J. Physiol. (1982), **325**, *pp.* 79–91
With 6 text-figures
Printed in Great Britain

A COMPARISON OF THE STRUCTURES OF α- AND γ-SPINAL MOTONEURONES OF THE CAT

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(*Received 13 July 1981*)

SUMMARY

1. The structures of seven γ-motoneurones (axonal conduction velocities of 15–48 m/sec) were compared with those of nine α-motoneurones (axonal conduction velocities of 71–91 m/sec) by using histochemical methods to reveal horseradish peroxidase which had previously been injected intracellularly into indentified motoneurones in the cat lumbosacral spinal cord.

2. The size of the cell bodies of the motoneurones, and the diameters of their intramedullary axons, were related to their axonal conduction velocities over the whole range studied.

3. Despite the smaller size of the cell bodies of the γ-motoneurones, their dendritic trees extended as far as those of the α-motoneurones. However, γ-motoneurones had fewer main dendrites than the α-motoneurones and these branched much less, so that the dendritic trees of the γ-motoneurones were much simpler than those of α-motoneurones. Although the extents of the dendritic trees were not related to axonal conduction velocity, the complexity of the dendritic trees was clearly related to axonal conduction velocity and to cell body size.

4. The total surface area of each cell, taken as an indication of the area available for synaptic contact, was much smaller for γ- than for α-motoneurones, and was related to axonal conduction velocity.

5. Only one of the seven γ-motoneurones studied had axon collaterals whereas five of the nine α-motoneurones had well developed collaterals. This finding is consistent with the relative contribution that each group of motoneurone axons makes to recurrent inhibition.

6. One of the γ-motoneurones had two axons, of different diameter, which emerged from the spinal cord at the same level but in different ventral rootlets.

7. These features of motoneurone structure are related to aspects of their physiological properties.

INTRODUCTION

α-Motoneurones have axonal conduction velocities greater than 55 m/sec. They innervate mostly extrafusal skeletal muscle fibres and are therefore skeletomotor in function. Gamma-motoneurones have axonal conduction velocities less than 55 m/sec. They mostly innervate intrafusal muscle fibres and so are fusimotor in function (Kuffler, Hunt & Quilliam, 1951). Conduction velocity is only an approximate

guide to function as overlap of the functional subgroups probably occurs, and the finding of motoneurones with skeletofusimotor functions (β-motoneurones) and a wide range of conduction velocities is a complication (Laporte & Emonet-Dénand, 1976). Although these types of motoneurone have some common features, there are important differences between their physiological properties (Hunt, 1951; Hunt & Paintal, 1958; Murthy, 1978). The experiments reported in the present paper were undertaken to compare the structures of α- and γ-motoneurones because differences in structure may relate to differences in functional characteristics.

A variety of methods has been used to investigate the structure of α-motoneurones, and a good picture of this is emerging (eg. Barrett & Crill, 1974; Brown & Fyffe, 1981). However, because of technical difficulty, little is known of the detailed structure of γ-motoneurones. They have cell bodies and axons of smaller diameter than the α-motoneurones but are known to lie in the same region of the spinal cord (Bryan, Trevino & Willis, 1972; Burke, Strick, Kanda, Kim & Walmesley, 1977).

The intracellular injection of horseradish peroxidase now offers a means of exploring in detail the structure of neurones, and it has proved possible to use this method to study γ-motoneurones (Cullheim & Ulfhake, 1979; Westbury, 1979). The results presented in this paper show that the structure of γ-motoneurones is different from that of α-motoneurones in several ways, and that the differences are relevant to a discussion of the differences in function between these two types of motoneurone.

METHODS

These experiments were performed upon adult cats of both sexes, weighing 2·2–4·7 kg, anaesthetized with pentobarbitone sodium (Sagatal, May & Baker Ltd.). Using conventional techniques, intracellular recordings were made from lumbosacral motoneurones following laminectomy.

The animals were immobilized with pins driven into the pelvis and vertebrate bodies. To improve mechanical stability of the preparation, the animals were paralysed with gallamine triethiodide (Flaxedil, May & Baker Ltd.) and artificially ventilated following bilateral pneumothorax. Ventilation was adjusted to maintain end-tidal CO_2 concentration at 4–4·5%. During paralysis, an adequate level of anaesthesia was maintained by regular supplements of pentobarbitone sodium and this was monitored by continuous recording of blood pressure and heart rate. At intervals, recovery from the neuromuscular paralysis was permitted so that the level of anaesthesia could be confirmed.

Motoneurones were identified by their antidromically conducted responses recorded from the soma following electrical stimulation of the sciatic nerve above the origin of the hamstring nerve. The dorsal roots from L5 to S3 were cut to prevent orthodromic inputs to the spinal cord. The axonal conduction velocity of each motoneurone was determined from the latency of the antidromic response at the soma. Further identification was obtained by electrical stimulation of the central end of the cut dorsal roots at difference strengths. Alpha-motoneurones display prominent monosynaptic e.p.s.p.s following discharge of group 1A afferent axons, whereas γ-motoneurones do not. The dividing line between the α and γ conduction velocity ranges has been set arbitrarily at 55 m/sec. Direct functional identification was not possible in these experiments; however motoneurones with conduction velocities greater than 60 m/sec and monosynaptic e.p.s.p.s from 1A afferent axons are almost certainly skeletomotor, and those with conduction velocities of less than 45 m/sec and without monosynaptic 1A e.p.s.p.s are almost certainly fusimotor in function (Hunt & Paintal, 1958; Kemm & Westbury, 1978). The properties of skeletofusimotor (β) motoneurones have not been investigated fully but their conduction velocities probably span the α range and also the higher γ conduction velocities (Laporte & Emonet-Dénand, 1976).

