

# Cells of Origin, Course, and Termination Patterns of the Ventral, Uncrossed Component of the Mature Rat Corticospinal Tract

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## ABSTRACT

The cells of origin, the course, and termination patterns of the ventral, uncrossed component of the rat corticospinal tract (CST) was investigated by using retrograde and anterograde tracing methods. Anterograde tracing with biotin dextran-amine (BDA) revealed the position and detailed morphology of CST fibers in the spinal cord. Cross sections on spinal levels C4, T8, and L4 showed labeled fibers in the ipsilateral ventral funiculus on all levels. Although ipsilateral ventral CST fibers run close to the midline in the cervical cord, they were found to disperse more in the ventromedial funiculus at lower spinal levels. To study the termination patterns of the ipsilateral ventral projection, a dorsal spinal cord hemisection was performed at level T8, severing the crossed dorsomedial and dorsolateral components but leaving ipsilateral ventral running fibers intact. These fibers were observed to have sometimes several collaterals with terminal arbors extending into different spinal segments, innervating mostly laminae III-VI. Structures closely resembling synaptic boutons were identified in these arbors. By retrograde tracing in animals with dorsal spinal cord hemisection, we found labeled cells equally distributed throughout the spinally projecting cortical areas corresponding to the level of tracer injection. Labeled cells were found in layer V. The diameter of the labeled cells was not significantly different from other spinally projecting cortical neurons. In summary, a neuroanatomically complete ipsilateral, ventral corticospinal projection down to low spinal levels was found. The large extension of the terminal arborizations in intermediate laminae of the spinal cord suggests a modulatory role of this CST component. *J. Comp. Neurol.* 386:293-303, 1997. © 1997 Wiley-Liss, Inc.

**Indexing terms:** anatomy; pyramidal tract; ventral funiculus; spinal cord; pyramidal decussation

The corticospinal tract (CST) of the rat and other rodents is one of the best studied mammalian fiber tracts. It has served as a powerful model system in the investigation of central nervous system (CNS) tract development (Stanfield and O'Leary, 1985; Joosten et al., 1987, 1989, 1992; Stanfield, 1992), anatomical plasticity (Kalil and Reh, 1982; Bregmann et al., 1989; Kuang and Kalil, 1990), motor physiology (Castro, 1972; Hicks and D'Amato, 1975; Kartje-Tillotson et al., 1987; Stewart et al., 1990; Babalian et al., 1993), and CNS regeneration (Schnell and Schwab, 1990; Schnell et al., 1994; Bregman et al., 1995; Joosten et al., 1995; Cheng et al., 1996). Most studies have focused on its main crossed component, which is located at the ventromedial aspect of the dorsomedial funiculus of the rat spinal cord (Hicks and D'Amato, 1975; Armand, 1982; Miller, 1987). Although, as in other mammals (Armand, 1982, review), minor components of the rat CST have been

known to exist for a long time (Goodmann et al., 1966; Vahlsing and Feringa, 1980), their exact course and position are not well described, and their functions are unknown (Casale et al., 1988; Rouiller et al., 1991). Casale et al. (1988) and Rouiller et al. (1991) reported minor CST components in the ipsilateral dorsomedial, contralateral lateral, and ipsilateral ventromedial funiculi of the rat spinal cord. Particularly unclear was how far caudal these minor CST components extend into the spinal cord. By

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anterograde horseradish peroxidase (HRP) tracing, an extension of ipsilateral ventral CST fibers down to high lumbar levels during the first postnatal week was shown to be present (Joosten et al., 1992). However, this projection was described to retract from the second postnatal week on and could not be shown beyond level T 4 after postnatal day 28. Also, Joosten et al. (1992) did not observe ventral fibers growing into gray matter areas and, therefore, concluded that functional contacts of the uncrossed, ventral CST fibers are absent. By application of the recently introduced anterograde tracer biotin dextran-amine (BDA), which combines high sensitivity with superior single-fiber resolution (Brandt and Apkarian, 1992; Veenman et al., 1992), we show here that the ipsilateral, ventral CST projection extends to low spinal levels also in adulthood. These fibers have profuse collateral arborizations into gray matter areas and may, therefore, be a fully functional CST component.

## MATERIALS AND METHODS

### Anterograde tracing of CST fibers

All procedures involving animal experiments were approved by the Veterinäramt of the canton of Zurich. Lewis rats, between 4 and 7 weeks of age, were deeply anesthetized by an intraperitoneal injection of a combination of Hypnorm (0.3 mg/kg) and Midazolam (0.6 mg/kg). The scalp was opened, and a hole was drilled into the skull overlying the right sensorimotor cortex. By means of a Hamilton syringe, 1.5  $\mu$ l of 10% BDA (Molecular Probes, Eugene, OR) in 0.01 M phosphate buffer (PB) were applied in three shallow injections to the right cortex. The scalp was closed with tissue glue (Histoacryl blue, Braun, Melsungen, Germany). In rats in which the termination patterns of the ventral, ipsilateral CST fibers were studied, a laminectomy was performed at T8, and the dorsal half of the spinal cord was transected with iridectomy scissors at the time of tracer injection, leaving only the ventral projection uninjured. After a survival period of 11 days, the animals were killed with pentobarbital (500 mg/kg) and perfused transcardially with a Ringer solution containing 100 000 IU/liter of heparine and 0.25% NaNO<sub>2</sub>, followed by 4% paraformaldehyde solution in 5% sucrose in 0.1 M PB as fixative. The spinal cords were removed, postfixed overnight in 4% formaldehyde, and embedded in a gelatin-egg albumin protein matrix polymerized by glutaraldehyde.

