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Distribution patterns of dendrites in motor neuron pools of lumbosacral spinal cord of the chicken

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Summary. The morphology of dendritic trees (dendroarchitecture) of motor neurons innervating specific hindlimb muscles (motoneuron pools, MNP) was studied in the chick spinal cord. Motoneurons were labelled by intramuscular injections of horseradish peroxidase conjugated with cholera toxin subunit B. MNPs of posterior iliotibial and femorotibial muscles were located at the dorsolateral part of lateral motor column of lumbosacral segments (LS) 1–4 and 1–3, respectively. Although the dendritic profiles of femorotibialis motoneurons were fewer than those of posterior iliotibialis, these two MNPs had a similar distribution pattern of dendrites. Dendritic profiles were about equally distributed in the gray and white matter. Dendrites from the MNP of posterior iliotibialis radiated in all directions. A large number of dendrites penetrated into the white matter, and some even reached to the subpial regions of the lateral funiculus. One array of dendrites that projected dorsomedialwards extended to the base of the posterior horn. MNPs of both the iliofibularis (LS 4–7) and caudilioflexorius (LS 6–8) had dendritic trees with similar distribution patterns. There were two main arrays of dendritic extensions; one along the dorsal, and another along the ventral border of the lateral motor column. Dendrites from the iliofibularis and caudilioflexorius motoneurons were located more frequently in the white matter than in the gray matter. A large number of dendrites extended in all directions from the MNP of the adductor muscle, which was located in the medial region of lateral motor column of LS 1–2. The distribution of dendrites from a few other MNPs was also examined. From these observations, we conclude that there are major differences in the distribution of dendrites of MNPs innervating different chick hind limb muscles. We discuss the possibility that these differences may be associated with differences in the quantity or quality of afferent inputs received by motoneurons in the various MNPs.

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Introduction

It is now well established that individual limb muscles in vertebrates are innervated by longitudinally arranged motor neuron pools (MNP) located in the lateral motor column of the spinal cord. The location of MNPs has been examined by using both retrograde degeneration techniques (Romanes 1964; Cruce 1974; Ohmori et al. 1984) and retrograde labelling with horseradish peroxidase (HRP) (Landmesser 1978; Hollyday 1980; Martin and Hrycyshyn 1981; Nicolopoulos-Stournaras and Iles 1983; Straznickey and Tay 1983; Berger et al. 1984; Ruigrok and Crowe 1984; Hardman and Brown 1985; Haase and Hrychshyn 1986), as well as by analyses of pathological material from paralysed patients (Sharrard 1955).

In addition to the locations of neuronal somata, the determination of dendritic configurations and of overall dendritic dimensions has important implications for understanding the function of motoneurons. Golgi methods have been used to demonstrate dendritic arborization, and have revealed several important aspects of the dendritic branching pattern of spinal motoneurons (Scheibel and Scheibel 1970). Silver impregnation techniques, however, have several drawbacks: they are rather capricious; it is often difficult to impregnate a specific group of cells (for example, MNP) and the technique is most effective with immature neurons.

By contrast, *intracellular* injection of HRP (or dye) is a reliable technique, and has greatly increased our knowledge of the detailed dendritic morphology of *single* spinal motor neurons (Barrett and Crill 1971, 1974; Lux and Schubert 1975; Jankowska et al. 1976; Snow et al. 1976; Egger et al. 1980; Rose 1981; Ulfhake and Kellerth 1981a, b; Ruigrok et al. 1984; Fetcho 1986; Cullheim et al. 1987a, b). However, this procedure is not only time consuming, but also difficult to use if one

wants to investigate the overall morphology of dendritic trees for several different MNPs in a comparative study.

Because of the limitations of both Golgi and intracellular labelling techniques, we have instead used a new retrograde HRP labelling method in which HRP conjugated with cholera toxin subunit B (CHRP) (Trojanowski et al. 1982; Wan et al. 1982; Furicchia and Goshgarian 1987) provides an effective and reliable tool for studies on overall morphology of dendritic trees of MNPs.