Following this identification, γ- and α-motoneurones were injected with horseradish peroxidase (Sigma Ltd., type VI) by passing current through the recording micro-electrode. The electrodes were filled with a solution of the enzyme in Tris HCl buffer, pH 7·6, with 0·2 M-KCl added (Snow,

Rose & Brown, 1976) and they had resistances of 20–50 MΩ. The electrode was made positive for 450 msec in each 600 msec, with currents of 10–20 nA. For γ-motoneurones, adequate staining was obtained with a total charge of between 120 and 270 nA . min. For α-motoneurones, charges of 220–510 nA . min were used. These currents were sufficient to outline the whole of the dendrites of the neurones satisfactorily and there was no significant correlation between the measured extents of the dendritic trees and the charge passed for each group.

The animals were allowed to survive for 1–5 hr following injection, and then were perfused with saline at 37 °C followed by fixative (1% paraformaldehyde and 1·25% glutaraldehyde in 0·1 M-phosphate buffer, pH 7·6). The spinal cord was then removed and allowed to stand overnight in fixative at 4 °C. There was no significant correlation between the extent of the dendritic trees outlined by subsequent staining and the survival times before fixation for each of the groups of motoneurones.

100 μm serial sections were made on a freezing microtome and processed to display horseradish peroxidase using the method of Hanker, Yates, Metz & Rustioni (1977). The sections were mounted serially and a light microscope with a drawing tube was used to make camera lucida drawings to reconstruct the shapes of the neurones. These composite drawings were reconstructions of the neurones as projected onto a transverse plane of the spinal cord. Dendrites which ran rostro-caudally were thus foreshortened, and for this reason measurements of the sizes of the dendritic trees were made both from the drawings and directly from the slides. No correction for shrinkage during fixation has been made, and a factor of 15–20% is to be expected.

RESULTS

The structures of seven motoneurones with axonal conduction velocities between 15 and 48 m/sec were studied in detail. All but one of these (conduction velocity, 48 m/sec) lacked a monosynaptic input from group 1A afferent axons and so may be presumed to be fusimotor in function. For comparison, nine α-motoneurones with axonal conduction velocities between 71 and 91 m/sec were also studied. In all of these a monosynaptic e.p.s.p. could be recorded following stimulation of dorsal roots at a strength just above threshold for group 1A axons.

Dendritic trees

Fig. 1 shows diagrams of reconstructions of four γ-motoneurones displayed as if projected onto a transverse plane. The dendritic trees of these neurones were much simpler in their architecture than those of α-motoneurones, but extended over almost as large a distance, even though the cell bodies and axons were of smaller diameter. Fig. 2 shows reconstructions of two α-motoneurones for comparison.

In both α- and γ-motoneurones, the proximal dendrites were of larger diameter than the distal ones. The processes of the cells as outlined by the reaction product were sometimes varicose and irregular. The drawings presented here do not attempt to reproduce the diameter of the dendritic profiles.

The seven γ-motoneurones had dendritic trees which extended for $1{\cdot}70 \pm 0{\cdot}20$ mm in the dorso-ventral, $1{\cdot}22 \pm 0{\cdot}11$ mm in the medio-lateral, and $1{\cdot}34 \pm 0{\cdot}20$ mm in the rostro-caudal dimension (mean ± S.E. of mean). For the nine α-motoneurones studied here, the extents of the dendritic trees averaged $1{\cdot}35 \pm 0{\cdot}15$ mm in the dorso-ventral, $1{\cdot}22 \pm 0{\cdot}10$ mm in the medio-lateral, and $1{\cdot}44 \pm 0{\cdot}16$ mm in the rostro-caudal dimension. In most of the motoneurones, the actual lengths of the dendrites were greater than these dimensions would imply as they often pursued irregular paths through the ventral horn. The average extent of the dendritic trees of the motoneurones, calculated simply as the mean of the rostro-caudal, medio-lateral and dorso-ventral