Sagittal and cross sections (50  $\mu$ m) were taken on a Vibratome and processed in a semifree floating way as described earlier (Herzog and Brösamle, 1997). Briefly, tissue sections were collected consecutively from the collecting buffer of the Vibratome in a way that one end of the sections came to lay onto a frosted stripe along the longitudinal side of the slide, thus preserving the proper orientation and sequence of the sections. The sections were fixed to the frosted stripe with a droplet of cyanoacrylic glue (Cyanolith, 3M, Rüslikon, Switzerland). The slide with the sections glued to it was then transferred, the glued side up, to a staining jar with 50 mM Tris buffered saline, pH 8.0, containing 0.5% Triton X-100 (TBST), and washed for three times, 30 minutes each, on a magnetic stirrer. The slides were then placed in a humid incubation chamber and incubated overnight with an avidin-biotin-peroxidase complex in TBST (ABC elite, Vector Labs, Burlingame, CA) according to the instructions of the

manufacturer. After washing for three times, 30 minutes each, in TBST in the jar and a short rinse in 50 mM Tris buffer, pH 8.0 (TB), the sections were placed into the incubation chamber again and preincubated for 10 minutes in 0.4% ammonium nickel sulphate (Sigma, St. Louis, MO) in TB followed by a second preincubation with 0.4% ammonium nickel sulphate and 0.0015% 3,3'-diaminobenzidine (DAB, Sigma) in TB. Sections were then reacted with 0.4% ammonium nickel sulphate, 0.0015% DAB and 0.004% H<sub>2</sub>O<sub>2</sub> in TB. The reaction was monitored under a microscope and stopped by washing extensively in TB in a staining jar. Sections were dried on the slides, dehydrated through alcohol and xylene, and coverslipped in Eukitt (Kindler, Freiburg, Germany).

Sections were viewed on an Olympus microscope, and drawings were made with an attached camera lucida tube. Fiber numbers on cross sections of the ipsilateral ventral, the ipsilateral dorsomedial, and the contralateral dorsolateral component of the CST were determined either directly at the microscope or from high-resolution digital images on the computer screen. Due to the high density of labeled fibers in the main, contralateral dorsomedial CST, single fibers could not be distinguished when BDA was detected with the ABC DAB method, and hence, no fiber counts could be established for this component on different spinal levels. For publication figures, electronic images were acquired by using a Xillix Microimager slow-scan, high-resolution CCD camera, contrast enhanced, sharpened, and mounted by using Photoshop software and subsequently printed on a Kodak dye sublimation printer.

### Fluorescence detection of BDA-traced fibers

To assess the total number of ventral fibers, the efficiency of the BDA tracing was estimated by detection of the BDA label at level C1 with fluorescein-avidin, which allowed for better counting of fibers in the main CST component. Obtained average numbers were compared with total CST fiber counts in the dorsomedial funiculus at C1 established by Casale et al. (1988) from electron photomicrographs. In eight animals, 50  $\mu$ m Vibratome cross sections were taken and processed semifree-floating as described above. After washing for three times, 30 minutes each, in TBST and incubation overnight in 10  $\mu$ g/ml fluorescein-avidin (DCS, Vector Labs) in TBST, unbound fluorescein-avidin was washed out for three times, 30 minutes each, in TBST, and the sections were mounted in Mowiol (Calbiochem, La Jolla, CA) containing 0.1% DABCO (Aldrich, Steinheim, Germany) as an antifading agent. Sections were viewed under epifluorescent illumination, and digital images were acquired by using a Xillix Microimager slow-scan, high-resolution CCD camera. Fibers in the main component of the CST were counted automatically, by using the ImageTool software package (UTHSCSA, San Antonio, TX).

### Retrograde labeling of ventrally, ipsilaterally projecting CST neurons

Five Lewis rats at the age of 5 weeks were deeply anesthetized by an intraperitoneal injection of a combination of Hypnorm (0.3 mg/kg) and Midazolam (0.6 mg/kg). A laminectomy was performed at level T6, and the exposed dorsal half of the spinal cord was cut bilaterally as described above, thus interrupting all dorsally running CST components but leaving the ventral, ipsilateral CST components intact. A small piece of gelfoam was placed on

the site of injury, and the adjacent muscle tissue was sutured. At approximately levels T10 and L2, partial laminectomies were performed, and the spinal cord was exposed. At each site, the spinal cord was injected medially with 1.5  $\mu$ l of a 5% solution of the retrograde neuronal tracer Fluorogold (Fluorochrome, Englewood, CO) in phosphate-buffered saline (PBS) containing 2% dimethylsulfoxide. The wounds and the skin were sutured. After a survival time of 6 days, the animals were killed and transcardially perfused as described above.

To mark reference points in the cortex, the skull was fixed in a stereotaxic frame. Two holes were drilled in the skull lateral to Bregma, and by means of a glass capillary filled with a saturated solution of DiI (Molecular Probes) in 100% ethanol, a point was marked 3 mm lateral to Bregma on each hemicortex. The brain was then dissected from the skull, postfixed overnight in 4% formaldehyde and 5% sucrose in 0.1 M PB and embedded in agar. Tangential Vibratome sections of 100  $\mu$ m were taken of the cortex, transferred to slides, and coverslipped with Mowiol. All sections were viewed and analyzed on a Zeiss Axiophot fluorescence microscope with a digital camera and a computer running Image 1 (Universal Imaging, West Chester, PA) image analysis software. Only strongly retrogradely labeled cortical neurons were mapped by measuring the distance from the DiI reference points. Cells with weak label were not included in the analysis, because dye spread via the cerebrospinal fluid from the injection site to the site of the CST lesion could not be completely excluded. The diameters of labeled cells were measured where the nucleus was visible in the section, to ensure consistency of measurement. The depth of the cells in the cortex was estimated from the number of sections from the cortical surface. Two of the 10 hemicortices were not included in the analysis because too many cells had been labeled, either by spreading of the dye to the site of the dorsal hemisection or by an incomplete lesion. For comparison of the cell diameters and depths of ventral, ipsilateral projecting neurons to other CST neurons, in two control rats, Fluorogold was injected into the spinal cord as described above, but without transecting the dorsal half of the cord rostral to the injections. Cell diameter and depth were analyzed as described above.

