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The Neurons of the Medial Geniculate Body in the Mustached Bat (*Pteronotus parnellii*)

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ABSTRACT

The neurons in the medial geniculate body were studied in Golgi preparations from adult mustached bats (*Pteronotus parnellii*). Their somatic and dendritic configurations were compared with those of cells in other, nonecholocating mammals. A second goal was to use the thalamic nuclear subdivisions derived from Golgi material to integrate the findings in parallel studies of cytoarchitecture, immunocytochemistry, and tectothalamic connections.

Three primary divisions are defined. The ventral division is large and has a stereotyped neuronal organization. Medium-sized perikarya (about 10 μm in diameter) represent tufted neurons; the fibrodendritic plexus forms laminae in the lateral part along which midbrain axons terminate. A smaller, possibly intrinsic, neuron with thin, sparse dendrites is rarely impregnated. Neurons in the larger, medial part, which represents frequencies of 60 kHz and higher, have more spherical dendritic fields; their branching pattern remains tufted, and the laminar organization was less evident. The dorsal division is about equal in size, and it has many nuclei and a corresponding neuronal diversity. These neurons are medium-sized except in the suprageniculate nucleus, where many cells are larger. Four dorsal division nuclei are recognized. Each has neurons with radiate or weakly tufted dendritic arbors. Superficial dorsal nucleus neurons are oriented from medial to lateral, imparting a slightly laminated appearance to the neuropil. A few smaller, stellate neurons with modest dendritic domains are present. Suprageniculate nucleus neurons have radiating dendritic fields that project spherically; they have fewer branches than dorsal nucleus neurons. The posterior limitans nucleus is dorsomedial to the suprageniculate nucleus; it has small neurons with long, sparsely branched dendrites. The rostral pole nucleus, included in the dorsal division on cytoarchitectonic grounds, had too few neurons impregnated to reveal its neuronal architecture. The medial division, the smallest of the main parts, is one nucleus with at least six types of cells, including the magnocellular, bushy tufted, disc-shaped, medium-sized multipolar, elongated, and small stellate neurons. There is no laminar arrangement.

Many of the neurons resemble those in rodent, marsupial, carnivore, and primate auditory thalamic nuclei. Despite such morphological correspondences, functional differences, such as the evolution of combination sensitivity, suggest that structurally comparable auditory thalamic neurons may subserve diverse physiological representations.

Key words: comparative anatomy, thalamus, dendrites, cytoarchitecture, homology

A central postulate of comparative neurology is that it is possible to identify homologous populations of neurons and comparable neural circuits in different species. This issue is especially pertinent in microchiropteran bats, which are clearly differentiated from an insectivore heritage on the basis of the enormous relative expansion of their central auditory system (Baron, 1974). This hypertrophy dwarfs even that of carnivores and primates, in whom hearing is

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considered to be advanced (Masterton et al., 1969). The primary question addressed here is whether the neuronal organization that subserves auditory thalamic function in an echolocating mammal can be compared with its terrestrial counterparts.

A related issue is whether peripheral specializations, such as a fovea or enhanced vibrissal sensibility, have a central neural correlate throughout their sensory pathways, as they appear to have in the thalamic visual (Malpeli and Baker, 1975) and somatic sensory (Mountcastle and Henneman, 1949; Woolsey and Van der Loos, 1970) representations. The mustached bat, *Pteronotus parnellii,* whose cochlea is specialized both mechanically (Pollak et al., 1972, 1979; Henson, 1978) and neurally (Suga et al., 1975; Kössl and Vater, 1985) for the 60 kHz constant frequency component of its echolocation call (Novick, 1963), also has an expanded representation of this frequency in its cochlear nucleus (Ross et al., 1988; Zook and Leake, 1989), inferior colliculus (Zook et al., 1985; O'Neill et al., 1989), and auditory cortex (Suga and Jen, 1976; Suga, 1984). A precise pattern of tonotopic organization has been demonstrated within the mustached bat's medial geniculate complex (Olsen, 1986). This arrangement undoubtedly reflects and also transforms the systematic pattern of best frequency prevailing in hindbrain and midbrain auditory centers (Pollak and Casseday, 1989). While a fovea may conserve one stimulus dimension (for example, frequency), other axes may be superimposed upon or interleaved within it. The relatively enormous 60 kHz neural map in the central nucleus of the mustached bat's inferior colliculus contains local aural subregions within which binaural subclasses of neurons are segregated spatially (Wenstrup et al., 1986), and chemically specific subregions have been identified in several central auditory nuclei in the mustached bat (Winer et al., 1994). If similar arrangements exist in the auditory thalamus, then a more refined architectonic treatment would be required to identify them. One goal of this study is to delineate architectonic boundaries that reflect neuronal structure. Another question is whether the central substrates for sharply tuned representations of frequency necessarily entail a laminar fibrodendritic organization.

Comparative neuroanatomy reveals both parallels and significant species differences in medial geniculate body organization. In the ventral division, which represents the lemniscal auditory pathway, the principal neurons in most species have bushy dendrites with a tufted branching pattern (Morest, 1965; Winer, 1985). Their long dendritic axis is parallel to isofrequency representations (Aitkin and Webster, 1972; Imig and Morel, 1985a,b) and receives topographically organized input from tonotopically arranged inferior colliculus neurons (Andersen et al., 1980; Kudo and Niimi, 1980). While comparable tufted neurons occur in the ventral division of the rat (Winer and Larue, 1987), opossum (Morest and Winer, 1986), cat (Winer, 1985), and human (Winer, 1984b) medial geniculate body, their arrangement in bats is unknown. There are equally striking species differences, which suggest that a single common pattern of auditory thalamic organization cannot suffice for all mammals. Rats have comparatively few auditory thalamic γ-aminobutyric acid-containing (GABAergic) neurons (Winer and Larue, 1988), while cats (Rouiller et al., 1990) and monkeys (Smith et al., 1987) have many more. Perhaps species-specific patterns in the functional organization of local thalamic circuits reflect differences in intrinsic and architectonic organization that remain to be defined with anatomical methods or tested physiologically.

Another question is the concordance among different methods for subdividing the thalamus in comparative anatomy. This study, which is part of a correlative series, considers the cellular and fibrodendritic architecture. The other investigations examine cytoarchitecture (Winer and Wenstrup, 1994), immunocytochemical patterns (Winer et al., 1992), and, finally, the distribution of tectothalamic axons (Wenstrup et al., 1994) to achieve a clearer picture of auditory thalamic organization.

Abbreviations

BIC	brachium of the inferior colliculus
BSC	brachium of the superior colliculus
CG	central gray
CP	cerebral peduncle
D	dorsal nucleus or dorsal division of the medial geniculate body
DS	superficial dorsal nucleus of the medial geniculate body
GABA	γ-aminobutyric acid
GAD	glutamic acid decarboxylase
IC	inferior colliculus
M	medial division of the medial geniculate body
MB	mammillary body
MRF	mesencephalic reticular formation
MZ	marginal zone
PL	posterior limitans nucleus
SC	superior colliculus
Sg	suprageniculate nucleus
Spf	subparafascicular nucleus
SpN	suprapeduncular nucleus
Vl	lateral subdivision of the ventral nucleus of the medial geniculate body
Vm	medial subdivision of the ventral division of the medial geniculate body

Planes of section:

D	dorsal
L	lateral
M	medial
V	ventral

MATERIALS AND METHODS

Animals

Mature male mustached bats, *Pteronotus p. parnellii* (11–14 g) were captured at Windsor and Mt. Plenty Caves, Jamaica, West Indies. They were anesthetized with sodium pentobarbital (60 mg/kg, i.p.) until areflexic, and then cooled in an ice bath laced with alcohol while the brain was removed. The brain was immersed in potassium dichromate for Golgi-Cox impregnation (Ramon-Moliner, 1970) in the dark, at room temperature, for 10–14 days.

Histology

After rinsing in alcohol, the tissue was dehydrated in ascending alcohols and ethyl ether, infiltrated with low-viscosity nitrocellulose, and sectioned at 120 μm in an unbroken series from the dorsal column nuclei through the basal ganglia. Sections were mounted onto albuminized slides, the mercuric salt was precipitated in a strong ammonia-alcohol solution, and the tissue was dehydrated and then coverslipped. Series were prepared in each of the cardinal anatomical planes; the plane of section in the

TABLE 1. Summary of Types of Neurons in the Mustached Bat's Medial Geniculate Complex

Division	Subdivision	Neuron type	Somatic shape and size[1]	Dendritic branching pattern and field size	Figure no.
Ventral	Lateral	Tufted	Oval or round; 9 × 10–12 μm	Polarized bushy tufts arising from the somatic poles; 150 × 300 μm	3, 8
		Stellate	Oval or elongated; 8–9 × 10 μm	Weakly tufted; 140 × 200 μm	12A
	Medial	Tufted	Oval or round; 8 × 10–12 μm	Polarized bushy tufts less developed than those of other ventral division cells; 300 × 300 μm	4, 9
		Stellate[2]	As above	As above	Similar to 12A
Dorsal	Superficial dorsal	Weakly tufted	Elongated; 8 × 12 μm	Bushy tufts arising from the somatic poles; 200 × 100 μm	5:2; 10:2
	Dorsal	Radiate	Oval or round; 10 × 10 μm	Weakly tufted; 200 × 200 μm	5:1, 3; 10:1
		Stellate	Round or elongated; 10 × 8–10 μm	Radiating or weakly stellate; 200 × 200 μm	12:4–6
	Suprageniculate	Large radiate	Oval; 14 × 14 μm	Radiate and with a spherical field; 200 × 200 μm	10:3
		Small stellate[2]	Oval; 8 × 10 μm	Irregularly radiate; 120 × 100 μm	6:6
	Posterior limitans	Elongated	Almond-shaped; 6 × 15 μm	Conforms to the shape of the nucleus, with elongated arbor; 100 × 300 μm	6:1, 2
Medial		Magnocellular	Oval; 15 × 18 μm	Radiate; 250 × 300 μm	7:6; 11:1, 6
		Bushy	Elongated; 10 × 15 μm	Weakly stellate or weakly tufted; 200 × 150 μm	7:1, 4, 7
		Disc-shaped	Oval or slightly elongated; 10 × 12 μm	Radiate and stellate; 250 × 250 μm	11:3–5
		Multipolar	Oval; 10 × 12 μm	Weakly stellate or weakly tufted; 200 × 250 μm	7:3
		Elongated	Almond-shaped; 12 × 18 μm	Irregularly radiate; 300 × 150 μm	7:8
		Small	Round; 8 × 10 μm	Stellate; 120 × 150 μm	7:2, 5; 12:7

[1]Width by height.
[2]Probable γ-aminobutyric acid-positive (GABA) neuron (Winer et al., 1992, 1994).

transverse and horizontal material closely approximated that used in a prior study of the mustached bat inferior colliculus (Zook et al., 1985).

Data analysis

Low-magnification cartoons (Figs. 1, 2) were made by drawing neurons through a camera lucida from several sections and arranging them without dendritic overlap for purposes of clarity. For each neuron, the location relative to nuclear borders and the orientation were preserved.

Every section containing the medial geniculate body was studied; only representative examples of well-impregnated neurons were drawn. Criteria for inclusion were 1) that the dendrites were free of artifactually impregnated debris, particularly that attributable to the thin, filamentous profiles of poorly fixed protoplasmic astrocytes which often enveloped them and obscured fine, smooth processes; 2) that the bulk of the cell's dendritic field was contained in the section; 3) that the quality of dendritic preservation and morphology was consistent with the level observed in plastic-embedded, toluidine blue-stained, semithin preparations (Winer and Wenstrup, 1994); and 4) that somatic size and shape matched those in Nissl preparations. Estimates of somatic size and dendritic field dimensions are based on measurements of the cells from the Golgi preparations (Table 1).

A library of material stained either by the Nissl method, with toluidine blue, with cytochrome oxidase, and with antisera to glutamic acid decarboxylase (GAD) or GABA was available for reference.

Optics

Semi-, planachro-, and planapochromatic objectives were used to study the neurons, and the high power drawings were made on a Zeiss WL microscope. Dendritic appendages were classified under oil immersion.

RESULTS

Three primary divisions of the medial geniculate complex were defined, and these correspond closely to those in other mammals, with some significant exceptions. Within two of these divisions, other, finer regional subdivisions were recognized (see Table 1 for a summary). This conclusion was supported by observations from the Golgi preparations in the present account and conclusions from the companion cytoarchitectonic (Winer and Wenstrup, 1994) and tectothalamic connectional experiments (Wenstrup et al., 1994).