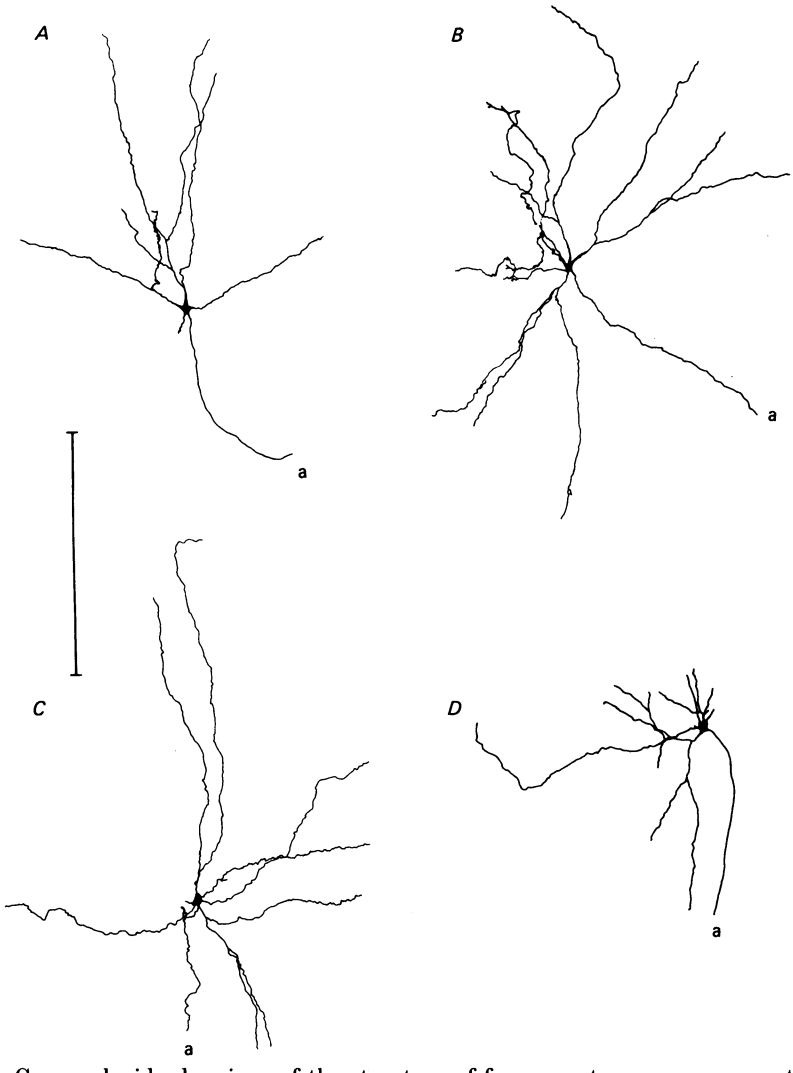

Fig. 1. Camera lucida drawings of the structure of four γ-motoneurones, reconstructed from serial sections. The neurones are displayed as if projected onto the transverse plane of the spinal cord. The calibration bar is 1 mm. 'a' indicates the axon in each case. The axonal conduction velocities of these neurones were: *A*, 18; *B*, 16; *C*, 15; *D*, 31 m/sec.

dimensions, was not correlated with the size of the cell body from which they were derived, or with the axonal conduction velocity (see Fig. 5*D*).

Whereas the dendrites of the α-motoneurones were well distributed in both the transverse plane and rostro-caudally, the dendrites of the γ-motoneurones were concentrated mostly in the transverse plane. Although all of the γ-motoneurones had dendrites that ran rostro-caudally and these extended almost as far as those of α-motoneurones, only a minority of dendrites went in this direction. For most of the γ-motoneurones, nearly all of the dendritic tree could be contained within a transverse section about 300 μm thick.

Because the muscles of destination were not fully identified, detailed comparisons of the orientations of the dendrites were not worthwhile. In general terms, the dendritic patterns conformed to the earlier descriptions. All of the motoneurones had an apical group of dendrities which ran dorsally, and lateral and medial groups which were less well defined. Some of the lateral dendrities of all the motoneurones penetrated the white matter of the ventro-lateral funiculus.

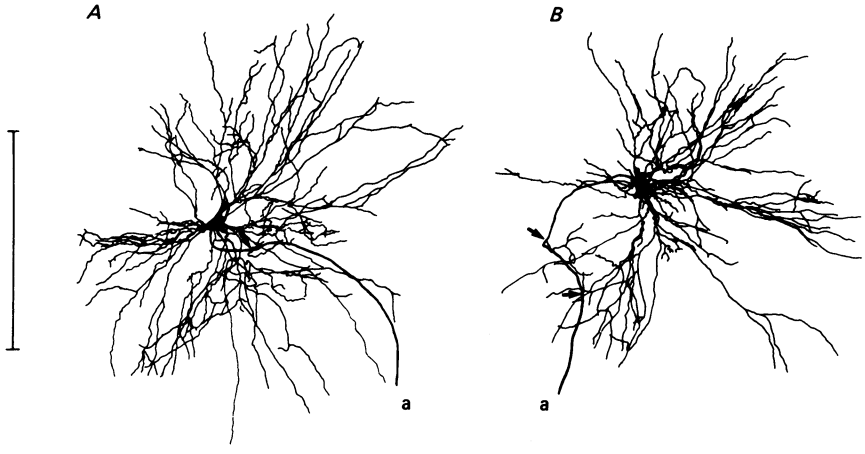

Fig. 2. Camera lucida drawings of two α-motoneurones with axonal conduction velocities of *A*, 83 m/sec and *B*, 81 m/sec. 'a' indicates the axon. Small arrows indicate the origin of axon collaterals, but these have not been fully traced for reasons of clarity. The calibration bar represents 1 mm.

The dendritic trees of the γ-motoneurones were all less complex than those of α-motoneurones. They had 4–7 (mean, 5·6) main dendrites compared with 7–11 (mean, 9·2) for α-motoneurones, and their dendrites branched much less. The little branching which did occur in γ-motoneurones was close to the soma, in contrast to the branching of α-motoneurone dendrites where subdivisions occurred both proximally and distally. This meant that the α-motoneurones had a much greater peripheral dendritic area when compared with the γ-motoneurones. This difference is emphasized if the dendritic trees are represented as equivalent schematic diagrams, as in Fig. 3*A* and *B*.

The complexity of the dendritic trees was well correlated with the conduction velocity of the axon for each motoneurone. The simplest measure of the complexity of branching is given by counting the total number of terminals for each neurone. This reflects the number of main dendrites and the number of times each divides. The neurone of Fig. 3*A* had nineteen terminals and that of Fig. 3*B* had sixty-nine terminals. Fig. 3*C* shows that the number of dendritic terminals for the whole population of motoneurones (α and γ) increased with conduction velocity.

