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Neural architecture of the rat medial geniculate body

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Abstract

The rat medial geniculate body was subdivided using Nissl preparations to establish nuclear boundaries, with Golgi-Cox impregnations to identify projection and local circuit neurons, and in fiber stained material to delineate the fiber tracts and their distribution. Three divisions were recognized (ventral, dorsal and medial); the first two had subdivisions. The ventral division had lateral and medial parts. The main cell type had bushy tufted dendrites which, with the afferent axons, formed fibrodendritic laminae oriented from dorso-lateral to ventro-medial; such laminae were not as regular medially, in the ovoid nucleus. The dorsal division contained several nuclei (dorsal superficial, dorsal, deep dorsal, suprageniculate, and ventrolateral) and neurons with radiating or bushy dendrites; the nuclear subdivisions differed in the concentration of one cell type or another, and in packing density. A laminar organization was present only in the dorsal superficial nucleus. Medial division neurons were heterogeneous in size and shape, ranging from tiny cells to magnocellular neurons; the various cell types intermingled, so that no further subdivision could be made. This parcellation scheme was consistent with, and supported by, the findings from plastic embedded or fiber stained material. There were very few small neurons with locally ramifying axons and which could perform an intrinsic role like that of Golgi type II cells. Their rarity was consistent with the small number of such profiles in plastic embedded or Nissl material and the few GABAergic medial geniculate body neurons seen in prior immunocytochemical work. While similar neuronal types and nuclear subdivisions are recognized in the rat and cat, there may be major interspecific differences with regard to interneuronal organization in the auditory thalamus whose functional correlates are unknown.

Key words: Thalamus; Golgi type II cell; Interneuron; Thalamocortical auditory system

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1. Introduction

Thalamic sensory nuclei occupy a key position in the synaptic sequence between the periphery and the representation of experience in the cerebral cortex. They process information several synapses removed from the receptors and then they convey this information towards the cerebral cortex (Fitzpatrick et al., 1983 [squirrel monkey]; Vaudano et al., 1991 [rat]; Shi and Cassell, 1997 [rat]). They serve also as a hub for descending cortical influences (Pedroarena and Llinás, 1997 [guinea pig]) which could modify thalamocortical (Castro-Alamancos and Connors, 1997) and thalamo-amygdaloid (LeDoux et al., 1985 [rat]; Shinonaga et al., 1994 [cat]) information. These complementary roles place the thalamus in an important position in the representation of experience in the brain. This centrality underscores the importance of the thalamus in the hier-

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Abbreviations: Aq, cerebral aqueduct; APt, anterior pretectum; BIC, brachium of the inferior colliculus; BSC, brachium of the superior colliculus; BV, blood vessel; CG, central grey; CP, cerebral peduncle; D, dorsal nucleus or dorsal division; DC, dorsal nucleus, caudal part; DD, deep dorsal nucleus; DS, dorsal superficial nucleus; eml, external medullary lamina; Hip, hippocampus; LGB, lateral geniculate body, dorsal nucleus; LGBv, lateral geniculate body, ventral nucleus; LMN, lateral mesencephalic nucleus; LP, lateral posterior nucleus; LPc, lateral posterior nucleus, caudal part; M, medial division; MB, mamillary body; ML, medial lemniscus; MRF, midbrain reticular formation; MZ, marginal zone; OT, optic tract; Ov, pars ovoidea of the ventral division; PIN, posterior intralaminar nucleus; PL, posterior limitans nucleus; Pt, pretectum; SC, superior colliculus; Sg, suprageniculate nucleus; SN, substantia nigra; Spf, subparafascicular nucleus; SpN, suprapeduncular nucleus; V, pars lateralis of the ventral division; Vb, ventrobasal complex; Vl, ventrolateral nucleus; Planes of section: D, dorsal; L, lateral; M, medial; V, ventral

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Table 1
Summary of neuronal types in the rat medial geniculate body

Division	Neuron type	Shape of dendritic field	Size of dendritic field[a]	Somatic shape and size[b]	Figure(s)
Ventral	1. Bushy tufted	Elongated vertically in pars lateralis, horizontally in pars ovoidea	50×100 μm	Oblate or round; 10×8 μm	Fig. 2C: 1, Fig. 3: 1, Fig. 6A,B: 1
	2. Small stellate	Oval	50×30 μm	Flask-shaped; 10×6 μm	Fig. 2C: 2, Fig. 3: 2, Fig. 6A: 2
Dorsal	3. Tufted	Polarized laterally	200×100 μm	Oblate; 12×8 μm	Fig. 2B: 3, Fig. 4: 3, Fig. 6C,D: 3
	4. Radiate	Oval and often asymmetrical	80×80 μm	Spindle-shaped; 8×10 μm	Fig. 2B: 4, Fig. 4: 4
	5. Small stellate	Circular	Uncertain; 40×100 μm	Round or flask-shaped; 6×6 μm	Fig. 4: 5, Fig. 6C,D: 5
Medial	6. Magnocellular	Irregularly radiate	250×500 μm	Elongated; 15×25 μm	Fig. 2A: 6, Fig. 5: 6, Fig. 6E: 6
	7. Wide field	Elongated in all principal planes	250×200 μm	Triangular; 20×15 μm	Fig. 2A: 7, Fig. 5: 7
	8. Tufted spindle	Vertically oriented	300×100 μm	Fusiform; 15×8 μm	Fig. 2A: 8
	9. Horizontal	Laterally oriented with few vertical processes	300×150 μm	Oblate or oval; 8×6 μm	Fig. 2A: 9, Fig. 5: 9
	10. Small stellate	Spherical	80×80 μm	Oblate or oval; 8×6 μm	Fig. 2A: 10, Fig. 5: 10, Fig. 6E: 10

[a] Estimates of lateral versus vertical dimensions.
[b] Width versus height.

archy of sensory processing, and it is a stimulus for asking whether subdivisions of the thalamus have structural differences that might distinguish them from one another in the functional domain.

The goal of the present account is to analyze the anatomical organization of the rat medial geniculate body, a structure implicated both in auditory information processing (Hu et al., 1994 [rat]) and in associative changes involved in learning and memory (McIntosh and Gonzalez-Lima, 1995 [rat]). This approach contrasts and compares the results from studies of neuronal architecture in Golgi preparations to that of cytoarchitectonic patterns derived from Nissl material, and integrates these data with myeloarchitectonic patterns from fiber stained and plastic embedded sections. These results provide a context for the accompanying study on auditory thalamic input to physiologically defined subregions of neocortex (Winer et al., 1999 [rat]). A final objective is to integrate these results with the outcomes from prior investigations on rat medial geniculate body neurochemical organization (Winer and Larue, 1988) and with those of experimental connectional studies on thalamocortical-corticothalamic reciprocity (Winer and Larue, 1987). This approach will encourage more explicit hypotheses about the functional role of the various subdivisions of the medial geniculate body. These observations may have implications for understanding species parallels and differences in the evolution of sensory thalamic circuitry (Winer and Larue, 1996 [rat, bat, cat, and monkey]) or the basis for developmental differences among medial geniculate body subdivisions.

Two other reasons justify further study of the rat auditory thalamus. The first pertains to the conclusion that the medial geniculate body contains functionally distinct subregions. The principal distinction is between the ventral division, which is entirely auditory (Aitkin and Webster, 1972 [cat]), and the medial division, which is polysensory (Wepsic, 1966 [cat]), and projects both to auditory cortex and to the limbic system (LeDoux et al., 1987 [rat]; Turner and Herkenham, 1991 [rat]). While the dorsal division is auditory, its neurons have broad tuning curves and are part of a secondary (paralemniscal, lemniscal adjunct) pathway from the lateral

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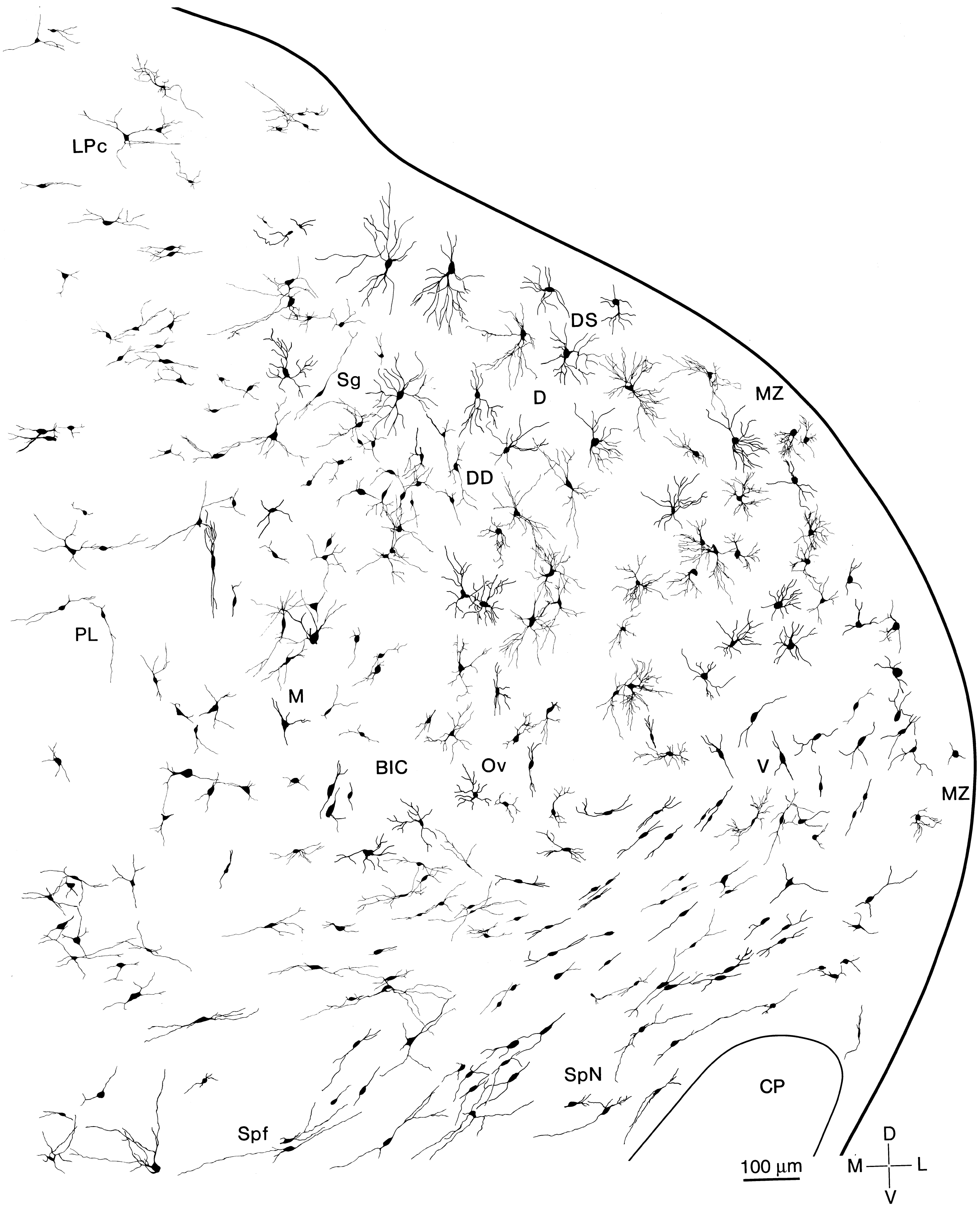
Fig. 1. Composite drawing showing the principal medial geniculate body nuclei in a transverse view from an adult rat midway through the auditory thalamus (see Fig. 10 for the comparable level in Nissl stained material). The cardinal features were the prevalence of bushy tufted cells in the ventral division (V, Ov), the prominent radiate dorsal division (D, DS) neurons, and the much larger, heterogeneous medial division (M) cells. Ventral division neurons contributed to fibrodendritic laminae that were most evident in the pars lateralis (V); cells in the pars ovoidea (Ov) were still tufted but the laminae were displaced by fibers. Dorsal division neurons often had radiating dendrites and a spherical shape; the largest dorsal division neurons were in the suprageniculate nucleus (Sg). The latter cells were clearly distinguished from the still larger and more diverse medial division neurons (M). The inferior face of the medial geniculate complex abutted the posterior intralaminar nuclei, two of whose representatives, the subparafascicular (Spf) and suprapeduncular (SpN) nuclei, were well developed in the rat; these neurons had long, slender, sparsely branched dendrites (Winer et al., 1988 [opossum and cat]). Axons ascending in the inferior brachium (BIC) dominated the ventro-medial quadrant of the medial geniculate body. Neurons from different sections were drawn and superimposed. Golgi-Cox impregnation, 140 μm thick sections. Planachromat, N.A. 0.65, ×396.