Our previous studies (Homma et al. 1988; Okado et al. 1988) demonstrated that MNPs innervating the extensor muscles of hip joint (for standing) in the chicken received a dense innervation by serotoninergic fibers. Differential innervation of MNPs by serotoninergic fibers appeared to be related to whether or not the motor neurons and muscles were involved in maintaining an upright standing posture. MNPs that mediate tonic excitation for standing may also receive a dense input from primary afferents from muscle spindles (Liddell and Sherrington 1924, 1925). It is, therefore, reasonable to propose that the degree of expansion and arborization of dendrites may vary depending on differences in the amount of afferent input to different MNPs. The primary aim of the present study was to elucidate the distribution pattern of dendrites of different MNPs by use of the CHRP retrograde labelling technique. These data will serve as a foundation for future experimental studies on the plasticity of dendritic arborization following the perturbation of afferent input to motoneurons.

Materials and methods

Forty adult (6 month-old) and ten postnatal (1 to 7 days after hatching) White Leghorn chickens were used in this study.

The animals were deeply anesthetized by an intramuscular injection of ketamine (Parke-Davis) (8 mg per 100 g body weight) and a subsequent intraperitoneal injection of Chloropent (Fort-Dodge Laboratories) (0.15 ml per 100 g body weight).

A 50–100 µl solution of 0.1% CHRP (List Biological Labs., Campbell, CA) was injected diffusely into each of the thigh muscles (sartorius, posterior iliotibialis, femorotibialis, ischioflexorius, accessorius, adductor, iliofibularis, caudilioflexorius) shown in Fig. 1.

Although there is a potential problem of HRP diffusing to adjacent muscles, we have found that preservation of an intact fascial sheath can prevent this diffusion. (Haase and Hrycyshyn 1986). After a survival time of 2 days, the chickens were deeply anesthetized and perfused with a Zamboni's fixative composed of 4% paraformaldehyde and 0.2% picric acid in a 0.15 M sodium phosphate buffer (pH 7.3). Spinal cords were immediately removed and cut into segments according to the location of dorsal roots. They were left in the fresh fixative for a few hours, and then immersed in graded concentrations (5%, 10%, 30%) of sucrose solutions in a 0.1 M phosphate buffer. Each spinal cord segment was embedded in Tissue-Tek (Miles Inc.) using dry ice-acetone, and embedded tissues were kept for indefinite periods (days to months) at −80° C.

Transverse or parasagittal sections were cut at 30 µm on a cryostat. The sections were processed according to the tetramethyl benzidine technique of Mesulam et al. (1980). Sections were mounted on chrome alumn-coated slides, and counterstained with neutral red. Labelled dendrites of motoneurons were delineated using a drawing tube at magnification × 25. The laminar organization of the spinal cord was adapted from the study of Martin 1979).

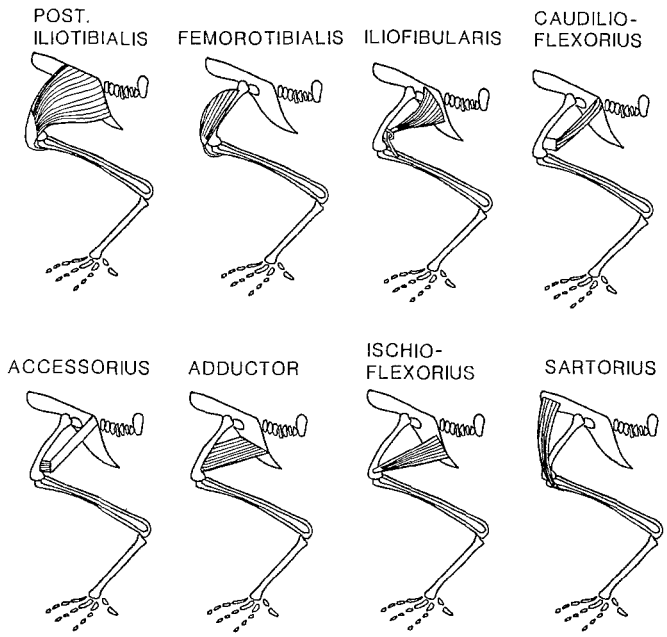

Fig. 1. Schematic location of the muscles around the hip joint of the chick in which CHRP was injected

Results

The retrograde labelling technique employed in the present study was very stable and reliable, providing consistently satisfactory results in labelling of the motoneuron somata (Fig. 2), dendrites (Figs. 2–4) and axons (Fig. 2, arrowheads). The labelled axons of primary afferent fibers derived from the muscle were located in the dorsal horn. No labelled axons of primary afferent were found in the ventral half of the spinal cord (Fig. 7, arrowheads). Motoneuron somata within a MNP were contained in a coherent cluster, with only a few cells lying outside of the cluster. Motoneuron somata innervating each hindlimb muscle formed a longitudinally arranged MNP. The location of MNPs was identical to those reported in a previous study by Landmesser (1978).

