (DSCT). On the basis of their input, which is primarily from hindlimb group II muscle afferents and cutaneous afferents, these neurones appear to make up a population which is functionally separate from Clarke's column neurones (Edgley & Jankowska, 1988).

In the present experiments we have investigated the location, axonal projections and morphology of these dorsal horn spinocerebellar tract neurones. A comparison of these properties with those of Clarke's column neurones and of other ascending tract neurones which are found in the same part of the dorsal horn has been made. Two groups of dorsal horn neurones with ipsilaterally ascending axons and extracerebellar targets have already been identified and investigated morphologically. These are spinocervical tract neurones, which have axons in the dorsolateral funiculus (Jankowska, Rastad & Westman, 1976; Brown, Rose & Snow, 1977*a*), and neurones with axons in the dorsal columns (postsynaptic dorsal column neurones; Brown & Fyffe, 1981). Our aim has been to determine whether dorsal horn spinocerebellar tract neurones are anatomically similar or distinct from these other types of ascending tract cells. In particular, we have investigated the size of the somata, the morphology of the dendrites, the trajectory of the axons and the presence or absence of axon collaterals. Lack of initial axon collaterals would indicate that the cells function mainly as ascending tract cells, as do Clarke's column neurones (Randic, Miletic & Loewy, 1981; Houchin, Maxwell, Fyffe & Brown, 1983), whereas their presence would indicate that the cells also play a role in local circuitry, as is the case for spinocervical tract neurones (Jankowska *et al.* 1976; Rastad, Jankowska & Westman, 1977; Brown *et al.* 1977*a*) and postsynaptic dorsal column neurones (Brown & Fyffe, 1981).

In addition to these properties we have also investigated the cerebellar termination of the axons, for comparison with the termination of the DSCT.

An abstract describing some aspects of this work has been published (Edgley & Gallimore, 1986).

METHODS

The bulk of the data described in this report were obtained from experiments on six adult cats, prepared with the anaesthetic and surgical procedures described in the preceding paper (Edgley & Jankowska, 1988). Our data are supplemented by some data derived from the experiments of the preceding paper.

Intracellular staining with horseradish peroxidase (HRP)

In order to investigate the morphology of dorsal horn spinocerebellar tract neurones, they were penetrated and filled with HRP in four experiments. In these experiments electrodes tip-filled with a solution (15% w/v) of HRP (Sigma, type VI) were used for recording. Pipettes with impedances of 15–30 MΩ were selected for use. Total current × time used for ionophoresis into successfully stained neurones ranged from 75 to 250 nA min. At the end of the experiment the cats were perfused through the descending aorta using Mesulam's (1982) procedure. The fixed spinal cords were sectioned either transversely (three cats) or horizontally (one cat) and processed according to the method of Hanker, Yate, Metz & Rustioni (1977). The processed section were counter-stained with Toluidine Blue.

Cerebellar stimulation

In the initial experiments silver ball electrodes placed on the cerebellar surface (with the dura intact) were used for antidromic activation of the neurones. A large exposure of the ipsilateral cerebellar cortex was made from the foramen magnum caudally to the tentorium rostrally and as far laterally as possible without causing excessive bleeding. In the early part of these experiments the most effective locations for antidromic activation of Clarke's column neurones (recorded in the L3 segment) were determined, to allow a comparison with the lowest threshold locations for antidromic activation of dorsal horn neurones.

In other experiments varnished tungsten needle electrodes were inserted into the cerebellar cortex. For access to the anterior lobe they were passed through a small slit in the dura approximately at the level of the fissura prima and were angled rostrally by 30–45 deg. For access to the posterior lobe electrodes were inserted through the paramedian lobule, with an angle of 20–30 deg, tip rostral. Two reconstructed electrode tracks are illustrated in Fig. 6. As for the surface electrodes, the most effective locations for antidromic activation of Clarke's column neurones in each stimulating electrode track were determined at the beginning of the experiment. At the end of each experiment an electrolytic lesion was made (500 μA for 15–30 s) in each electrode track and these were subsequently reconstructed histologically.

RESULTS

Distribution and location of cell bodies

Observations have been made on seventy-nine dorsal horn neurones which were antidromically activated from the cerebellum. All of the neurones were recorded in a region extending from the middle of the L5 segment to the middle of the L3 segment. At either end of this region neurones were encountered only infrequently, whereas they were common in the caudal half of the L4 segment. Consequently we have focused our attention on this region.