Ventral division

The ventral division represented a little less than half of the volume of the medial geniculate complex. In transverse sections, it began about 200 μm from the caudal tip of the auditory thalamus and ended just behind its anterior pole (Winer and Wenstrup, 1994, their Figs. 6–11). Two principal architectonic subdivisions were recognized: a smaller, lateral part, where fibrodendritic laminae were readily apparent, and a larger, medial part where no laminar arrangement was evident. Two much smaller nuclei—the ventrolateral nucleus and the marginal zone—lie within it; since neither is part of the lemniscal auditory system, they are not considered further.

Ventral nucleus, lateral part. The ventral and lateral margins of the medial geniculate body were formed by the

Fig. 1. (See overleaf.) A cartoon from Golgi preparations from the caudal one-third of the medial geniculate body of the mustached bat. Tufted principal neurons with bushy dendritic branches dominated in the lateral part of the ventral nucleus (Vl), while neurons in more medial ventral nucleus territories (Vm) had a similar branching pattern but more spherical dendritic fields. Dorsal division neurons had flattened and polarized dendritic fields in the superficial dorsal nucleus (DS); dorsal nucleus (D) neurons were radiate and had spherical dendritic domains; suprageniculate nucleus (Sg) neurons were larger and their radiating processes distinguished them from the thin strip of sparsely branched, elongated posterior limitans nucleus (PL) neurons. In the medial division (M), several neuronal varieties were impregnated. The most conspicuous were the large multipolar radiate or magnocellular neurons. See text for further analysis. *Insets* here and in Figure 2 show the architectonic borders of the principal subdivisions. Golgi-Cox technique. This protocol and the scale apply to Figures 1 and 2. Planachromat, N.A. 0.65, ×500.

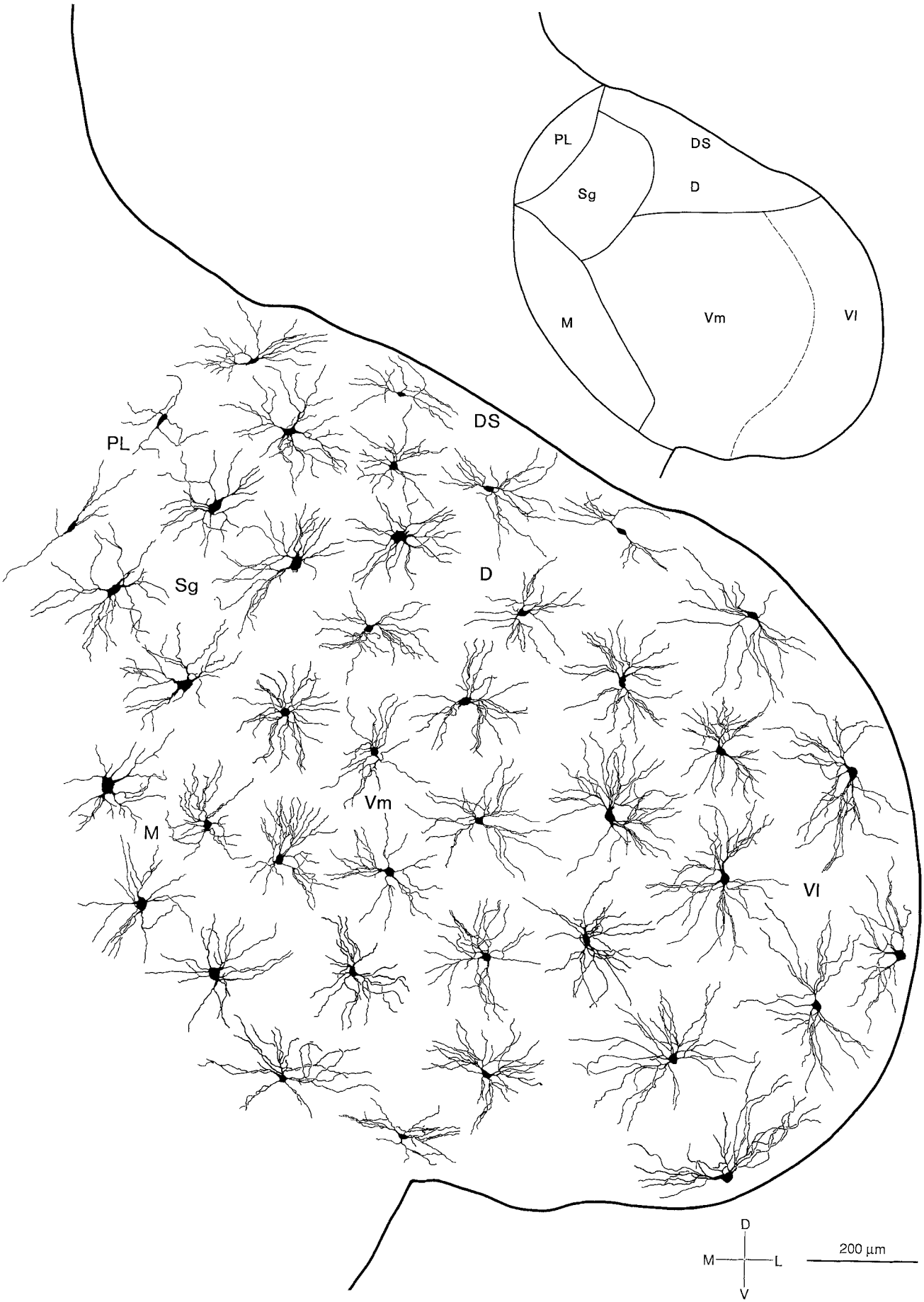

Figure 1 (See legend on previous page.)

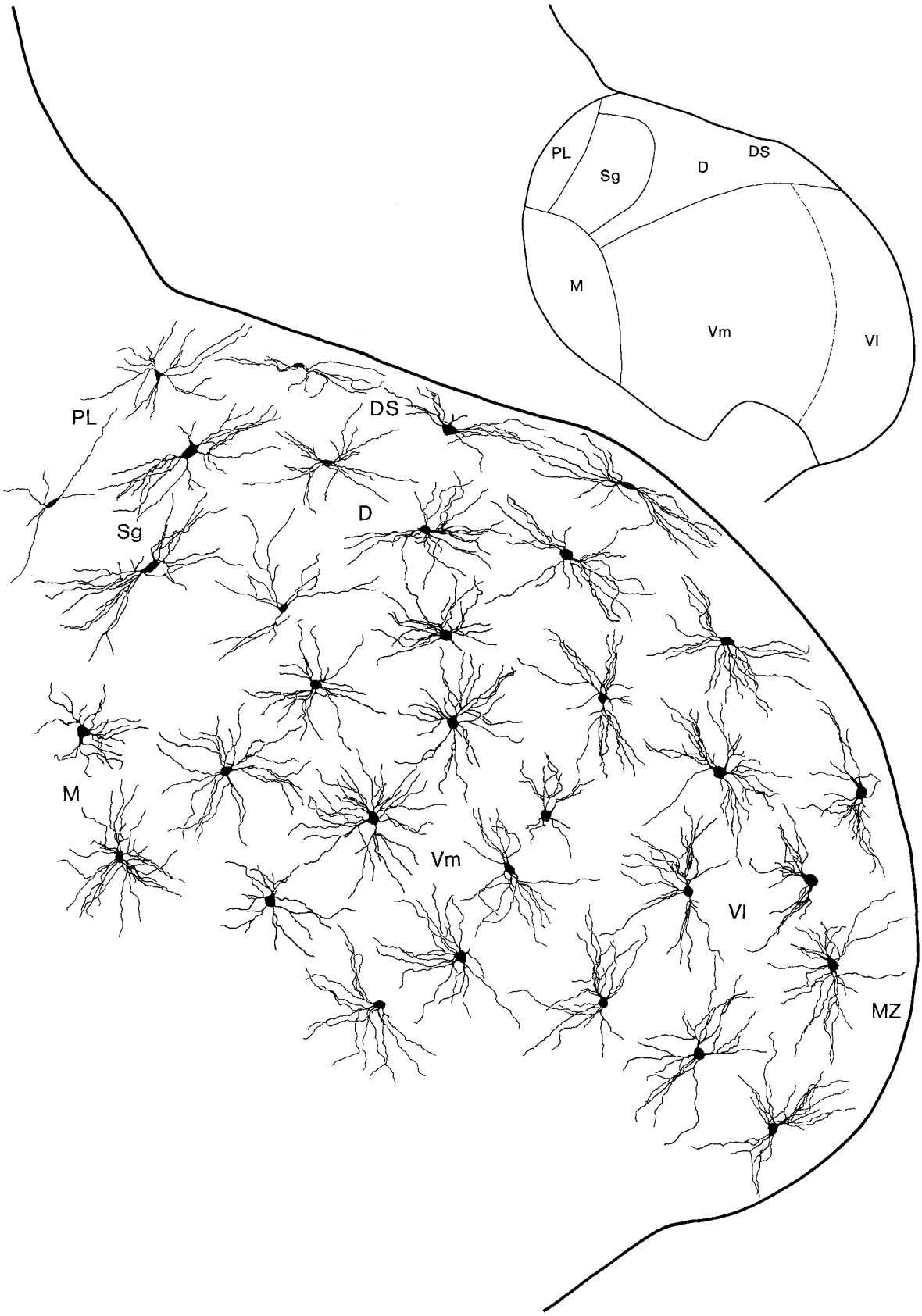

Fig. 2. More rostrally, many of the same features described above were present. The lateral (low frequency; see Olsen, 1986) part of the ventral nucleus (Vl) was comparatively small, and the medial part (Vm) far larger. These subdivisions formed much of the medial geniculate complex at this anteroposterior level. Each cartoon was composed by drawing the neurons individually, and then arranging them on a silhouette at the appropriate auditory thalamic level; this procedure minimized dendritic overlap. See Figure 1 for protocol.

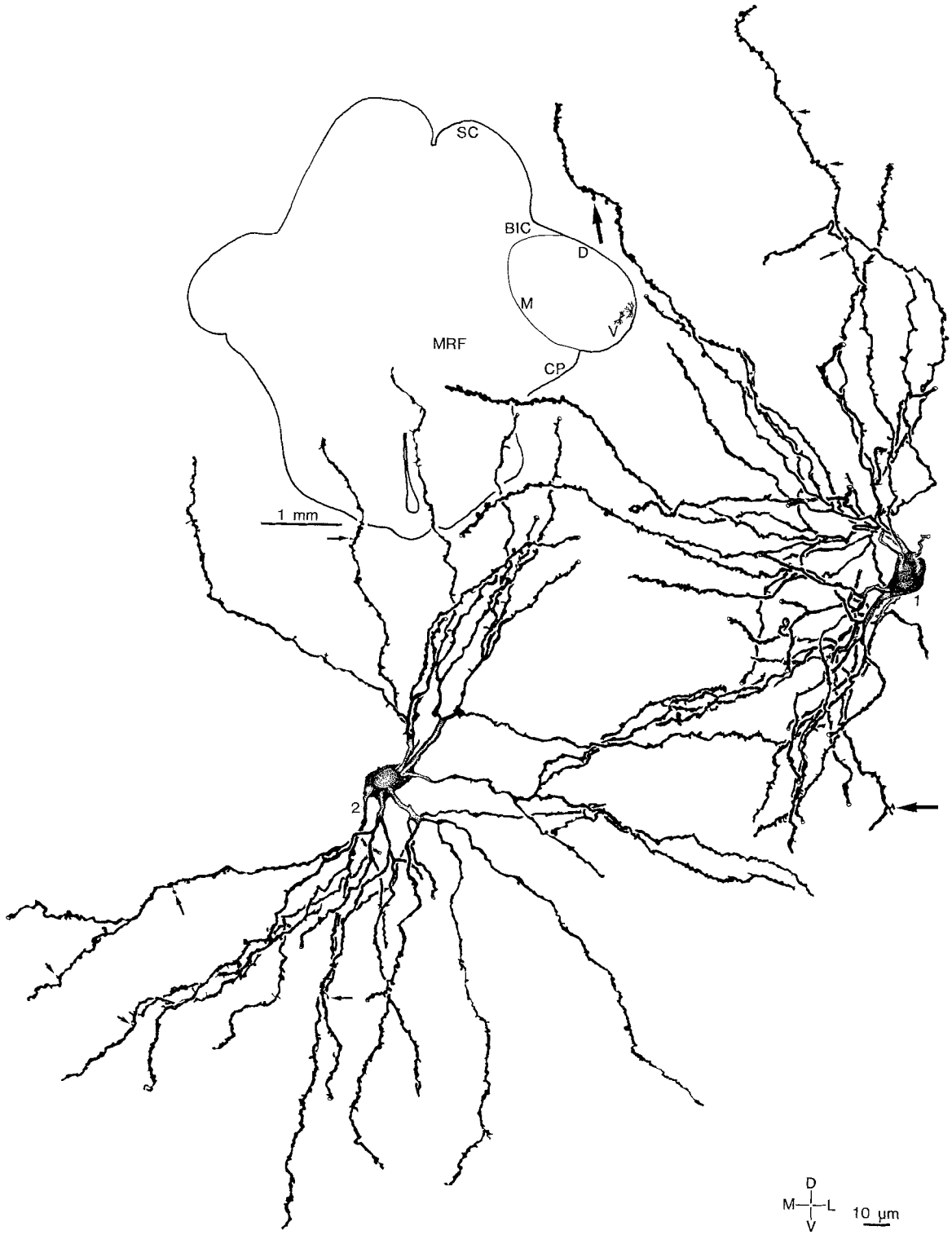

Fig. 3. Tufted neurons with bushy dendrites from the lateral part of the ventral division. Some bushy dendritic tufts (1) were largely confined to one fibrodendritic lamina (that is, within a 25–80-µm-wide strip immediately adjoining the lateral and medial borders of the neuron); others (2) projected much farther. Small arrows, short and fine dendritic appendages; medium-sized arrows, medium-sized spines; large arrows, long or very thick appendages. Protocol for Figures 3–13: planapochromat, N.A. 1.32, ×2,000. In this and succeeding figures, where a dendrite has been transected or has not been followed farther is indicated by an open circle at the tip. Neurons rarely, if ever, extended their dendrites beyond their nucleus of origin.