Labelled axons were found coexisting with dendritic profiles in the lateral part of the ventral funiculus near the ventral root exit zone (Figs. 2, 8). However, it was easy to differentiate between axons and dendrites, because dendrites were always thinner than axons, and because the diameter of single dendritic profiles was generally more variable compared to axonal profiles (Fig. 5). We did not observe any recurrent collateral axons from motoneurons.

The distribution pattern of dendrites was considerably different as between MNPs of specific thigh muscles. Although the shape of dendritic trees was basically the same for individual motor neurons located along the rostrocaudal extent of each MNP, the density and length of dendritic profiles differed considerably for motoneurons located in the middle of the MNP (Figs. 2, 8) versus those at the rostral and caudal ends (Fig. 6). Unless otherwise noted, all descriptions regarding the shape of dendritic trees in the following sections are based on data

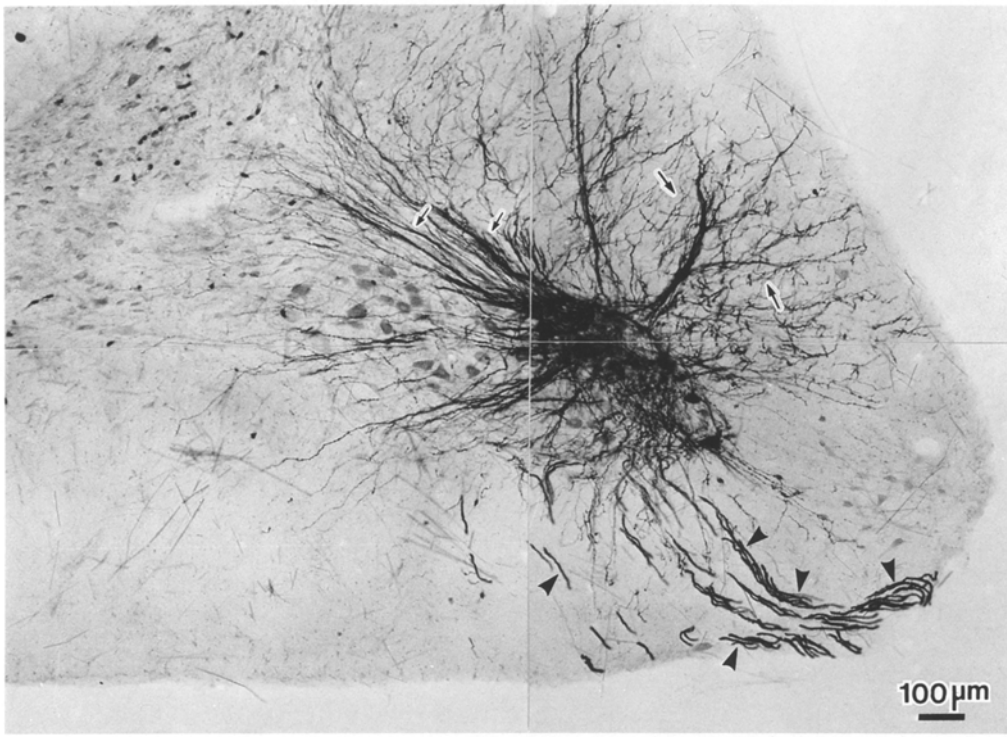

Fig. 2. A photograph taken from the ventral half of the spinal cord following CHRP injections into the posterior iliotibial muscle. Detailed explanation in the text

obtained from motoneurons located in the midpoint of a MNP. The distribution pattern of dendritic fields was quite similar in adjacent sections taken from the middle of a MNP.