The location of the cell bodies of spinocerebellar tract neurones has been defined either by leaving the microelectrode in the track in which a neurone was penetrated (nine cases), or after intracellular staining with HRP (fourteen cases). Figure 1 shows the location of these neurones in two transverse planes. The cell bodies were distributed across the entire width of the dorsal horn and were usually close to the border of Rexed's laminae IV and V. During any particular experiment, dorsal horn spinocerebellar tract neurones could easily be differentiated from Clarke's column neurones. First, many were located caudal to Clarke's column, which usually ends in the rostral part of the L4 segment (Rexed, 1954). Secondly, they were found more superficially in the spinal cord, 1·2–1·8 mm deep to the surface of the dorsal columns, whereas Clarke's column neurones were generally more than 2·0 mm deep. Finally, dorsal horn spinocerebellar tract neurones had a characteristic input, from group II

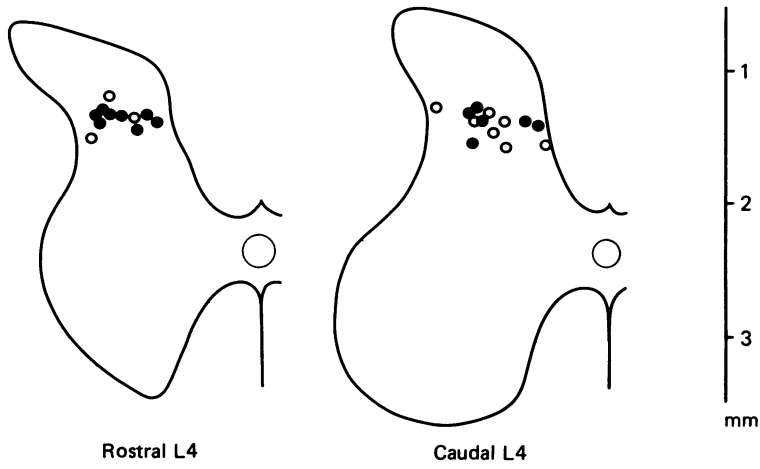

Fig. 1. Locations of dorsal horn spinocerebellar tract neurones. The locations of the cells determined after filling with HRP (●) or from reconstructions of electrode tracks (○) are shown in two transverse planes: in the rostral half of the L4 segment to the left and in the caudal half of the L4 segment and the rostral half of the L5 segment to the right.

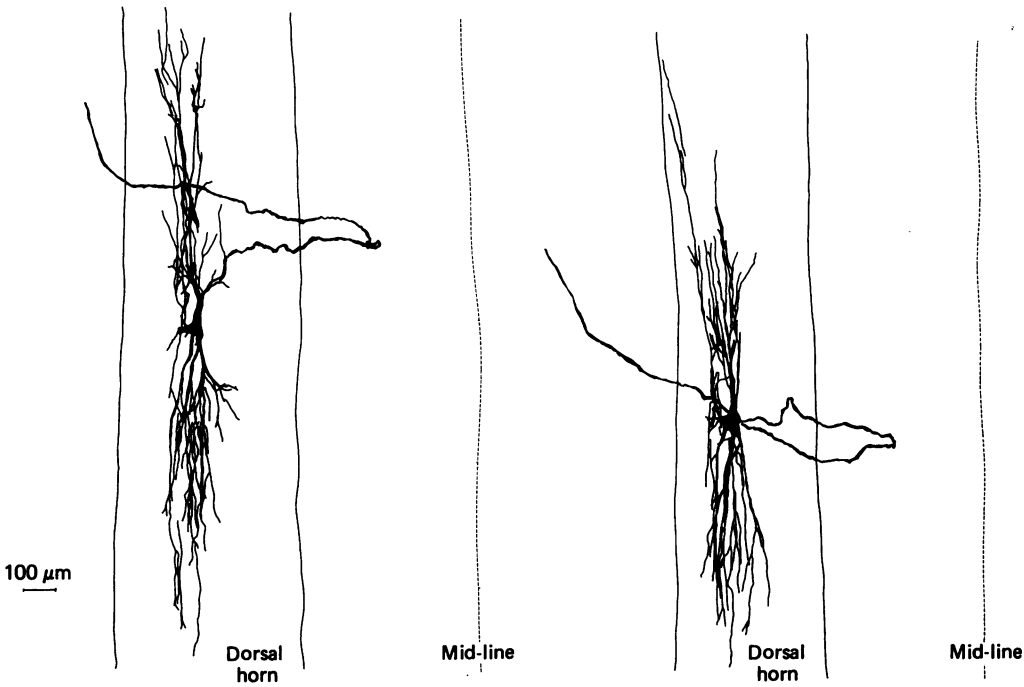

Fig. 2. Morphology of dorsal horn spinocerebellar tract neurones in the longitudinal plane. Reconstructions of two neurones are shown; the continuous lines represent the borders of the dorsal horn at the level of the cell body and the dotted lines mark the mid-line. Note that the axons first run medially before turning to pass into the lateral funiculus.

muscle afferents and cutaneous afferents, which has not been found in Clarke's column neurones. Consequently they were encountered in parts of the dorsal horn where large synaptic field potentials were evoked by group II, but not by group I, muscle afferents (Edgley & Jankowska, 1987) whereas field potentials from group I muscle afferents are found close to Clarke's column.