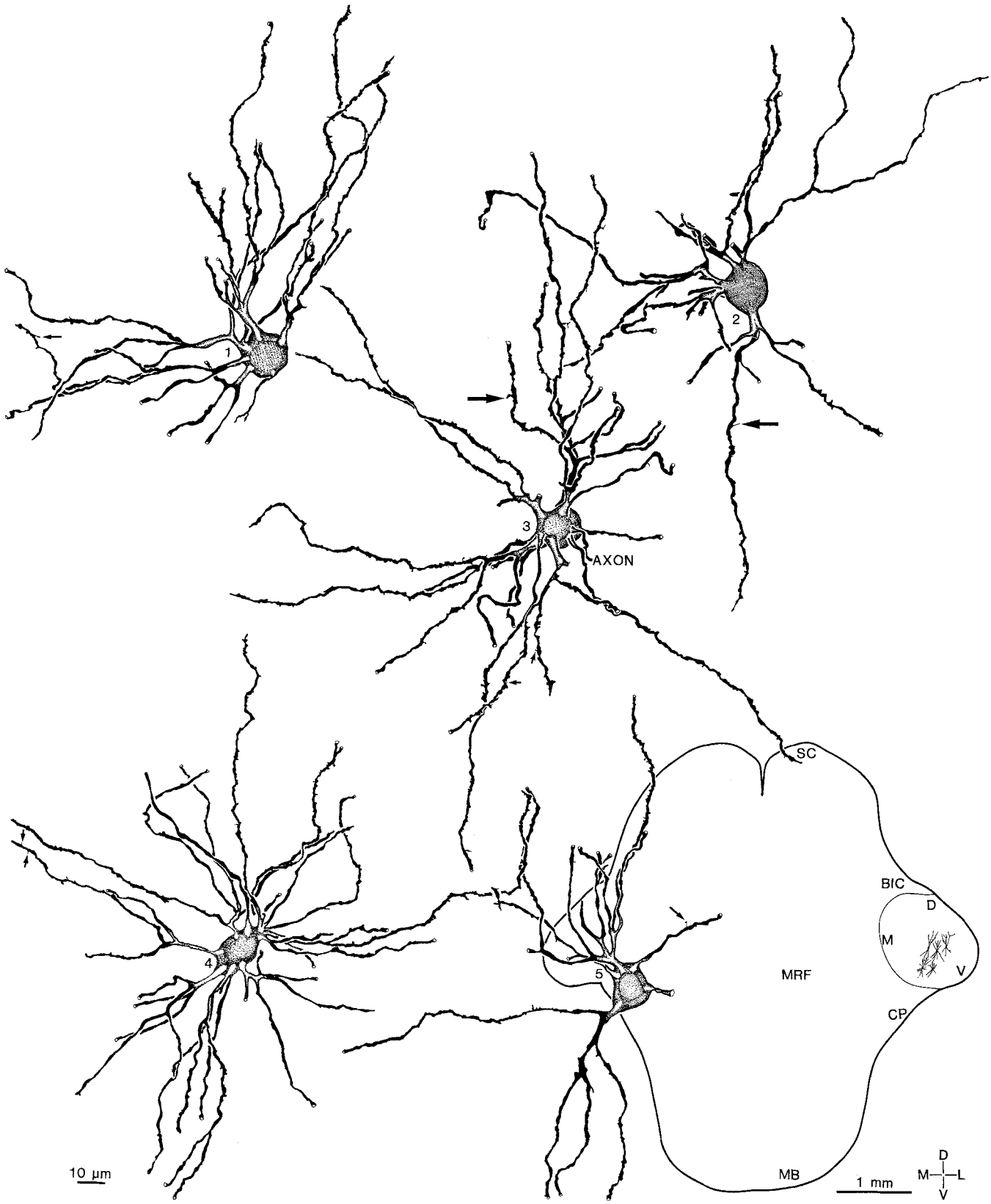

Fig. 4. Neurons from the medial part of the ventral division. Their primary dendrites were less tufted and their dendritic field more spherical than those of cells in the lateral part (see Fig. 3). 1, a tufted cell whose primary dendrites branch primarily in one lamina; 2, a less tufted cell with a thick, perhaps myelinated, axon; 3, a tufted cell with unusually long dorsomedial and ventrolateral dendritic trunks; 4, a tufted neuron with a highly developed, spherical dendritic field; 5, a tufted neuron with fewer than the usual number of appendages (compare with numbers 1 and 3). Arrows, varieties of dendritic appendages considered further in the text; see legend to Figure 3 for details. Where possible, the AXON is denoted.

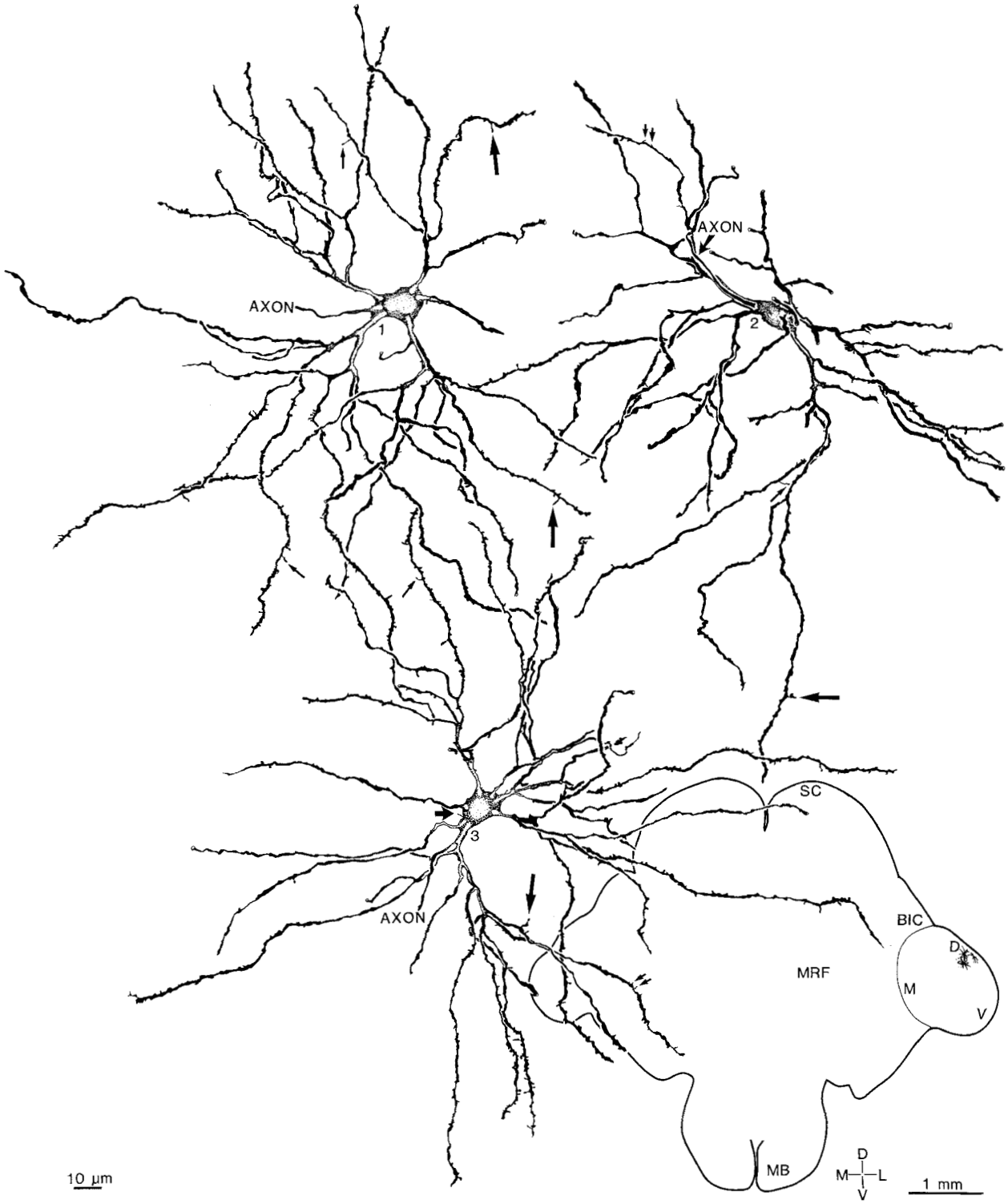

Fig. 5. Dorsal division neurons from the dorsal nucleus (1, 3) and the superficial dorsal nucleus (2). 1, radiate cell with weakly tufted dendritic segments and a moderate number of dendritic appendages; 2, more strongly tufted neuron near the extreme superficial margin of the dorsal nucleus, and with a dorsomedial-to-ventrolateral orientation; these neurons were responsible for the modest fibrodendritic lamination in this nucleus; 3, a radiate neuron with a spherical dendritic field; some dendrites had appendages, and there was a somatic spine (thick arrowhead). See Figure 3 legend for details.

ventral nucleus, save for a thin sheet of neuropil, the marginal zone, along the free surface. In Nissl preparations, ventral nucleus neurons had an average somatic area (99.6 μm^2) that was within 10 μm^2 of the values for the cells in the other medial geniculate subdivisions; a few smaller neurons occurred. There was no statistically significant difference in perikaryal size between the three divisions.

The tufted neuron (Fig. 1A,B:Vl; Fig. 3:1, 2) had an oval, elongated soma whose long axis ran approximately from dorsal-to-ventral within the lateral part of the ventral nucleus. These somata formed long, vertical rows, while neurons situated more medially were inclined up to 45°. Some five-to-six main dendrites about 2–3 μm thick arose from the somatic poles; far thinner branches issued occasionally from the lateral part of the perikaryon. Primary trunks formed four-to-six secondary dendrites within 25–50 μm, and then extended up to 200 μm before terminating, usually without branching further. Secondary tufts ran parallel to each other, contributing to a strongly polarized profile. Dendritic tufts were not limited to a single or simple orientation, however. Even on adjacent neurons, some tufts formed lateral-to-medial arrangements (Fig. 3:1), while others projected through the full, caudal-to-rostral extent of the 120-μm-thick section (Fig. 9:1, upper dendritic segment), or beyond it (Fig. 9:2, dorsalmost dendrites).

Tufted neuron dendritic fields characteristically formed rows; their long dendritic axis contributed to the fiber-rich laminae. Their dorsoventral axis exceeded the mediolateral one, a tendency that was most marked in the dorsal and lateral parts of the ventral division. In the medial part, equally well-developed dendritic tufts might arise from almost any part of the somatic surface (Fig. 2:Vm). Dendritic laminae were estimated to be about 80 μm wide in the lateral part of the ventral division (Fig. 1). This value varied for single dendritic tufts, particularly along the mediolateral axis. The complexity of such tufts was best seen at higher power, where they formed parallel, serpentine arrays (Fig. 8).

The dendritic appendages of these cells were varied. They included small, delicate spines about 0.5 μm long (Fig. 8: small arrows), thicker, medium-sized appendages up to 1 μm in length (Fig. 8: medium-sized arrows), and thick or thin, sometimes pedunculated, spines 3–4 μm long (Fig. 8: large arrows). Most appendages lay along the middle dendritic segments, forming small clusters of three-to-five spines. Some cells had more appendages (Fig. 8:2) than others (Fig. 8:3), and no neurons were devoid of appendages.