Posterior iliotibialis and femorotibialis

The MNP of the posterior iliotibial muscle was located in the dorsolateral region of the lateral motor column of lumbosacral segments (LS) 1–4. Dendritic profiles extended in virtually all directions from the MNP (Figs. 2, 8). Large numbers of dendrites were found extending into the lateral funiculus (Fig. 2, large arrows; Figs. 3, 8), with some dendrites reaching to the outer surface of the white matter (subpial regions). "Dendritic bundles" (Scheibel and Scheibel 1970) were most frequently located in the lateral funiculus (Figs. 2, 3). The dendritic bundles were formed by several first or second order dendrites, which joined together at the border regions between the lateral motor column and the white matter (Fig. 4, arrows).

There were large numbers of dendrites (Fig. 2, small arrows) which extended dorsomedially along the border between the gray matter and lateral funiculus. These dendrites were followed up to the base of the dorsal horn (laminae V and VI). Dendrites extending medialwards traversed the lateral motor column, and in a few cases they were found to project to the medial motor column. There was another group of dendrites extending toward the ventral funiculus which reached as far as the midpoint of the dorsal-ventral extent of the white matter.

The MNP of the femorotibial muscle was located at the midpoint (mediolateral) of the lateral motor column in LS 1–3 (Fig. 8). Although the femorotibial MNP contained fewer dendrites compared to the posterior iliotibial MNP, the distribution pattern of dendrites in these two MNPs was generally similar.

About 50% of the dendritic profiles of both the posterior iliotibial and femorotibial MNPs were located within the white matter.

Iliofibularis and caudilioflexorius

The MNPs of the iliofibularis and caudilioflexorius muscles (Fig. 8) are located in the lateral portion of the lateral motor column of LS 4–7 and LS 6–8, respectively. The overall morphology of the dendritic trees was very similar in these two MNPs. There were two main arrays of dendritic profiles: one consisted of clusters of dendritic profiles that extended along the dorsal, the other along the ventral border of the lateral motor column. For both MNPs there appeared to be more dendrites located in the white matter than in the gray matter. However, only a few dendrites from those MNPs reached the subpial region, and similarly only a few dendritic profiles extended medially across the lateral motor column.

Adductor, ischioflexorius and accessorius

The MNPs of these three muscles (Fig. 8) were located in medial regions of the lateral motor column of LS 1–2 (adductor), 3–4 (ischioflexorius) and 5–7 (accessorius). The dendritic trees of the MNP of the adductor extended in all directions. Although large numbers of dendrites were found in the lateral and ventral funiculi, they only extended to the mid-point between the border of the gray matter and the subpial region. Many den-