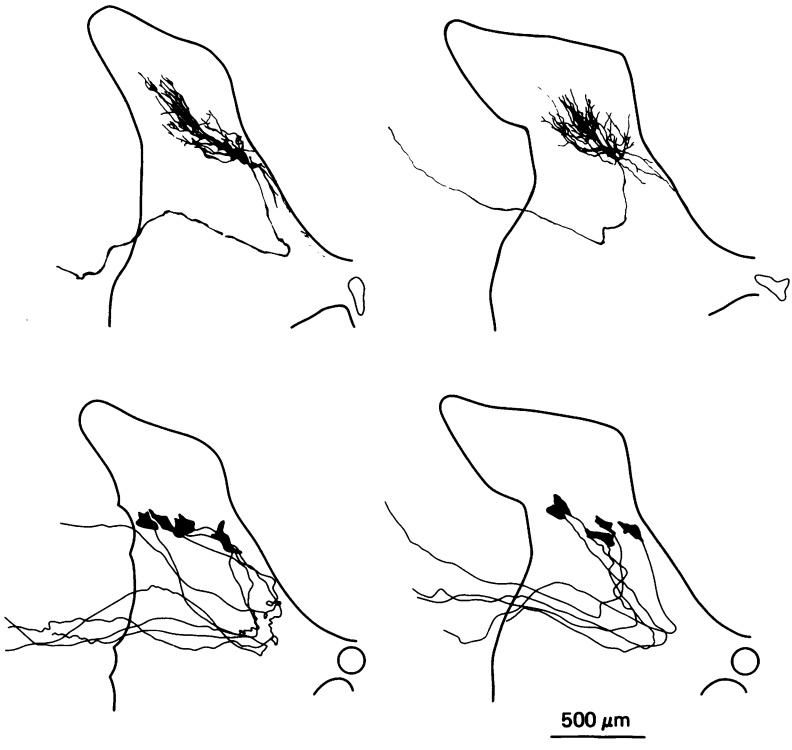

Fig. 3. Morphology of dorsal horn spinocerebellar tract neurones in the transverse plane and trajectories of the axons. Reconstructions of the dendritic trees of two neurones are shown in the upper diagrams. The lower diagrams show the cell bodies and axon trajectories of all of the ten stained neurones which were reconstructed in the transverse plane. Note that the initial portion of each axon is directed ventrally before turning to enter the lateral funiculus.

Although the neurones were readily found in the L4 segment, they were not clustered together as Clarke's column neurones are: in any individual electrode track extracellular recordings from only a single or exceptionally two neurones could be made.

Morphology of dorsal horn spinocerebellar tract neurones

Fourteen well-stained neurones were recovered from the four experiments in which intracellular HRP injections were made. They had large cell bodies with minimum mid-somal diameters of 23–38 μm. However, they were considerably elongated and usually extended for 80–100 μm in the rostro-caudal direction. Typically there were between five and nine primary dendrites and these gave rise to extensive dendritic

arborizations. Reconstructions of two neurones from horizontal sections are shown in Fig. 2, and two neurones from transverse sections are shown in the upper diagrams of Fig. 3.

One feature common to all of the neurones was the rostro-caudal elongation of the

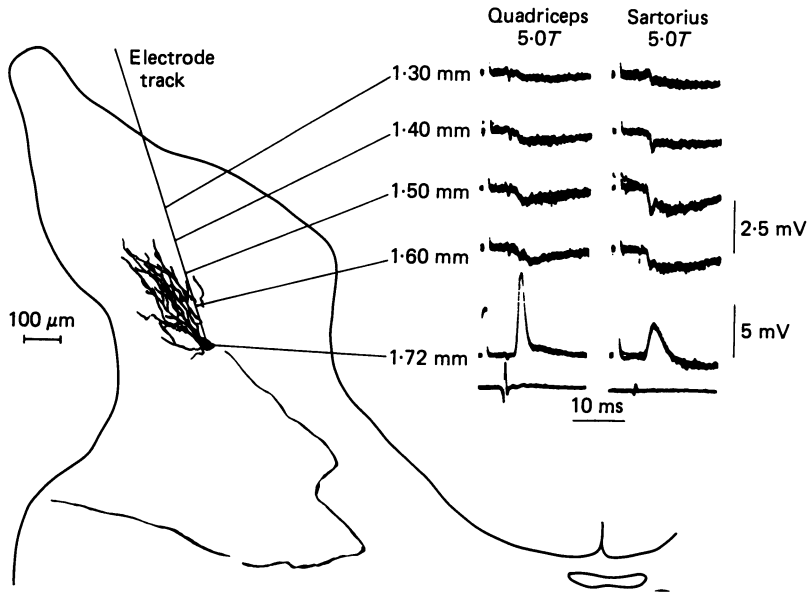

Fig. 4. Location of the dendrites in relation to the field potentials evoked by group II muscle afferents in the dorsal horn. To the left the soma, axon and main dendrites of one of the stained neurones are shown, with the electrode track in which the neurone was penetrated. The traces on the right are field potentials recorded at the marked positions along the electrode track (upper four traces) and intracellular records from the cell soma. The lowermost traces are from the surface of the spinal cord and show the arrival of volleys in muscle afferents at the L5 segment. In all of the traces the stimuli were kept at 5 times threshold for the most excitable fibres, in order to activate most of the group II afferents.