tegmental region of the midbrain (Morest, 1965 [cat]) through the dorsal and medial divisions of the auditory thalamus (Winer and Morest, 1983a [cat]) and terminating in the nonprimary auditory cortex (Winer et al., 1977 [cat]). This diversity of connections and physiology endows the medial geniculate body with a nuclear complexity not immediately evident in either the lateral geniculate body or the ventrobasal complex, neither of



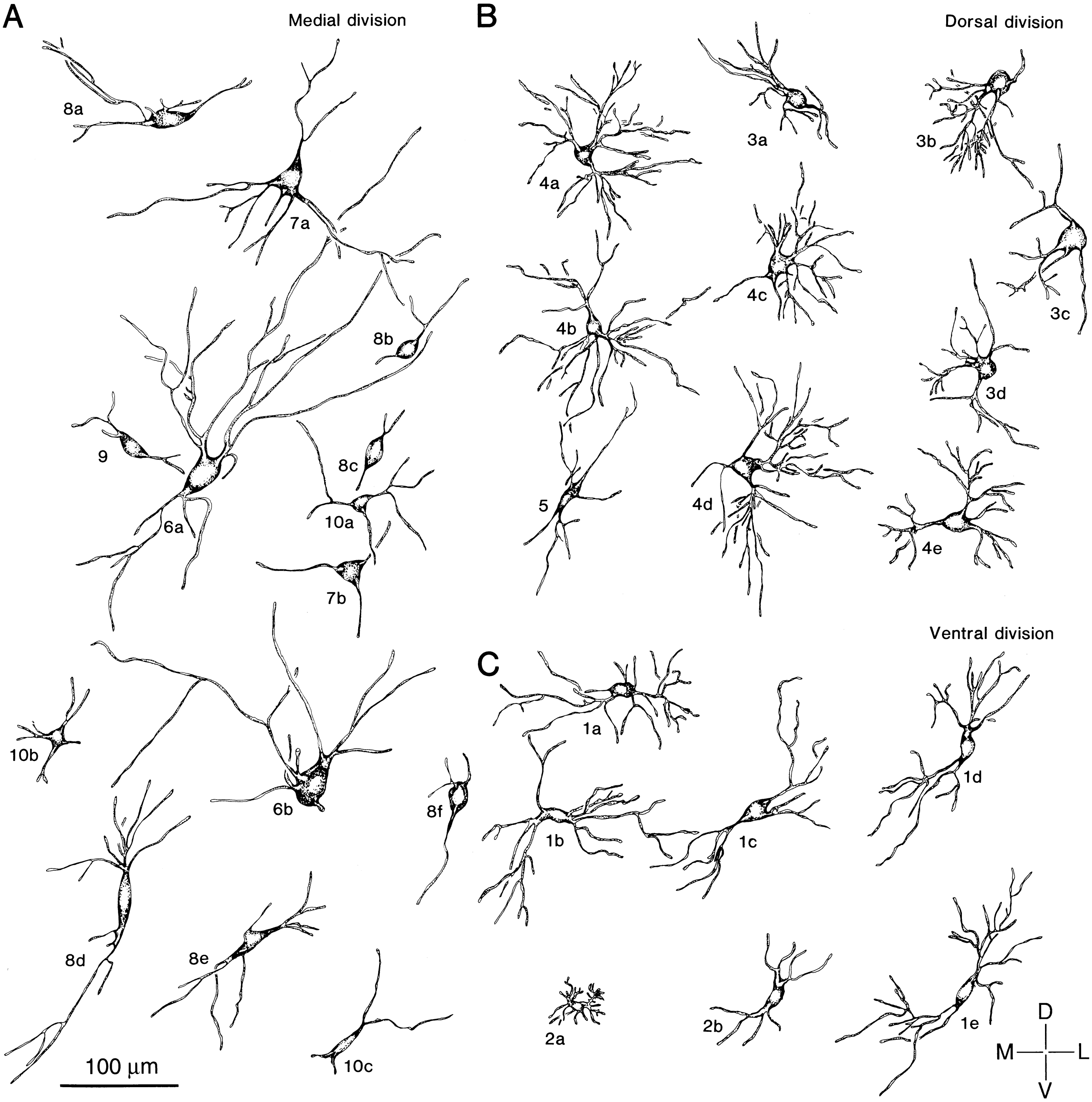


Fig. 2. Representative Golgi impregnated neurons (see Table 1) from medial geniculate body divisions (compare with Fig. 1). A: Medial division cells had a wide array of sizes and shapes. Magnocellular neurons (6) had the largest somata in the medial geniculate body and distinctive, radiating dendritic fields. Wide field neurons (7) had the next largest dendritic fields, which spanned both the long and short axes of the medial division, while the tufted spindle cell (8) was elongated vertically and had a more complex mode of branching. Horizontal cells (9) had their main dendritic plane oriented medio-laterally, across the short axis of the medial division. Small stellate neurons (10) were rare here and in other parts of the medial geniculate complex. Protocol for all panels: Planachromat, N.A. 0.65, ×500. B: Dorsal division neurons had tufted (3), radiate (4) or stellate (5) dendritic branching patterns. Tufted cells predominated in the superficial dorsal nucleus, while radiate cells were numerous in the dorsal and deep dorsal nuclei; small stellate neurons were impregnated so rarely that no conclusion about their preferred locus can be made. C: Ventral division principal tufted neurons (1) had the most prominent dendritic tufts in the medial geniculate body. Their processes contributed to the laminar fibrodendritic plexus. A second, much smaller stellate cell (2) was also present.

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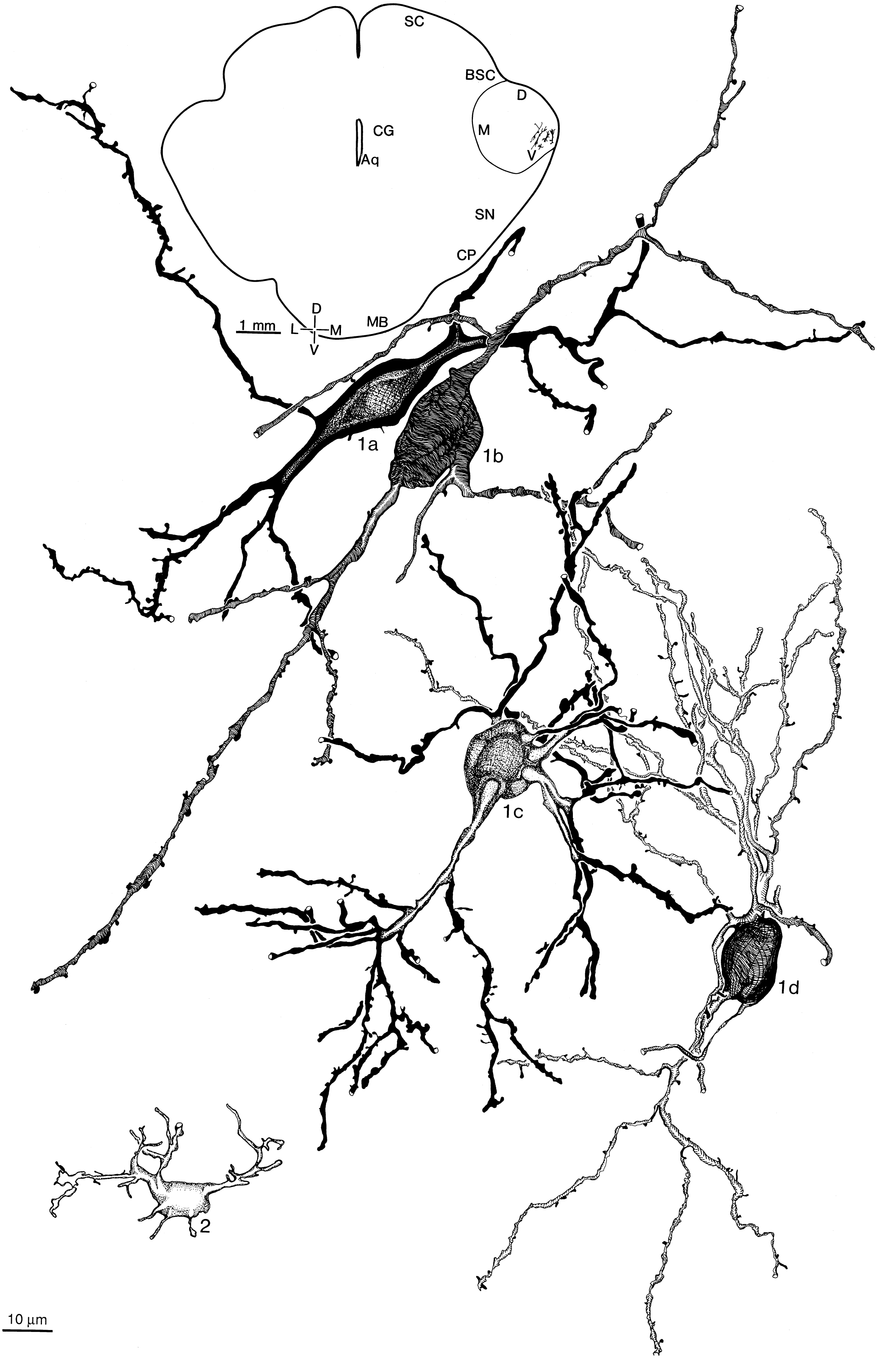
Fig. 3. Ventral division neurons. Bushy tufted neurons (1) predominated, and their primary dendrites ran parallel to one another while the distal segments intertwined. The axon usually originated from the soma (1c, near the top) or a proximal dendrite (1b, lower right dendrite) and soon became myelinated and was refractory to impregnation. Appendages were present in modest numbers on the intermediate dendrites. Some lateral dendrites (1a) were long enough possibly to cross laminar borders. A much smaller, presumptive Golgi type II cell (2) was also impregnated, though no axon could be identified and the dendrites had some elaborate appendages (discussed further in the text). Open circles at dendritic tips denote transected processes (Figs. 3–6). Inset, schematic view of the locus of the impregnated neurons. Protocol for Figs. 3–6: Planapochromat, N.A. 1.32, ×2000.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which has any direct affiliations with the limbic forebrain or appears to serve more than one modality (Jones, 1985). A more detailed account of the rat auditory thalamus is required to specify comparative differences in thalamocortical processing and the implications of these findings for a more general theory of mammalian thalamic sensory function.

A third rationale is comparative. There are significant species specific differences in the proportion of intrinsic γ-aminobutyric acid-containing (GABAergic) neurons in the medial geniculate body, ranging from $< 1\%$ (rat and mustache bat) to $> 30\%$ (cat and macaque monkey) (Winer and Larue, 1996). These might endow the auditory thalamus with a range of neurochemical variation not found in the lateral geniculate body, whose proportion of GABAergic neurons seems to be strongly conserved in different species (Ohara et al., 1983 [rat]; Penny et al., 1983 [cat and prosimian primate]; Hendrickson et al., 1983 [monkey]). It remains, however, to be seen whether the same types of local circuit neurons can be identified.

