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The human medial geniculate body

Jeffery A. Winer

Department of Physiology – Anatomy, University of California, Berkeley, CA 94720, U.S.A.

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The medial geniculate body in non-human species is divided into several parts, each with a different structure, physiological organization, and pattern of connections. Which parts of the human medial geniculate body and which types of neurons might be homologous to those of other species is unknown, and the object of the present study.

The cytoarchitecture, fiber architecture, and neuronal organization of the adult human medial geniculate body were studied in Nissl, Golgi, and other preparations. Three divisions, comparable to those in other mammals, were described. The ventral division had a bimodal distribution of somatic sizes in Nissl material which, in Golgi impregnations, may correspond, respectively, to a larger neuron with bushy dendrites and a tufted branching pattern, and a smaller stellate cell with a radiating, spherical dendritic field. The large neurons formed clusters surrounded by a particular pattern of neuropil which, together, constituted fibro-dendritic laminae whose long axis was oriented medio-laterally in parallel sheets or rows. The dorsal division was dominated by small and medium-sized somata representing at least three populations of neurons in the Golgi preparations. The large stellate cell had a radiate dendritic field and a dichotomous branching pattern; an equally large neuron with an elongated, multiangular perikaryon and bushy dendritic arbors forming tufts also occurred. Blended among these larger neurons were many smaller cells with tiny, flask-shaped, round, or drumstick-like perikarya, limited dendritic fields and thin dendrites, and poorly developed stellate or bushy dendritic configurations. In the medial division, larger somata were more common than in the other medial geniculate divisions, but small cells were present in considerable numbers.

The fiber architecture and the different kinds of neurons distinguished the three major divisions and the nuclei within them. Thus, the ventral nucleus had long fascicles of axons running parallel to the dendrites of bushy neurons, while the marginal and ovoid nuclei had a different organization. The dorsal division had a more diffuse, irregular arrangement of thinner axons interspersed among bundles of coarser fibers, whereas the medial division was traversed by many coarse preterminal axons passing laterally and dorsally from the brachium of the inferior colliculus; these imparted a striated pattern to the neuropil. Regional variation in cytoarchitecture and the fiber plexus defined several nuclei in each subdivision, except in the medial division, where the density of the staining made further subdivision impossible.

A singular morphological feature of the human medial geniculate body was the enormous development of the neuropil, such that single neurons or small groups of cells were often surrounded by expanses of fibers and clusters of glial cells 200 μm or more in diameter. Since these interstices must be partially filled by dendrites, afferent fibers, and intrinsic axons, it implies that the neuropil might have a somewhat different, perhaps elaborated, role in human hearing, in contrast to infrahuman species, in whom it appears to be comparatively reduced.

medial geniculate body, auditory thalamus, cytoarchitecture, neuronal architecture, neuropil organization, human thalamus, tonotopic organization, auditory system

Introduction

The history of neuroanatomy in general, and of the study of the great sensory systems in particular, is one of progressive subdivision, both anatomical and physiological. Structures and functions once believed to be uniform and isomorphic are reluctantly but nonetheless inevitably subdivided in the name of more precise localization of cerebral function. The infrahuman medial geniculate body is no exception to this pattern, and since 1900 it has been subdivided anatomically into, for example, two [55] or three [53] main parts and as many as thirteen [40,70] nuclei. A corresponding refinement in functional organization followed, such that certain parts (for example, the ventral

division) were regarded as principally auditory in view of the narrow tuning curves of the cells and their pattern of tonotopic organization [3]. Other parts (for example, the medial division) contain neurons with much broader, often polysensory tuning curves, and an unknown number of representations of the basilar membrane [1]. Moreover, the pattern of brain stem input to these divisions is different [4,42]. Thus, not all parts of the medial geniculate body can be considered as exclusively or equally auditory based on their connections, form, or function.

In previous work the human medial geniculate body has been analyzed mainly in terms of its topographic location [33], cortical connections [67], development [13,14,48], or functional organization [64,65]. However, its neuronal architecture has never been described in much detail, nor have systematic distinctions been made among the types of neurons and the patterns of neuropil organization between nuclei. In fact, the human medial geniculate body has usually been treated as containing rather few discrete architectonic territories, each with relatively homogeneous types of cells – generally large or small, with little effort made to systematically correlate these findings with those from studies of non-human species.

A cardinal principle of comparative neurology is that certain neuronal populations are homologous in different species [20,35]. However, the criterion of common ancestral origin used to support a claim of homology rarely permits a direct comparison of prototypical and extant brain structures. Thus, other anatomical criteria, such as analogous position [6,58], patterns of connections [23], mode and tempo of development [15,51,58], or similar functional organization [75], are often adduced to justify homology. These issues and their possible functional implications are the main questions addressed here. Insofar as the human medial geniculate body (or parts of it) may be considered as homologous to the corresponding neuronal populations in the non-human medial geniculate body, similar kinds of neurons, and perhaps a comparable architectonic organization, might occur in both. The present study describes several nuclei and types of neurons which could be homologous on the bases of structure and position, and a pattern of neuropil organization whose degree of development may be related to human verbal and auditory behavior.

Method

Brain stems including the medial geniculate bodies from seven adult male or female humans (fourteen complete thalami) were available for study. The range of ages was 47–64 years and the cause of death in each case was of non-neurological origin. Audiograms were not available but an examination of the clinical history excluded persons with gross hearing defects. The brain was removed within a few hours of death and immersed in fixative (10% formalin–saline) or Golgi–Cox fluid.