Some of the dendrites of both α- and γ-motoneurones did not branch at all; others branched several times to form many terminals. A number of topological methods have been used to describe the branching of dendritic trees. In this investigation, the centrifugal ordering method was used to establish the order of branching of each

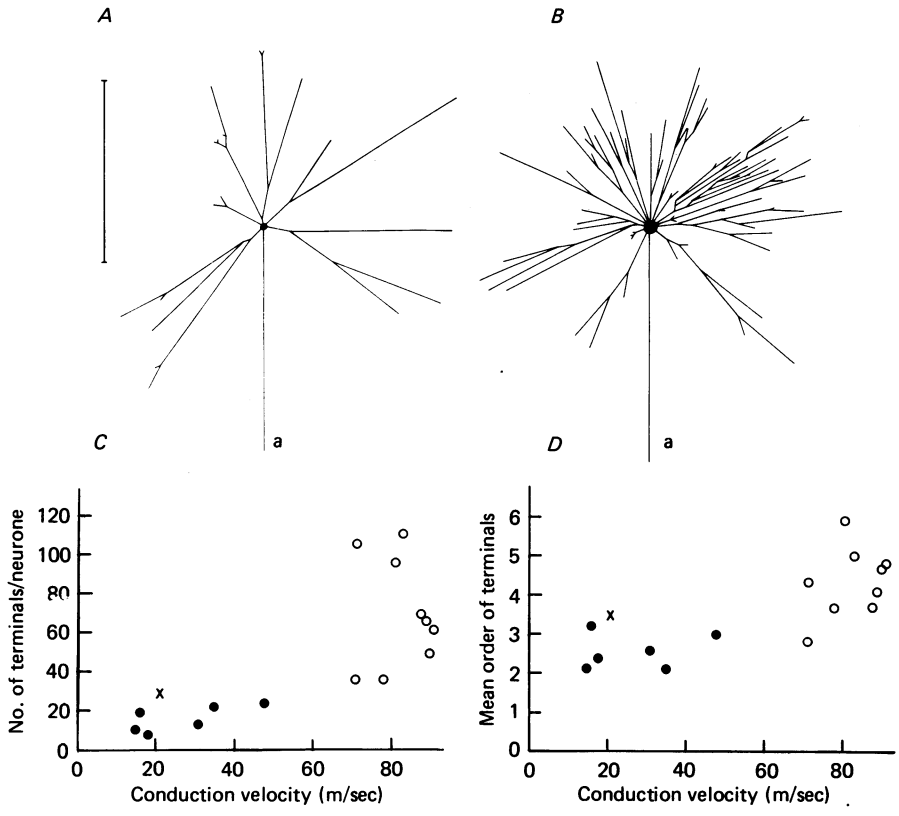

Fig. 3. Schematic diagrams showing the pattern of branching of the dendrites in *A*, a γ-motoneurone with an axonal conduction velocity of 16 m/sec and *B*, an α-motoneurone with an axonal conduction velocity of 88 m/sec. 'a' marks the axons. The bar represents 1 mm. In these diagrams, the length of the dendritic segments has been preserved, but no attempt has been made to represent the angle of branching or the physical relationships between individual branches. *C* shows the relationship between the complexity of branching in the dendritic tree as represented by the total number of dendritic terminals per neurone and the axonal conduction velocity. *D* shows the relationship between the complexity of dendritic branching as represented by the mean order of branching in the dendritic tree of each neurone and the axonal conduction velocity. The order of branching of each terminal was assigned by using the centrifugal ordering method (see text). In *C* and *D*, the measurements for γ-motoneurones (conduction velocity < 55 m/sec) are represented by ● (× indicates those for the γ-motoneurone with two axons, see Fig. 6), and those for α-motoneurones are shown by ○.

dendritic terminal. In this method, the proximal, main dendrites are assigned the order 1 and, progressing outward through the dendritic tree, the order of branching is increased by 1 at each branching point until each terminal is reached. The mean order of branching of the terminals was found by averaging the orders of the terminals. This method gives a useful picture of the branching complexity (Uylings, Smit & Veltman, 1975). The simplicity of the γ-motoneurones was reflected in low mean orders of branching, whereas the more complex α-motoneurones had higher values. For the whole population of motoneurones, there was a clear relationship

between the mean order of the dendritic terminals and the axonal conduction velocity (Fig. 3*D*).

Accurate reconstruction of the dendritic trees of the motoneurones depended upon careful superimposition of the serial sections in the camera lucida. In simple dendritic fields, for example in all of the γ-motoneurones described here, there is little ambiguity so that reconstruction is very good. With the α-motoneurones, the increased branching complexity led to instances of ambiguity in the reconstruction, and this was made more likely by the small distortions that are inevitable in the histological processing. For these reasons, the complexity of the dendritic fields of the α-motoneurones is likely to have been underestimated in this work, but this is much less likely for the γ-motoneurones.

As the size of the cell body and the diameter of the axon of a motoneurone are also related to its axonal conduction velocity (see later and Fig. 5) the complexity of branching of the dendritic tree was also well correlated with these aspects of the structure of the neurones.

There was considerable variation in the architecture of the dendritic trees of the γ-motoneurones, as can be seen from a comparison of Figs. 1*A* and 6*B*. These two drawings represent the extremes of complexity encountered in the sample of γ-motoneurones studied.

The motoneurone with an axonal conduction velocity of 48 m/sec was unusual in several respects. It received a monosynaptic e.p.s.p. following stimulation of the dorsal root at a strength just above the threshold for group 1*A* axons, and this might be taken to indicate that it was of the α (or β) type. However, study of its dendritic tree (Fig. 6*C*) suggested that it had more in common with the other γ-motoneurones than with the α-motoneurones in its structure. The position of this neurone in the ventral horn was also unusual in that it was placed laterally, with its soma close to the border between the grey and white regions.