2. Methods

A large collection of normal histological (Winer and Larue, 1987), immunocytochemical (Winer and Larue, 1996) and experimental tract tracing (Games and Winer, 1988) material from the rat was available. Only the salient information appears here; details are given in the appropriate references. All of the observations that follow are from mature (< 12 months old) and healthy albino male Sprague-Dawley rats (160–600 g). One animal (Fig. 5) was older than most of the others (10 months versus < 3 months) and therefore larger (600 g versus ~160 g). Procedures followed the approved institutional animal care and use protocol and were performed under veterinary supervision and by trained personnel.

2.1. Golgi method

The Golgi-Cox method was used to impregnate neurons (see Winer and Wenstrup, 1994 [bat]). Rats were anesthetized with sodium pentobarbital (40 mg/kg) and cooled in an alcohol-laced ice water solution while the brain was dissected. The tissue was immersed in the impregnating solution, then embedded in celloidin and cut serially at 140 μm. Sections were developed using the on-the-slide method. After dehydration, clearing, and coverslipping, neurons were jet black on a clear background (Ramón-Moliner, 1970).

Representative examples of well impregnated neurons were drawn with a drawing tube. The objective used appears in the accompanying figure legend.

2.2. Plastic embedded material

Several rats were anesthetized at a level that suppressed corneal, pedal, and nociceptive cutaneous reflexes, then perfused intracardially with phosphate buffered (PB) saline, followed by fixative (2% paraformaldehyde/3% glutaraldehyde at ~15°C). The brain was blocked in the stereotaxic transverse plane and sectioned on a Vibratome into slabs 400 μm thick which were dehydrated through ascending ethanols and propylene oxide, then embedded in plastic. The slabs contained the entire medial geniculate body and were faced with glass knives. Semithin sections 0.5–2 μm thick were heat annealed onto glass slides and stained with toluidine blue to reveal neurons and myelinated axons. The diameters of the axons were estimated from drawings made with oil-immersion planapochromatic objectives at 100×.

2.3. Fiber stained tissue

To visualize fiber tracts, material was prepared with the Spielmeyer method (Mallory, 1942). Frozen sections 25–50 μm thick were cut to reveal the axonal plexus and the course of myelinated fibers.

3. Results

3.1. Cytoarchitectonic parcellation

The medial geniculate body was, in transverse sections, about 1200 μm long (Figs. 9–12), some 1000 μm high and almost 1500 μm wide at its maximum (Fig. 8B). As in the other species (Winer, 1992 [rat, bat, opossum, and monkey]), three main parts were distinguished in Nissl material (Fig. 10); this conclusion was confirmed in Golgi preparations (Fig. 1). The ventral division was dominated by bushy tufted neurons (Fig. 2C; Table 1). The dorsal division had cells with either a tufted or a stellate configuration (Fig. 2B). In contrast, the medial division had a heterogeneous neuronal pop-

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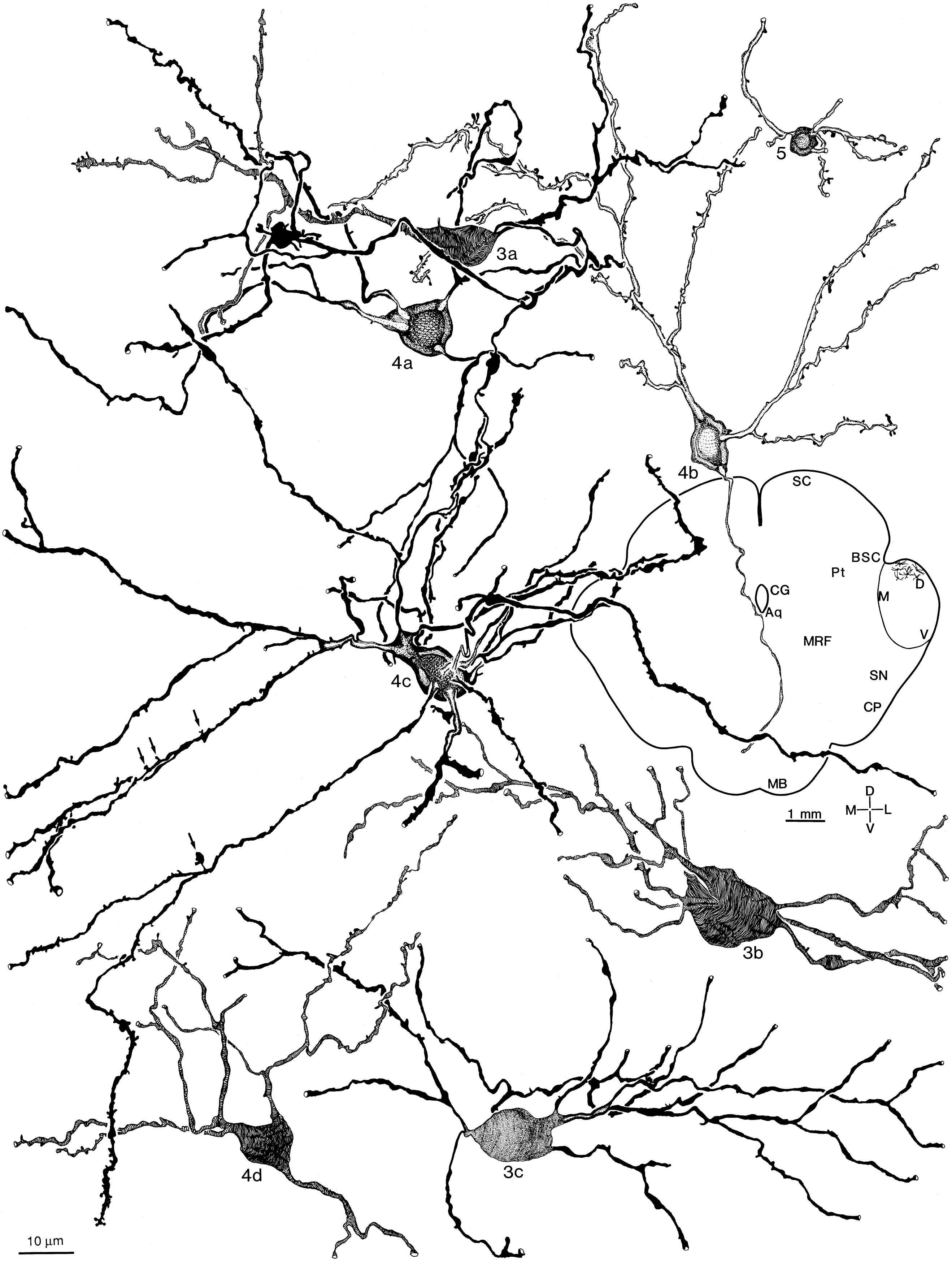
Fig. 4. Dorsal division neurons had only a limited laminar organization and more diverse cell types than the ventral division (Fig. 3). While tufted neurons (3) were present, they neither formed regular laminae nor were they more numerous than the radiate cells (4), whose dendritic configuration was irregularly spherical. Various appendages were present along the intermediate and distal dendrites (4c, arrows). Some dendrites (for example, 4a) were varicose and irregular, with a few bulbous segments at irregular intervals. In contrast, the small stellate cell (5) had a far simpler dendritic arrangement, with sparse processes radiating into adjoining sections. Protocol as in Fig. 3.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ulation in which tufted cells were rare (Fig. 2A); the neurons will be described more fully in Section 3.3.

Proceeding caudo-rostrally, the posterior tip of the medial geniculate body was relatively cell-poor as axons ascending via the brachium of the inferior colliculus (Fig. 9A: BIC) displaced the resident neurons of the bed nucleus of the inferior brachium. The dorsal division appeared first. Its neurons lacked the prominent fibrodendritic laminae that were a hallmark of the ventral division. Just 25% of the distance from its caudal tip, the medial geniculate body reached its peak in size (Fig. 8B), and every major nucleus was present. The ventral division formed the ventrolateral surface of the auditory thalamus. The neurons in the lateral part were aligned in the dorso-ventral axis (Fig. 9B: V); more medially, in the pars ovoidea, the cells were not oriented as regularly. The junction between the ventral and the dorsal divisions was often marked by a prominent thalamoperforating vessel.

Dorsal division neurons were present from the most caudal (Fig. 9A) to the extreme rostral (Fig. 12) poles of the medial geniculate body. The dorsal division proper contained several nuclei (Figs. 1 and 9B). Three of these nuclei – the superficial dorsal (Fig. 9B: DS), the dorsal (Fig. 10: D) and the deep dorsal (Fig. 11: DD) – were closely related but differed in regional cytoarchitecture. Neurons in the dorsal superficial nucleus had somata arranged in flattened sheets oriented dorsomedially to ventrolaterally; cells in the dorsal nucleus were more dispersed by the rich fiber plexus (see below) and did not form such layers, while deep dorsal nucleus neurons were a clustered mass lateral to the much larger neurons of the suprageniculate nucleus (Fig. 10: Sg). The latter was present at every level except the caudal tip and it was well-developed midway through the caudo-rostral extent of the medial geniculate body (Figs. 9–12).

The medial division was the smallest of the three parts and had the most heterogeneous collection of neurons (Fig. 1: M). While the large neurons were conspicuous (Fig. 6E: 6; Fig. 9B: M), a wide range of somatic sizes and shapes was present. The medial division extended the full length of the medial geniculate body as a slender (~200 μm wide at its maximum) lentiform nucleus (Figs. 9–12).

3.2. *Fiber architecture*

The myeloarchitectonic patterns were consistent with the plan for the subdivisions proposed above. The ventral nucleus neuropil was moderate in density (Fig. 7B: V); preterminal axonal fascicles ascended between rows of thalamocortical relay neurons (Fig. 6B: below 1). The dorsal division, especially caudally (Fig. 7A: D, DD), was remarkably pale and appeared to have little myelin; in fact, the fine caliber of these fibers was noteworthy in thicker sections, while the semithin material demonstrated that, many axons, while myelinated, were ~0.5 μm thick (Fig. 6D). Dorsal division fibers often formed prominent fascicles that ran medio-laterally (Fig. 6D; Fig. 7B: above DD). These axons could represent fine preterminal processes of cortical origin (Winer and Larue, 1987; see Winer and Morest, 1984 for similar fibers in the cat).

As might be expected from its proximity to the brachium of the inferior colliculus, the medial division had many more axons than the other subdivisions. Some fibers were sectioned face-on, suggesting that they were ascending towards more remote targets (Fig. 6F). The most prominent axons were among the largest caliber (2–3 μm in diameter) in the medial geniculate body and ran in bundles among the dendrites (Fig. 6F, open profiles). The abundant fibers imparted a striated, heavily myelinated texture to this division that set it apart from the ventral and dorsal divisions.

3.3. *Neuronal organization*

The structure of Golgi impregnated neurons and their nuclear arrangement confirmed and reinforced the cytoarchitectonic interpretation proposed above. One difficulty that frustrated more definitive conclusions was the refractoriness of the adult material to complete impregnation. This had two implications. It hampered any definitive account of the organization of nuclei such as the caudal dorsal nucleus (Fig. 9A: D) since too few neurons were available to permit firm conclusions. Thus, analysis of this and some other nuclei (such as the rostral pole, anterior to Fig. 12, and present through about one-quarter of the length of the medial geniculate body) was necessarily incomplete. A second difficulty was that the axons of Golgi impregnated cells were often unstained, making impossible any systematic analysis with regard to the axons arising from local circuit neurons.