## RESULTS

Injection of BDA into the right sensorimotor cortex of young adult rats resulted in a strong anterograde labeling of corticofugal fibers. Ipsilateral projections to thalamic nuclei, mesencephalic nuclei, pontine nuclei, inferior olive, and dorsal column nuclei could be identified. Also, contralaterally projecting callosal fibers were clearly visible. In the spinal cord the strongest label was found in the ventral most part of the contralateral dorsomedial funiculus, the typical location of the main CST in the rat (Fig. 1A). Another, much smaller portion of CST fibers was found in the contralateral dorsolateral funiculus (Fig. 1B) and in the ipsilateral ventromedial funiculus (Fig. 1C). Small numbers of labeled fibers were observed in the ipsilateral dorsomedial funiculus (i.e., in the main CST of the other cortical hemisphere; Fig. 1A) and occasionally in the ipsilateral lateral funiculus (Fig. 1D). The described CST fibers were found on all investigated spinal levels (i.e., down to L4/5) in all animals.

## Course of ventral, ipsilateral fibers

Sagittal sections of the medulla oblongata at the level of the pyramidal decussation showed that the pyramidal tract, which runs as a compact fiber bundle at the ventral surface, defasciculates into many smaller fiber bundles that turn dorsally and cross to the contralateral spinal cord. Some fibers, however, do not turn and continue their path into the ipsilateral ventral funiculus (Fig. 2). Because no bifurcations could be observed, we concluded that these fibers are distinct, separate axons rather than collaterals from other, crossing fibers.

In the cervical and upper thoracic spinal cord the uncrossed ventral CST fibers run very close to the ventral median fissure. At lower spinal levels they disperse more into the ventromedial funiculus (Fig. 3). This pattern parallels that of the main CST projection in the contralateral dorsomedial funiculus that runs as a compact fiber bundle at upper spinal levels and usually defasciculates into several bundles at lower spinal levels (Fig. 3).

We have counted the number of labeled ventral uncrossed fibers at different spinal levels and found at C4 an average of  $65.6 \pm 1.15$  (SD,  $n = 3$ ), at T8  $26.3 \pm 10.12$ , and at L4  $7 \pm 2.64$  fibers (Fig. 4A). This represents a decrease from cervical levels (100%) to approximately 40% at mid-thoracic and 11% at midlumbar levels (Fig. 4B). A very similar decrease in fiber numbers along the rostrocaudal axis of the spinal cord was observed also for the other minor components of the CST (Fig. 4B).

## Termination patterns

BDA-labeled ipsilateral ventral CST fibers were observed to bypass the dorsal hemisection lesion undisturbed in the ventromedial funiculus (Fig. 5A). Other CST components were interrupted by the lesion, thus allowing for the detailed analysis of the termination patterns of the ipsilateral ventral projection. On all spinal levels collaterals branching into gray matter areas were seen. Interestingly, single ventral CST fibers sometimes gave rise to several collateral arborizations on different spinal levels. Ventral fibers often made a sharp turn perpendicular to the longitudinal cord axis and ascended into the gray matter where they branched profusely in both rostrocaudal and lateral directions (Fig. 5B, Fig. 6). Most branches were found in intermediate regions corresponding to Rexed's laminae III–VI (Fig. 6). This region has also been described as the predominant target area of the main CST component (Liang et al., 1991), although CST fibers have also been reported to innervate superficial layers (Bregman and Goldberger, 1983; Barth and Stanfield, 1990; Kuang and Kalil, 1990) and the ventral horn (Bregman and Goldberger, 1983; Barth and Stanfield, 1990; Kuang and Kalil, 1990). Terminal arbors extended for several millimeters in the rostrocaudal and approximately 1 mm in the lateral direction. At higher magnifications numerous structures closely resembling synaptic boutons could be seen (Fig. 5C–E).

## Cells of origin of the ipsilateral, ventral CST projection

Cortical neurons projecting to the ipsilateral, ventral spinal cord were identified by retrograde tracing from T10 and L2 after interrupting the other CST components by a dorsal hemisection of the cord at level T6. Strongly labeled neurons were mapped from tangential section series onto a