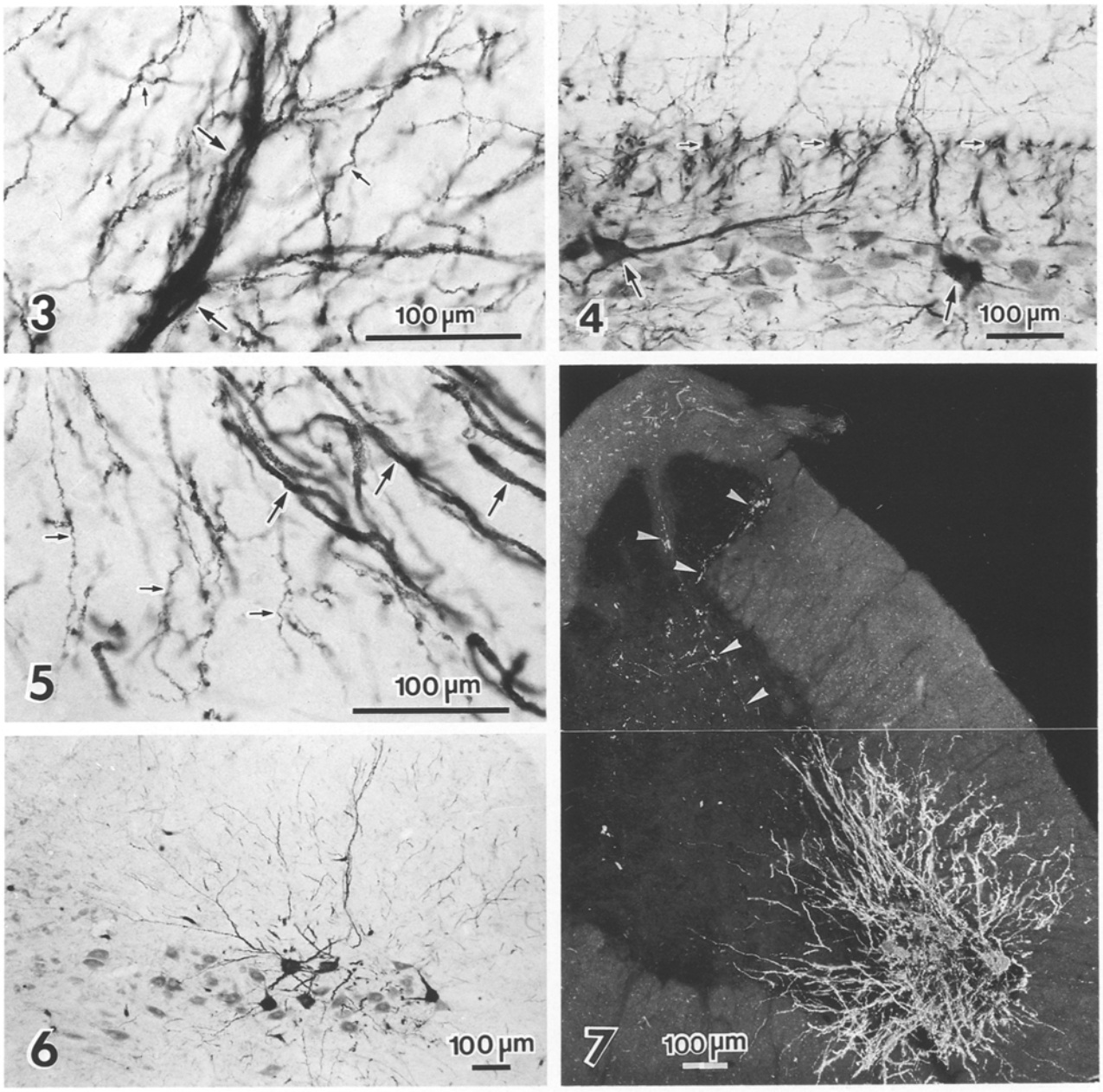

Fig. 3. Dendritic profiles in the lateral funiculus following CHRP injections into the posterior iliotibial muscle. *Large* and *small arrows* indicate dendritic bundles and fine dendrites, respectively

Fig. 4. A photograph taken from a sagittal section of lumbosacral spinal cord segment. 3. Motoneurons (*large arrows*) and dendrites (*small arrows*) of posterior iliotibialis NMP are labeled

Fig. 5. A high power field photograph taken from the ventral funiculus near the ventral root exit. Retrogradely labeled axons (*large arrows*) and dendrites (*small arrows*) are easily recognized

Fig. 6. Retrogradely labeled motoneurons and dendrites observed in the lumbosacral segment 1 following CHRP injections into the posterior iliotibial muscle

Fig. 7. A dark field photograph taken from third lumbosacral spinal cord segment in the chick one week after hatching. *Arrowheads* indicate primary afferent fibers from the posterior iliotibial muscle

drites from the adductor MNP were found in the medial motor column. Although there were fewer dendrites overall in the accessory MNP compared to the adductor MNP, the basic distribution pattern of dendrites from these two MNPs was similar. One difference, however, was that there appeared to be somewhat fewer dendrites from the accessory pool that extended in a ventromedial direction.

Three arrays of dendritic profiles extended from the MNP of the ischioflexorius. They were oriented in the dorsolateral, ventrolateral and medial directions. The former two groups of dendritic extensions were located