Ventral division neurons were among the most highly tufted cells in the medial geniculate body (Fig. 1: V), especially those in the pars lateralis. The term,

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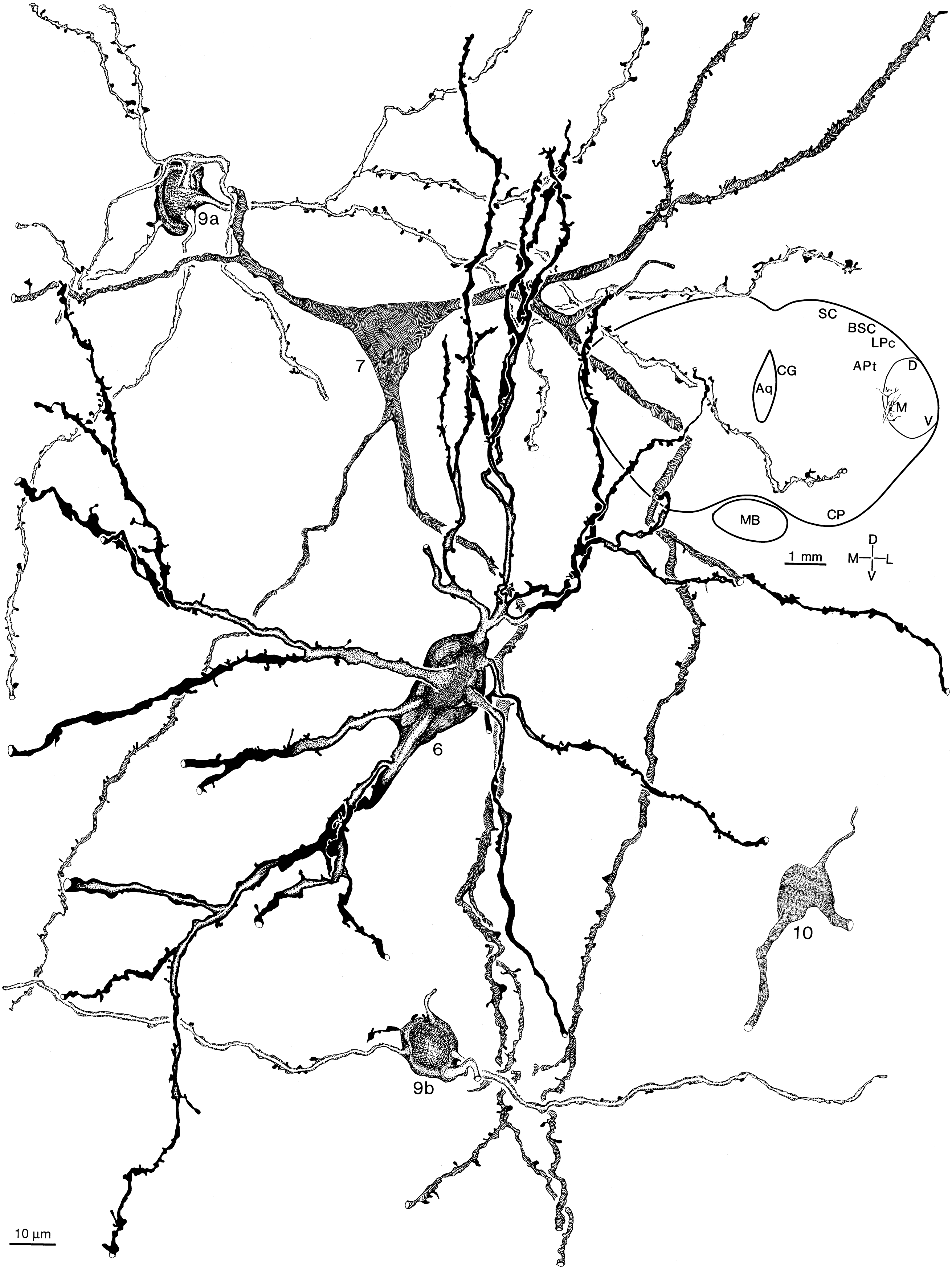
Fig. 5. Medial division cells encompassed a wide range in size and shape, from massive magnocellular neurons (6) to small stellate cells (10). The neurons also had the most diverse dendritic architecture in any division; some cells had a horizontal orientation (9b) while others were devoid of a specific directional configuration (7). The magnocellular neuron was classified as a radiate cell, despite its irregular dendritic field, and the processes had complex arbors in which single processes coiled about one another, especially distally (6). The appendages on most neurons were diverse in size and shape and concentrated along the intermediate dendrites. For the tufted spindle cell, see Fig. 2A: 8d and Table 1. Protocol as in Fig. 3.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tufted, encompassed a range of dendritic variation (see Fig. 2C). The laminae formed by these dendrites and the ascending axons had a long, gently curved dorso-ventral axis; the laminae were inclined at ∼40° from the stereotaxic vertical plane. Tufted cells in the more medial pars ovoidea had more radiate dendritic fields than neurons situated laterally in the ventral division. The laminae were short, coiled, contorted, and irregular in shape.

Other features were evident at higher magnification. The soma was typically elongated or oval, with the long axis oriented dorso-laterally to ventro-medially; it was often smooth, though some cells had a few fine appendages (Fig. 3: 1a). Primary dendrites usually arose at the somatic poles (with some exceptions: see Fig. 3: 1c) and branched either sparsely (Fig. 3: 1b) or profusely (Fig. 3: 1d). The most highly tufted examples had 8–10 compactly organized dendrites. Neurons in the pars ovoidea had a more radiate three-dimensional shape than cells in the pars lateralis, though the branching pattern was still tufted. Dendrites had a moderate number of spines, chiefly on their intermediate segments. Appendages were variable in shape and ranged from 0.5–3 μm in length. The axon arose from the soma and was never impregnated past the initial segment.

A second, much smaller neuron with a stellate dendritic configuration and a far simpler, dichotomous branching pattern was impregnated (Fig. 3: 2; Table 1). Examples of these cells were so rare that any more detailed description was not possible.

Dorsal division neuronal architecture had parallels and differences with the ventral division. Only one nucleus, the dorsal superficial, contained neurons with a consistent orientation (Fig. 9B: DS). Here, the tufted neurons lay in slender sheets along the dorso-lateral surface of the medial geniculate body, their primary dendrites arranged medio-laterally (Fig. 4: 3). Their dendritic configuration resembled that of principal cells in the pars lateralis of the ventral division. Their tufted processes arose at the poles and extended laterally as flattened dendritic sheets or were sometimes oriented vertically. However, the tufts were rarely as elaborate or as highly branched as the corresponding processes of ventral division principal neurons.

A second class of neuron, the radiate cell (Table 1), was the most prevalent type elsewhere in the dorsal division, including the suprageniculate nucleus (Fig. 1: Sg) where, despite their much larger size, the cells had essentially the same branching pattern. Radiate cells differed from their tufted counterparts in having a simpler dendritic arbor with dichotomous rather than tufted branches, and in lacking a preferred orientation. They often had larger dendritic domains which were not filled homogeneously (Fig. 2B: 4b); their processes often extended beyond the tissue section (Fig. 4: 4b,c, open circles at dendritic tips). They were never as radiate as those of their feline counterparts (Winer and Morest, 1983a). The few appendages lay along the intermediate dendrites and had surprisingly heterogeneous shapes, ranging from small, squat spines to longer and much more complex varieties (Fig. 4: 4c, arrows).

As in the ventral division, a far smaller stellate neuron was also impregnated (Fig. 4: 5). It had a soma ∼6 μm in diameter and 3–4 primary dendrites that radiated irregularly and projected outside the section. These neurons were equally rare in the Golgi preparations (< 1% of the sample) and in plastic embedded material (Fig. 6C,D: 5).

Medial division neurons (Figs. 1 and 2A, and Fig. 5) differed from cells in the ventral (Fig. 2C, Fig. 3) and dorsal (Fig. 2B, Fig. 4) divisions in having no laminar organization, in their wide range of structural diversity, and in their larger size. In Nissl preparations, medial division neurons formed a slender shell between the lateral mesencephalic nucleus (Fig. 9A: LMN) and the nuclei of the dorsal division (Fig. 10: Sg). Internally, the medial division was traversed by brachial axons (Fig. 6F) that obscured any obvious laminar arrangement. In the rat (present results) and cat (Winer and Morest, 1983a) it was the only medial geniculate body division without discernible nuclear subdivisions.