The axon arose from an apical dendrite (Fig. 8:1, 3) or the perikaryon (Fig. 8:2) and projected medially before the impregnation terminated abruptly. The absence of further staining was probably a consequence of myelination.

Stellate neurons (Fig. 12:1–3) represented a second, much less common neuronal population, and such cells were found both in the lateral and medial parts of the ventral division. Since most ventral division neurons were less than 100 μm^2 in average somatic area, uniform in size, and had a tufted branching pattern, a definitive identification of prospective Golgi type II cells was problematic, particularly since the axon was almost always unimpregnated in these adult specimens. Nevertheless, a few such neurons were identified based on their comparatively small somata, their sparse, thin primary dendrites, and their restricted dendritic fields.

Ventral nucleus, medial part. This subdivision was readily distinguished from adjoining nuclei on several grounds. The dorsal nucleus, which lies above it, had somewhat smaller neurons whose more radiating pattern of dendritic branching was conspicuous (Fig. 1). Suprageniculate nucleus cells, which lay dorsomedial to the medial nucleus, were much larger, with a radiate branching pattern and moderately developed dendritic tufts. Medial division neurons formed the medial border and had still larger somata and dendritic fields with a heterogeneous architecture.

The medial part of the ventral nucleus also contained neurons with a tufted pattern of bushy dendrites. Such cells were found throughout the medial geniculate complex, in both the caudal one-third (Fig. 1:Vm) and midway through the auditory thalamus (Fig. 2). These neurons were distinguished from cells in the lateral ventral nucleus in two ways. First, their dendritic fields were more spherical (Fig. 4:4) and their primary dendrites arose anywhere on the soma (Fig. 4:3); second, their somatic orientation was sometimes from dorsomedial-to-ventrolateral (Fig. 4:2). Thus, they had smaller dendritic fields and simpler arbors than those of the more lateral neurons (compare Figs. 3 and 4, and Figs. 4:1 and 2:1; and see Fig. 1). However, some of the medial cells were indistinguishable from those in the lateral part of the ventral nucleus (compare Figs. 4:1 and 8:1). The laminar fibrodendritic organization was most pronounced medially in sections through the caudal part of the auditory thalamus (Fig. 1) and less evident in the more rostral and dorsal territories in the medial subdivision (Fig. 2).

Some dendrites branched only once or twice before ending (Fig. 9:1, 3). Dendritic appendages like those in the lateral part of the ventral nucleus occurred, including small, fine ones or much longer and more complex types (Fig. 9: small, medium-sized, and large arrows, respectively), as well as an occasional somatic spine (Fig. 9:3, thick arrow).

Dorsal division

The dorsal division nuclei represented about 45% also of the volume of the medial geniculate body. If the rostral pole nucleus is included in the dorsal division, then the dorsal and ventral divisions are of equal size while the medial division is far smaller (see below, and Winer and Wenstrup, 1994 for further consideration). The dorsal division was present throughout the entire caudal-to-rostral extent of the auditory thalamus. It differed from the ventral division since it consisted of several nuclei, each with a different neuronal population.

Superficial dorsal nucleus. This nucleus formed a thin, crescent-shaped sheet about 500 μm wide above the dorsal nucleus and lateral to the much larger neurons in the suprageniculate nucleus (Fig. 2). It contained weakly tufted, small neurons distinct from the cells in the lateral part of the ventral nucleus. Their tufted dendritic branching pattern (Fig. 5:2) was much simpler, and their dendritic fields far smaller, than those of ventral division neurons with bushy dendritic arbors. Moreover, their long somatic axis was oriented from lateral-to-medial (Fig. 1:DS).

Primary dendrites arose at the elongated somatic poles and branched profusely within a few micrometers. Most dendrites had a tufted mode of branching (Fig. 10:2), although the bushes on other neurons were rarely as elaborate as those found on ventral division principal cells (compare Fig. 5:2 and Fig. 1:Vl). Dendritic fields ran from lateral-to-medial and were 100–500 μm long, and most dendrites ended in the nucleus of origin. As in the ventral division, varied dendritic appendages were present, and these were concentrated along the intermediate processes (Fig. 10:2).

Dorsal nucleus. The radiate neurons mingled among the superficial dorsal nucleus neurons whose dendritic tufts were less developed. They were distinct from the tufted cells with spherical dendritic fields found in the medial part of the ventral division (Figs. 1, 2:D). Radiate cell perikarya were oval or round (Fig. 5:1, 3) rather than elongated as in the superficial dorsal nucleus (Fig. 5:2). Six or more primary dendrites arose from any part of the soma to form one or two tufts or to bifurcate. As in the superficial dorsal nucleus, the tufts were simpler than those of ventral division cells (compare Figs. 5:1 and 3:1), and slightly smaller. While the tufted dendritic branching pattern was a cardinal feature of *Pteronotus* medial geniculate organization, dorsal division dendritic fields were far more spherical, and the branching pattern less strongly tufted, than in the ventral division.

Dorsal nucleus radiate cell dendrites were thinner and more delicate (Fig. 10:1) than those of tufted neurons in either the dorsal (Fig. 10:2) or the ventral (Fig. 8:1) divisions. Despite the complex branching of some dendrites, few overlapped or formed elaborate arrays. Appendages, though smaller, were no less elaborate (Fig. 10:1, arrows).

Other, much rarer dorsal nucleus neurons may not belong to this class. For example, cells with a more tufted branching pattern (Fig. 12:4) that was reminiscent of the superficial dorsal nucleus (Fig. 10:2) were impregnated, as were neurons with only three-to-four primary dendritic branches (Fig. 12:5) or cells with up to ten primary, radiating dendrites (Fig. 12:6). While their dendrites were relatively smooth for appreciable distances, some had a few appendages (Fig. 12:4–6, arrows). The limited axonal impregnation did not permit them to be classified definitively as local circuit neurons, although their comparative rarity and unique dendritic form (but not their somatic size) were consistent with this interpretation.

Suprageniculate nucleus. This nucleus formed much of the dorsal division, especially in the caudal half of the auditory thalamus. It was located between the posterior limitans nucleus medially and the dorsal and superficial dorsal nuclei laterally (Figs. 1, 2). It had large, sparsely branched neurons with comparatively simple dendritic fields.

The large radiate neuron was prevalent throughout the suprageniculate nucleus. With a perikaryon up to 240 μm^2 in area, it was bigger than all but a few medial division cells (see below). Up to six thick dendrites arose from the somatic poles (Fig. 6:3), or more widely and without preferential origin (Fig. 6:5). The branching pattern was tufted, but simpler and less polarized (Fig. 6:4) than the arrangement in the ventral (Fig. 3:2) or medial (Fig. 7:1) divisions. Despite their tufted arbors, the dendritic field was more-or-less spherical and radiate. The dendrites were comparatively short for such a large cell (for example, compare Fig. 6:2, from the posterior limitans nucleus, with the suprageniculate cells in Fig. 6:3–5). Appendages varied in number, ranging from comparatively sparse (Fig. 6:4) to numerous (Fig. 6:3), and they were as diverse (if not as common) as those in the ventral (Fig. 3:1, arrows) and medial (Fig. 7:6, arrows) divisions.

Smaller stellate neurons had thin, sparse dendrites (Fig. 6:6). Their perikaryon was almost as large as that of the large radiate neurons (Fig. 6:3–5), but their dendritic fields were less than one-fourth the size. They had various dendritic appendages and some surprisingly long, pedunculated spines (Fig. 6:6, large arrows).

Posterior limitans nucleus. Lying beneath the brachium of the inferior colliculus (see Winer, 1992) and above the suprageniculate nucleus, these elongated neurons formed a thin wedge that ended midway through the length of the auditory thalamus (Figs. 1, 2). The long nuclear axis ran from dorsolateral-to-ventromedial, a pattern recapitulated by the dendritic trajectory of the principal neurons (Fig. 6:1, 2).

Elongated neurons were the main cell type. Each almond-shaped soma had three-to-five primary dendrites that arose at the poles. These trunks divided once or twice, usually parallel to the long axis, and extended through the nucleus, with little further branching. Primary dendritic segments were smooth, while the distal surfaces received various appendages; many were short and pedunculated, and others were long and filiform.

Medial division

The smallest of the three primary medial geniculate divisions represented only about 10% of the volume of the auditory thalamus. It was situated between the medial face of the ventral nucleus and, more medially, various nonauditory midbrain and diencephalic nuclei (Winer and Wenstrup, 1994). Despite its modest size, the medial division nevertheless contained the most diverse neuronal population of any auditory thalamic subdivision.

The magnocellular neurons were the largest cells (Fig. 7:6) in the medial geniculate body. Three or more thick primary dendrites arose from a round soma and, considering the size of the cell, projected for a comparatively short distance within the medial division. The dendrites branched sparsely and simply, and radiated to form a spherical dendritic field. Dendritic tufts were rare. Their surface had an irregular, varicose texture, with few appendages (Fig. 11:1). Most spines were short and pedunculated (Fig. 11:6, medium-sized arrows).

Bushy neurons were smaller and had many more primary dendrites (Fig. 7:1, 4, 7). With a soma about half the size of

Fig. 6. Suprageniculate (3–6) and posterior limitans nucleus neurons (1, 2). 1, sparsely branched cells had slender dendrites confined to a narrow strip forming the borders of the posterior limitans nucleus; 2, neuron with heterogeneous dendritic appendages; 3–5, suprageniculate neurons were large and had spherical dendritic fields, some poorly tufted dendrites, and primarily short and medium-sized appendages (arrows); 6, small stellate neuron with fine dendrites and a few long dendritic spines, some of which were pedunculated.