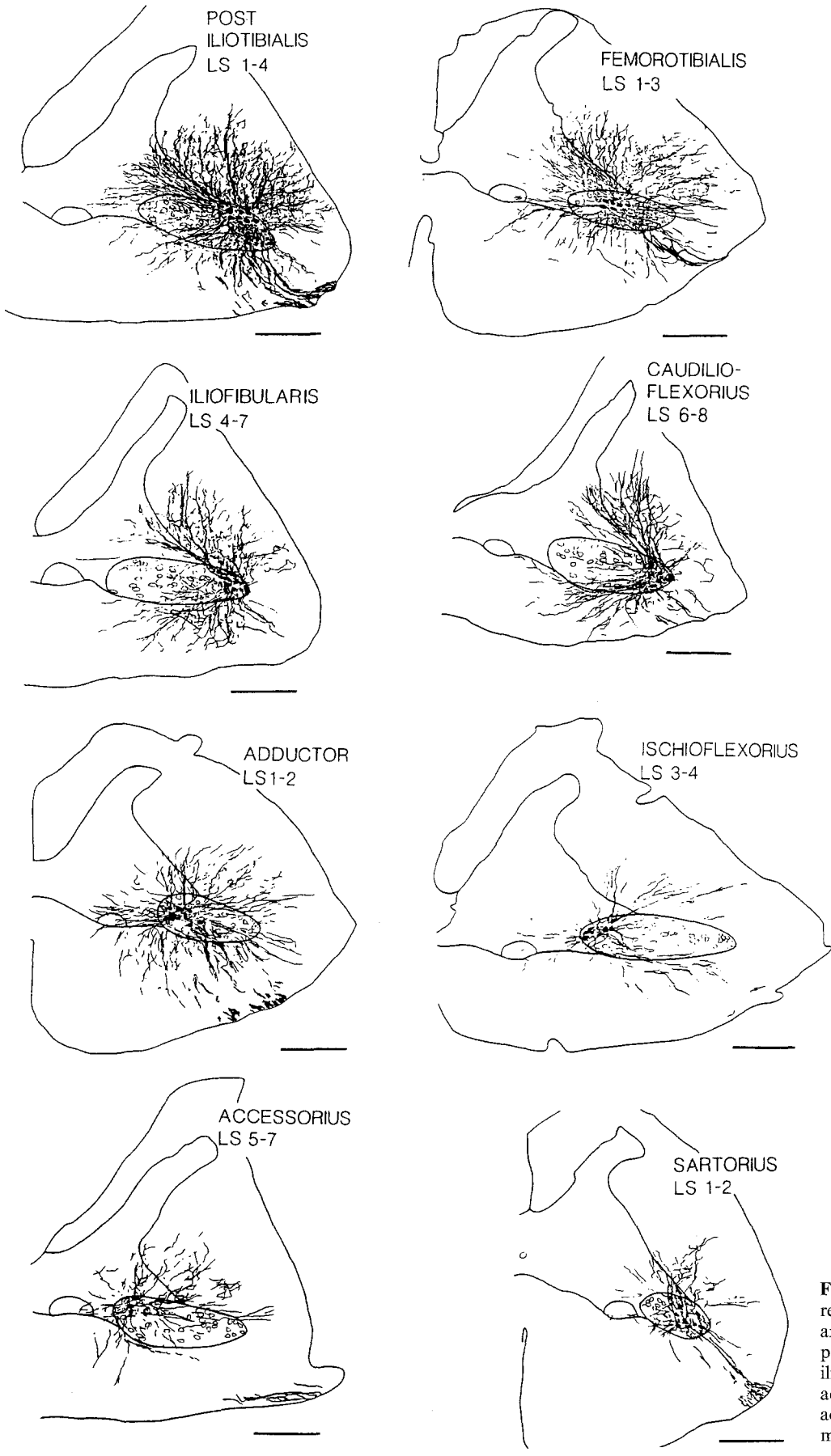

Fig. 8. Camera lucida drawings of retrogradely labeled motoneurons and dendritic trees of the posterior iliotibial, femorotibialis, iliofibularis, caudilioflexorius, adductor, ischioflexorius, accessorius and sartorius motoneuron pools. Bars 500 μm

at both ventral and dorsal aspects of the lateral motor column.

The dendritic profiles from these three MNPs were distributed about evenly in both the white and gray matter.

Sartorius

The MNP of the sartorius muscle (Fig. 8) was located in the lateral part of the lateral motor column of LS 1–2. Although dendritic arborization was not as extensive as some of the other MNPs, sartorius motor neuron dendrites extended in all directions, except towards the ventral funiculus.

Discussion

Sensitivity of retrograde labelling with CHRP

Because there have been no studies on dendritic morphology and branching of spinal motoneurons of the chick spinal cord using intracellular injection techniques, it is difficult to know whether the retrograde labelling technique used in the present study is as sensitive as intracellular injection techniques for labelling the most distal dendritic extensions. However, the dendrites of labelled motoneurons could be followed, presumably to their distal branches, often as far as the subpial regions of the lateral funiculus, or the base of the posterior horn. From this, it seems reasonable to conclude that the retrograde labelling technique used in the present study is a reliable method for comparative studies on the structure of dendritic trees of different MNPs.