Eight thalami were studied with Nissl and various fiber preparations. Each thalamus was sectioned serially in either the transverse plane, with an orientation similar to that of atlases of the human thalamus [5,18], or horizontally, in a plane intersecting the habenula, the caudolateral extremity of the pulvinar, and the inferior colliculus. Four thalami were embedded in low viscosity nitrocellulose or frozen sectioned at 30–60 μm thickness, and alternating series were stained for Nissl substance with cresylecht violet, or for fibers with the Weil or Weigert technics. Four other thalami were embedded in paraffin and sectioned at 10–20 μm and stained for cells or fibers.

Six thalami were prepared by the Golgi–Cox method [16,54]. These were immersed in potassium dichromate–mercuric chloride fixative at room temperature in darkness for 30–45 days, then dehydrated in ascending concentrations of alcohol, embedded in low viscosity nitrocellulose, and sectioned serially at 160 μm. The mercuric salts were precipitated in strong ammonia and the reaction was stopped with 1% sodium thiosulfate using the on-the-slide method of Ramon-Moliner [54]. After dehydrating, clearing, and coverslipping, the sections were studied on a Zeiss WL microscope with a drawing tube and through semi-, planachro-, or planapochromatic lenses having long working distance (300 μm or more) and high numerical aperture (N.A. 0.65–1.4). The particulars of the lens used to make each drawing are indicated in the figure legend.

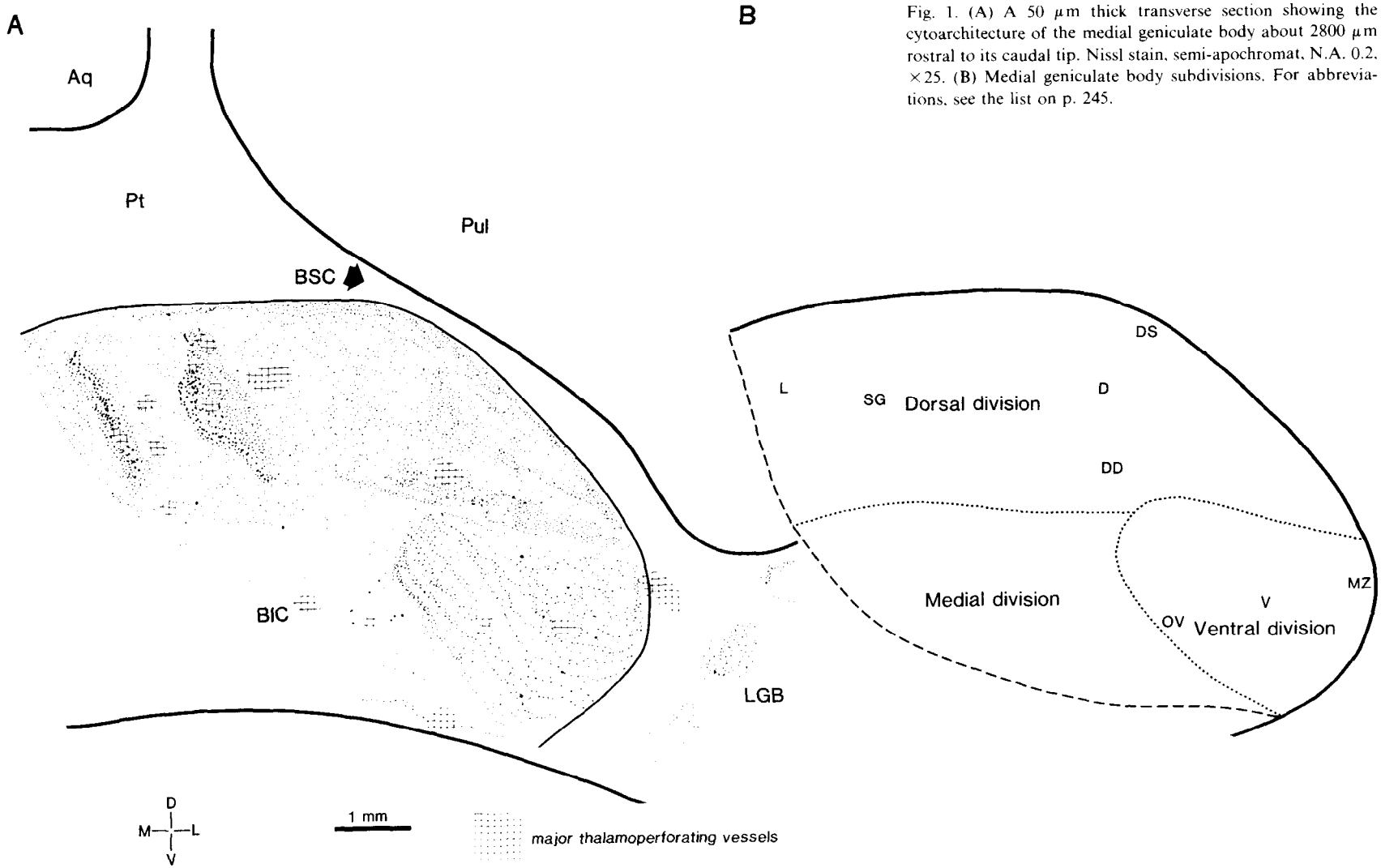

Fig. 1. (A) A 50 μm thick transverse section showing the cytoarchitecture of the medial geniculate body about 2800 μm rostral to its caudal tip. Nissl stain, semi-apochromat, N.A. 0.2, $\times$25. (B) Medial geniculate body subdivisions. For abbreviations, see the list on p. 245.