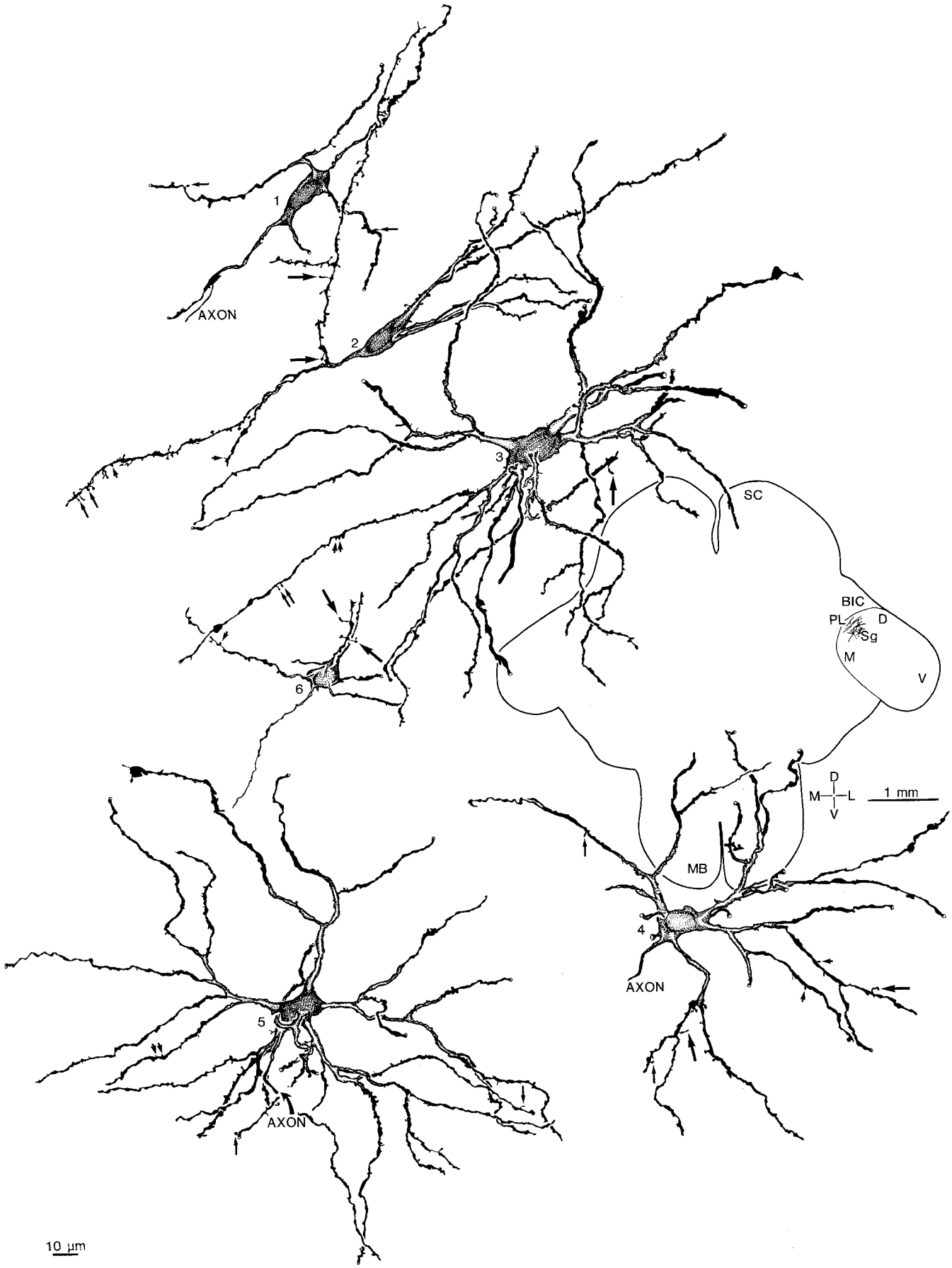

Figure 6

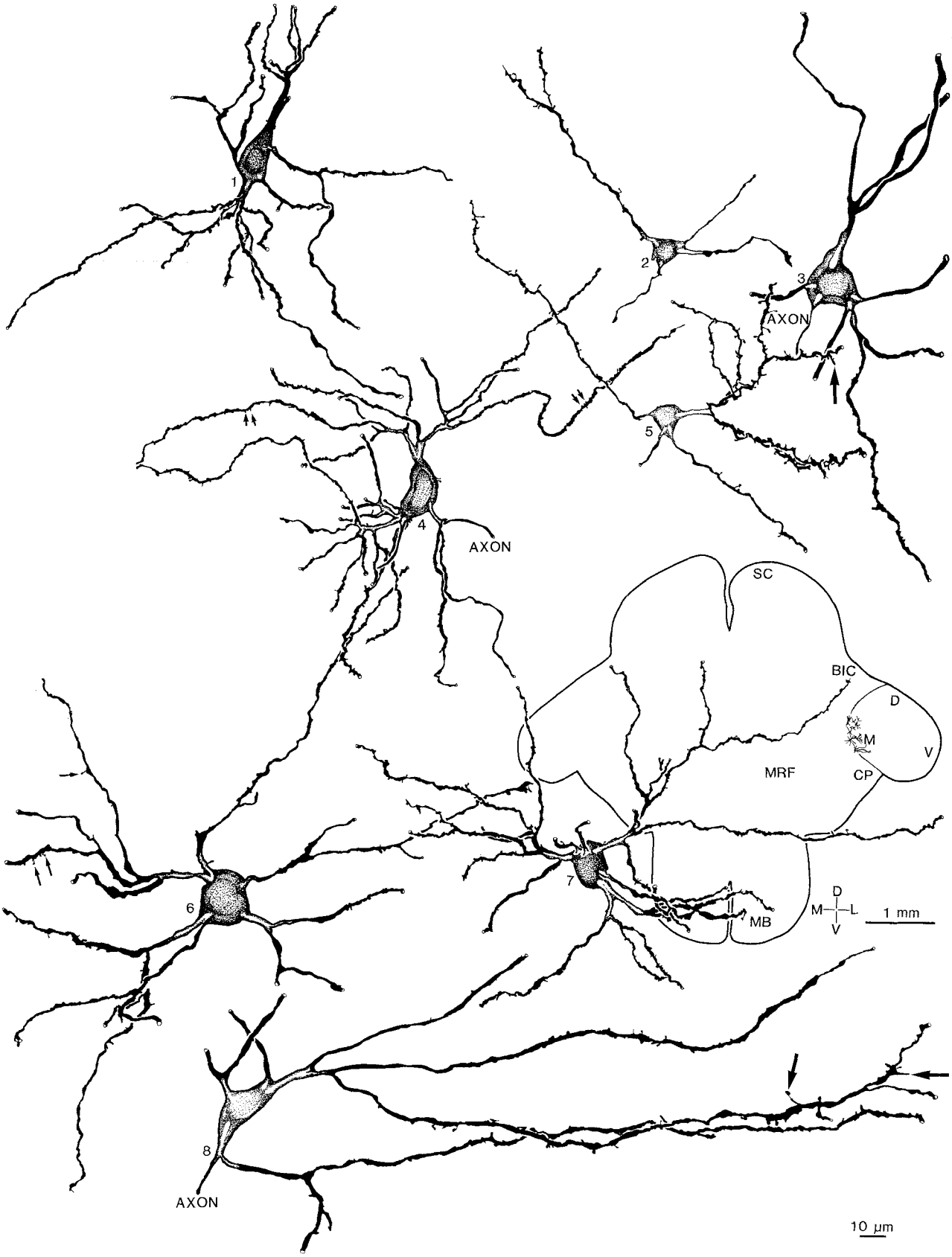

Fig. 7. Medial division neurons (1–8). 1, 4, 7, bushy neurons with medium-sized somata and dendritic tufts that had varied orientations; 2, 5, small stellate neurons with a few slender dendrites, and rare, much larger, tufted arbors (5); 3, a medium-sized multipolar cell with thick, smooth dendrites; 6, a magnocellular neuron with large, sparsely branched dendrites and an irregularly spherical dendritic field; 8, an elongated neuron with dendritic arbors oriented from medial-to-lateral, and a moderate number of appendages, some pedunculated or with other complex shapes.

that of the magnocellular neuron, they also had a different neuronal architecture. Their four-to-five principal dendrites arose at intervals, and then branched to form tufts. The orientation of the tufts was from dorsal-to-ventral (Fig. 7:1, 4) or medial-to-lateral (Fig. 7:7), and the dendritic field was irregular and radiating since many of the dendritic extremities were transected as they projected remotely. Appendages were mainly short and plentiful on the intermediate dendrites; a few somatic spines occurred (Fig. 7:4).

The dendritic form of the disc-shaped neurons (Fig. 11: 3–5) contrasted sharply with that of the bushy neurons (Fig. 7:1, 4, 7). Most of their dendritic field lay within the confines of the 120-μm-thick sections, except for their tips. The oval somata had eight-to-ten primary dendrites, most about 2 μm in diameter (Fig. 11:3–5). These arose like spokes from a wheel (Fig. 11:4) or somewhat less regularly (Fig. 11:5). The processes radiated equally in the same, disc-like plane, so that branches running far rostrally or caudally were rare. Most dendrites had simple branching patterns that overlapped or converged to impart a tufted appearance on some arbors (Fig. 11:3). The dendrites had a rough surface but comparatively few appendages. Most spines were short and simple, but some were more complex (Fig. 11:4, large arrows).

Medium-sized multipolar neurons resembled the disc-shaped neurons in somatic size, and had a much simpler dendritic branching pattern. Their three-to-five thick main dendrites were widely spaced and branched as weak tufts or had a simpler, dichotomous design (Fig. 7:3). These cells were as big as the large radiate suprageniculate neurons (Fig. 10:3), and only a little smaller than the magnocellular neurons (Fig. 11:6).

Elongated neurons had an unusual dendritic orientation, with the mediolateral axis (Fig. 7:8) up to 200 μm wide. It was one of the few cells with dendrites extending outside the nucleus of origin. They had a simple branching pattern, thick processes, and a modest number of appendages, including long, smooth, or pedunculated spines.

Small stellate neurons complete the survey of medial division cell types. Their soma was 10 μm or less in diameter, and three-to-five dendrites arose irregularly and radiated in a weakly stellate configuration (Fig. 7:2, 5; Fig. 12:7, arrows). The appendages included small, fine spines less than 1 μm long, medium-sized ones about 1–2 μm long, and others longer than 2 μm, some with an elaborate shape.

Rostral pole nucleus

The architectonic affiliations of the rostral pole nucleus, which was prominent in the most anterior one-third of the medial geniculate complex, were uncertain. These neurons appeared largely continuous with neurons that, more caudally, were identified as belonging to the ventral division. However, the cytoarchitecture of this region differed from that of the ventral division (see Winer and Wenstrup, 1994 for a more complete discussion). This nucleus had an entirely different pattern of midbrain input that aligned it more closely with the dorsal division (Wenstrup et al., 1994).

Very few neurons were impregnated in the rostralmost one-half of the medial geniculate body, probably as a consequence of the robust myelination in this region and the adult status of the specimens available for study. Consequently, no conclusion can be made about the neuronal architecture.

DISCUSSION

This study confirms that the principal medial geniculate body subdivisions recognized in other mammals exist in the mustached bat. It also demonstrates interspecific differences in neuronal form, in the proportion of different neuronal types, and in the fibrodendritic laminar architecture. The main points relate to the reliability of the Golgi method as a structural tool for defining medial geniculate subdivisions; the comparative analysis of neuronal structure; the congruence of the proposed architectonic plan with findings from other methods; and the meaning of these results for deriving principles of auditory thalamic organization.

Methodological issues

The subdivisions described here depend on local variations in dendritic form as revealed by the Golgi method. While dendritic architecture alone may not distinguish every subdivision, the present data can be compared readily with nuclei seen in other species. This scheme agrees with the independent findings from several different methods.

Confidence in the reliability of the Golgi method comes from studies that have compared the types of neurons and the architectonic boundaries with those defined by other methods, for example, Nissl counterstaining of Golgi impregnations (Pasternak and Woolsey, 1975; Shimono and Tsuji, 1987). Each major class of neurons recognized using one method were also identified with others. While the auditory thalamus was not part of these studies, there is no reason to believe that it would be different. Such correlations are evidently much less secure when features other than the somatodendritic form of the neuron are considered. The type or distribution of afferent synapses, or the form of the axon are not definitive, since a single type of neuron may include a wide range of structural variability (Peters and Harriman, 1988). While dendritic architecture alone may not identify functionally distinct neuronal populations, it was adequate for the types of neuron considered here, and it reliably defined even small thalamic subdivisions, such as the posterior limitans nucleus, whose short axis is less than 100 μm wide.

The conclusions from the Golgi studies support the subdivisions drawn by other, independent methods. These include the nuclei recognized in Nissl preparations, the neuropil arrangements revealed in toluidine blue-stained material (Winer and Wenstrup, 1994), the distribution of GABA-immunoreactive elements (Winer et al., 1992), and the connectional pattern of inferior colliculus axons afferent to the medial geniculate complex (Frisina et al., 1989; Wenstrup et al., 1994).

Comparative anatomy of auditory thalamic subdivisions

Rodents. In rats, a pattern of medial geniculate organization exists that resembles that in the mustached bat, with significant variations in nuclear size, neuronal orientation, and the proportion of the auditory thalamus devoted to one