For eleven of the motoneurones, the total surface area of the cell with its dendrites was estimated so giving a measure of the area available for synaptic contact. These measurements showed that there was a clear relationship between the neuronal surface area and the axonal conduction velocity as would be expected from the branching patterns of the neurones. The mean surface area for four α-motoneurones was 237,600 μm^2 and the mean area for seven γ-motoneurones was 58,400 μm^2. The relationship is shown in Fig. 4. The mean ratio of dendritic surface area to somatic surface area was 19·7 for the seven γ-motoneurones, and 29·6 for the four α-motoneurones. Because of the difficulty in determining the shape and size of the cell body in sections of 100 μm thickness, these ratios are approximate.

To obtain an estimate of the surface area for each neurone, the dendritic tree was subdivided into segments and the average diameter of each segment was measured under the high power of the light microscope. To the dendritic surface area obtained by summing the area of the segments was added the area of the cell body. No part of the axon was included. The dendrites were sometimes varicose so that their diameters were difficult to measure accurately, and they pursued irregular courses in the spinal cord. The estimates of the surface areas are therefore approximate only. The errors are likely to be greater for measurements of α-motoneurones than for γ-motoneurones because of the greater complexity of the former. Many of the motoneurones of both types lacked a clear division between the soma and the main dendrites so that the values for the ratio of dendritic area to somatic area could not be clearly determined.

Axons and cell bodies

For each of the motoneurones, the diameter of the intramedullary axon cylinder and the size of the cell body, as outlined by horseradish perioxidase reaction product, were measured.

The diameters of the axons distal to the initial segments were measured under the high power of the light microscope. The axons varied in diameter along their course, and the values plotted in Fig. 5 are the means of ten observations of each axon.

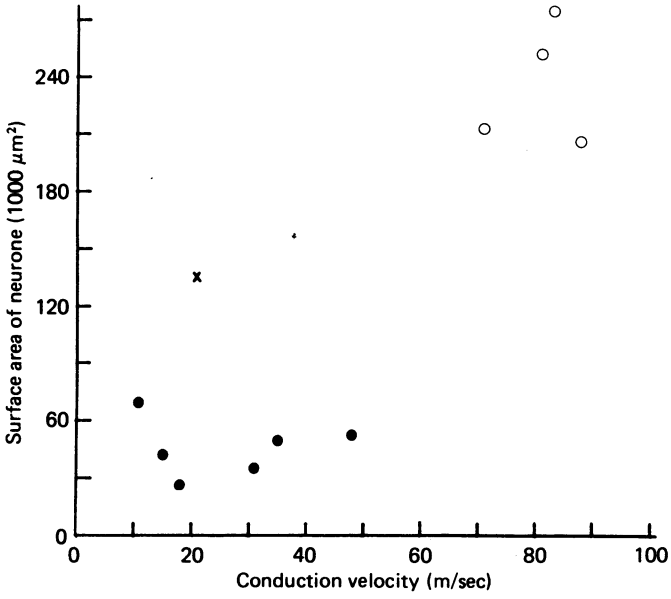

Fig. 4. The relationship between the estimated total surface area of the cell and the axonal conduction velocity for eleven motoneurones. The symbols are as in Fig. 3.

The size of the cell bodies was assessed from the mean of the maximum and minimum diameters in the transverse plane. To avoid main dendrites, the actual measurements were made of an ellipse fitted into the profile of the cell body (Cullheim, 1978). Such measurements disregard the frequent irregularities of shape but they are probably a reasonable representation of neurone size.

The diameters of the axons were clearly related to their conduction velocities (correlation coefficient, $r = 0{\cdot}88$, $P < 0{\cdot}01$). Such a relationship has previously been shown for α-motoneurones (Cullheim, 1978) and the measurements for γ-motoneurones are consistent with an extension of that relationship (Fig. 5*A*). The diameters of the axons were also clearly related to the size of the cell body ($r = 0{\cdot}67$, $P < 0{\cdot}01$), and this relationship also extends into the range of the γ-motoneurones (Fig. 5*C*). Fig. 5*B* illustrates the relationship between cell body size and axonal conduction velocity which follows from the above relationships ($r = 0{\cdot}72$, $P < 0{\cdot}01$). All of these relationships are similar to those found by Cullheim & Ulfhake (1979).

By contrast, the average extents of the dendritic trees of the motoneurones were not related significantly to the cell body size ($r = -0{\cdot}20$, $P \simeq 0{\cdot}45$) (Fig. 5*D*), the axon diameter ($r = 0{\cdot}09$, $P \simeq 0{\cdot}74$) or the axonal conduction velocity ($r = -0{\cdot}21$, $P \simeq 0{\cdot}45$).