Results

The human medial geniculate body formed a small oval eminence protruding from the caudal extremity of the diencephalon, where it nestled beneath the immensely expanded pulvinar (Fig. 1A). It was flanked ventrolaterally by the lateral geniculate body, immediately dorsally by the tectal-pulvinar fibers, dorsomedially by the caudal surface of the pretectum, and rostrally by a large fiber capsule comprised of medial lemniscal and corticofugal axons which separated it from the caudal extension of the ventrobasal complex, with some of whose neurons it shared certain structural features. Grossly, the medial geniculate body was about 5 mm wide, 4 mm deep, and 4–5 mm long, and formed an oblate, slightly convex spheroid which was truncated somewhat along its ventromedial edge; rostrally, the various subnuclei formed small bulges on its dorsal surface. The ventromedial border was slightly concave. Many axons afferent to the medial geniculate body entered it from its inferior aspect (Fig. 2A, solid black) and from its rostral pole, too.

Cytoarchitecture and fiber architecture

In Nissl (Fig. 1A) and fiber stained preparations (Fig. 2) three major divisions were distinguished in the medial geniculate body. Each division differed in perikaryal size (Fig. 6), fiber plexus (Fig. 2), somatic packing density (Fig. 4), and neuronal morphology (Figs. 7–11). The ventral division filled the ventrolateral quarter, the medial division occupied the ventromedial margin, and the dorsal division formed a tier extending the length and breadth of the medial geniculate body.

Ventral division

The lateral border of the ventral division was bounded by fibers from the optic tract and axons which may be tectofugal, thalamofugal, or corticofugal (Fig. 3, inset). Few if any fibers destined for the ventral division or other parts of the medial geniculate body appeared to enter laterally. In the capsule of neuropil abutting the ventral division a few cells were dispersed; this slender lamella, comprised chiefly of axons and small, multipolar neurons, is the *marginal zone*, which extended ventrally to the lateral border of the cerebral peduncle (Fig. 3, MZ) and rings the free surface of the caudal pole of the medial geniculate body. It was distinguished from the ventral nucleus proper by the diffuse distribution of cells and the lack of any obvious laminar organization (Fig. 4A, MZ).

The *ventral nucleus* (Figs. 3, 4A) is the chief part of the ventral division. Its neurons were clearly separated from the dorsal (Fig. 3) and medial divisions (Fig. 1A) by cell-poor zones and differences in the orientation, fiber caliber, and texture of the axonal plexus (Fig. 2A), and by a distinctive pattern of neuronal architecture (see below). In somatic size, ventral nucleus cells clearly formed a bimodal (though continuous) distribution: small neurons (less than 100 μm^2 in somatic area) were nearly as numerous as the medium-sized perikarya (100–400 μm^2); very large cells (above 500 μm^2) were much less common (Fig. 6A, B). Smaller cells often have sparse cytoplasm, little Nissl substance, a round or oval somatic profile with few obvious dendrites, and a displaced nucleus (Fig. 4A). They appear scattered without any apparent pattern in the neuropil.

The medium-sized multipolar or bipolar neurons were roughly as numerous but had a different architectonic arrangement. They sometimes formed clusters of 5–20 cells which included the smaller neurons. However, in contrast to the small cells, they often had a preferred somatic orientation which was relatively constant from cluster-to-cluster (Fig. 5). Their long somatic axis may form slender rows which run from medial-to-lateral. More superficially in the ventral nucleus, the rows were more steeply inclined (Fig. 4A), and ventrally

Fig. 2. Fiber stained, transverse, 40 μm thick section, some → 3000 μm from the caudal tip. (A) The fiber plexus. The size and density of the lines and dots is proportional to fiber caliber and concentration. Dashed lines, fiber tracts. Weil stain, semi-apochromat, N.A. 0.2, ×23.5. (B) Ventral nucleus – marginal zone myeloarchitecture. In the ventral nucleus alternating strips of straight (thick arrowheads) and coiled (thin arrowheads) fibers are aligned, forming fibrous laminae possibly corresponding to the width (open circles) of the dendritic fields of the bushy cells with tufted dendritic branching (see Fig. 7A). The laminae are not present in the marginal zone. Protocol for panels (B, C) planachromat, N.A. 0.35, ×200. (C) Dorsal nucleus fibers without apparent laminar orientation, some forming axonal fascicles.