Is the pattern of dendritic arborization determined by axonal inputs?

There was considerable diversity in the pattern of dendritic arborization between different MNPs in the chicken spinal cord. This indicates that different sets of dendritic processes extending in different directions receive diverse combinations of inputs to MNPs, that may in turn regulate the characteristic activity patterns of the motoneurons and muscles (Jacobson and Hollyday 1982b).

Although the number of labeled dendritic profiles differed, the MNPs of the posterior iliotibialis and femorotibialis were found to have an identical spacial distribution pattern of dendritic trees. It is interesting to note that femorotibialis and posterior iliotibialis are both extensors (Jacobson and Hollyday 1982a) that are co-activated during limb movements (Landmesser 1978). Thus, motoneurons innervating muscles acting as synergists may receive similar inputs. Some support for this idea was provided by our recent observations (Homma et al. 1988; Kojima et al. 1988; Okado et al. 1988) that serotoninergic fibers differentially innervate a group of MNPs projecting to the hip joint extensors of the chick.

In the present study each MNP was found to have a distinct dendritic branching pattern. Similar results have been reported for the human spinal cord (Abdel-Maguid and Bowsher 1979; Schoenen 1982) and for the spinal cord of the Japanese toad (Oka et al. 1987). Although no statistical differences could be found for the dendritic distribution pattern of white matter dendrites of turtle spinal motoneurons, clear differences were demonstrated for the dorsal dendritic trees located in the gray matter (Ruigrock et al. 1985). The distribution patterns of dendritic trees are similar for MNPs of the quadriceps, posterior biceps, gastrocnemius, soleus and short intrinsic planter muscles in the cat (Ulfhake and Kellerth 1983), and for the triceps, subscapularis and pectoralis muscles of the bullfrog (Lichtman et al. 1984). Furthermore, there is evidence that different subtypes of motoneurons innervating the same muscle may have anatomical differences other than patterns of dendritic arborization. Although triceps surae motoneurons of different size and type (fast-twitch or slow-twitch types) have the same dendritic arborization pattern, dendrites of the fast-twitch-type motoneurons are reported to be more complex compared to those of slow-twitch-type motoneurons (Cullheim et al. 1987a, b).

Although all of the factors that might determine the distribution pattern of dendritic trees are not known at present, there are several lines of evidence indicating that axonal inputs are at least one candidate that may influence dendritic orientation (Das 1975; Steffen and Van der Loos 1980; Bellinger and Anderson 1987). Moreover, dendrites atrophy following elimination of axonal inputs (Smith 1974; Deitch and Rubel 1984). The dendritic profiles of spinal motoneurons are also altered by deafferentation (Bernstein and Standler 1983) and by ablation of somatomotor cortex (Standler and Bernstein 1984).

Although the basic distribution pattern of dendrites was similar for the MNPs examined in the present study, rather marked differences were found in the density and length of dendrites of motoneurons located in the middle of the MNP versus those at rostral and caudal ends of each MNP. Some muscles are organized into "compartments" (English 1984) with each compartment receiving a different amount of axonal input from a single MNP. It is conceivable that this compartmental organization is reflected in the differences in dendritic extensions between the midpoint and the ends of a MNP.

Axonal inputs to MNPs

Although primary afferent fibers are located more medially in the dorsal horn of mammalian species (Ishizuka et al. 1979; Smith 1983; Hongo et al. 1987; Kudo and Yamada 1987), in avian species they are distributed in the lateral aspects of the dorsal horn (Fig. 7) and lateral motor column (Robert and Cohen 1975). This area coincides with the region where groups of dendritic profiles extend from the MNPs of posterior iliotibialis (Fig. 2, arrows), femorotibialis, iliofibularis and caudilioflexorius. Thus, these MNPs may have direct synaptic connections with primary afferents.