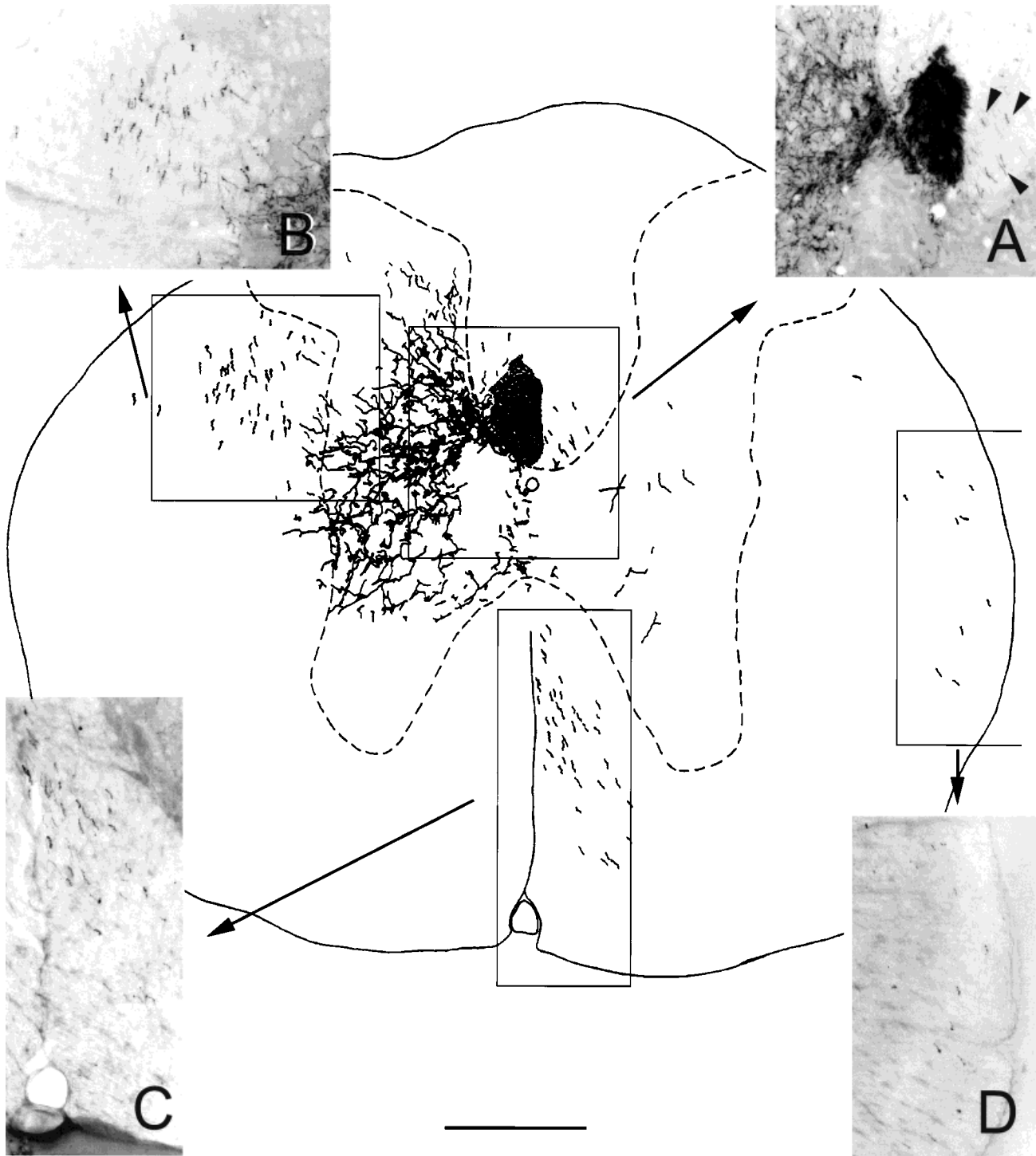


Fig. 1. Biotin dextran-amine (BDA) tracing of the adult rat corticospinal tract from the right hemicortex reveals several components of the corticospinal tract (CST). Cross section at midthoracic level. Camera lucida drawing with the areas of the different components photographed (A–D) and marked in the drawing as boxes. **A:** The main CST component with by far the most fibers runs as a compact bundle in the contralateral dorsomedial funiculus. Some fibers originating from the right sensorimotor cortex can be found in

the ipsilateral dorsomedial funiculus (arrowheads), the location where most of the CST fibers from the other hemisphere are running. **B:** A second minor contralateral component is located dispersely in the dorsolateral white matter area. **C:** Ipsilateral (uncrossed) fibers are found in the ventromedial funiculus. **D:** Occasionally, CST fibers are found that run in the ipsilateral lateral white matter. The dashed line delineates the border between gray matter and white matter. Scale bar = 250  $\mu$ m.

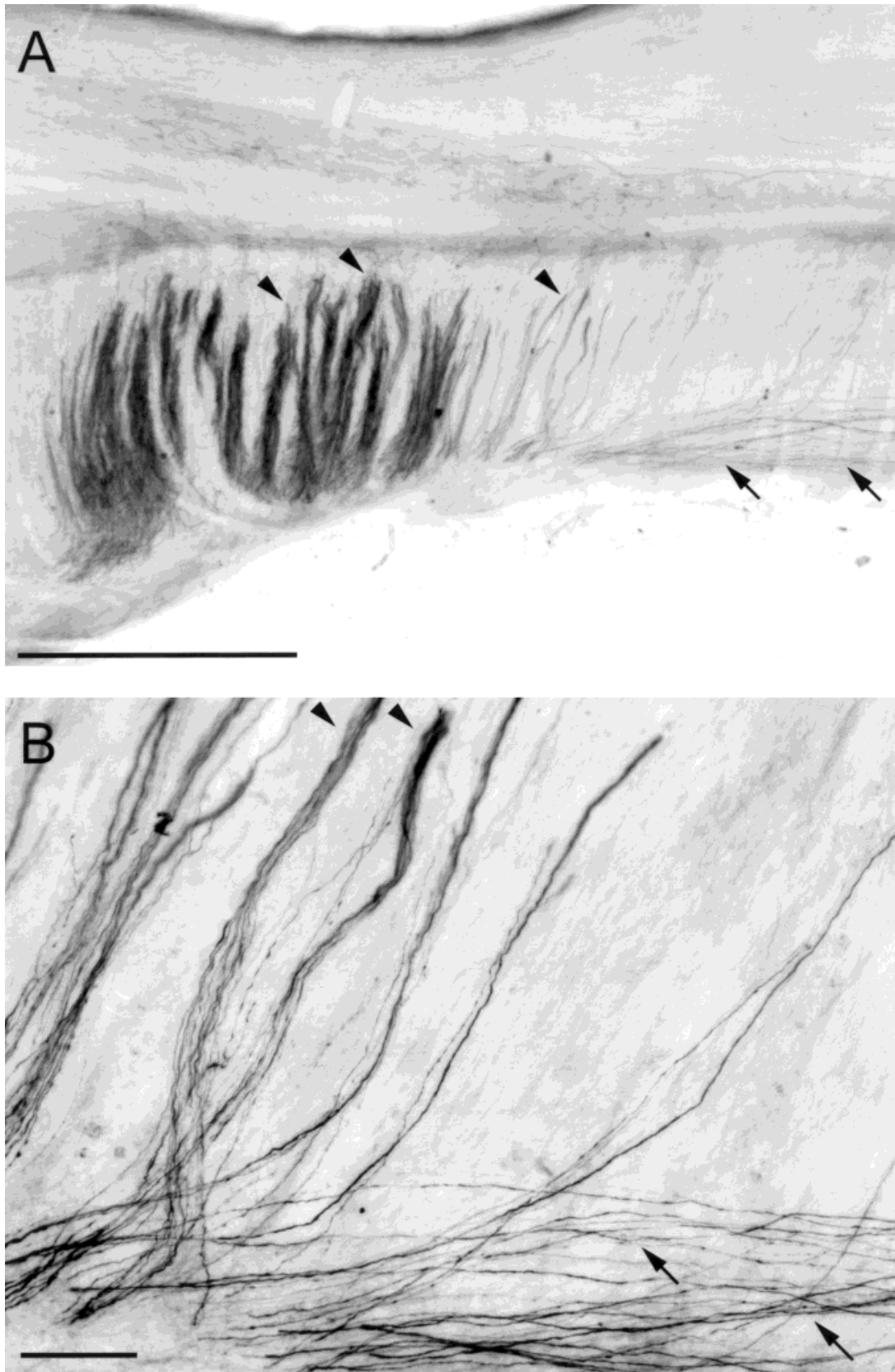


Fig. 2. Sagittal section of the medulla oblongata at the pyramidal decussation. **A:** Overview. Although most fibers turn dorsal and decussate to the contralateral spinal cord (arrowheads), some fibers do not and continue to run in the ipsilateral ventromedial funiculus