In Golgi preparations medial division cells had a

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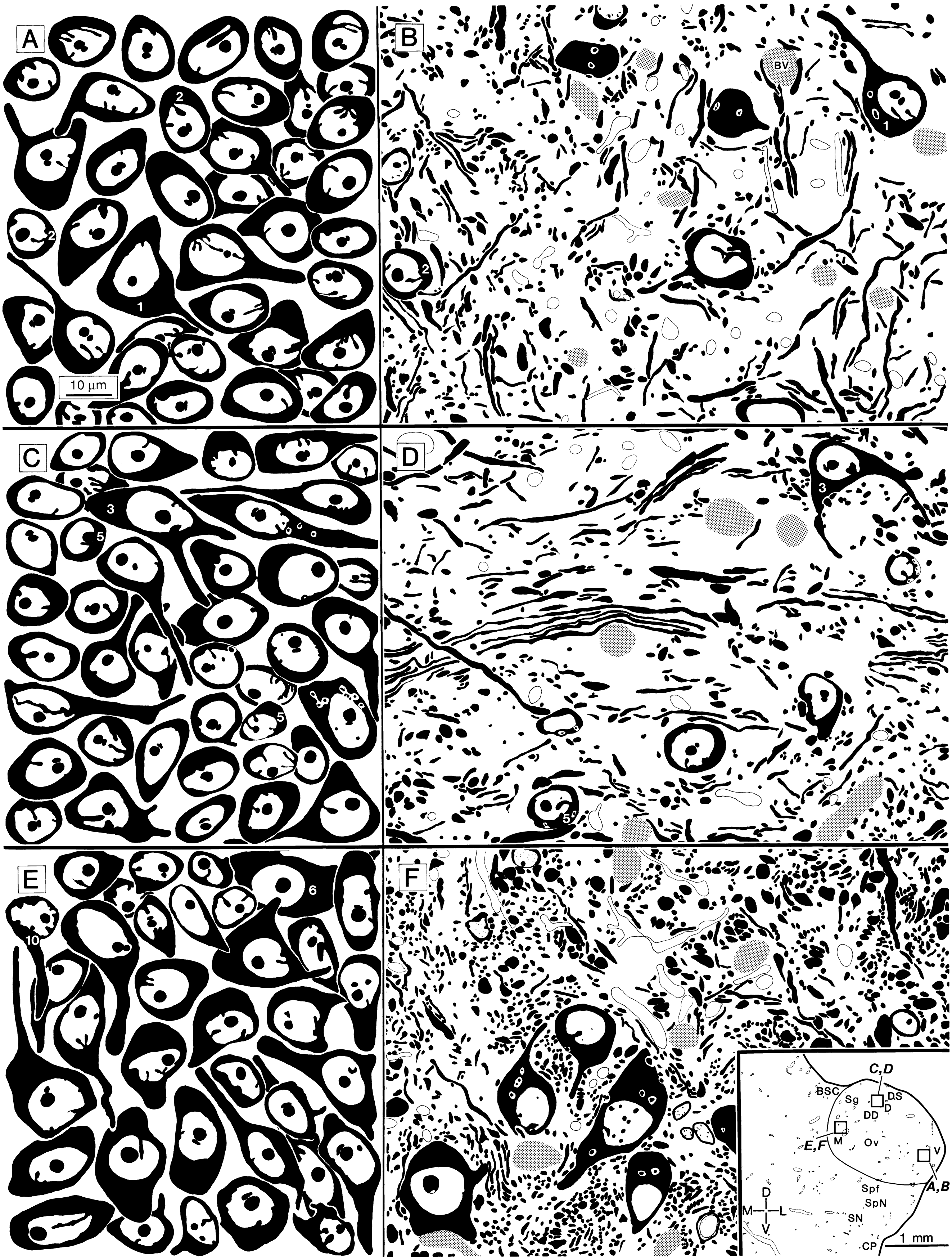
Fig. 6. Views of medial geniculate body divisions from plastic embedded, semithin material. In panels A, C, and E representative neurons were selected and drawn in close proximity. The actual density of cells is depicted in panels B, D, and F. A: Ventral division neurons in a 1 μm thick section. The large, presumptively principal (type I) cells (1; see Table 1) had round somata, smooth contours, an occasional dendrite, and a nuclear envelope with few invaginations. In contrast, the smaller, presumptive Golgi type II interneurons were far less common, had smaller somata, no or only rare dendrites, and a more elaborately invaginated nuclear perimeter. Inset at lower right in F: boxes, locus of observations. Toluidine blue stained section. B: Ventral division neuropil and associated somata were dominated by a vertical axonal plexus. Preterminal axons (solid black profiles) formed thin fascicles entering the ventral division; some fibers (small round profiles) cut en face were passing elsewhere. Dendrites (open elongated profiles) and glia (small open profiles) and small blood vessels (BV, stippled) were included in this and panels D and F. C: Dorsal division neuronal somata included possible tufted (3) and small stellate (5) neurons. The neuron at the extreme lower right may be a radiate cell. The many cells with long lateral dendrites suggest that these processes were aligned in register. D: The neuropil organization was marked by fascicles of slender axons oriented medio-laterally, with few fibers ascending. Some bundles may represent corticofugal preterminal fibers (see text). Myelinated axons passed near the soma of a presumptive tufted neuron (3). The neuropil contained many unmyelinated fibers. E: Medial division cells were the most heterogeneous in size and shape in this survey. While the magnocellular neurons (6) were the most striking, the wide range in size included cells with somata ∼10×7 μm (10), matching those of possible Golgi type II cells (Fig. 5: 10; Table 1: 10). F: The medial division neuropil contained many more large caliber axons than either the ventral (B) or dorsal (D) divisions, and there were bundles of myelinated axons ranging from 0.5 μm to ∼3 μm in diameter.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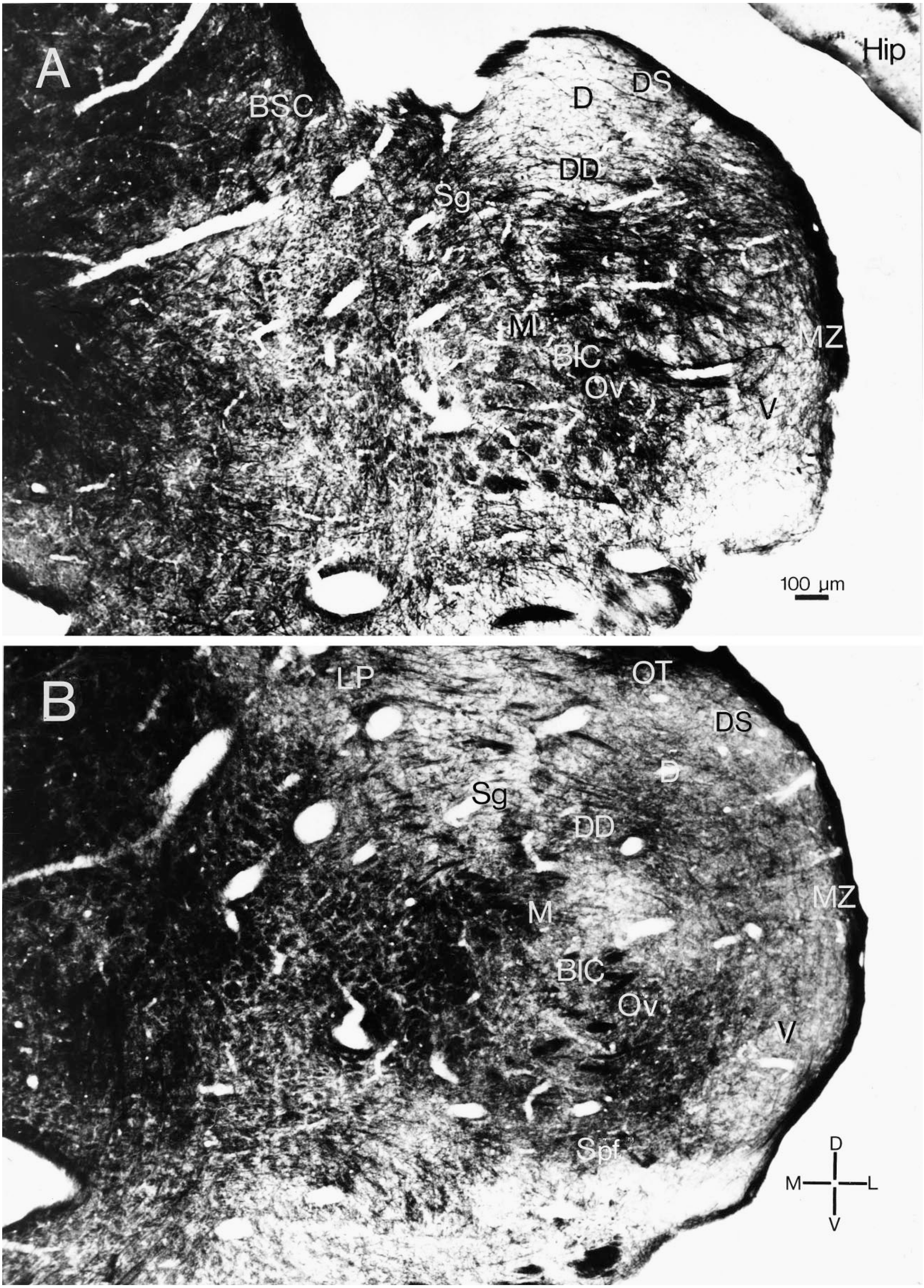
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BIC
Ov
V
Spf
D
M
L
V

Fig. 7. Fiber architecture of the auditory thalamus. A: From the caudalmost one-third (at a level corresponding approximately to Fig. 9B), all the principal nuclei were present. The ventral division (V, Ov), though not yet at its maximum size (see Fig. 8C), nevertheless had distinct subregions of lighter myelination in the pars lateralis and many more fibers in the pars ovoidea. The more caudal and lateral dorsal division territories (DS, D, DD) had much finer myelin, in contrast to the suprageniculate nucleus (Sg), where the staining was far darker. More medial, non-auditory parts of the midbrain-diencephalic transition had a uniformly dark myeloarchitecture. Spielmeyer stain. Planachromat, N.A. 0.32, ×125. B: More rostrally (corresponding approximately to Figs. 8C and 10), the ventral division (V, Ov) was developed fully and the myelin density was intermediate to the paler dorsal division (DS, D) and the more darkly stained medial division (M; see also Fig. 6F). Myelinated axons were even finer in the posterior intralaminar region between the ventral face of the medial geniculate complex and the cerebral peduncle, near the subparafascicular nucleus (Spf). At this level, the inferior brachium (BIC) was fully developed, and the prospective descending axons crossing the dorsal division ventrolaterally (above DD) were evident.
←

wide variety of dendritic configurations (Fig. 1). Some neurons had processes that ran parallel to the long axis of the medial division (Fig. 2A: 8d), others crossed this plane (Fig. 2: 8a), and some dendrites had both vertical and lateral processes (Fig. 2A: 6b). Many of the principal cell dendrites conformed to the lentiform shape of

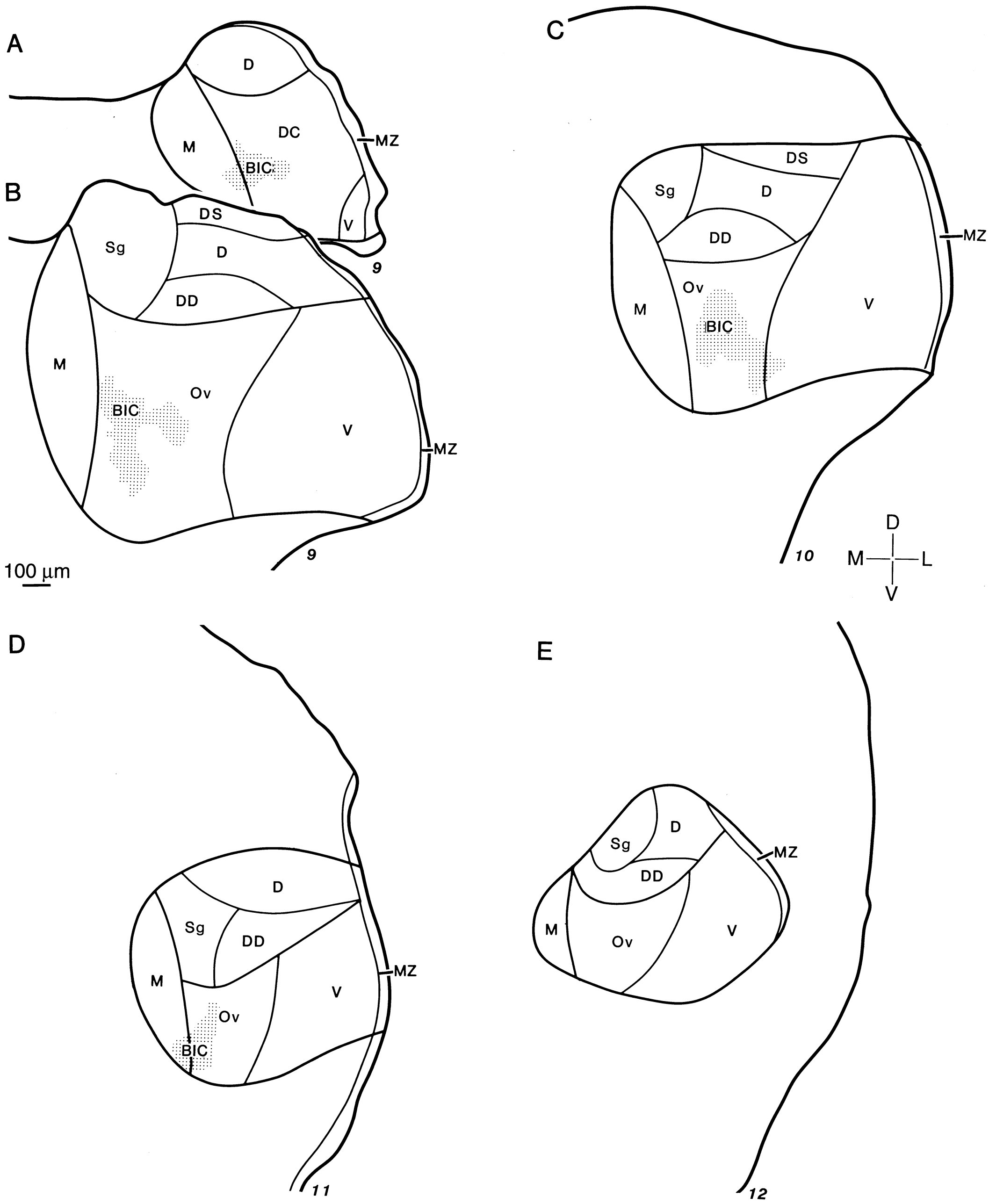

Fig. 8. Nuclear boundaries of subdivisions of the medial geniculate body derived from the sections in Figs. 9–12. The brachium of the inferior colliculus is represented by stippling.

the nucleus. Few processes of medial division neurons extended into the adjoining reticular formation or entered the dorsal and ventral divisions of the medial geniculate body.

The most striking medial division neuron was the magnocellular neuron (Table 1) whose 5–7 primary dendrites arose from any part of the soma to fill an irregularly shaped, spherical domain. Some branches were strongly tufted, others bifurcated simply (Fig. 5: 6). Unlike many other medial geniculate body neurons, dendritic appendages arose within 30 μm of the soma, and the intermediate and distal dendrites had a modest number of diverse processes, a few of which were pedunculated or unusually elaborate. Many dendrites projected for 200 μm or more, and some extended beyond the nucleus or the plane of the section (Fig. 1: M, Fig. 5: 6, upper and left lateral upper branches).