dendritic arborizations as can be seen in Fig. 2. In general the dendrites did not extend more than 300 μm medio-laterally and so did not reach both borders of the dorsal horn. Longitudinally, however, they were very extensive; all four of the neurones reconstructed in the horizontal plane had dendrites which extended for 2·0 mm. Dorso-ventrally most of the dendrites were confined to the area of, or just dorsal to, the cell body. In addition, a few fine dendrites which ran ventrally and medially close to the border of the dorsal columns could be found in some neurones. These dendrites passed towards the central canal, but always ended before reaching the substantia grisea centralis. The dorsally directed dendrites were most dense in laminae IV and V, extending to lamina III but not to lamina II. Each of the neurones therefore occupied a cigar-shaped territory, confined mainly to lamina IV. This is the region of the dorsal horn in which large synaptic field potentials are evoked by stimulation of group II afferents in muscle nerves (Edgley & Jankowska, 1987). The correspondence between the foci of these field potentials and the dendritic

arborization of a dorsal horn spinocerebellar tract neurone can be seen in Fig. 4. A reconstruction showing the locations of the soma, axon and main dendrites of a stained spinocerebellar tract neurone is shown to the left, together with the electrode track in which it was penetrated (as determined from the point of entry of the microelectrode and the location of the cell soma). Recordings made at different points along the track are shown to the right. The amplitude of the field potentials was maximal approximately 200 μm dorsal to the cell soma (1·5–1·6 mm deep to the surface of the dorsal column). Field potentials ventral to the cell body were not taken in this electrode track, in order not to destroy the cell. However, in other experiments the short-latency dorsal horn field potentials have been found to decline sharply below lamina V (Edgley & Jankowska, 1987).

Trajectory and conduction velocity of the axons

The axons of all fourteen stained neurones were well filled and could be followed for several millimetres as they ascended. The two lower diagrams in Fig. 3 show reconstructed axon trajectories for the ten cells which were sectioned in the transverse plane. All of them followed a similar but indirect course through the grey matter. Initially, they ran ventrally, and usually also medially, for more than 500 μm to a position at the ventro-medial border of the dorsal horn almost at the level of the central canal. At this point they turned, often after a series of complex convolutions, to pass laterally across the grey matter and into the ipsilateral lateral funiculus. A similar course could also be reconstructed for the four neurones which were cut in horizontal sections as illustrated in Fig. 2. Although all of the axons eventually ascended within the ipsilateral lateral funiculus, the initial ventrally directed parts of the axons did not always pass rostrally, but sometimes ran caudally for some distance before turning and entering the white matter to ascend.

Within the white matter the axons could be traced to the superficial half of the lateral funiculus. The stained axon ascended at this location, at the level of or dorsal to the central canal. Despite careful inspection of the stained sections of all of the axons throughout their course in the grey matter and well into the white matter, initial axon collaterals were never seen.

Because of the limited extent of the HRP staining of the axons, the course of the axons could only be followed for a few millimetres within the ipsilateral lateral funiculus. However, all of the neurones were antidromically activated by stimulation of the ipsilateral lateral funiculus in the thoracic region and, whenever tested (n = 24), from the first or second cervical segments. In all cases the stimuli were delivered via a pair of silver ball electrodes placed on the surface of the dura. Since small currents (often less than 50 μA) were sufficient to antidromically activate the neurones, it seems likely that the axons were large and travelled superficially within the funiculus.

The neurones were antidromically activated from the cerebellum with latencies of between 2·6 and 4·7 ms. Estimates of conduction velocity for the neurones have been obtained from the latency of antidromic activation and the total conduction distance from recording point to cerebellum. The values obtained range from 62 to 112 m s^{-1} and the mean was 84·2 (S.D. $\pm$ 10·1) m s^{-1}. A histogram of the distribution of conduction velocities is given in Fig. 5*A*. These values are approximate since the

precise conduction distance from the recording point to the cerebellum cannot be measured. However, a more accurate estimate of conduction velocity along the spinal cord has been obtained for those neurones which were antidromically activated from the cervical and thoracic segments (Fig. 5*B*). These values fall into the same range (mean 88·7, S.D. $\pm$ 11·5 m s^{-1}).