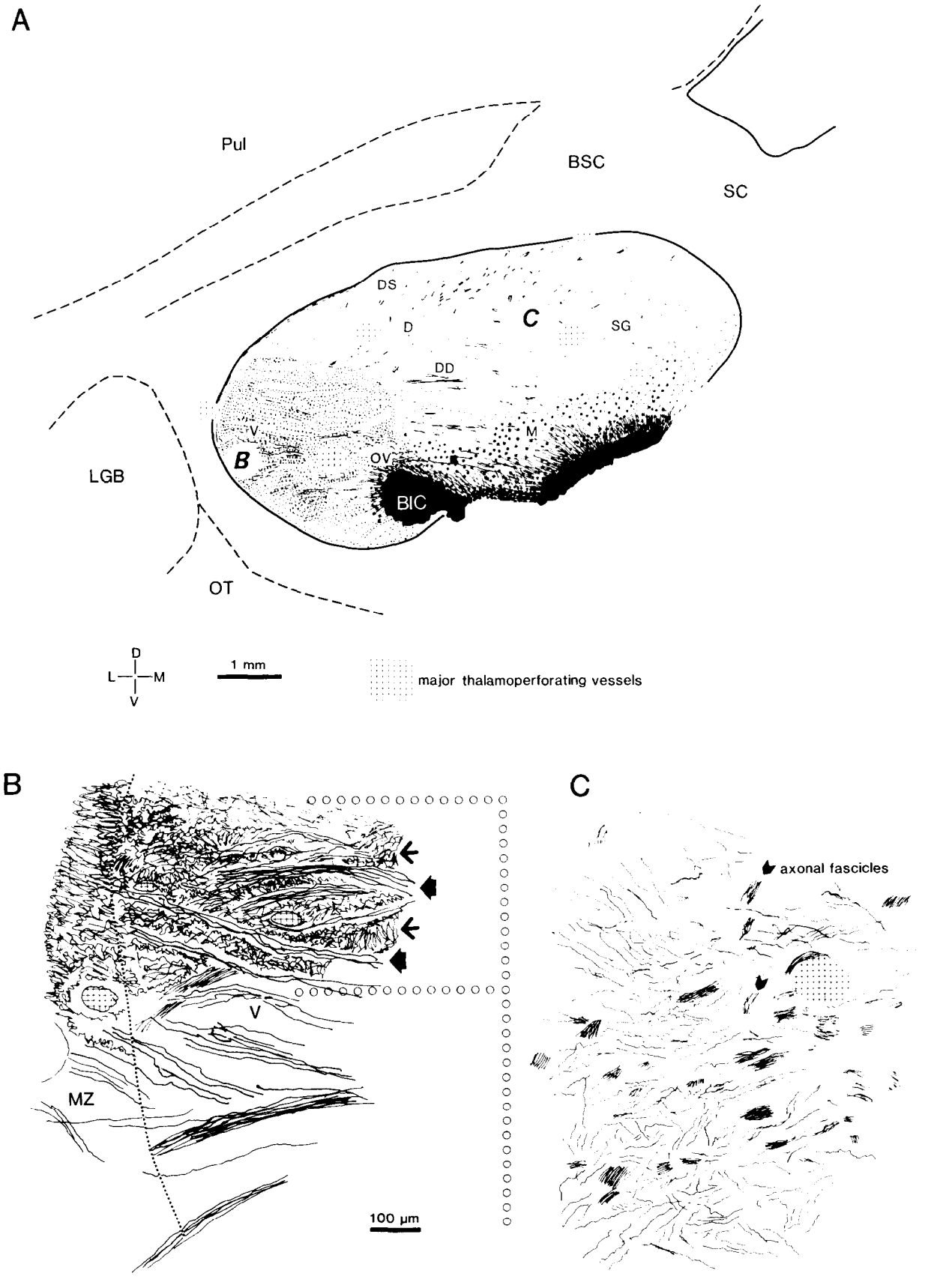
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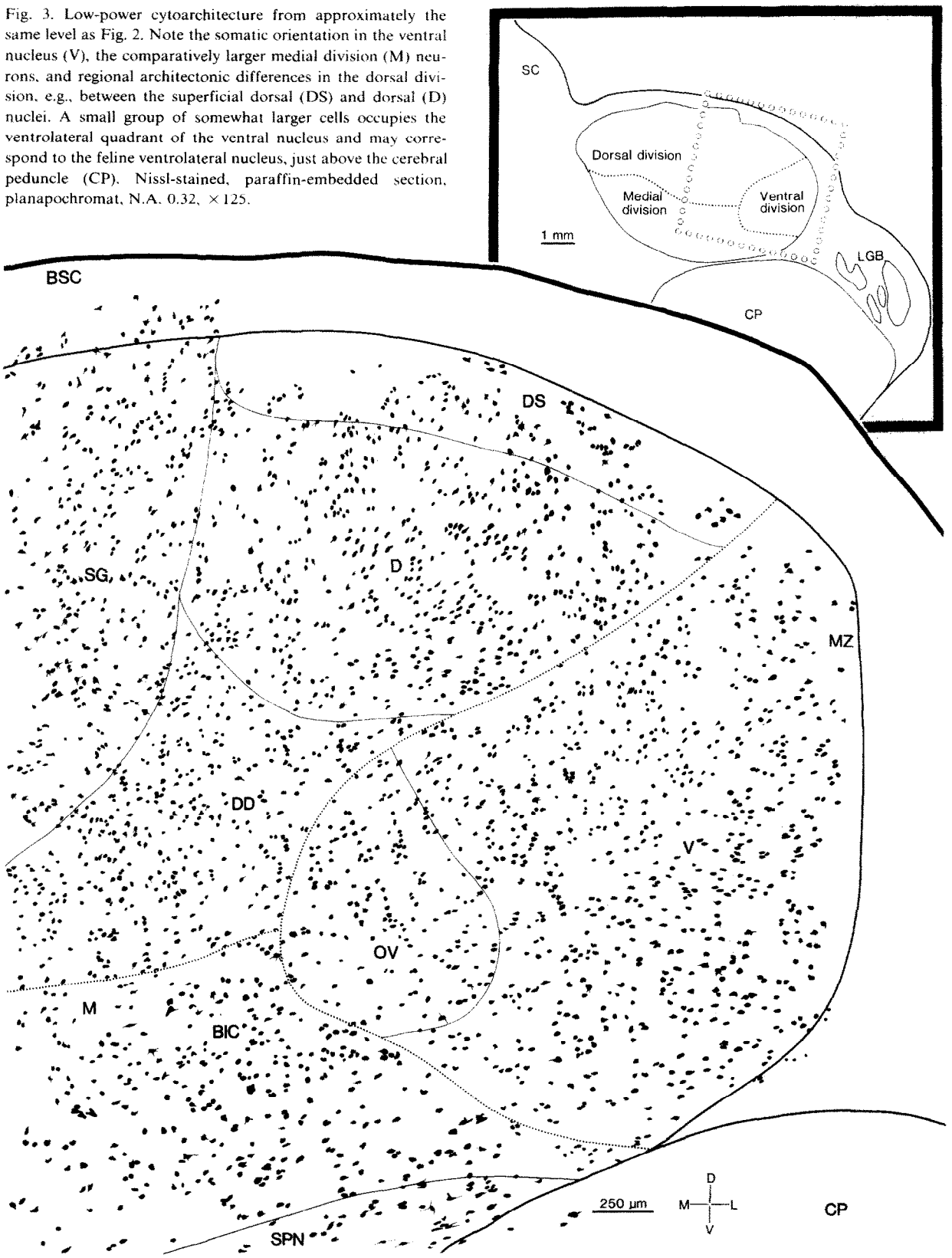
Fig. 3. Low-power cytoarchitecture from approximately the same level as Fig. 2. Note the somatic orientation in the ventral nucleus (V), the comparatively larger medial division (M) neurons, and regional architectonic differences in the dorsal division, e.g., between the superficial dorsal (DS) and dorsal (D) nuclei. A small group of somewhat larger cells occupies the ventrolateral quadrant of the ventral nucleus and may correspond to the feline ventrolateral nucleus, just above the cerebral peduncle (CP). Nissl-stained, paraffin-embedded section, planapochromat, N.A. 0.32, ×125.