Wide field neurons, seen only in the medial division, had triangular somata from which several processes projected irregularly (Fig. 5: 7). Their branches never formed the tufts that were characteristic of large principal cells in the ventral (Fig. 2C: 1) and dorsal (Fig. 4: 3c) divisions. The dendrites of wide field neurons divided dichotomously and often gave rise to vertical or lateral branches. These spanned considerable distances, up to 500 μm or more, and were the definitive feature of this neuron. Appendages were restricted largely to the intermediate dendrites and were neither numerous nor especially elaborate (Fig. 5: 6).

Tufted spindle cells were the sole medial division neuronal type with bushy dendrites (Fig. 2A: 8). Their tufts were simpler than those of bushy neurons in either the ventral (Fig. 2C: 1) or dorsal (Fig. 4: 3b) divisions, and sometimes only one of the two main trunks was tufted. The soma was fusiform and the dendrites arose at the poles, giving the neuron a bitufted appearance. These neurons had more robust branching and a different orientation than neurons in the adjoining subparafascicular nucleus (Fig. 1: Spf). Like most other medial division cell types, their dendritic surfaces were smooth rather than spinous.

Horizontal neurons had the simplest dendritic architecture of any medial division neuron (Fig. 5: 9), with their long, undivided lateral processes extending up to 200 μm, thus spanning most of the short axis of the medial division (Fig. 1: M) or even extending beyond it (Fig. 11: M). Branching was usually simple and dichotomous. The processes were thin and had a few (Fig. 5: 9b) or a moderate (Fig. 5: 9a) number of appendages clustered on the intermediate dendrites.

Small stellate cells were rare (Fig. 2A: 10), as elsewhere on the rat medial geniculate body. These neurons were recognized in Nissl or plastic material by their modest somatic size and highly invaginated nuclear membrane (Fig. 6E: 10), and by their characteristic branching. The few examples impregnated had a round soma with 3–4 primary dendrites that divided weakly and projected for < 100 μm. Their dendrites divided rarely and never formed tufts, and many were relatively smooth.

4. Discussion

4.1. Functional interpretation

The emerging picture of medial geniculate body organization suggests that it contains functional subdivisions that process auditory and extra-auditory information and which constitute largely parallel pathways to the cerebral cortex and to subcortical telencephalic nuclei. The subsequent account is based largely on work in the cat, for which a larger body of evidence is available, except where noted otherwise. Considering the strong concordance across species in medial geniculate body neuronal architecture (Winer and Wenstrup, 1994 [rat, mustache bat, cat, opossum, human], it is appropriate to use this as a device to propose functional correlations and to summarize species differences.

The ventral division is considered to be entirely auditory on the basis of strong ascending connections arising from the central nucleus of the inferior colliculus (LeDoux et al., 1987 [rat]). Despite the importance of this pathway, damage to the ventral division alone in the rat results in little or no deficit in sound localization with trains or bursts of noise; only at high frequencies was a modest impairment evident (Kelly and Judge, 1985 [rat]). This is consistent with the corresponding absence of significant deficits in sound localization after bilateral ablation of rat auditory cortex (Kelly, 1980;

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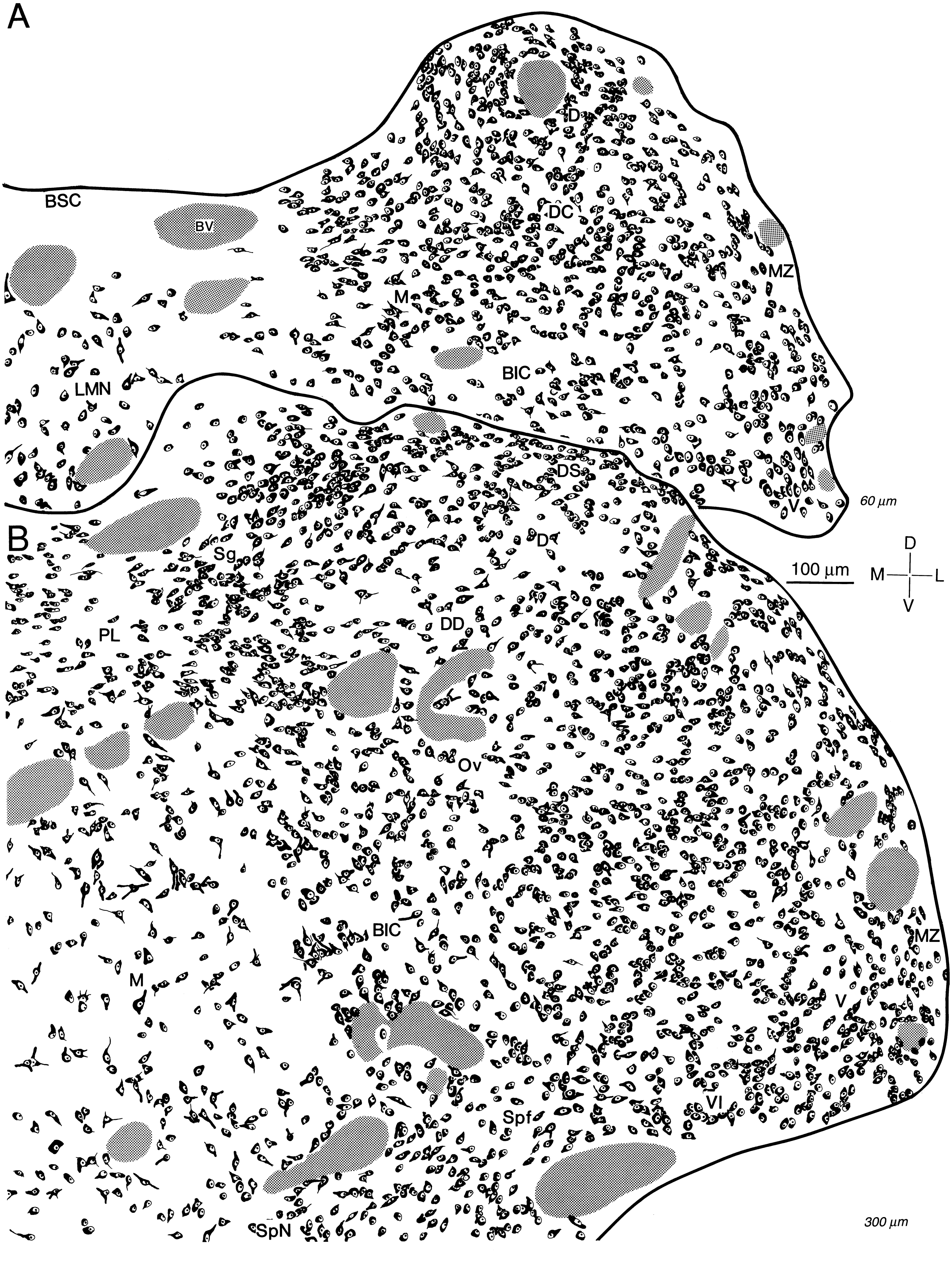
Fig. 9. Cytoarchitecture of the caudal medial geniculate body. A: At the extreme caudal tip, dorsal division nuclei (D) and the medial division (M) were dominant. Neurons in the most superficial dorsal nucleus were oriented parallel to the nuclear perimeter, while deeper-lying dorsal nucleus neurons had a wide variety of arrangements. Protocol for Figs. 9–12: Nissl preparation, 25 μm thick section. Planachromat, N.A. 0.65, ×500. The number at the lower right in each panel is the distance from the caudal tip of the medial geniculate body. B: At ~25% of the caudo-rostral length of the auditory thalamus, all the main nuclei were well developed. Somata in the lateral part of the ventral division (V) had a dorso-lateral to ventro-medial orientation, while pars ovoidea (Ov) neurons were dispersed by brachial axons (see Fig. 8B: BIC). Dorsal superficial nucleus (DS) neurons formed a sheet ~200 μm deep by 700 μm wide along the dorso-lateral surface of the medial geniculate body. Neurons in the subjacent dorsal nucleus (D) were packed more loosely and had no consistent orientation; while the same neuronal types were present, radiate neurons with spherical dendritic fields dominated. The deep dorsal nucleus (DD) was just beginning as a group of slightly larger neurons that became prominent more rostrally (Fig. 10: DD). Suprageniculate nucleus (Sg) neurons sometimes were more clustered and smaller than medial division (M) neurons. The latter cells were dispersed in small groups in the thalamic neuropil (Fig. 6F).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L
V
PL
DD
Ov
BIC
MZ
M
V
VI
Spf
SpN
300 µm

Kelly and Kavanagh, 1986 [rat]). This result contrasts with the more severe effects observed commonly in other species (Diamond and Neff, 1957; Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984 [cat]); Kavanagh and Kelly, 1987 [ferret]; Heffner and Masterton, 1975 [monkey]). These species differences suggest a functional non-equivalence in rodent thalamocortical organization compared to that in other species.

The physiological responses of ventral division neurons are well documented in the cat and consistent with the idea that it is a primary hub in the thalamic auditory system, though the physiological data available in rodents are limited. These cells have a systematic spatial distribution of unit characteristic frequency (Imig and Morel, 1985 [cat]), they respond preferentially to auditory stimuli and their Q_{10dB} values exceed those of neurons in other auditory thalamic regions (Aitkin and Webster, 1972 [cat]), and they project exclusively onto auditory cortex (Winer et al., 1977 [cat]). In the rat, few of these parameters have been examined systematically. One study found that the postsynaptic response in the ventral division to brachial stimulation in an in vitro slice preparation is a single (or sometimes two) short latency spike(s) (Hu, 1995). This could allow these neurons to encode signal onset or offset with temporal fidelity, and it is consistent with the behavior of ventral division cells as reported in other species. A combined physiological-anatomical investigation found a monosynaptic pathway from the inferior colliculus to the medial geniculate body from GABAergic collicular neurons (Peruzzi et al., 1997 [rat]). This suggests that even the classical lemniscal pathway contains more than one transmitter-specific projection. Since there are so few Golgi type II neurons in the ventral division (present results, and Winer and Larue, 1988 [rat]) this suggests that the postsynaptic target of the many GABAergic colliculogeniculate neurons must be principal cells and that the (presumptively excitatory) amino acidergic inputs must converge on the same neurons (Winer et al., 1996 [cat]).

The physiological response of rat dorsal division neurons contrasts with that of ventral division cells. Dorsal division neurons responded to brachial shocks with delayed bursts in which a low threshold spike is elicited by excitatory postsynaptic potentials, while ventral division cells appear to lack this mechanism. Moreover, dorsal division neurons were more hyperpolarized at rest and did not have inwardly rectifying channels that might block long latency burst responses (Hu, 1995 [rat]). These features are consistent with the extracellular responses of cat dorsal division neurons, which have little capacity to encode temporal events precisely since their onset-offset behavior correlated so poorly with that of the stimulus (Aitkin and Prain, 1974 [cat]).

Dorsal division neurons have some features in common with neurons in the other divisions. For example, they receive both inferior colliculus input and projections from the lateral tegmental system of the midbrain (LeDoux et al., 1985 [rat]), a region whose role in hearing is not clear (Morest, 1965 [cat]). While dorsal division cells respond to auditory stimuli, their tonotopic arrangement was neither as precise as that of ventral division neurons nor as diffuse as those of the medial division (but see Gross et al., 1974 [squirrel monkey]). Though the neurons respond best to auditory stimuli, pure tones were often ineffective in driving them (Aitkin and Dunlop, 1968 [cat]). These properties are consistent with a role in processing species specific communication signals which might be involved in reproduction or territoriality or social behavior; such signals often have complex spectral and temporal profiles that might selectively excite dorsal division neurons with the appropriate filter properties. Other dorsal division neurons, especially those in the suprageniculate nucleus, had polymodal affiliations (Benedek et al., 1997 [cat]). Electrical stimulation of the dorsal and ventral divisions blocked high frequency ($\sim$40 Hz) cortical gamma potentials, while stimulating the nearby posterior intralaminar nucleus elicited them. Thus, extra-auditory nuclei as well as the medial geniculate body may play a role in coordinating cortical discharges between different architectonic fields (Barth and MacDonald, 1996 [rat]).