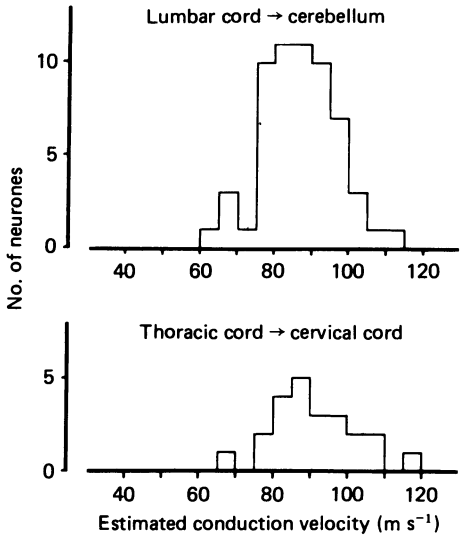

Fig. 5. Conduction velocities of the axons of dorsal horn spinocerebellar tract neurones. The upper histogram shows the distribution of conduction velocities for fifty-nine cells, calculated using the antidromic latency from the cerebellum and an estimate of the total conduction distance. The lower histogram shows the distribution of conduction velocities for those neurones which were antidromically activated from both the cervical and thoracic segments ($n = 23$) for which the conduction distance was determined more accurately.

Cerebellar termination of the axons

In the experiments in which surface stimulation was used for mapping, twenty-seven neurones were investigated. Currents of 150–500 μA were necessary to antidromically invade the neurones, at the lowest threshold point. A likely reason for these high thresholds was the distance between the axon terminals and the stimulating electrodes. With the dura intact the closest possible apposition between the mossy fibre terminals and the electrodes is 500 μm (the width of the dura mater, the molecular layer and the Purkinje cell layer). However, much larger separations are possible in the case of neurones which do not project to superficial parts of the cerebellar folia directly below the ball electrodes. Two low-threshold areas were found using surface mapping, one rostral on the anterior lobe with the electrodes placed under the tentorium and a second caudal on the posterior lobe with the electrodes placed on the paramedian lobule. A large majority of neurones (24/27:89%) could be activated from both regions.

To avoid the necessity for large stimuli and to define more precisely the position of the lowest threshold points, tungsten needle electrodes inserted into the cerebellum were used in the other experiments. In six experiments an electrode was inserted into

the anterior lobe and in three of them another was successfully inserted into the posterior lobe. Using these electrodes the neurones could usually be activated by stimuli of less than 100 μA and often less than 50 μA.

In the anterior lobe the most effective location for antidromic activation of the neurones was 9–12 mm deep to the cerebellar surface when the electrodes were inserted at the fissura prima. Reconstructions of the electrode tracks revealed that

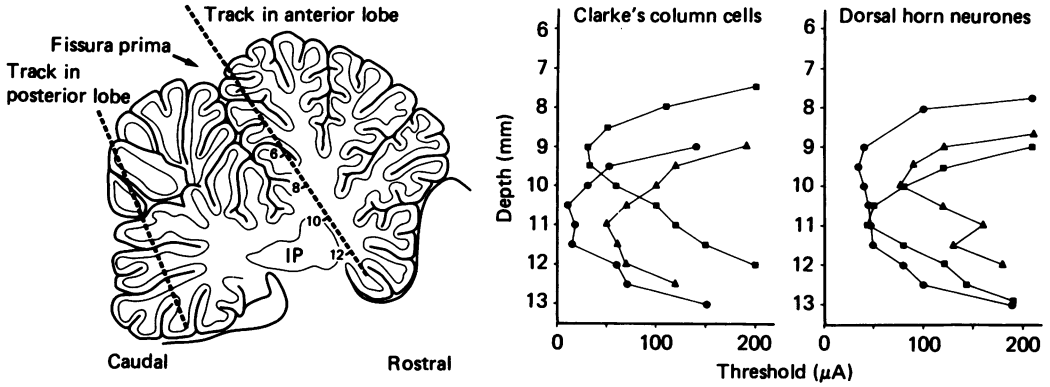

Fig. 6. Projection of the axons into the cerebellum. To the left is a sagittal section through the cerebellum showing the locations of two stimulating electrode tracks in the posterior and anterior lobes. The graphs are depth–threshold plots showing the positions along the anterior lobe electrode track from which three Clarke's column cells (left-hand plot) and three dorsal horn spinocerebellar tract cells (right-hand plot) were antidromically activated. The lowest threshold points for both types of cell were at 9–12 mm depth. IP, nucleus interpositus.

this location corresponds to the base of lobules III and IV, just anterior to nucleus interpositus anterior. One such reconstruction is illustrated in Fig. 6 (rostral track). The depth–threshold plots to the right show the best points for antidromic activation of three dorsal horn spinocerebellar tract neurones. For comparison, depth–threshold profiles for three Clarke's column neurones which were antidromically activated from the same electrode track are shown in the middle plot. These had their lowest thresholds at similar depths.

In the posterior lobe the most effective locations were 2–3 mm deep to the surface of the paramedian lobule (one track is illustrated in Fig. 6*A*). Sixteen neurones were recorded in the three experiments where electrodes were placed in both anterior and posterior lobes and twelve of them (75%) were antidromically activated from both locations. Together with the results from surface mapping, these data suggest that a substantial proportion of dorsal horn spinocerebellar tract neurones project to both the anterior and the posterior lobes of the cerebellum.