(arrows). At higher magnifications (**B**), it can be seen that these fibers do not arise from crossing collaterals but are independent fibers. Scale bars = 1 mm in A, 100  $\mu$ m in B.

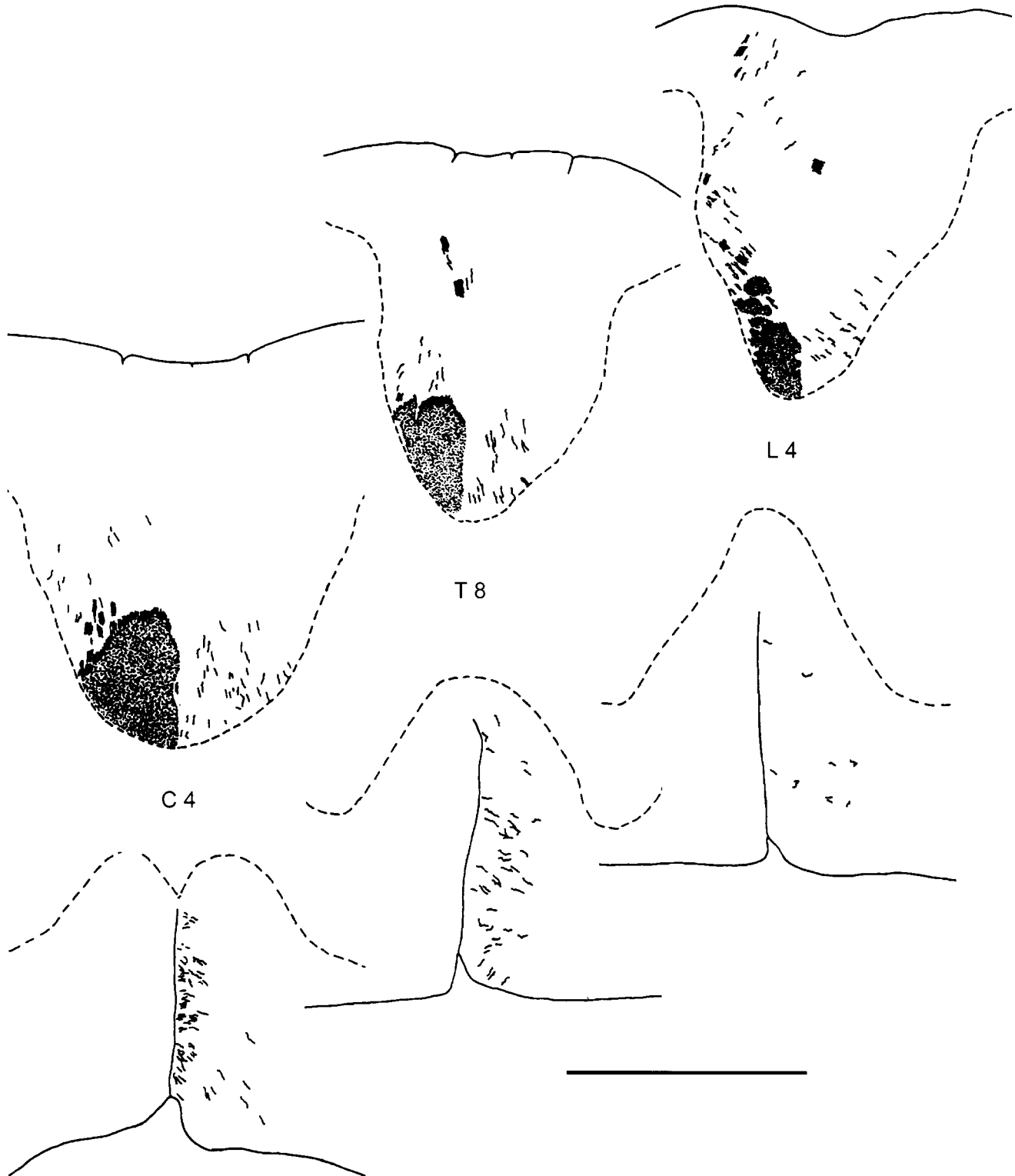


Fig. 3. Camera lucida drawings of traced CST fibers in the dorsomedial and ventromedial funiculi at different spinal levels. Ipsilateral ventral CST fibers are found on all spinal levels. At high levels (C4) most of them run close to the midline. At lower levels (T8

and L4), as their number declines, they disperse more in the ipsilateral ventral funiculus. This corresponds to the main CST tract that runs as a compact bundle on high lumbar levels and tends to defasciculate at lower levels. Scale bar = 500  $\mu$ m.