This suggests that different thalamic nuclei may have dissimilar roles in cortical modulation. Thus, in other rodents, pharmacological inactivation of caudomedial parts of the medial geniculate body affected the middle latency response in both the midline cortex and in the temporal lobe, while ventral division inactivation involved only the temporal lobe (McGee et al., 1992 [guinea pig]). Likewise, the mismatch negativity response was under specific control by the caudomedial, and not the ventral, part of the auditory thalamus, and the tone-evoked response to stimulation was seen only

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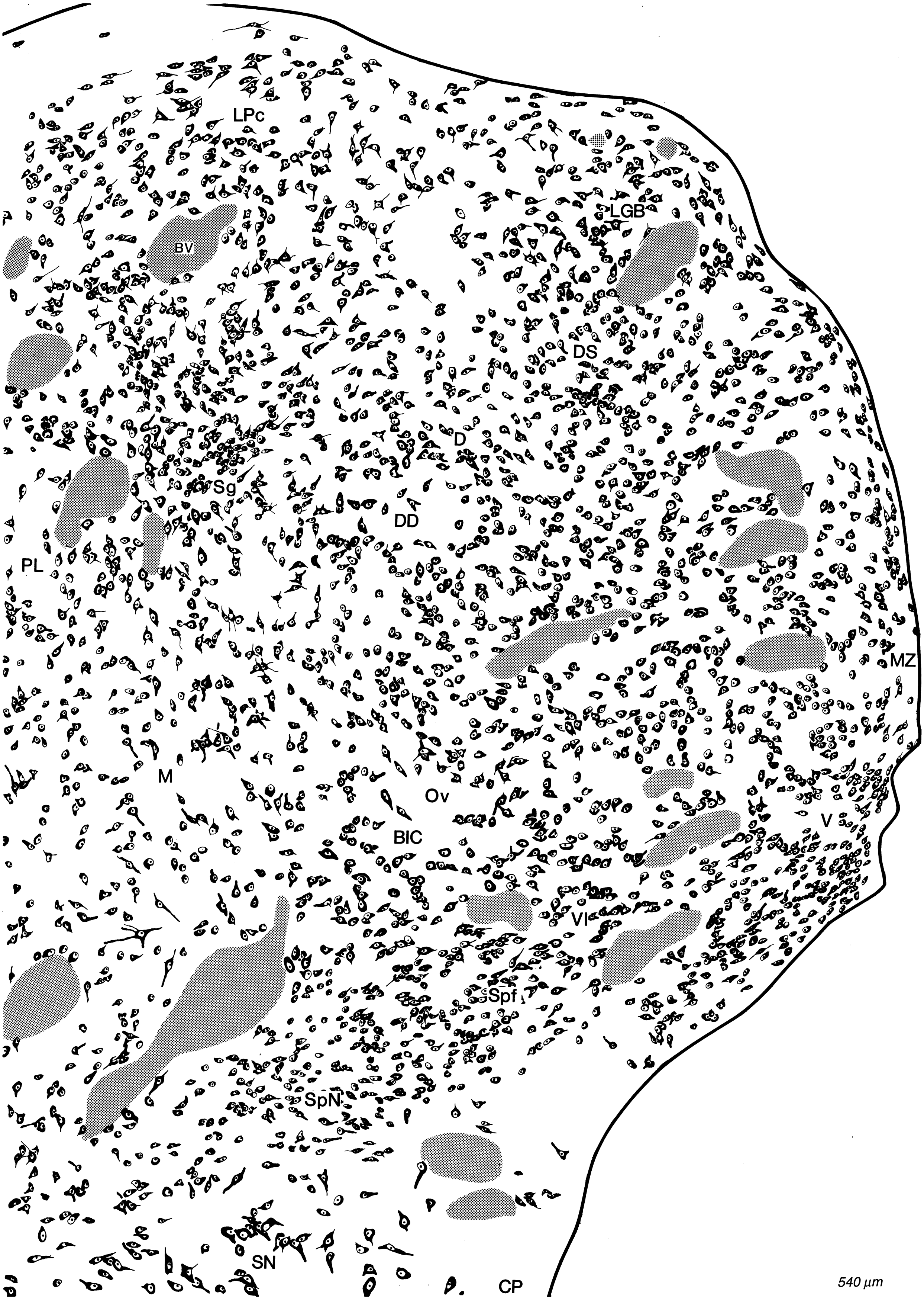
Fig. 10. Just caudal to the midpoint of the medial geniculate body, the principal divisions on the medial wall adjoined non-auditory nuclei. The ventral division (V, Ov) had attained its zenith, the dorsal division nuclei (D, DD) were each bordered by a fibrous capsule that aided their identification, and the posterior intralaminar (represented by the subparafascicular [Spf] system) was well developed. The medial division provided a clear example of the criteria used to distinguish medial geniculate body divisions: (i) its neurons were bigger and more loosely packed than those of the overlying suprageniculate nucleus (Sg); (ii) the cells were larger and had more dendritic staining than those of the lateral mesencephalic nucleus, which it abutted medially (unlabeled); (iii) neurons in the subparafascicular nucleus were oriented dorso-laterally to ventro-medially, while medial division cells were more vertical; (iv) neurons in pars ovoidea (Ov) were smaller and in continuity with pars lateralis cells (V); (v) these boundaries were in accord with those in Golgi (Fig. 1) and fiber stained material (Fig. 6F, Fig. 7); and (vi) they were in agreement with the distribution of tectothalamic axons in connectional studies (LeDoux et al., 1987 [rat]).


LPc
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540 μm

in the midline cortex (Kraus et al., 1994b [guinea pig]). Certain synthesized speech sounds selectively activated the dorsal division (Kraus et al., 1994a [guinea pig]). Taken together, these results, in conjunction with the distinct pattern of midbrain input to the dorsal division (LeDoux et al., 1987 [rat]), support the idea that the rodent dorsal division has a different, but no less specific, functional arrangement than the ventral division.

Finally, the chief target of dorsal division projections is nonprimary auditory cortex (Winer and Larue, 1987; Arnault and Roger, 1990 [rat]), areas without a clear tonotopic organization. Perhaps these regions have a role in the discrimination of sound patterns rather than the exact representation of peripheral auditory events.

In the medial division, the pattern of organization is unique: there is little or no systematic spatial representation of sound frequency except in a gradual or coarse fashion (Rouiller et al., 1989 [cat]), and the Q_{10dB} values of single neurons are low enough to suggest that many may not have precisely definable characteristic frequencies (Aitkin, 1973 [cat]). These neurons respond to extra-auditory input (Wepsic, 1966 [cat]), and they project to auditory and non-auditory cortex (Winer et al., 1977 [cat]) and to the limbic system as well (LeDoux et al., 1985 [rat]). Certain other features also distinguish the medial division from other auditory thalamic nuclei. For example, its neurons are the last to migrate during prenatal ontogenesis (Altman and Bayer, 1989 [rat]), and its connections with the cortex terminate chiefly in layers I and VI (Patterson, 1976 [rat]; Vaughan, 1983 [rat]).

The projection of the medial division to the amygdala (LeDoux and Farb, 1991 [rat]) also links the extralemniscal and multisensory output of the auditory thalamus with widespread areas of the limbic forebrain and beyond. Besides the obvious influence that this auditory thalamic input might have on autonomic responses via forebrain amygdalofugal projections, the central amygdaloid nucleus projects to the caudal part of the pontine reticular nucleus, which may be implicated in the acoustic startle reflex (Rosen et al., 1991 [rat]). Both the central and the lateral amygdaloid nuclei are targets of the medial division (LeDoux et al., 1990 [rat]), whose projection is believed to be glutamatergic (LeDoux and Farb, 1991 [rat]) and to form asymmetric synapses chiefly on dendritic spines (LeDoux et al., 1991 [rat]; but see Moriizumi and Hattori, 1992 [rat]). This suggests that the few glutamic acid decarboxylase-immunoreactive (GABAergic) neurons in the medial division have a purely intrinsic role (Winer and Larue, 1988 [rat]). The medial division and the posterior intralaminar nucleus both project to the caudoputamen as well as the amygdala, and this input is recapitulated by a corticostriatal projection arising from nonprimary auditory cortex, field TE3 (Arnault and Roger, 1990 [rat]). One possible role for the amygdala is integrative, since single neurons receive convergent auditory thalamic, hippocampal, and basal forebrain input (Mello et al., 1992 [rat]). The medial division thus acts as a polymodal hub for the redistribution of thalamocortical and thalamolimbic influence. Since medial division neurons show enduring associative changes in learning paradigms (McEchron et al., 1996 [rabbit]), they could exert a polysynaptic influence on the responses of cortical, subcortical and brain stem neurons to acoustic and non-auditory stimuli.

4.2. *Comparison with other species*

Extending these findings to those in other species is problematic, since limited physiological data are available for the rat auditory thalamus (Hu et al., 1994; Hu, 1995). The many parallels between the rat and the cat suggest that certain features of medial geniculate body organization are highly conserved. For example, in the ventral division, the principal type of neuron is a bushy tufted cell (Morest, 1964 [cat]; Clerici and Coleman, 1990 [rat]; Winer and Wenstrup, 1994 [bat]) which is the target of lateral lemniscal axons (Morest, 1975 [cat]; LeDoux et al., 1987 [rat]); these neurons project topographically onto primary auditory cortex, ending chiefly in layers III–IV (Sousa-Pinto, 1973 [cat]; Winer, 1992 [cat]; Romanski and LeDoux, 1993 [rat]). The medial division, likewise, has many features conserved across species. The neuronal architecture in both cat and rat is heterogeneous and several presumptively homologous classes of neuron can be identified (Winer and Morest, 1983a [cat]; Clerici et al., 1990 [rat]). In each species the medial division projects to layers I and VI in auditory and periauditory cortex (Mitani et al., 1984 [cat]; Vaughan, 1983 [rat]) and to the amygdala as well (LeDoux and Farb, 1991 [rat]; LeDoux et al., 1991 [rat]; Huang and Winer, 1997 [cat]). It is possible to draw analogous parallels for the dorsal division.