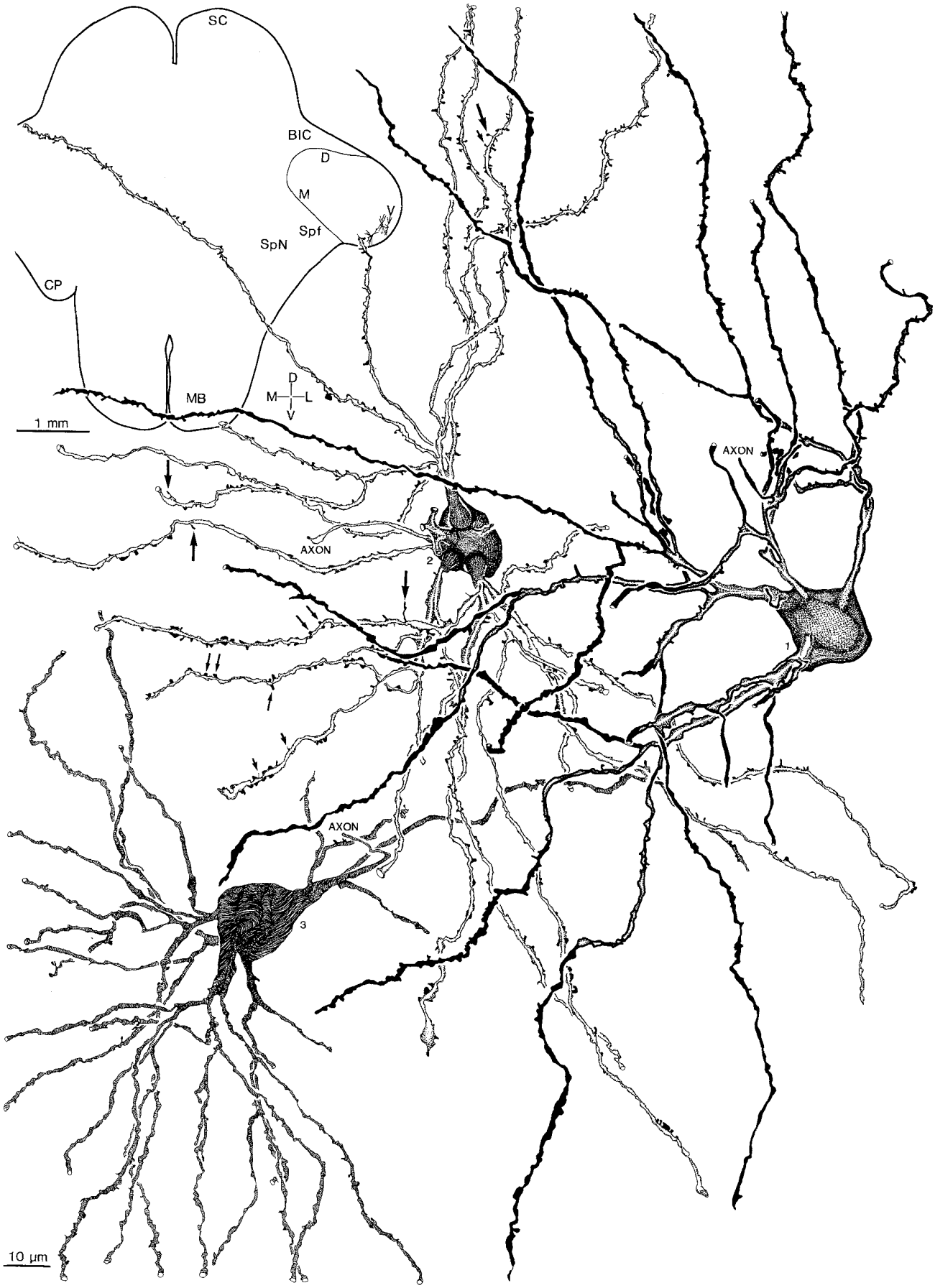

Figure 8

subdivision or another. For example, tufted principal neurons in the rat ventral division never display the extreme bushiness characteristic of the presumptively corresponding neurons in the mustached bat (compare Fig. 13A and B). However, the relative simplicity in dendritic branching among rat bushy tufted cells reveals a far clearer pattern of fibrodendritic laminae than in the bat, where the tufted arbors are so complex that they obscure the limits of single laminae among overlapping dendritic fields (compare Fig. 1 in the present account with Fig. 3 in Winer and Larue, 1987). In general, mustached bat neurons are more strongly tufted than cells in other species. In other subdivisions in the rat, comparable types of cells are readily identified, such as the magnocellular neurons in the medial division, and the radiate cells with spherical dendritic fields in the dorsal division, to name just two.

A second distinction between the rat and mustached bat is the relative proportion of the dorsal and medial divisions in the rat, while in the bat the ventral and dorsal divisions increase at the expense of the medial division. The functional significance of these differences are obscure. They may reflect species-specific functional adaptations related to behavioral plasticity (reviewed in Winer, 1992) or the emergence in the bat dorsal division of combination sensitive neurons (see Olsen, 1986).

It has proved impossible, so far, to identify intrinsic neurons with confidence in the auditory thalamus of either the rat or the bat. While such cells may be refractory to Golgi impregnation, their comparative rarity, in both Nissl and in semithin, plastic-embedded material (Winer and Wenstrup, 1994), suggests that somatic size alone is not adequate, as it often may be in the cat medial geniculate body (Winer, 1984a; Huchton et al., 1991) and in the primate visual thalamus (Hendrickson et al., 1983). GAD- or GABA-immunoreactive rat and bat medial geniculate neurons are likewise sparse, supporting the view that few local circuit neurons occur (Winer and Larue, 1988; Winer et al., 1992). Several independent lines of evidence suggest that these neurons are rather rare in the mustached bat's auditory thalamus. This raises the intriguing question of what the role of so few neurons might be, and how it would be expressed synaptically. The issue of whether Golgi type II cells have a perfect correspondence with GABA-immunostained neurons remains open. This case is in sharp contrast to the cat inferior colliculus, in which both small and large neurons have extensive local axonal collateral systems (Oliver et al., 1991), and in which the biggest cells are GABAergic (Oliver et al., 1994). Many large GABAergic cells are present in the mustached bat inferior colliculus and auditory cortex (Winer et al., 1992, 1994). While no quantitative estimates exist that might be compared directly with the proportions of such neurons in the cat, in both the colliculus and the cortex they are far more numerous than in the auditory thalamus (J.A. Winer, L.M. Bui, J.H. Hong, and D.T. Larue, unpublished observations). The small number in the medial geniculate body does not appear to reflect any compensatory numerical increase in the midbrain or cortex, nor is any progressive decrease along a caudal-to-rostral sequence evident. A similar principle applies in the cat primary auditory cortex, where a wide range of nonpyramidal cells—including the largest and the smallest—are GABAergic (Prieto et al., 1994a,b). Perhaps the small GABAergic neuron with a locally projecting axon is a hallmark of the auditory thalamus.

Marsupials. Subdivisions of the opossum auditory thalamus correspond closely to those in the mustached bat. The overall configuration of the caudal two-thirds of the medial geniculate body is surprisingly similar (Winer, 1992, his Fig. 6.5B,C), despite some differences in neuronal architecture. The ventral division in both species is relatively large and well developed, with clear fibrodendritic laminae predominating laterally, while the *pars ovoidea* neurons have predominantly spherical dendritic fields and a bushy branching pattern, which is reminiscent of that of cells in the medial part of the mustached bat's ventral division (compare Figs. 4:3, 4 and 13C). The dorsal division is reduced compared with the analogous region in the cat (Winer and Morest, 1984), while the posterior limitans nucleus represents only a thin strip of sparsely branched cells next to the large, radiating suprageniculate principal neurons (Morest and Winer, 1986, Fig. 3). By the same token, the opossum interlaminar nuclei are prominent (Winer et al., 1988), much as they are in the mustached bat (Winer and Wenstrup, 1994).

The modest development of the interlaminar neuropil in the ventral division is similar in the two species. Perhaps the opossum has only a few Golgi type II cells, as suggested by their rarity both in Golgi preparations (see Morest and Winer, 1986, Fig. 5) and in immunocytochemical studies (Penny et al., 1984). Such cells are predominantly small, with a flask-like somatic shape and sparse cytoplasm. This finding is consistent with the rarity of mustached bat auditory thalamic GAD- or GABA-immunoreactive neurons (Winer et al., 1992) and corresponds as well to the few examples of well-impregnated Golgi type II cells (present results).

Carnivores. There are many differences between the cat and mustached bat medial geniculate complex: in the cat, the dorsal and medial divisions are relatively much larger, the dorsal division forms much of the caudal extremity of the auditory thalamus, the number of local circuit neurons is far larger, and there is a concomitant relative expansion of the neuropil. The comparatively large size of individual nuclei and local difference in neuronal architecture, thalamocortical connectivity, and neurochemistry permit further subdivisions to be recognized readily (Winer, 1984b, 1985, 1991, 1992).

Parallels between the cat and bat include the highly developed tufted neurons, especially in the lateral part of the ventral nucleus, where in the cat these cells closely resemble their bat counterparts. In the cat *pars ovoidea*, which may correspond to the medial part of the bat ventral nucleus, dendritic fields overlap less and have narrower fibrodendritic laminae (Fig. 13D; Morest, 1965), while in the bat the analogous neurons have a less polarized arrangement. Such patterns might reflect differences in physiological organization. While it may be tempting to correlate

Fig. 8. Neurons from the lateral part of the ventral division, showing their dendritic arbors and their appendages (arrows) at higher resolution. These ranged from very slender or slightly thicker spines about 0.5 μm long (small arrows), to 1–2-μm-long appendages (medium-sized arrows), a few of which are pedunculated, to spines as long as 5 μm (large arrows). 1–3, tufted neurons showed the characteristic, complex dendritic branching arrangements (see also Fig. 3).

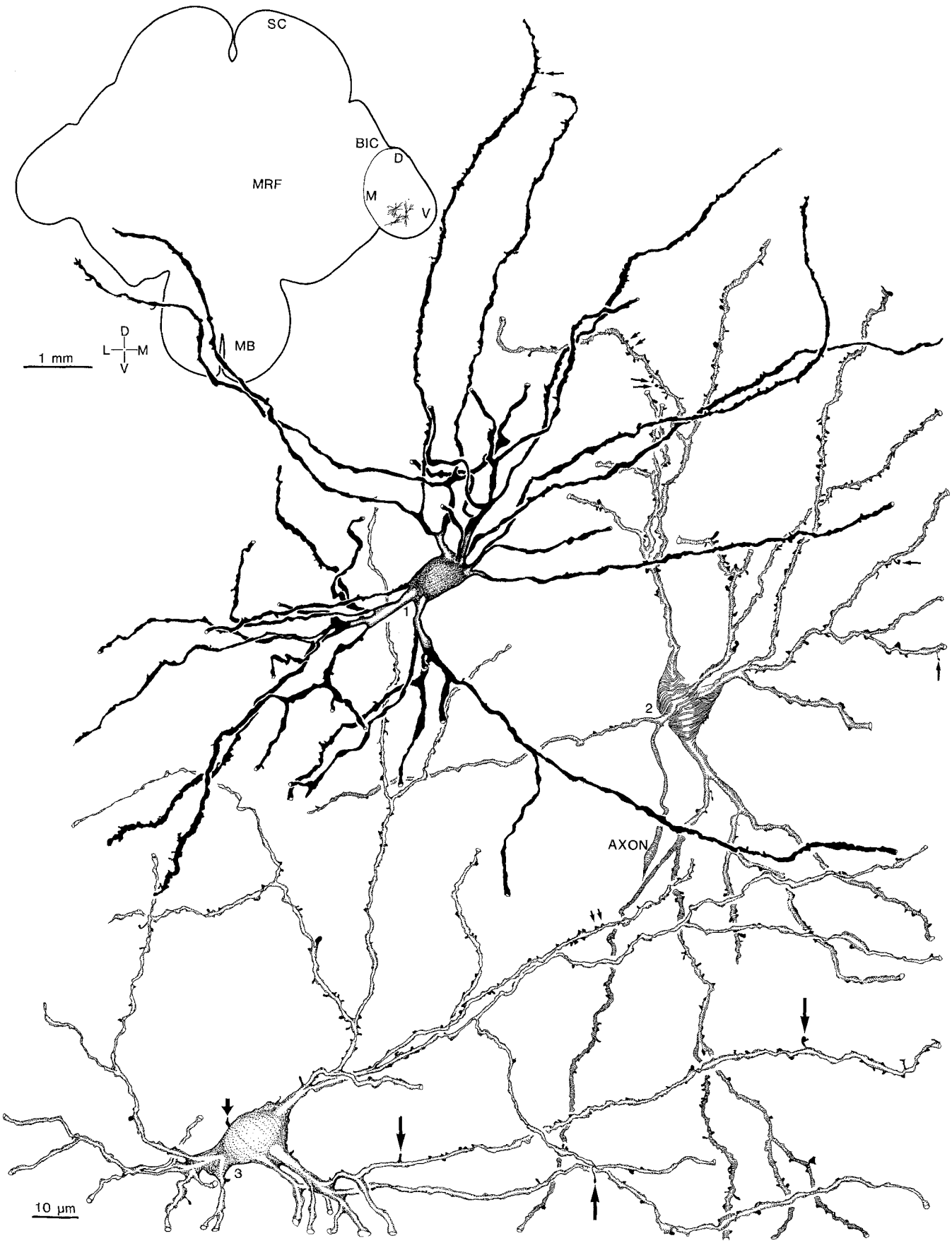

Fig. 9. Neurons in the medial part of the ventral division had tufted dendrites and large, irregularly shaped dendritic fields. 1, a tufted cell with well-developed dendritic bushes, some with lateral dendrites up to 200 μm long; 2, a neuron with more vertically arranged dendritic arbors and moderate numbers of spines; 3, a tufted cell with a somatic spine (thick arrow), a more medial-to-lateral orientation, and long dendrites (see also Fig. 4).