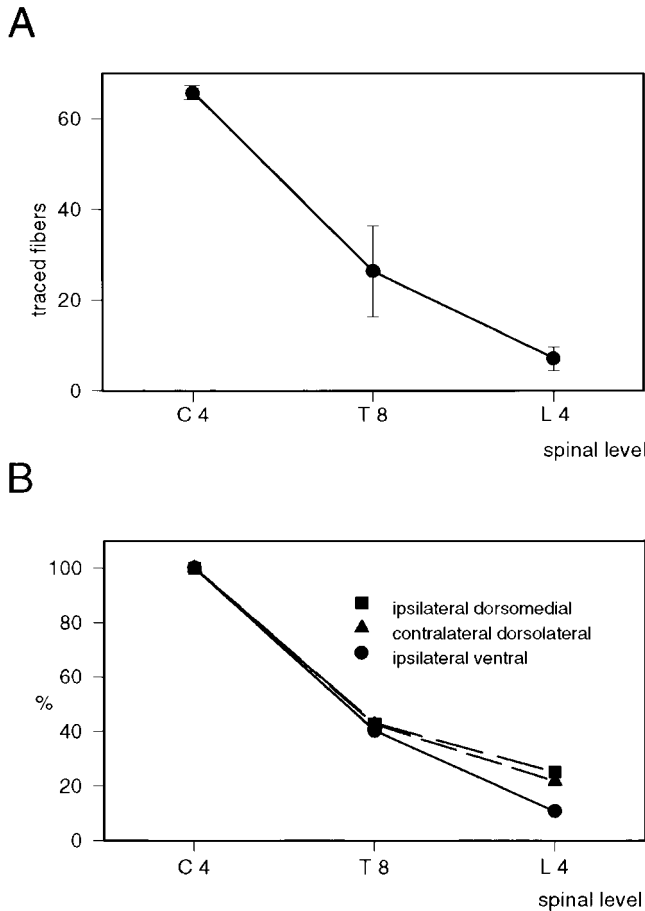


Fig. 4. Ipsilateral ventral CST fibers gradually decrease in number at lower spinal levels but are present on all levels. **A:** Counts of traced ipsilateral ventral CST fibers. Actual fiber numbers are likely to be much higher as the tracing efficiency was estimated to be 1–2%. **B:** The decline of ipsilateral ventral CST fiber numbers along the spinal cord exactly parallels that of the other minor CST components.

coordinate system and were found to be distributed over the whole hind limb projection area and adjacent fields (Fig. 7). The average cell diameter was  $22.12 \pm 2.63 \mu\text{m}$  (SD,  $n = 55$ ), which was not significantly different from that of other corticospinal projection neurons of that area ( $21.92 \pm 2.55 \mu\text{m}$ ,  $n = 53$ ). An average of  $49.38 \pm 16.8$  cells (SD,  $n = 8$ ) was found to be labeled per hemicortex from spinal levels T10 and L2. Compared with the number of spinal cord fibers seen by anterograde BDA tracing, this result points to a slightly higher efficiency of the retrograde tracer. Cells projecting to the ipsilateral, ventral CST were found in the same cortical depth (layer V) as other corticospinal projecting neurons.

#### Estimation of absolute fiber numbers in the ipsilateral ventral CST component

Fiber counts of fluorescence detected BDA-labeled fibers in the contralateral dorsomedial main CST component yielded at C1 an average number of  $1,222 \pm 314$  (STD,  $n = 8$ ) traced fibers. If compared with the data of previous work, where electron microscopic observations show 81,000 CST fibers, our BDA tracing protocol has an overall tracing

efficiency of  $1.51 (\pm 0.39)\%$ . Because the cell bodies of the corticospinal neurons that project to the ipsilateral ventral portion are distributed over the same area as those of the main CST component, one can assume that their tracing efficiency is very similar too. If extrapolated, this means that at level C4 there are approximately 4,350 ipsilateral ventral fibers, and at levels T8 and L4 1,750 and 450 fibers, respectively.

#### DISCUSSION

We have shown that the ipsilateral, ventral component of the mature CST is a distinct, although minor, part of the adult rat CST system. The cells of origin of the ipsilateral, ventral projection were found in layer V of the sensorimotor cortex, indistinguishable in terms of size and distribution, from other corticospinal projection neurons. Because no branch points of crossing and noncrossing CST fibers were observed at the pyramidal decussation, we conclude that each CST neuron has only one axon descending to the spinal cord, either crossed or uncrossed. Ventral, ipsilateral CST fibers were present at all spinal levels, but their number decreased along the rostrocaudal axis of the cord with approximately the same rate as that of other studied minor CST components. Terminal branches and collaterals from these ventral, uncrossed fibers into areas of spinal gray matter corresponding mostly to Rexed laminae III–VI were observed. These fibers arborized profusely over large areas and showed many structures resembling synaptic boutons and en passant synaptic contacts. It cannot completely be excluded that the dorsal hemisection that allows to study exclusively the ventral CST fibers influences the termination patterns of the latter. However, in mammals axonal sprouting of CNS fibers into denervated areas is limited to a permissive period during development and fiber growth in response to a lesion is very limited in the adult (Bregman and Goldberger, 1983; Barth and Stanfield, 1990; Kuang and Kalil, 1990). Therefore, the termination patterns of the ipsilateral, ventral CST fibers should only be minimally modified by the dorsal hemisection, if at all.

Earlier studies in rats have not found ventral, uncrossed fibers below thoracic levels and claimed an absence of branches of these fibers into the spinal gray (Vahlsing and Feringa, 1980; Joosten et al., 1992). This difference, compared with our present data, is most likely due to the more sensitive tracing methods now available. BDA and its detection by the semifree floating method (Herzog and Brösamle, 1997) shows low numbers of fibers over long distances in excellent single fiber resolution. The transient uncrossed, ventral CST projection to lumbar levels observed in postnatal rats (P5–7) by Joosten et al. (1992) probably reflects the transient presence of axons that, in the adult, have other projection targets and are retracted during the maturation of the nervous system (Stanfield et al., 1982; Stanfield and O'Leary, 1985). Alternatively, a more efficient labeling due to higher anterograde transport of tracer during the growth phase of the axons may also occur.