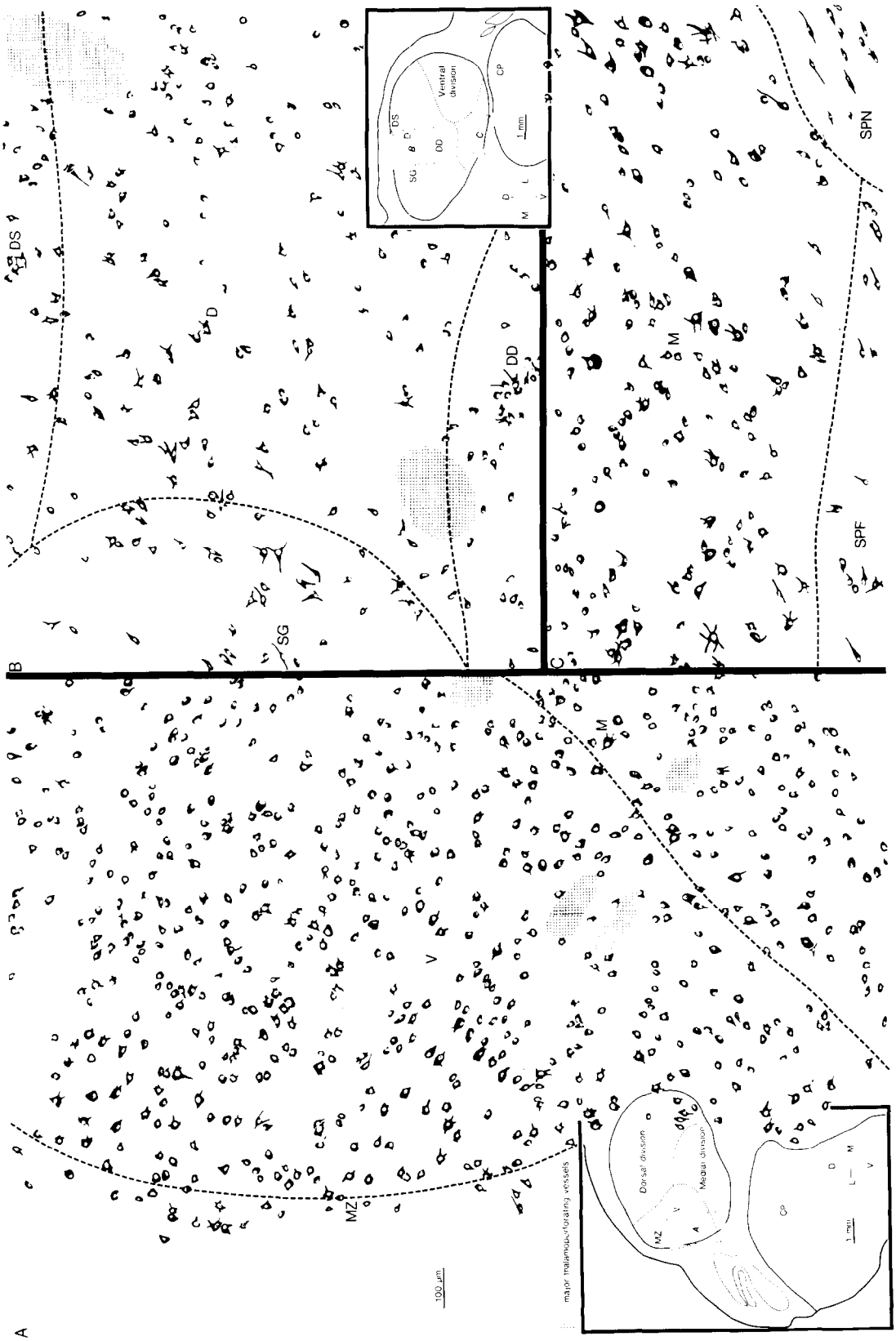
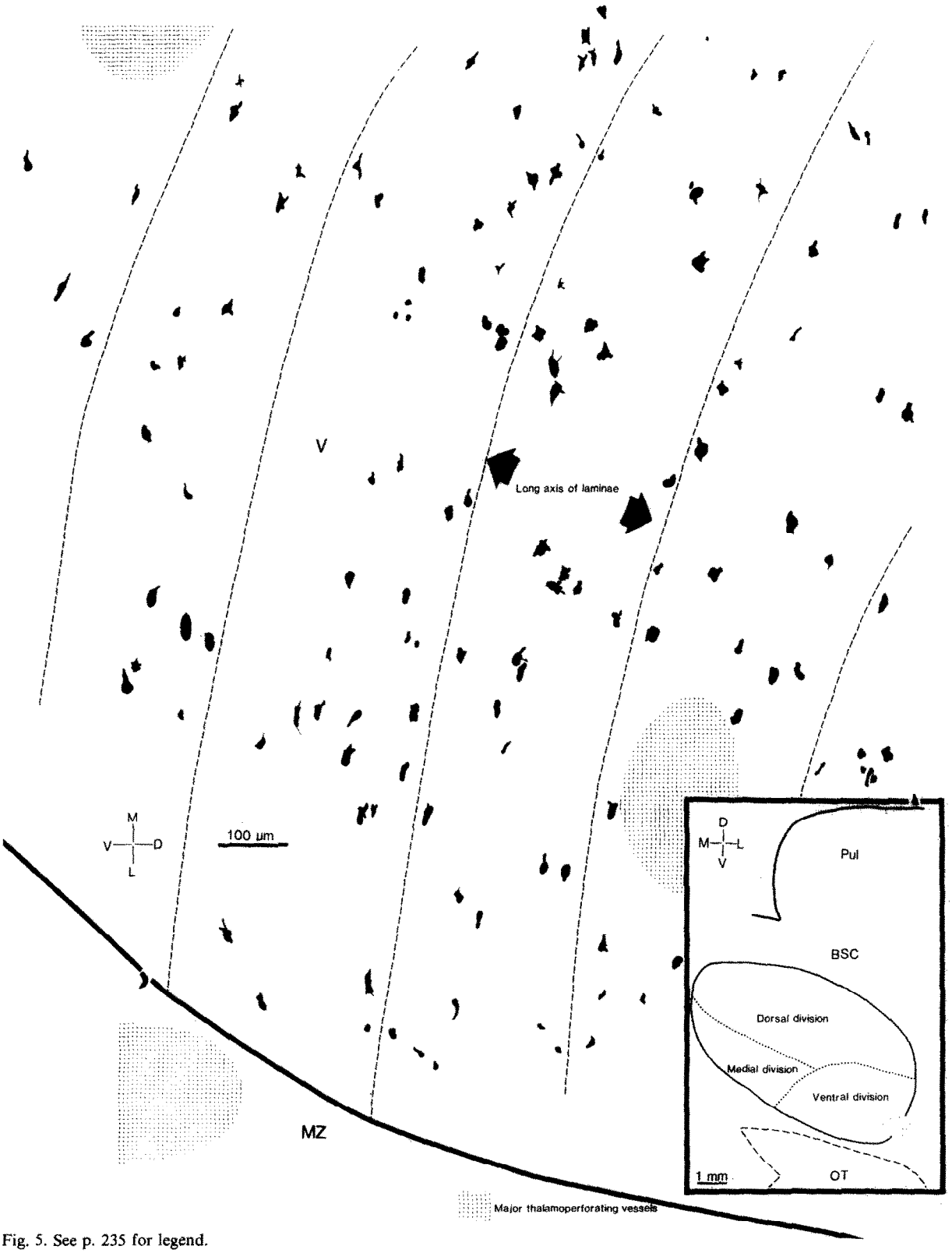