Axon collaterals

Although a careful scrutiny of the sections showed that there were no axon collaterals in six of the seven γ-motoneurones, one neurone had extensive axon collaterals reminiscent of those seen in most α-motoneurones (for example, Fig. 2; Cullheim & Kellerth, 1978*a–c*). Fig. 6*A* shows a drawing of this neurone. There were four collaterals, with origins 380, 680, 1200 and 1550 μm from the cell body. Each

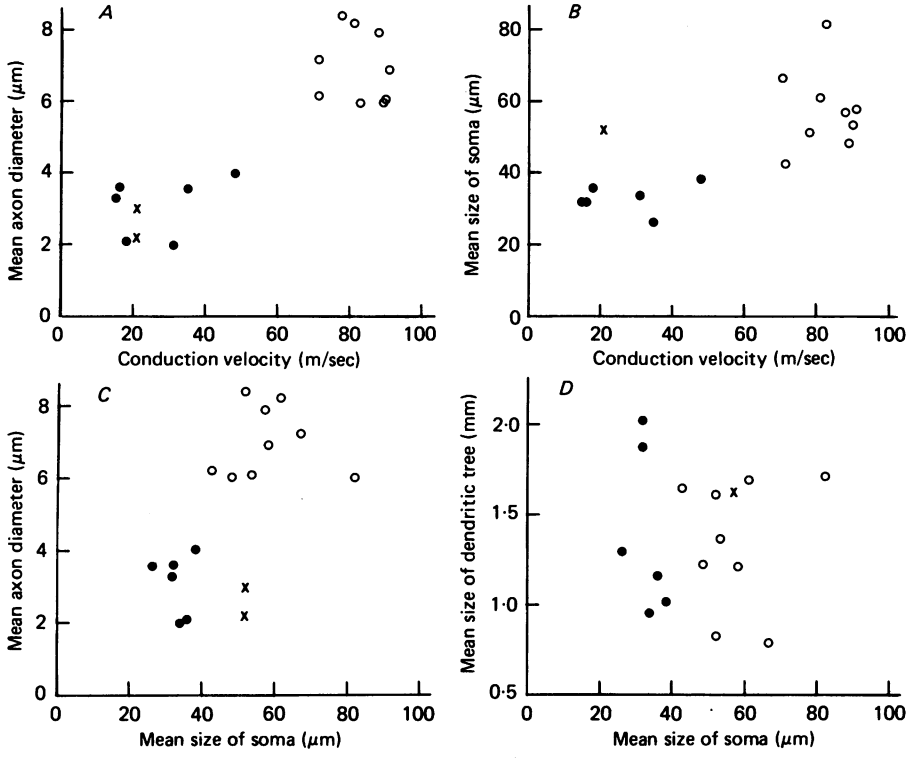

Fig. 5. *A*, the relationship between the diameter of the axon cylinder (mean of ten measurements of the intramedullary axon, avoiding the initial segment) and the axonal conduction velocity for each motoneurone. × indicates measurements from the neurone with two axons, where ten measurements were taken from each axon. *B*, the relationship between the mean diameter of the cell body of the motoneurones measured in the transverse plane and their axonal conduction velocity. *C*, the relationship between the axon diameter (as above) and the mean cell body diameter. *D*, the relationship between the mean size of the dendritic tree (taken as the mean of the extents of the dendritic tree in the dorso-ventral, medio-lateral and rostro-caudal directions) and the mean cell body diameter. The symbols are as in Fig. 3.

of these collaterals subdivided in the ventro-lateral part of the ventral horn, an area that is similar to that occupied by collaterals of α-motoneurones with similar locations.

Six of the seven γ-motoneurones had single axons which pursued uncomplicated paths to the ventral root exit zones, the point of exit of the axon usually being caudal to the cell body. One γ-motoneurone, however, possessed two axons which emerged from the spinal cord at the same level but in different rootlets (Fig. 6*B*). These axons,

which were of different diameter, probably arose by division of a single axon about 70 μm from the cell body, though it was difficult to be quite sure of this because the origin of the second axon was obscured by an overlying proximal dendrite, and the possibility therefore remains that they arose separately, one from the soma and the second from a large proximal dendrite.

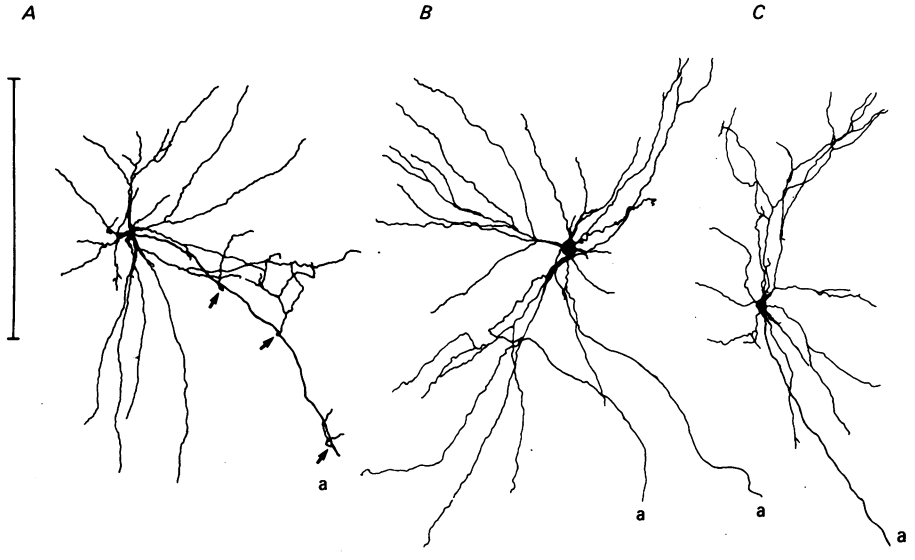

Fig. 6. Camera lucida drawings of γ-motoneurones. *A*, axonal conduction velocity, 35 m/sec; the axon is marked by 'a' and the origins of the three proximal axon collaterals are marked with arrows. A fourth set took origin 1550 μm from the soma, beyond this drawing. *B*, axonal conduction velocity was measured as 21 m/sec; each of the two axons are marked with 'a', and it is not known which of these corresponded with the electrophysiological measurement. *C*, axonal conduction velocity, 48 m/sec. The axon is marked by 'a'. The calibration bar represents 1 mm.