Both anterograde tracing with BDA as well as retrograde tracing with Fluorogold labeled only a small portion of all CST fibers. Retrograde tracing labeled approximately 50 cortical neurons per hemicortex from T10 and L2 and was slightly more efficient than the anterograde tracing with an average of 26 ventral fibers at spinal level

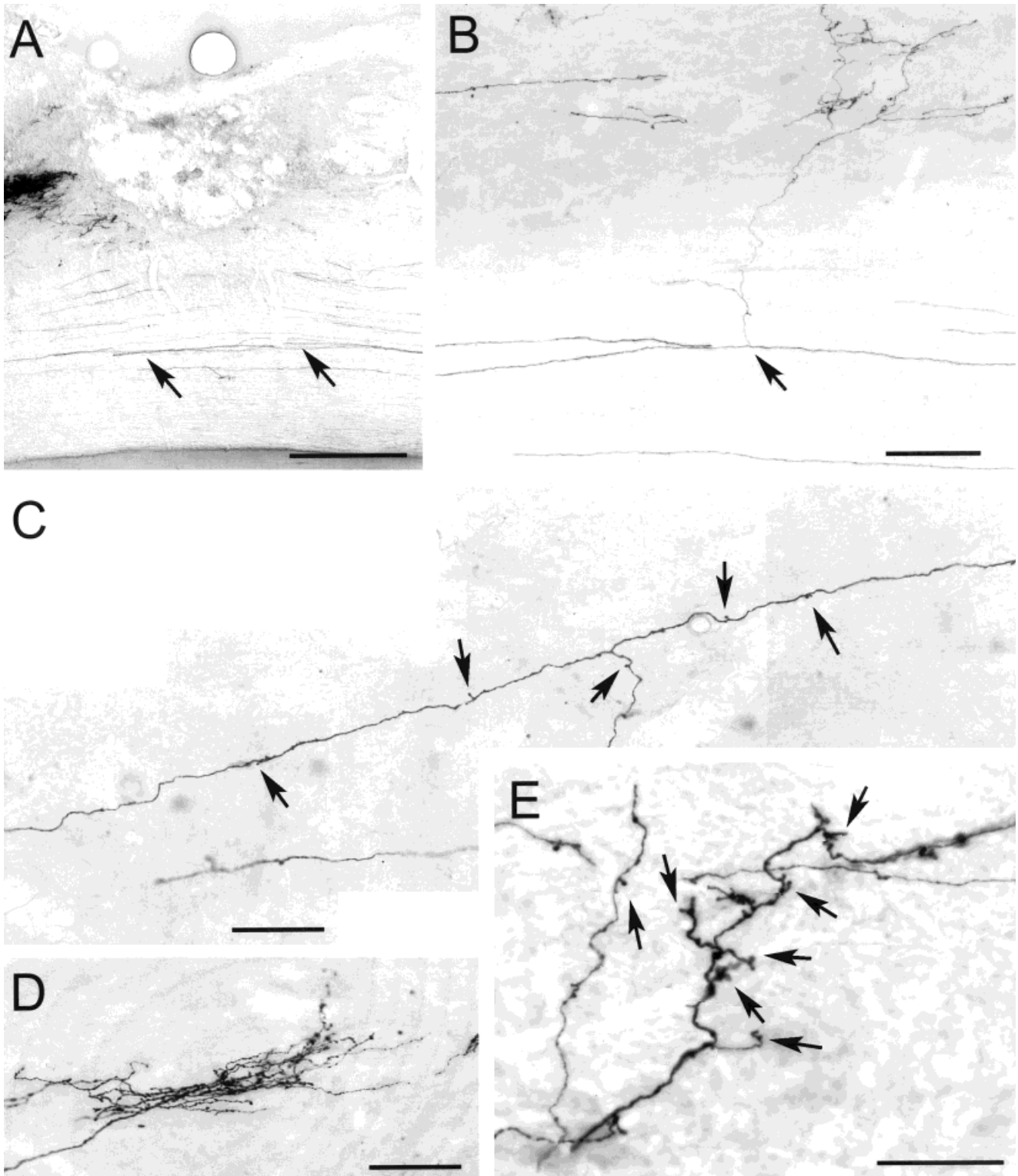


Fig. 5. Photomicrographs of ventral ipsilateral CST fibers in 50- $\mu$ m sagittal sections of the spinal cord. **A:** A dorsal hemisection at a midthoracic level interrupts the dorsal CST components leaving the ventral fibers (arrows) intact and thus allowing the analysis of their arborization patterns at lower spinal levels. **B:** Collaterals

(arrow) arise from ventral fibers and grow up into the spinal gray where they branch. **C-E:** In the spinal gray the terminal arbors extend over large distances where they branch profusely and show many terminal and en passant bouton-like swellings (arrows). Scale bars = 0.5 mm in A, 100  $\mu$ m in B, 50  $\mu$ m in C, D, 20  $\mu$ m in E.