DISCUSSION

Morphology of dorsal horn spinocerebellar tract neurones

Although only fourteen neurones were investigated by intracellular staining, the appearance of all of the neurones was remarkably uniform. All had an extensive

dendritic territory in lamina IV which was extremely elongated and could extend for more than 2 mm rostro-caudally.

The elongated territory occupied by the dendrites corresponds closely to the region where group II muscle afferents evoke large synaptic field potentials (Edgley & Jankowska, 1987) and since these neurones are powerfully excited by group II muscle afferents (Edgley & Jankowska, 1988) it seems highly probable that, at least to some extent, the field potentials reflect synaptic currents in their dendrites. Large synaptic field potentials can also be evoked in this same region by low (electrical)-threshold afferents from the hairy skin of the leg and afferents from hair follicles have been shown to project there (Brown, Rose & Snow, 1977*b*). This may be the basis for the powerful actions cutaneous afferents exert on dorsal horn spinocerebellar tract neurones (Edgley & Jankowska, 1988).

In general, the dendritic arborizations of dorsal horn spinocerebellar tract neurones resemble those of the large projection neurones of Clarke's column, which are also elongated rostro-caudally but restricted medio-laterally (Randic *et al.* 1981; Houchin *et al.* 1983). In contrast, they differ from spinocervical tract cells and postsynaptic dorsal column neurones. Both of these types of neurone are also found in laminae IV and V, and, although those studied morphologically have been in the caudal lumbar segments, both are present in the L4 segment (Rustioni & Kaufman, 1977; Brown, Fyffe, Noble, Rose & Snow, 1980). Spinocervical tract neurones do not form a homogeneous group and only those located at the lateral border of the dorsal horn have elongated dendritic trees like those of dorsal horn spinocerebellar tract neurones (Brown *et al.* 1977*a*). Other spinocervical tract neurones and postsynaptic dorsal column neurones have dendritic arborizations which are restricted rostro-caudally (Brown & Fyffe, 1981). Generally, the diversity of the dendritic trees and axonal trajectories of both of these types of neurone (Jankowska *et al.* 1976; Brown *et al.* 1977*a*; Brown & Fyffe, 1981) is in strong contrast to the relative uniformity of those of the dorsal horn spinocerebellar tract neurones we have investigated.

All of the dorsal horn spinocerebellar tract neurones had axons which took a similar, indirect course to the white matter (Fig. 3). We can only speculate as to why they take such a course. One possible explanation could be that they run with the axons of Clarke's column neurones (or, in the case of those neurones located caudal to Clarke's column, at the location where Clarke's column would lie). Alternatively the cell bodies might migrate after initial axonal out-growth during development. Another possibility might be that the axons take this course in order to provide axon collaterals to other parts of the spinal cord. Such axon collaterals were, however, never seen. This is a further point of similarity with Clarke's column neurones (Randic *et al.* 1981; Houchin *et al.* 1983). However, initial axon collaterals are a common feature of the axons of both spinocervical tract cells (Rastad *et al.* 1977; Brown *et al.* 1977*a*) and postsynaptic dorsal column neurones (Brown & Fyffe, 1981). The lack of initial axon collaterals indicates that these cells do not exert actions on other nearby neurones; we may therefore exclude the possibility that a recurrent inhibitory pathway is responsible for the IPSPs seen in some neurones (Edgley & Jankowska, 1988).

In common with Clarke's column neurones the axons of dorsal horn spinocerebellar tract neurones are large and rapidly conducting. Their axonal conduction velocities

are directly comparable to published values for Clarke's column neurones (60–120 m s^{-1}: Oscarsson, 1973; Mann, 1973) and are such that information impinging on the neurones may reach the cerebellum in 3–4 ms. Only the fastest conducting spinocervical tract and postsynaptic dorsal column neurone axons fall within this range (see Jankowska, Rastad & Zarzecki, 1979; Brown, 1981; Brown & Fyffe, 1981).

Although the input to dorsal horn spinocerebellar tract neurones differs strikingly from that of the large projection cells of Clarke's column, in terms of dendritic and axonal morphology and axonal conduction velocity they are closely similar.

Classification of dorsal horn spinocerebellar tract neurones as contributing to the dorsal spinocerebellar tract

The two classical hindlimb spinocerebellar tracts, the DSCT and the ventral spinocerebellar tract (VSCT), are both rapidly conducting and arise from large neurones located in segments rostral to those which contain the majority of hindlimb motoneurones. Dorsal horn spinocerebellar tract neurones share these features. The DSCT is generally thought to arise from neurones in Clarke's column (Oscarsson, 1973; Brodal, 1981) which have axons which ascend in the dorsolateral part of the ipsilateral lateral funiculus (Grant, 1962). The VSCT arises from the spinal border cells of Cooper & Sherrington (1940) and from scattered neurones in the ventral horn (cf. Oscarsson, 1973); its axons ascend contralaterally in the lateral funiculus.