Fig. 4. See p. 235 for legend.



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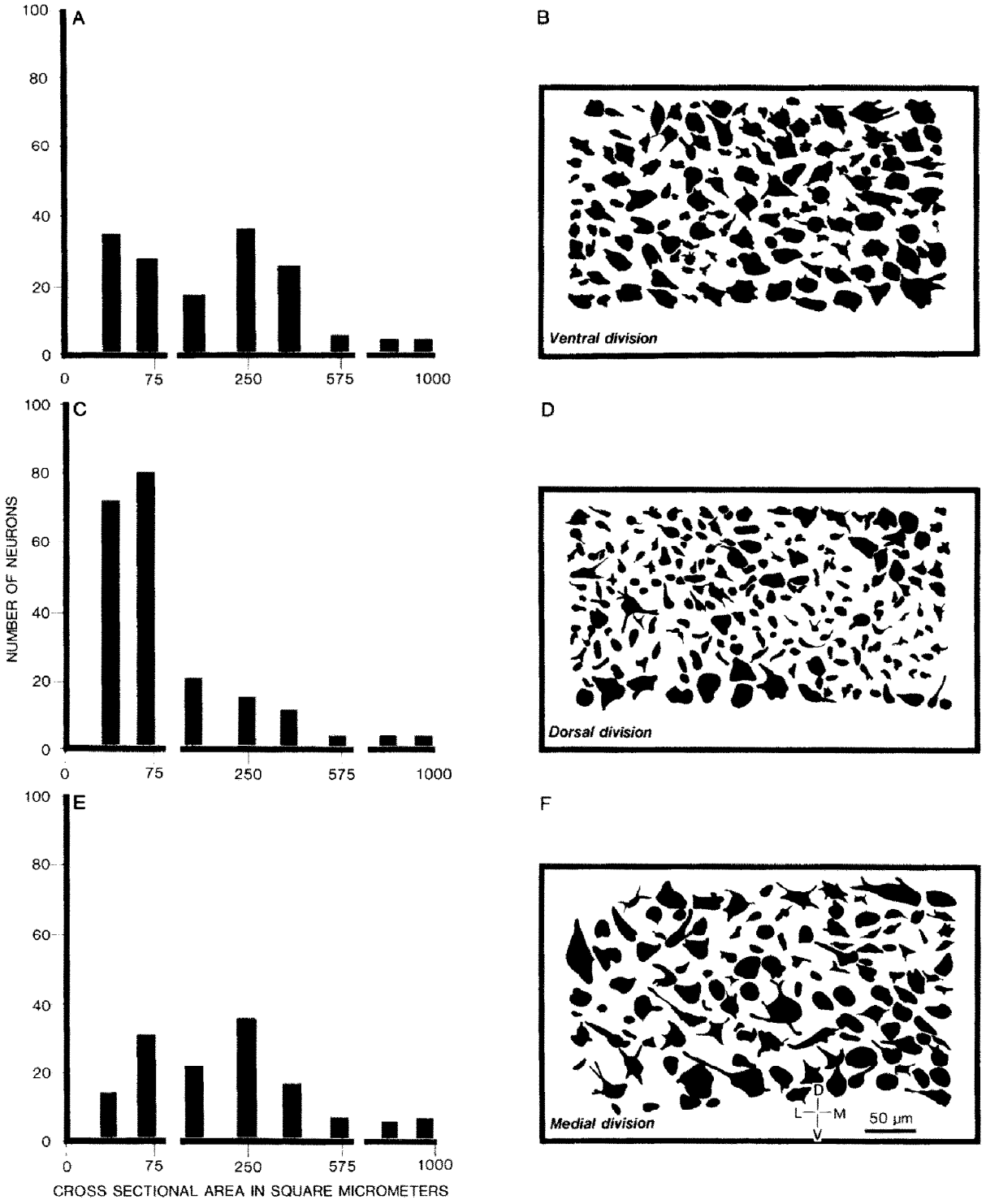

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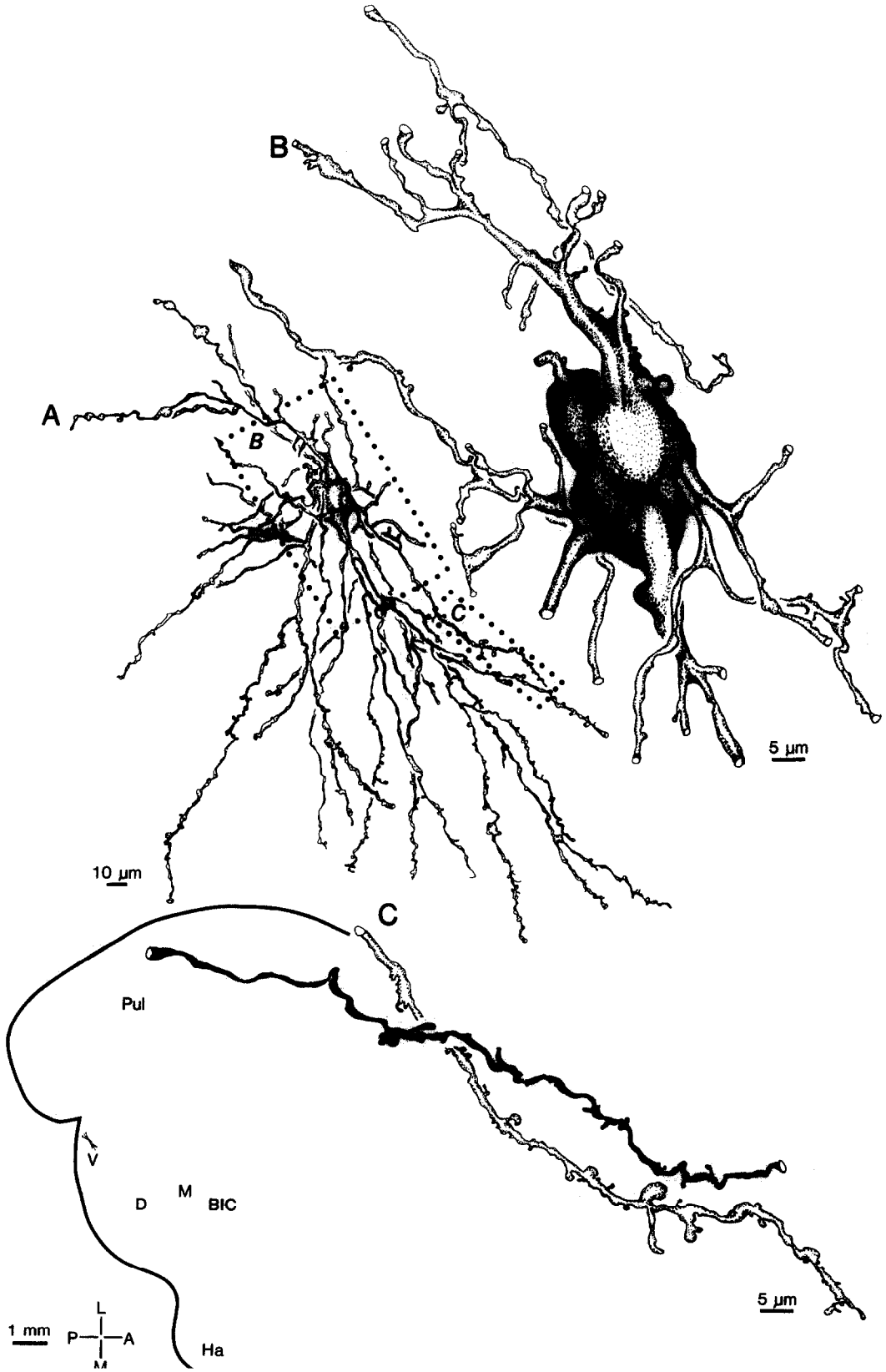
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they were longer and straighter (Fig. 5). In general, they resembled spokes radiating from a hub whose center lay in the medial division (Fig. 1A). The width of any single row cannot be estimated since particular cell clusters may overlap. In fiber stained material, fascicles of long, rather straight fibers (Fig. 2B, thick arrowheads) interlaced in an alternating pattern with finer, coiled axonal branches (Fig. 2B, thin arrowheads). These aggregations of straight and coiled fibers imposed a distinctive neuropil pattern throughout the ventral nucleus except at its juncture with the deep dorsal nucleus of the dorsal division, where a transitional zone occurred (Fig. 2A). The width of 5–8 of these fibrous laminae (Fig. 2B) and the span of single clusters of cells (Fig. 5) yielded a laminar breadth of 300–400 μm (Fig. 2B, open circles). Such laminae might include the dendritic arbors of roughly 2–3 of the large neurons believed to be principal cells (Fig. 7), and could easily include the bulk of the dendritic domains of the smaller cells with stellate dendritic fields (Fig. 8, stippled). The plexus of fibers in the marginal zone was different, consisting entirely of short, twisting axons abutting the curved, dorso-ventrally oriented visual radiations. Finally, in the ovoid nucleus of the ventral division, adjoining the dorsal, medial, and ventral divisions, the somata were still more dispersed, the conspicuous laminar arrangement of somata was absent, and massive bundles of brachial fibers ramified among the loose clusters of cells (Figs. 2A, 3).