DISCUSSION

Dendritic trees

The results of this study show that in many respects, the structures of γ-motoneurones are different from those of α-motoneurones. These differences are not only that the cell bodies and axons are smaller, with consequently lower axonal conduction velocities, but that the dendritic trees are different. Although the dendritic trees of γ-motoneurones were surprisingly extensive for neurones with small cell bodies, they were much less complex than those of α-motoneurones. There were fewer main dendrites in γ-motoneurones, and these branched much less than those of α-motoneurones. The branching occurred proximally so that the γ-motoneurones had many fewer peripheral branches. This was shown clearly in both of the simple topological measures of branching complexity; the number of dendritic terminals and the mean branching order of the terminals. This implies that the possibilities for peripheral synaptic input are much less for γ- than for α-motoneurones. This was supported by the estimates of neuronal surface area which showed that, on average,

γ-motoneurones had only a quarter of the surface area of α-motoneurones. The surface area of the smallest γ-motoneurone was about a tenth of that of the α-motoneurones. If synapses cover the whole of the neurones and if they occupy similar areas of contact, then γ-motoneurones receive many fewer synaptic contacts than α-motoneurones. This could be offset to some degree by the greater sensitivity of γ-motoneurones to injected current (Westbury, 1981). Whereas the dendritic surface area of α-motoneurones was well distributed over a considerable rostro-caudal length of the spinal cord, γ-motoneurones had dendritic trees that were much more restricted to a transverse 'slice' of spinal cord. In the transverse plane, the α- and γ-motoneurones, in general, had similar distributions of dendrites.

The extents and the complexities of the dendritic trees of the α-motoneurones in this study were greater than those described by Aitken & Bridger (1961) who found surface areas of up to 98,000 μm^2 using Golgi methods, and those studied by Barrett & Crill (1974) who found areas of up to 250,000 μm^2 in their detailed study using Procion Yellow. Intracellular injection of horseradish peroxidase is probably the best method at present available for the study of neuronal structure (Brown & Fyffe, 1981), and the structures found for α-motoneurones in the present study were of similar complexity to, but of slightly smaller dendritic extent than, those described by Brown & Fyffe. The neurones were, however, drawn from different populations. Comparisons of α- and γ-motoneurones within the present study should be valid because the methods used were the same for both groups.

Input resistance of γ-motoneurones

The input resistance of a neurone depends upon the surface area of its membrane and the way in which this is distributed between the cell body and the parts of the dendritic tree, and also upon the specific resistivity of the membrane itself. The input resistance of γ-motoneurones should be relatively high compared to α-motoneurones because of their small cell body size and the limited extent of their dendritic trees. In addition, because the ratio of dendritic area to somatic area was less for γ- than for α-motoneurones, the component of neuronal input conductance that could be attributed to the dendrites should be a smaller fraction of the total conductance.

It has been difficult to obtain adequate measurements of input resistance, but those that have been made have indicated values in the range 1·3–4·9 MΩ, comparable with those from the smaller α-motoneurones (Kemm & Westbury, 1978; Westbury, 1981). If these unexpectedly low values are correct, then the present results imply that the specific resistivity of the γ-motoneurone membrane is lower than that of α-motoneurones. This situation has been suggested for abducens motoneurones by the work of Grantyn & Grantyn (1978). Indeed, there would seem to be many similarities between abducens motoneurones and the γ-motoneurones studied here. Kernell & Zwaagstra (1981) have also recently raised the possibility that specific resistivity of the membrane is related to neurone size in their analysis of the properties of α-motoneurones of different size.

To establish whether or not the smaller γ-motoneurones have a lower membrane resistivity than the large α-motoneurones would require satisfactory measurement of input resistance coupled with careful reconstruction of the structure for each neurone in the way that Barrett & Crill (1974) employed for their study of

α-motoneurones. Such measurements have not been achieved in the present experiments on γ-motoneurones.

Branching of axons

There is clearly a difference in the proportion of α- and γ-motoneurone axons which give rise to axon collaterals. A large proportion of α-motoneurone axons have collaterals, all presumed to excite Renshaw cells and so to generate recurrent inhibition. Only one γ-motoneurone axon has so far been found with axon collaterals out of the seven neurones studied here and six more reported by Cullheim & Ulfhake (1979). This is a small proportion. This finding correlates well with electrophysiological studies of recurrent inhibition which have largely failed to find a component excited with a threshold appropriate for γ-axons (Eccles, Fatt & Koketsu, 1954; Westbury, 1980; Ellaway & Murphy, 1980). In general, however, the number of collateral terminations of motoneurone axons does decrease with axon diameter (Cullheim & Kellerth, 1978*b*), so the almost complete lack of γ-collaterals could be regarded as an extension of that relationship. Whether the present finding of a γ-axon with extensive collaterals can be dismissed as an anomaly is as yet unknown, but in at least one other situation axon collaterals of motoneurones have been found in the absence of significant recurrent inhibition (medial rectus motoneurones, Evinger, Baker & McCrea, 1979).

The finding of a γ-motoneurone with two axons cannot be assessed from the present result. It is compatible with the much greater variability in structure found for γ-motoneurones. However, in the many α-motoneurones studied by many investigators, none have been found with more than one axon within the spinal cord. It is not known from the present experiments whether both axons went to the same muscle by slightly different paths, or whether they had different destinations, implying a more general function and less specificity of action.