Although these groups of neurones give rise to a large number, most probably the great majority, of spinocerebellar tract fibres from the hindlimb, there have been reports from electrophysiological studies of other groups of spinocerebellar tract neurones (Aoyama, Hongo & Kudo, 1973; Tapper, Mann, Brown & Cogdell, 1975; Randic, Myslinski & Gordon, 1976). These neurones all have ipsilaterally ascending axons, but are located outside of Clarke's column. The existence of these neurones has not been easy to demonstrate using anatomical degeneration techniques because many spinocerebellar tract neurones do not show degeneration after cerebellectomy. However, with the introduction of HRP as a retrogradely transported neuroanatomical tracer it has become possible to identify the spinal sources of input to the cerebellum in detail (Matsushita, Hosoya & Ikeda, 1979; Grant, Wiksten, Berkley & Aldskogius, 1982). Several groups of spinocerebellar tract neurones other than the classical ones have been identified and by combining the HRP technique with limited spinal cord lesions, Matsushita *et al.* (1979) have determined the locations of the axons of these other groups. Spinocerebellar tract neurones with ipsilaterally ascending axons were found at two locations in the lumbar segments outside of Clarke's column: one group was ventro-medial in the dorsal horn, primarily in the sixth lumbar segment (approximately at the location of Clarke's column, but caudal to it) and the other group was in laminae IV and V of the dorsal horn. Matsushita *et al.* (1979) classified these cells as group II and group 9 respectively. It seems highly probable that the former group is that described by Aoyama *et al.* (1973). The locations and axonal trajectories of dorsal horn spinocerebellar tract neurones strongly suggest that they belong to group 9. The neurones described by Tapper *et al.* (1975) and by Randic *et al.* (1976) may also be part of the same group of cells. However, it is difficult to compare the neurones they

described with those we have described, since they did not report input from muscle afferents. The impression has in fact been given that spinocerebellar tract neurones in the dorsal horn relay only cutaneous information (Mann, 1973, p. 57), which would suggest that the neurones were not part of the population we have studied, all of which were readily discharged by volleys in group II muscle afferents (Edgley & Jankowska, 1988).

Most of the neurones we have described were located close to the border of laminae IV and V. A more precise localization is difficult because the border between these laminae is diffuse (Rexed, 1954). According to Matsushita *et al.* (1979), spinocerebellar tract neurones at this location extend rostrally throughout the thoracic spinal cord and into the cervical segments. We have restricted our investigation to neurones which are activated by group II afferents from hindlimb muscles and these seem to occupy only the caudal part of this group.

Experiments using selective spinal cord lesions provide strong evidence that dorsal horn spinocerebellar tract neurones have axons in the superficial part of the dorsolateral funiculus (Matsushita *et al.* 1979). This finding is in keeping with our observation that the neurones are antidromically activated when low-intensity electrical stimuli are applied to the dorsal part of the ipsilateral lateral funiculus and with the trajectory of the initial portion of the axons of the HRP-stained cells. Since the axons of the DSCT also run in the dorsolateral part of the ipsilateral lateral funiculus (Grant, 1962), this raises the possibility that not only the axons of Clarke's column neurones, but also the axons of dorsal horn spinocerebellar tract neurones contribute to the DSCT (see Tapper *et al.* 1975; Randic *et al.* 1976). Such a conclusion is also supported by our observations on the cerebellar termination of the axons. The most effective locations for antidromic activation of these neurones were in lobules III and IV of the anterior lobe and in lobule VIII of the posterior lobe, which are the termination areas of the DSCT (Grant, 1962). Furthermore, the lowest threshold locations corresponded well with the lowest threshold locations for antidromic activation of Clarke's column neurones (Fig. 6). We therefore suggest that the axons of dorsal horn spinocerebellar tract neurones contribute to the DSCT, a view in keeping with the observation that some DSCT axons originate caudal to Clarke's column in the fourth and fifth lumbar segments (Hongo, Okada & Sato, 1967).

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REFERENCES

AOYAMA, M., HONGO, T. & KUDO, N. (1973). An uncrossed ascending tract originating from below Clarke's column and conveying group I impulses from the hindlimb muscles of the cat. *Brain Research* **62**, 237–241.

BRODAL, A. (1981). *Neurological Anatomy*. Oxford: Oxford University Press.

BROWN, A. G. (1981). The spinocervical tract. *Progress in Neurobiology* **17**, 59–96.

BROWN, A. G. & FYFFE, R. E. W. (1981). Form and function of dorsal horn neurones with axons ascending in the dorsal columns in cat. *Journal of Physiology* **321**, 31–47.

BROWN, A. G., FYFFE, R. E. W., NOBLE, R., ROSE, P. K. & SNOW, P. J. (1980). The density, distribution and topographical organization of spinocervical tract neurones in the cat. *Journal of Physiology* **300**, 409–428.

BROWN, A. G., ROSE, P. K. & SNOW, P. J. (1977*a*). The morphology of spinocervical tract neurones revealed by intracellular injection of horseradish peroxidase. *Journal of Physiology* **270**, 747–764.