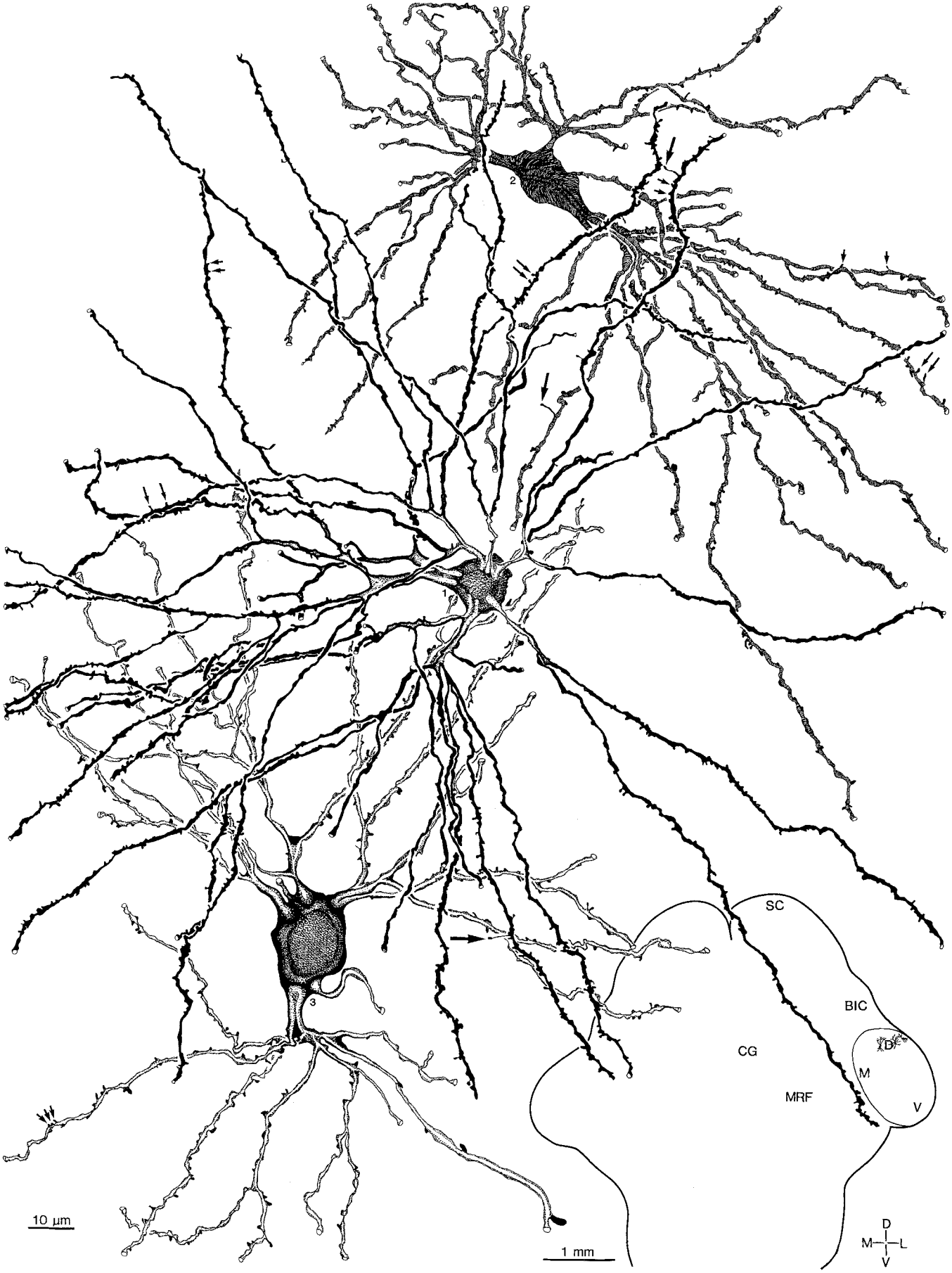

Figure 10 (See legend on following page.)

wider dendritic domains with broader primary afferent tuning, in the visual cortex at least there is no apparent relation between this structural feature and physiological attributes (Hübener and Bolz, 1992). In contrast to the ventral division, many cat dorsal division principal radiate cells have a rather simple stellate branching pattern, although tufted neurons do occur (Winer and Morest, 1984). In the bat, the tufted arrangement is even more obvious, though less prominent than in the ventral division.

Primates. In the human auditory thalamus the three principal divisions identified in bats, opossums, cats, and other species are also recognized. The human ventral division is reduced relative to the dorsal and medial divisions, particularly the former. Many of the analogous types of cells have been impregnated, including tufted cells with bushy arbors in the ventral division (Fig. 13E), large neurons with radiating dendritic fields in the dorsal division, and the magnocellular medial division neurons, among others (Winer, 1984a).

Comparing marsupial with carnivore with primate reveals a fundamental pattern of continuity in neuronal architecture in any given nucleus: the chief types of neurons are identified readily from species to species, with some exceptions. Many features of the neuronal architecture of the mustached bat's medial geniculate body have close affinities with those in other mammals. Even those adaptations that may be unique to the mustached bat—such as combination sensitivity—apparently use much of the same neuronal machinery. Many aspects of cellular architecture are literally indistinguishable in marsupials or rodents, such as the well-developed lateral arbors of bushy cells in the ventral division. In carnivores and humans the corresponding neurons have much narrower dendritic domains. Some bat neurons, especially those in the lateral (low frequency; Olsen, 1986) part of the ventral division, have dendritic arbors that resemble closely the fibrodendritic laminae present in cats.

Species-specific patterns of auditory thalamic organization

These parallels in comparative auditory thalamic organization do not obscure significant departures from a simple or singularly mammalian arrangement. The most salient species differences are the relative expansion or reduction of one thalamic subdivision compared with another, variability in the number and variety of Golgi type II neurons and the ensuing consequences for ultrastructural arrangements, and the relative homogeneity of perikaryal size among small mammals (see Winer, 1984a, Fig. 6). While other parallels undoubtedly exist, it is premature to make further conclusions without more data on connections, physiological attributes, and chemical architecture.

Some species differences may reflect the relative proportions of neuropil or cell density. Others, such as the number of presumptive synaptic nests (discussed in Winer and Larue, 1988) or the proportion of Golgi type II cells (Winer et al., 1992), may be involved in intrinsic processing and local thalamic circuitry. The physiological significance of the number of synaptic nests in the analysis of acoustic signals is unknown. The relative absence of GABAergic local circuit neurons in *Pteronotus* suggests that these or other ultrastructural specializations associated with them might also be rare (Winer et al., 1992). In the horseshoe bat (*Rhinolophus rouxi*) these neurons are far more numerous (Vater et al., 1992), and, by inference, the relative number of synaptic nests might be larger. If so, then the thalamic synaptic sequence may differ among bats, further complicating any simplistic assumptions about comparative auditory thalamic organization. Still other attributes, such as a larger number of cell types, may also reflect species-characteristic patterns of organization.

Other local differences are of unknown significance. In humans, the fibrodendritic laminae run from medial to lateral in the transverse plane, while in the mustached bat they have a more vertical arrangement, and the human *pars ovoidea* is relatively much smaller than the lateral sector of the ventral division, which is consistent with a massively expanded adaptation for low-frequency hearing.

Neuropil architecture also distinguishes the microchiropteran and human auditory thalamus. In bats the neuronal density is much higher, and in humans the neuropil contains small islands of neurons separated by relatively vast expanses of axons, dendrites, and glial processes (compare Winer and Wenstrup, 1994, their Fig. 1, with Winer, 1984a, his Figs. 3, 4). This finding suggests differences in intrageniculate circuitry.

There are a few other species differences in auditory thalamic organization. The emergence of combination sensitive neurons in the mustached bat may relate to physiologically specialized auditory thalamic subregions, such as the rostral pole nucleus, for which there seems to be no precise feline equivalent (Imig and Morel, 1985a,b). Two connectional differences further distinguish the mustached bat. The first is the apparent absence of any significant contralateral tectothalamic pathway (Zook, 1979; Wenstrup et al., 1994), even after very large inferior colliculus tracer injections (Paydar et al., 1993). In the cat, this projection is prominent (Andersen et al., 1980). A small descending input from the medial geniculate body and perigeniculate regions to the inferior colliculus occurs in the cat and rat but not in the mustached bat (Paydar et al., 1993). The mustached bat anterior pretectum receives a substantial projection from the inferior colliculus (Wenstrup et al., 1994) that apparently is absent in the cat (Andersen et al., 1980). The functional significance of these connectional patterns is not clear, and it emphasizes that species differences are not limited to thalamic microcircuitry, neuropil organization, or the relative proportions of the thalamic auditory nuclei alone. The essential continuity in organiza-

Fig. 10. (See overleaf.) Dorsal division neurons. 1, a radiate neuron from the dorsal nucleus with a spherical dendritic field; the appendages were concentrated on the intermediate dendritic segments; 2, a bushy neuron of the superficial dorsal nucleus with tufted dendritic branches that arose from the poles of an elongated soma (see also Fig. 5:2); 3, a suprageniculate nucleus large radiate neuron with a spherical dendritic field of modest size (see also Fig. 6:3–5).

Fig. 11. Medial division neurons had heterogeneous dendritic morphologies. 1, 2, 6, magnocellular neurons had large somata, and thick, sparsely branched, and comparatively smooth dendrites (see also Fig. 7:6); 3–5, disc-shaped neurons had richly divided, flattened dendritic fields whose branches lay within the section, except at their tips. Various appendages occurred, some up to 2–3 μm long.