This work was supported by a grant from The Wellcome Trust.

REFERENCES

AITKEN, J. T. & BRIDGER, J. E. (1961). Neuron size and neuron population density in the lumbosacral region of the cat's spinal cord. *J. Anat.* **95**, 38–53.

BARRETT, J. N. & CRILL, W. E. (1974). Specific membrane properties of cat motoneurones. *J. Physiol.* **239**, 301–324.

BROWN, A. G. & FYFFE, R. E. W. (1981). Direct observations on the contacts made between Ia afferent fibres and α-motoneurones in the cat's lumbosacral spinal cord. *J. Physiol.* **313**, 121–140.

BRYAN, R. N., TREVINO, D. L. & WILLIS, W. D. (1972). Evidence for a common location of alpha and gamma motoneurones. *Brain Res.* **38**, 193–196.

BURKE, R. E., STRICK, P. L., KANDA, K., KIM, C. C. & WALMESLEY, B. (1977). Anatomy of medial gastrocnemius and soleus motor nuclei in cat spinal cord. *J. Neurophysiol.* **40**, 667–680.

CULLHEIM, S. (1978). Relations between cell body size, axon diameter and axon conduction velocity of cat sciatic α-motoneurones stained with horseradish peroxidase. *Neurosci. Lett.* **8**, 17–20.

CULLHEIM, S. & KELLERTH, J-O. (1978*a*). A morphological study of the axons and recurrent axon collaterals of cat sciatic α-motoneurones after intracellular staining with horseradish peroxidase. *J. comp. Neurol.* **178**, 537–558.

CULLHEIM, S. & KELLERTH, J-O. (1978*b*). A morphological study of the axons and recurrent axon collaterals of cat α-motoneurones supplying different hind-limb muscles. *J. Physiol.* **281**, 285–299.

CULLHEIM, S. & KELLERTH, J-O. (1978*c*). A morphological study of the axons and recurrent axon collaterals of cat α-motoneurones supplying different functional types of muscle unit. *J. Physiol.* **281**, 301–313.

CULLHEIM, S. & ULFHAKE, B. (1979). Observations on the morphology of intracellular stained γ-motoneurones in relation to their axon conduction velocity. *Neurosci. Lett.* **13**, 47–50.

ECCLES, J. C., FATT, P. & KOKETSU, K. (1954). Cholinergic and inhibitory synapses in a pathway from motor-axon collaterals to motoneurones. *J. Physiol.* **126**, 524–562.

ELLAWAY, P. H. & MURPHY, P. R. (1980). A quantitative comparison of recurrent inhibition of alpha and gamma motoneurones in the cat. *J. Physiol.* **301**, 55–56*P*.

EVINGER, C., BAKER, R. & MCCREA, R. A. (1979). Axon collaterals of cat medial rectus motoneurons. *Brain Res.* **174**, 153–160.

GRANTYN, R. & GRANTYN, A. (1978). Morphological and electrophysiological properties of cat abducens motoneurons. *Expl Brain Res.* **31**, 249–274.

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. *Histochem. J.* **9**, 789–792.

HUNT, C. C. (1951). The reflex activity of mammalian small-nerve fibres. *J. Physiol.* **115**, 456–469.

HUNT, C. C. & PAINTAL, A. S. (1958). Spinal reflex regulation of fusimotor neurones. *J. Physiol.* **143**, 195–212.

KEMM, R. E. & WESTBURY, D. R. (1978). Some properties of spinal γ-motoneurones in the cat, determined by micro-electrode recording. *J. Physiol.* **282**, 59–71.

KERNELL, D. & ZWAAGSTRA, B. (1981). Input conductance, axonal conduction velocity and cell size among hindlimb motoneurones of the cat. *Brain Res.* **204**, 311–326.

KUFFLER, S. W., HUNT, C. C. & QUILLIAM, J. P. (1951). Function of medullated small-nerve fibres in mammalian ventral roots: efferent muscle spindle innervation. *J. Neurophysiol.* **14**, 29–54.

LAPORTE, Y. & EMONET-DÉNAND, F. (1976). The skeleto-fusiomotor innervation of the cat muscle spindle. *Prog. Brain Res.* **44**, 99–106.

MURTHY, K. S. K. (1978). Vertebrate fusimotor neurones and their influence on motor behaviour. *Prog. Neurobiol.* **11**, 249–307.

SNOW, P. J., ROSE, P. K. & BROWN, A. G. (1976). Tracing axons and axon collaterals of spinal neurones using intracellular injection of horseradish peroxidase. *Science, N.Y.* **191**, 312–313.

UYLINGS, H. B. M., SMIT, G. J. & VELTMAN, W. A. M. (1975). Ordering methods in quantitative analysis of branching stuctures of dendritic trees. *Adv. Neurol.* **12**, ed. KREUTZBERG, G. W., pp. 247–254. New York: Raven Press.

WESTBURY, D. R. (1979). The morphology of four gamma motoneurones examined by horseradish peroxidase histochemistry. *J. Physiol.* **292**, 25–26*P*.

WESTBURY, D. R. (1980). Lack of a contribution from gamma motoneurone axons to Renshaw inhibition in the cat spinal cord. *Brain Res.* **186**, 217–221.

WESTBURY, D. R. (1981). Electrophysiological characteristics of spinal gamma motoneurones in the cat. In *Muscle Receptors and Movement*, ed. TAYLOR, A. & PROCHAZKA, A., pp. 87–96. London: Macmillan.