BROWN, A. G., ROSE, P. K. & SNOW, P. J. (1977*b*). The morphology of hair follicle afferent fibre collaterals in the spinal cord of the cat. *Journal of Physiology* **272**, 779–797.

COOPER, S. & SHERRINGTON, C. S. (1940). Gower's tract and spinal border cells. *Brain* **63**, 123–134.

EDGLEY, S. A. & GALLIMORE, C. M. (1986). The morphology of dorsal horn spinocerebellar tract neurones in the cat. *Journal of Physiology* **371**, 56*P*.

EDGLEY, S. A. & JANKOWSKA, E. (1987) Field potentials generated by group II muscle afferents in the middle lumbar segments of the cat spinal cord. *Journal of Physiology* **385**, 393–414.

EDGLEY, S. A. & JANKOWSKA, E. (1988). Information processed by dorsal horn spinocerebellar tract neurones in the cat. *Journal of Physiology* **397**, 81–97.

GRANT, G. (1962). Spinal course and somatotopically organised termination of the spinocerebellar tracts. An experimental study in the cat. *Acta physiologica scandinavica* **56**, suppl., 193.

GRANT, G., WIKSTEN, B., BERKLEY, K. J. & ALDSKOGIUS, H. (1982). The location of cerebellar projecting neurones within the lumbosacral spinal cord in the cat. An anatomical study with HRP and retrograde chromatolysis. *Journal of Comparative Neurology* **204**, 336–348.

HANKER, J. S., YATES, P. E., METZ, C. B. & RUSTIONI, A. (1977). A new specific, sensitive and non-carcinogenic reagent for the demonstration of horseradish peroxidase. *Histochemical Journal* **9**, 789–792.

HONGO, T., OKADA, Y. & SATO, M. (1967). Corticofugal influences on transmission to the dorsal spinocerebellar tract from hindlimb primary afferents. *Experimental Brain Research* **3**, 135–149.

HOUCHIN, J., MAXWELL, D. J., FYFFE, R. E. W. & BROWN, A. G. (1983). Light and electron microscopy of dorsal spinocerebellar tract neurones in the cat: an intracellular horseradish peroxidase study. *Quarterly Journal of Experimental Physiology* **68**, 719–732.

JANKOWSKA, E., RASTAD, J. & WESTMAN, J. (1976). Intracellular application of horseradish peroxidase and its light and electron microscopical appearance in spinocervical tract cells. *Brain Research* **105**, 557–562.

JANKOWSKA, E., RASTAD, J. & ZARZECKI, P. (1979). Segmental and supraspinal input to cells of origin of non-primary fibres in the feline dorsal column. *Journal of Physiology* **290**, 185–200.

MANN, M. D. (1973). Clarkes column and the dorsal spinocerebellar tract. *Brain, Behaviour and Evolution* **7**, 34–83.

MATSUSHITA, M., HOSOYA, Y. & IKEDA, M. (1979). Anatomical organisation of the spinocerebellar system in the cat, as studied by retrograde transport of horseradish peroxidase. *Journal of Comparative Neurology* **184**, 81–106.

MESULAM, M.-M. (1982). *Tracing Neural Connections with Horseradish Peroxidase*. Chichester: J. Wiley.

MOLENAAR, I. & KUYPERS, H. G. J. M. (1978). Cells of origin of propriospinal fibres and of fibres ascending to supraspinal levels. An HRP study in cat and Rhesus monkey. *Brain Research* **152**, 429–450.

OSCARSSON, O. (1973). Functional organisation of spinocerebellar paths. In *Handbook of Sensory Physiology*, ed. IGGO, A. pp. 339–380. Berlin: Springer-Verlag.

RANDIC, M., MILETIC, V. & LOEWY, A. D. (1981). A morphological study of cat dorsal spinocerebellar tract neurones after intracellular injection of horseradish peroxidase. *Journal of Comparative Neurology* **198**, 453–486.

RANDIC, M., MYSLINSKI, N. R. & GORDON, J. H. (1976). Spinal localization of neurones receiving inputs from cutaneous afferents in the cat hindlimb. *Brain Research* **105**, 573–577.

RASTAD, J., JANKOWSKA, E. & WESTMAN, J. (1977). Arborization of initial axon collaterals of spinocervical tract cells stained intracellularly with horseradish peroxidase. *Brain Research* **135**, 1–10.

REXED, B. (1954). A cytoarchitectonic atlas of the spinal cord in the cat. *Journal of Comparative Neurology* **100**, 297–379.

RUSTIONI, A. & KAUFMAN, A. B. (1977). Identification of cells of origin of non-primary afferents to the dorsal column nuclei of the cat. *Experimental Brain Research* **27**, 1–14.

TAPPER, D. N., MANN, M. D., BROWN, P. B. & COGDELL, B. (1975). Cells of origin of the cutaneous division of the dorsal spinocerebellar tract. *Brain Research* **85**, 59–63.