The species differences are equally illuminating. The

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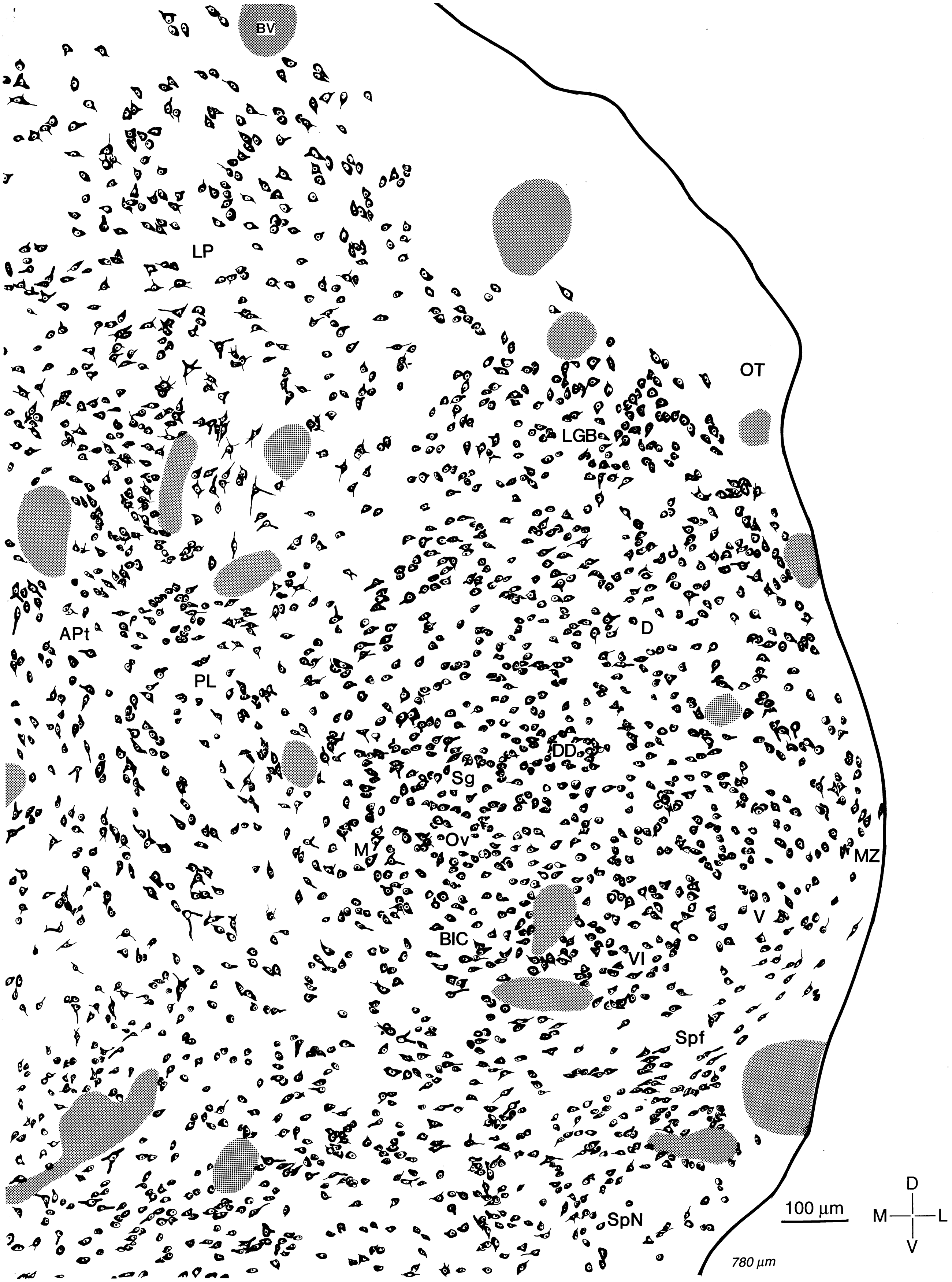
Fig. 11. About two-thirds of the way through the medial geniculate body (Fig. 8D), this section marked the beginning of the progressive diminution of the auditory thalamus as visual and other sensory nuclei and the posterior intralaminar system expanded. At this level, the entire medial geniculate body was embedded in a fibrous capsule of thalamofugal and thalamopetal axons. Ventrally, posterior intralaminar nuclear axons and corticofugal axons (Winer and Larue, 1987 [rat]) were present; medially, medial lemniscal fibers ascending toward the ventrobasal complex (Fig. 12: Vb, eml, ML) dominated, and axons from the brachium of the inferior colliculus were still present; and dorsally, corticofugal and thalamofugal systems contributed thin axons to the neuropil. While each medial geniculate subdivision was small, their boundaries were nevertheless established readily.


BV
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100 µm
D
M
L
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780 µm

few glutamic acid-decarboxylase (GAD) immunostained neurons in the rat medial geniculate body (Winer and Larue, 1988) is consistent with the paucity of Golgi type II cells impregnated in the present account. We have considered the implications of substantial species differences in the proportion of GABAergic neurons and Golgi type II cells elsewhere (Morest and Winer, 1986 [opossum, cat]). These range in number from $<1\%$ in the rat (Winer and Larue, 1988) and mustached bat (Winer et al., 1992, 1995) to $>30\%$ in the macaque monkey (Winer and Larue, 1996). The virtual absence in the rat somatic sensory thalamus of the dendrodendritic glomerular synaptic arrangements (Ohara and Lieberman, 1993) that are a hallmark of cat and monkey thalamic circuitry (Ralston, 1983) might suggest a species specific difference in kind in thalamic processing. An exception to this view is the finding that the rodent lateral geniculate body contains ~20% GABAergic neurons (Ohara et al., 1983). It remains to be seen how the processing and transfer of synaptic information differs in the ventrobasal complex in species with no (Harris and Hendrickson, 1987 [rat]), or a few (Penny et al., 1984 [rabbit]), or with many (Penny et al., 1983 [cat]) GABAergic neurons. Such differences raise again the question of what role a few GABAergic neurons might play physiologically (Arcelli et al., 1997 [rat, guinea-pig, cat, rabbit, monkey]), as well as the developmental basis for such a diverse range of neurochemical and synaptic patterns.

4.3. *Comparison with other studies*

There is substantial concordance between the types of neurons described here and the architectonic plans proposed in prior studies (LeDoux et al., 1985, 1987; Clerici and Coleman, 1990, 1998; Clerici et al., 1990 [rat]). Most of the same subdivisions are recognized, and the main neuronal types appear quite similar. Intracellular injections of single neurons in vitro have identified tufted cells in the ventral division and radiate neurons in the dorsal division (Hu et al., 1994 [rat]), whose configuration compares favorably with the Golgi impregnated neurons in the present investigation. The features of intrinsic type II cells remains a matter for further inquiry. The reasons for their relative rarity in Golgi impregnated material are better appreciated now (Winer et al., 1995 [bat]; Winer and Larue, 1996 [rat, bat, cat, and monkey]) than in prior work in the rat (Winer and Larue, 1987) and marsupial and carnivore (Morest and Winer, 1986; Winer et al., 1988) auditory thalamus, where their apparent refractoriness to impregnation was puzzling. The present study and an earlier immunocytochemical investigation (Winer and Larue, 1988 [rat]) provide the only direct, albeit limited, evidence for these neurons. Their most striking immunocytochemical feature in the latter investigation was dendrites up to 500 μm long with elaborate appendages; these neurons were rarely anaxonal. None of the prospective Golgi type II cells in our admittedly small sample had such long or complex dendrites. The possibility remains that either these processes are refractory to impregnation or that a type of neuron (the small cell) contains chemically specific subclasses that remain to be identified in Golgi preparations. The cat had many more, and different types of, the stellate neurons presumed here to have a local circuit role (Winer and Morest, 1983b).

Another unresolved issue is the precise territorial limits of the medial geniculate complex, particularly the rostral pole. In a companion study, we estimated the total caudo-rostral length at ~1200 μm in horizontally (Winer et al., 1999, Fig. 8C [rat]) or transversely (present account) sectioned material. Even the most rostral section in the present study (Fig. 12) leaves ~15% of the medial geniculate complex, as defined here, largely unexplored. Since thalamocortical projections arise from (Winer and Larue, 1987 [rat]; Winer et al., 1999 [rat]), and the tectothalamic input terminates in (LeDoux et al., 1987 [rat]), the entire medial geniculate body as we have defined it here, the rostral pole must play some role in thalamic auditory processing that remains to be explored. In the cat, the rostral pole contains a representation favoring the high frequency segment of the basilar membrane (Imig and Morel, 1985) and caudo-rostral gradients of thalamocortical projection and functional organization have also been reported (Rodrigues-Dagaeff et al., 1989). The rostral pole may therefore be a distinct architectonic entity in the rat as well.

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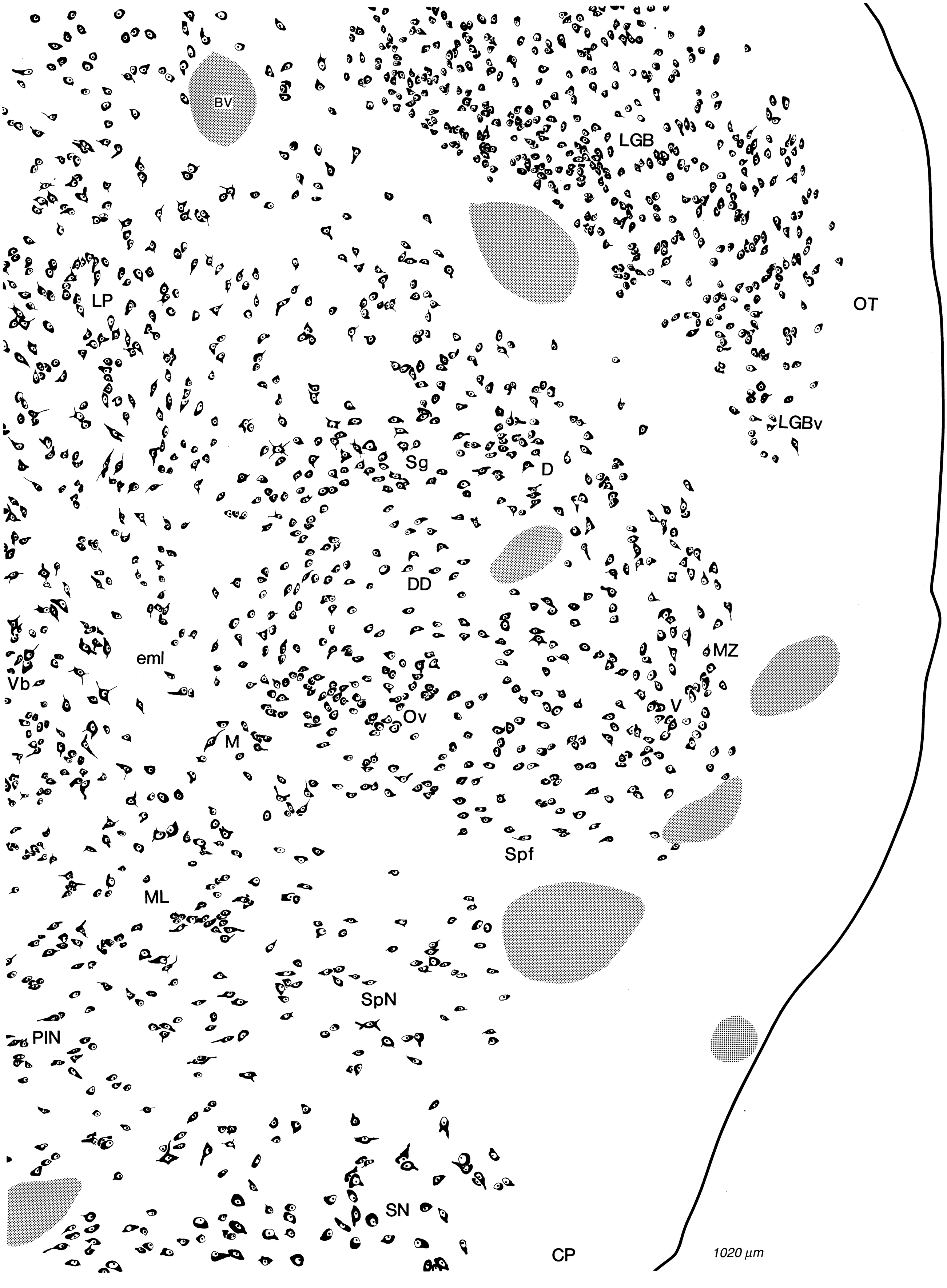
Fig. 12. This section was at ~80% of the caudo-rostral extent of the medial geniculate body, which assumed a teardrop shape and was now embedded in a matrix of axons. The inferior brachium could no longer be recognized as an entity. The continuity in neuronal structure between suprageniculate nucleus (Sg) and lateral posterior (LP) neurons was embodied by cells of similar size and shape in the ventrobasal complex neurons (Vb).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SpN
PIN
SN
CP
1020 µm

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