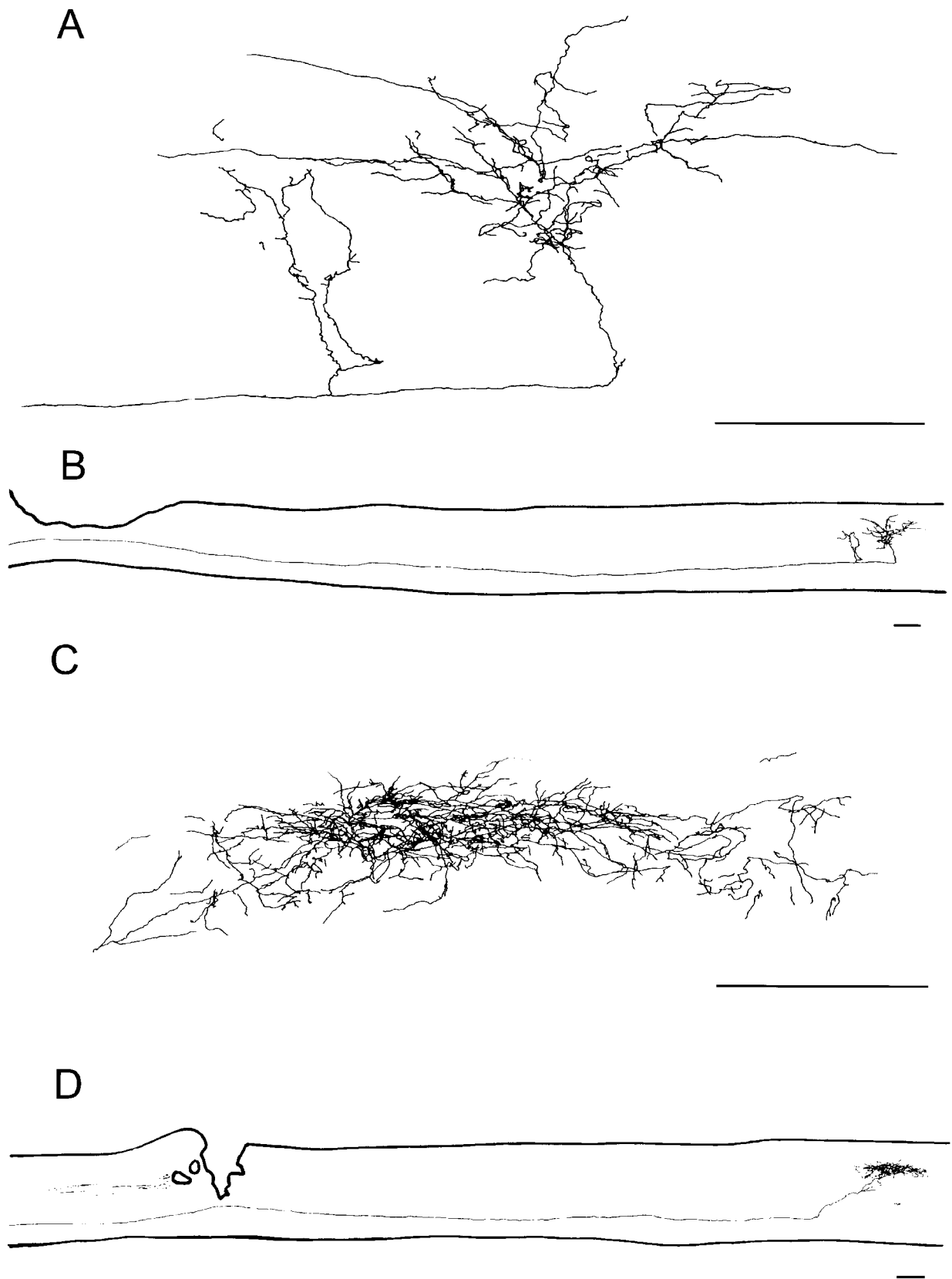


Fig. 6. Two examples of ventral ipsilateral CST fibers and their terminal arbors shown as Camera lucida reconstructions of multiple consecutive sagittal sections. **A,C:** High magnifications showing the profuse arborization mostly in layers IV–VI, the normal target areas of CST fibers in the rat. Reconstructed from 22 (A) and 16 (C)

sections corresponding to 1.1 (A) and 0.8 (C) mm lateral depth. **B,D:** The course of the corresponding ventral fibers from the dorsal hemisection that interrupts other CST components at T8, thus allowing for the study of the ventral fibers selectively. Scale bars = 0.5 mm.

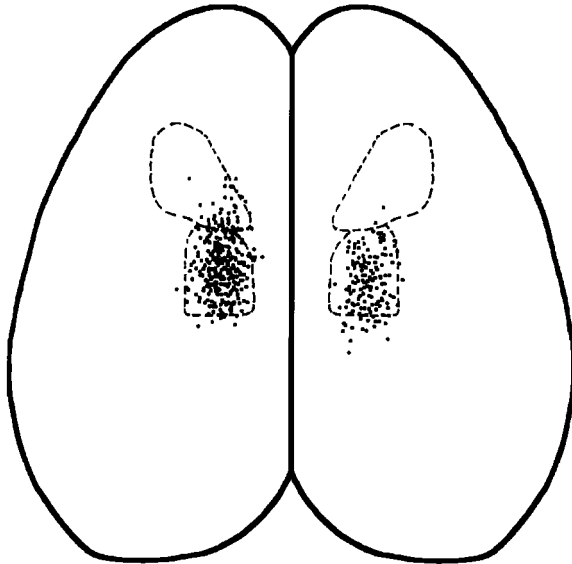


Fig. 7. Origin of ventral ipsilateral CST fibers as determined by retrograde labeling from T10 and L2. Cumulative map of 5 (left) and 3 (right) hemicortices. Cells of origin are scattered over the entire hindlimb area (lower encircled field). Some cells were also found more rostrally in the trunk-forelimb area (rostral encircled field) of the sensorimotor cortex (fields determined with intracortical microstimulation by Hall and Lindholm, 1974). Ipsilateral, ventral projecting cells are distributed over the same area as cells of origin of the other CST components.

T8. Absolute numbers of ventral CST fibers were estimated by a comparison with earlier electron microscopic data for the main CST (Leenen et al., 1985). The resulting fiber numbers range from several thousand ventral fibers at cervical levels to several hundred at lumbar levels. When compared with the main CST component, the number of fibers in the ipsilateral ventral CST components is small, approximately 5–6%. However, this does not necessarily mean that these fibers are not important functionally. Indeed, relatively few fibers can have strong effects on locomotion (Guth et al., 1980; Blight and Young, 1989; Bregman et al., 1995), presumably by activating and influencing spinal pattern generators (Grillner, 1975). The large size of their terminal arbors would correspond well with such a function.

Another interesting question that arises concerns the guidance cues that influence the decision that outgrowing corticospinal fibers have to make when reaching the pyramidal decussation. Several mechanisms for differential guidance are conceivable. First, intrinsic differences of the growing axons, possibly by different expression of receptors for local guidance cues or adhesion molecules, could be responsible for different routing (Joosten et al., 1990). Another possibility would be temporal changes in the cellular environment (Joosten and Gribnau, 1989) guiding earlier fibers in different directions than later ones.

Whether the ipsilateral CST component is specifically directed not to cross or whether this projection pattern forms 'by accident' cannot be decided at this point; however, the frequent and consistent occurrence of ipsilateral CST projections in many other mammalian species (Armand, 1982) suggests a normal innervation that may have

specific functional roles. As in other mammals, the ipsilateral ventral fibers in the rat persist in the adult and seem to find targets and to make functional synaptic contacts. Detailed physiological studies of the functions of the minor CST components will possibly allow us to answer questions about the specific functional roles of this system.

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