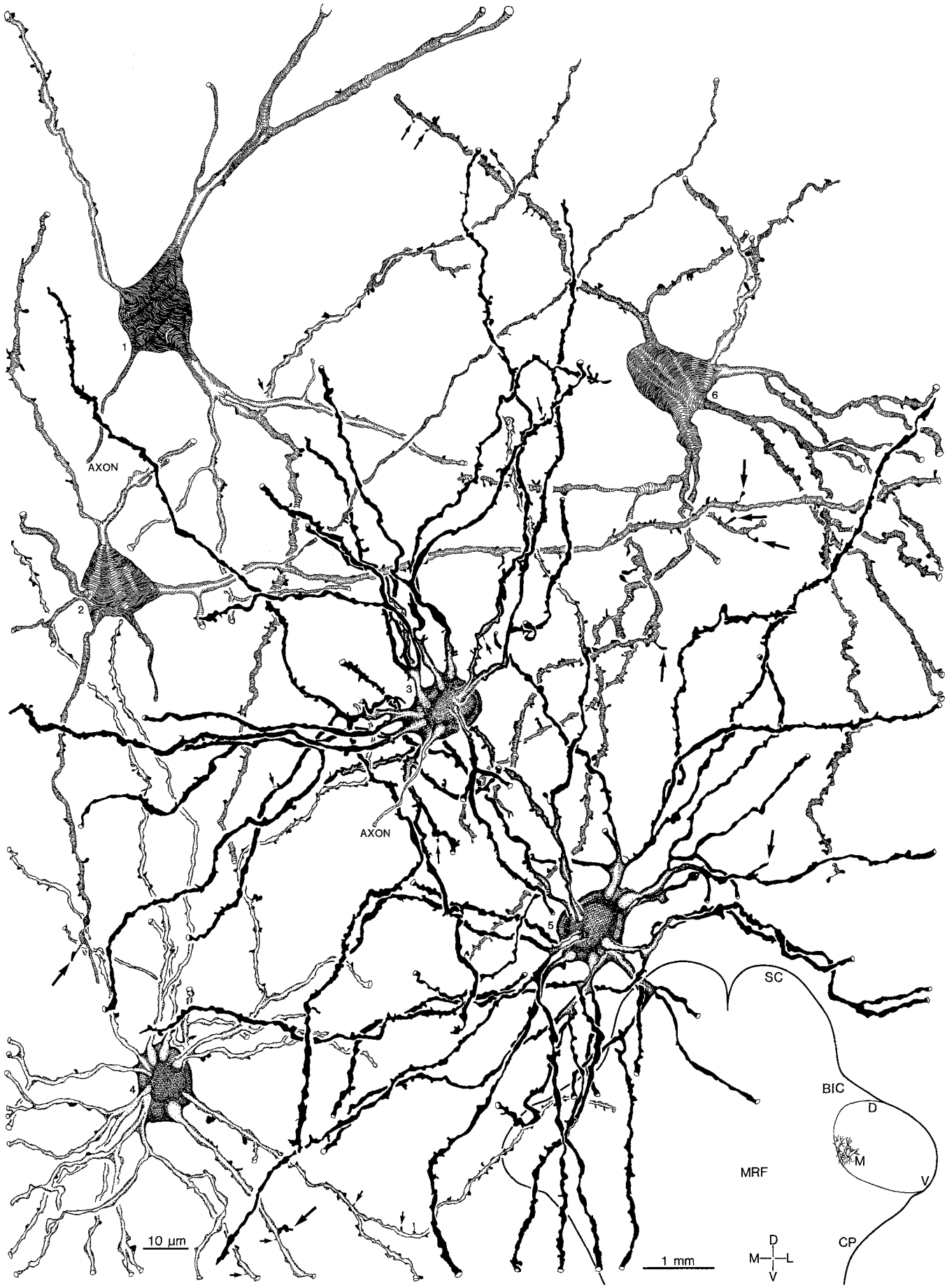

Figure 11

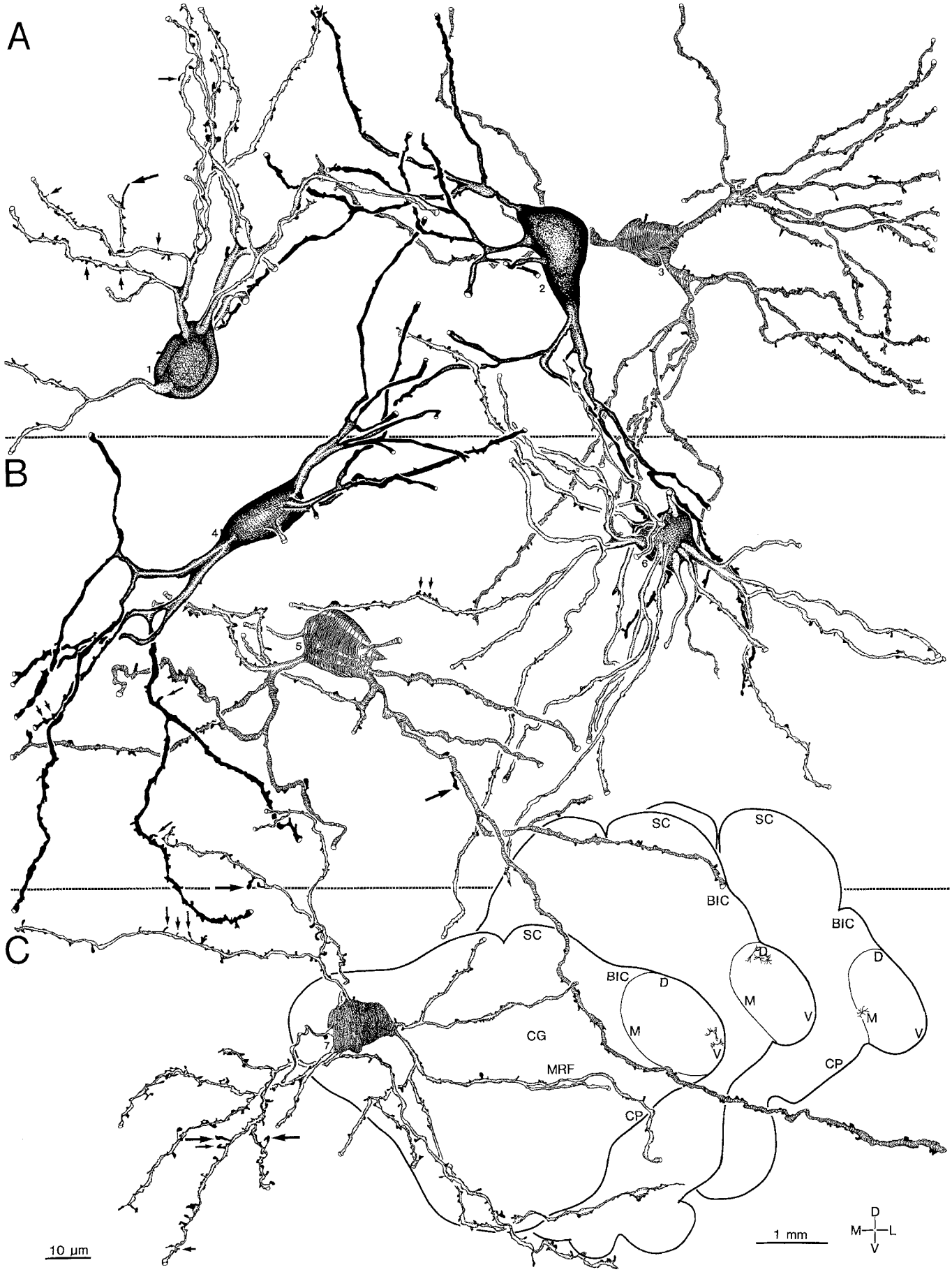
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Figure 12

tion across species occurs in parallel with species specific adaptations.

Correlation with other methods for subdividing the auditory thalamus

Cytoarchitectonic approaches. Other, independent methods validate many of the present conclusions. The architectonic boundaries drawn from Nissl material support this parcellation scheme, as do the local patterns of neuropil arrangement in plastic-embedded material (Winer and Wenstrup, 1994). In Nissl preparations, the long axis of ventral division neurons runs dorsoventrally, while dorsal division cells have oval somata ranging from medium-sized in the superficial dorsal nucleus to far larger in the suprageniculate nucleus, and medial division neurons are larger still. In the semithin sections, there are many medium-sized, myelinated axons in the medial part of the ventral nucleus, fewer in the dorsal nucleus, and many large and medium-sized myelinated preterminal fibers in the medial division (Winer and Wenstrup, 1994, their Figs. 2, 4).

Immunocytochemical studies. The regional form and nuclear distribution of glutamic acid decarboxylase- (GAD) immunoreactive puncta (axon terminals) also confirm this cytoarchitectonic scheme. In the ventral division, many medium-sized puncta occur, while those in the superficial dorsal and dorsal nuclei are smaller, more delicate, and sparser. In contrast, medial division puncta are much larger, coarser, and nearly as numerous as ventral division endings (Winer et al., 1992). The contention made in the prior study in this series—that architectonic boundaries are defined sharply—is reinforced by the immunocytochemical findings, in which the transitions between adjoining architectonic regions are only a few micrometers wide (see also Prieto et al., 1994b).

Connectional investigations. The few systematic comparative studies of auditory thalamic connectivity present a dilemma in evaluating global patterns of medial geniculate body organization. Despite these limitations, some common connectional themes are recognized in the mustached bat and other species. Subregions of the central nucleus of the inferior colliculus each project upon specific territories of the auditory thalamus in a topographic fashion (Wenstrup and Winer, 1987; Wenstrup et al., 1994; see also Frisina et al., 1989). These thalamic targets, in turn, send their axons to different cortical regions (Olsen, 1986), some following patterns with a striking resemblance to those in the cat (Winer et al., 1977; Niimi and Matsuoka, 1979; Imig and Morel, 1983). Auditory thalamic nuclei outside the classically defined lemniscal auditory pathway, such as the suprageniculate nucleus (Calford and Aitkin, 1983; B.A. Peterson and J.A. Winer, in preparation), receive brain stem afferents from extralemniscal sources and, in turn, project to extraauditory frontal lobe territories as well as to the auditory cortex (Kobler et al., 1987; Casseday et al., 1989). However, the mustached bat suprageniculate nucleus also receives topographically ordered input from the central nucleus of the inferior colliculus. This finding suggests that the rigid distinction between lemniscal and extralemniscal pathways is conserved in certain nuclei and violated in others.

The parallels enumerated above between nuclei and species are somewhat less secure with respect to an important area, the rostral pole nucleus. This region, which contains many combination sensitive neurons (Olsen, 1986; Olsen and Suga, 1991a,b), is distinguished architectonically (Winer and Wenstrup, 1994), and its neurons receive significant input from inferior colliculus regions representing frequency specific components of the bat's sonar signal (Frisina et al., 1989; Wenstrup et al., 1994). While the rostral part of the cat medial geniculate body also has a tonotopic organization (Imig and Morel, 1985a) and a cytoarchitecture (Winer, 1992) that sets it apart from the remainder of the ventral division, its affiliations are uncertain. The many myelinated preterminal axons have impeded efforts in the bat and cat to impregnate these neurons and to reach more definitive conclusions about their role in the medial geniculate body.

The interplay between these many methods leads to the conclusion that the principal auditory thalamic nuclei in the bat are related in a fundamental sense to those in other mammals. The main types of neurons within the medial geniculate complex representing frequency or aural interactions may be highly conserved in phylogeny. This inference includes some, but not all, elements of local auditory thalamic circuitry (Winer et al., 1992) and of tectothalamic connectivity (Wenstrup et al., 1994).

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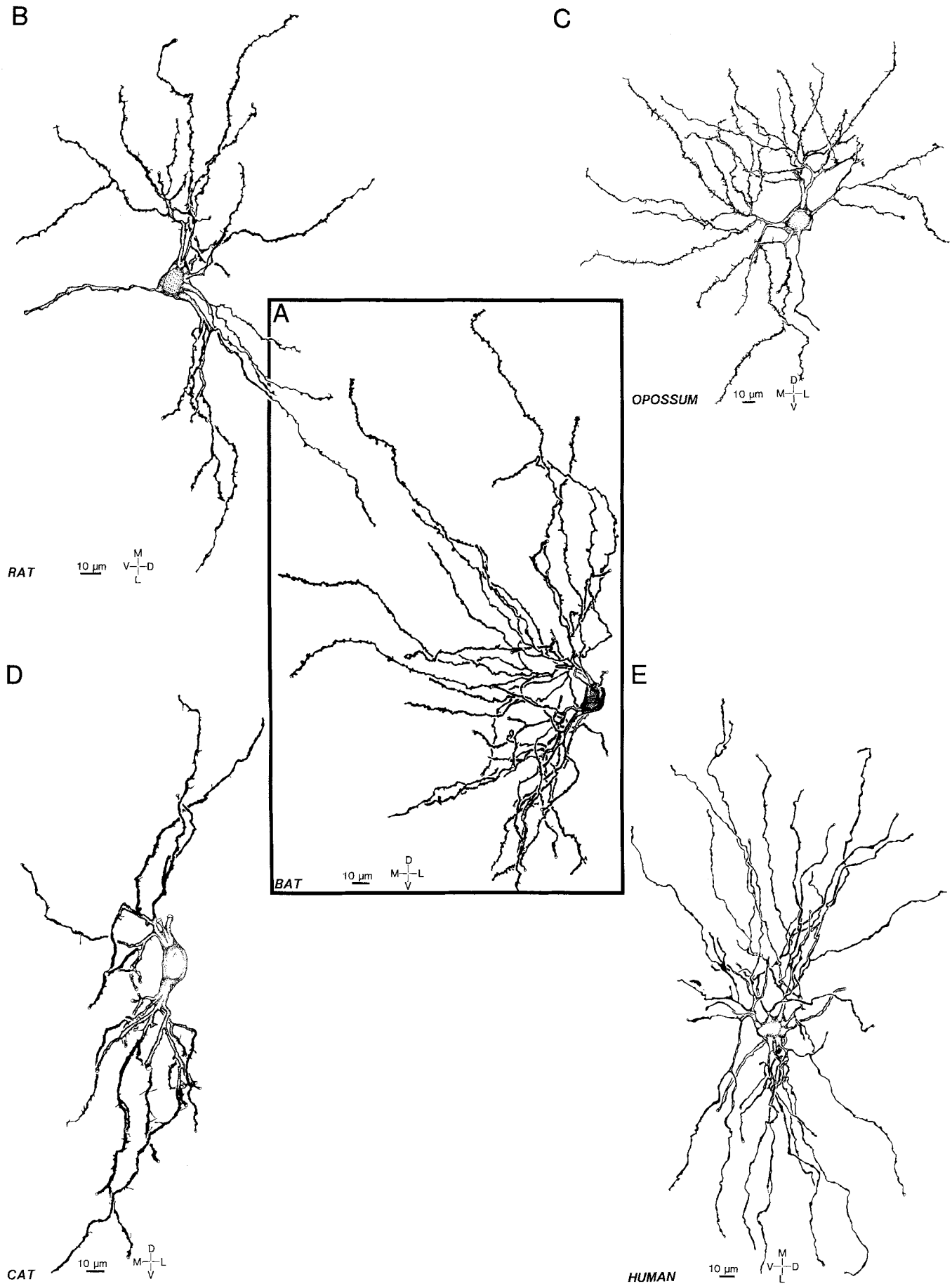
Fig. 12. Small, possibly intrinsic neurons from various medial geniculate body subdivisions. **A:** Cells from the ventral division (1–3) were differentiated from larger, more tufted neurons by the comparative simplicity of the dendritic branching, their smaller dendritic fields, and the slenderness of their processes. **B:** Dorsal division cells (4–6) had thin dendrites that often projected outside the plane of section. Some neurons were sparsely branched (5), while others divided more elaborately. **C:** A medial division stellate cell (7) had very fine dendrites and a variety of appendages, many of which were long, slender, and peduculated.

Fig. 13. (See overleaf.) Comparative dendritic architecture of Golgi-impregnated ventral division principal neurons from the medial geniculate body of a bat, a rodent, a marsupial, a carnivore, and a primate, respectively. Note the species differences in neuronal size and in the orientation of fibrodendritic laminae. Protocol for all panels: planapochromat, N.A. 1.32, ×2,000. **A:** Mustached bat (*Pteronotus parnellii*) neuron showing characteristically tufted, richly branched dendritic arbors typical of the lateral subdivision (Vl) of the ventral nucleus. **B:** The albino rat (*Rattus norvegicus*) had much simpler, but still well-tufted, dendritic arbors. **C:** In the Virginia opossum (*Didelphys virginiana*), the fibrodendritic laminae were broad, and the dendritic arbors retained their tufted branching patterns. **D:** In the cat (*Felis catus*), there was a narrow lateral dispersion of strongly tufted dendrites; several branches were transected, conveying a misleading impression of dendritic simplicity (see also Winer, 1984a, 1991). **E:** A neuron from an adult human (*Homo sapiens*) with many complex, well-tufted arbors.



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