Monosynaptic connection from the primary (muscle spindle) afferents is considered to be the exclusive affer-

ent source for increase in excitability of motoneurons during the tonic stretch reflex (Lloyd 1943). In addition recent studies (Crone et al. 1988; Hounsgaard et al. 1988) demonstrated that serotoninergic inputs to motoneurons in the cat extend the duration of the motoneuron excitability elicited by a train of Ia afferent impulses. It seems likely that MNPs of the posterior iliotibial, femorotibial, iliofibular and caudilioflexorius muscles, which may have monosynaptic connections with primary afferents as well as with serotoninergic fibers (Homma et al. 1988; Okado et al. 1988), mediate tonic excitatory responses involved in maintaining an upright posture in chickens.

Rubrospinal fibers in the pigeon (Wild et al. 1979) are located in the lateral border regions of the dorsal horn. Parts of dendritic fields from the posterior iliotibial, femorotibial, iliofibularis, and caudilioflexorius MNPs were found to overlap spacially with rubrospinal fibers. All of these MNPs are located in the dorsolateral region of the lateral motor column. This is consistent with a previous physiological study of the cat spinal cord, showing that monosynaptic rubrospinalmotoneuron connections are localized in the dorsolateral region of the lateral motor column (Shapovalov 1972). Anatomical studies also indicate that direct rubro-motoneuronal connections exist in the dorsolateral portion of the ventral horn of both cat (Motorina 1974) and monkey (Holstege et al. 1988; Ralston et al. 1988).

Kuypers (1982) has subdivided the brainstem-spinal pathways into medial and lateral groups. The medial group is composed of projections from the interstitial nucleus of Cajal, the mesencephalic reticular formation, the pontine and medullary medial reticular formation and the vestibular complex, and is involved in the control of the axial and proximal limb musculature. In mammals, the lateral group is composed of rubrospinal and corticospinal projections. The lateral group is thought to initiate movements, and to control movements of the distal extremity as well as highly specialized, detailed movements of the hand and digits (Shapovalov 1975; Kuypers 1982). Although it is not known what movements in the chicken may correspond to the distal extremity movements of mammals, the rubrospinal projection to MNPs in the chicken may have a similar function to that of the lateral group in mammalian species.

White matter dendrites

A remarkable feature of the dendritic trees of MNPs (posterior iliotibialis, femorotibialis, iliofibularis and caudilioflexorius) in the chicken lumbosacral spinal cord is the extensive spread of branches within the white matter. Axons from spinal descending as well as from propriospinal fibers may form synapses on these white matter dendrites (Oppenheim et al. 1975). Several descending pathways from supraspinal neurons have been demonstrated in the white matter of avian species. Serotoninergic fibers descend through the broad superficial regions of the lateral funiculus (Cabot et al. 1982; Sako et al. 1986), and tyrosine hydroxylase-positive fibers are located in the central regions of the lateral funiculus near lamina V (Okado et al. 1989). Reticulospinal pathways, which have not yet been studied in the chicken spinal cord, may be located in the lateral funiculus, as in the lizard (Wolters et al. 1984). Although vestibulospinal fibers have been shown to descend through localized regions near the surface of the ventral funiculus in the chicken (Wold 1978), a wider distribution of vestibulospinal fibers, extending mediolaterally in the ventral funiculus, is found in the pigeon spinal cord (Cabot et al. 1982). It seems likely that dendrites of MNPs penetrating into the white matter may have direct synaptic contacts with the above mentioned supraspinal descending fibers.

A considerable number of dendritic branches have been demonstrated in the spinal cord white matter of lower vertebrates (Szekely 1976; Bregman and Cruce 1980; Lichtman et al. 1984; Ruigrok et al. 1984; Oka et al. 1987). In the spinal cord of the bullfrog, dendrites traverse the white matter, and many branches were found running parallel to the surface of the cord after the dendrites reached subpial regions (Lichtman et al. 1984). In the turtle, most dendritic branches extend into the white matter, whereas the gray matter remains virtually free of dendritic arborizations. Although not as extensive as in lower vertebrates, many white matter dendrites have also been demonstrated in the cat (Aitken and Bridger 1961; Egger et al. 1980; Rose and Richmond 1981), and some of these penetrate deeply into the white matter, nearly reaching subpial regions. White matter dendrites of spinal motoneurons have been demonstrated in many species including man (Schoenen 1982). However, the extent of dendritic arborization in the white matter seems generally less in higher mammals. From a comparative point of view, dendritic extensions into the white matter of the chicken appear to fall between those of the turtle (Ruigrock et al. 1984) and cat (Egger et al. 1980).

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