Dorsal division

These nuclei extend from the caudal, free extremity of the medial geniculate body to its rostral tip where, much reduced in size, they form a cap separated by fibers from the caudal pole of the ventrobasal complex.

The cytoarchitecture of the dorsal division nuclei was dominated by small neuronal somata (less than 150 μm^2 in somatic area; Fig. 6C), most with an oblate profile (Fig. 6D). The medium-sized perikarya (150–500 μm^2) were either oval or elongated, and larger cells were rare. From cytoarchitecture, neuronal architecture (see below), and packing density, five dorsal division nuclei were distinguished. The *superficial dorsal nucleus*, like the marginal zone of the ventral nucleus, was surrounded by optic tract fibers and other axons, and had a dispersed, reticulated texture both in cell (Fig. 1A) and fiber (Fig. 2A: DS) preparations. Cellular packing density increased somewhat in the *dorsal nucleus* (Fig. 3) but, even here, large venues of the neuropil, territories as large as 200–400 μm, were virtually devoid of neurons (Fig. 4B: D). Undoubtedly, many of these spaces were filled with axons, some of which, perhaps of descending origin, formed fascicles oriented from dorsolateral-to-ventromedial (Fig. 2C, arrowheads). Other, much finer fibers imparted a lacy, filigreed texture to the dorsal nucleus axonal plexus without much consistent orientation. The *deep dorsal nucleus* was traversed by many thicker axons, including ones destined for the dorsal, superficial dorsal, and more medially placed dorsal division nuclei (Fig. 2A).

Dorsal nuclei somata were predominantly oval or multipolar. There was a slight increase in their packing density across the superficial dorsal, dorsal, and deep dorsal nuclei, but their shape was similar and they tended to cluster somewhat.

The *suprageniculate* and *posterior limitans nuclei* comprised, respectively, the medial and ventromedial limbs of the dorsal division. Suprageniculate

Fig. 4 (p. 231). Cytoarchitecture at a level midway through the medial geniculate body. (A) Ventral nucleus, showing dorsolateral-to-ventromedial disposition of somata. (B) Dorsal division nuclei. (C) Medial division and adjoining nuclei. Nissl-stained, paraffin-embedded section, planapochromat, N.A. 0.65, ×500.

Fig. 5 (p. 232). Cell clusters and presumptive laminar orientation in the ventral nucleus about 2500 μm from the caudal tip. Nissl-stained, frozen section, planapochromat, N.A. 0.35, ×200.

Fig. 6. (p. 233). Somatic size distributions taken from sections midway through the medial geniculate body. (A, B) Ventral nucleus of the ventral division. (C, D) Dorsal nucleus of the dorsal division. (E, F) Medial division. Nissl-stained, frozen section, planapochromat, N.A. 0.65, ×500.

← Fig. 7. (A) Large neuron in the ventral nucleus with bushy dendrites forming tufts. Semi-apochromat, N.A. 0.95, ×1060. (B) Soma and proximal dendrites at higher power. For panels B, C: planapochromat, N.A. 1.32, ×2000. (C) Dendrite (stippled) and a sinuous afferent axon (black) approaching it. *In this and the following figures where a process leaves the plane of section or is incomplete is shown by a hollow profile. The small inset drawing shows the position of the cell in the auditory thalamus.*

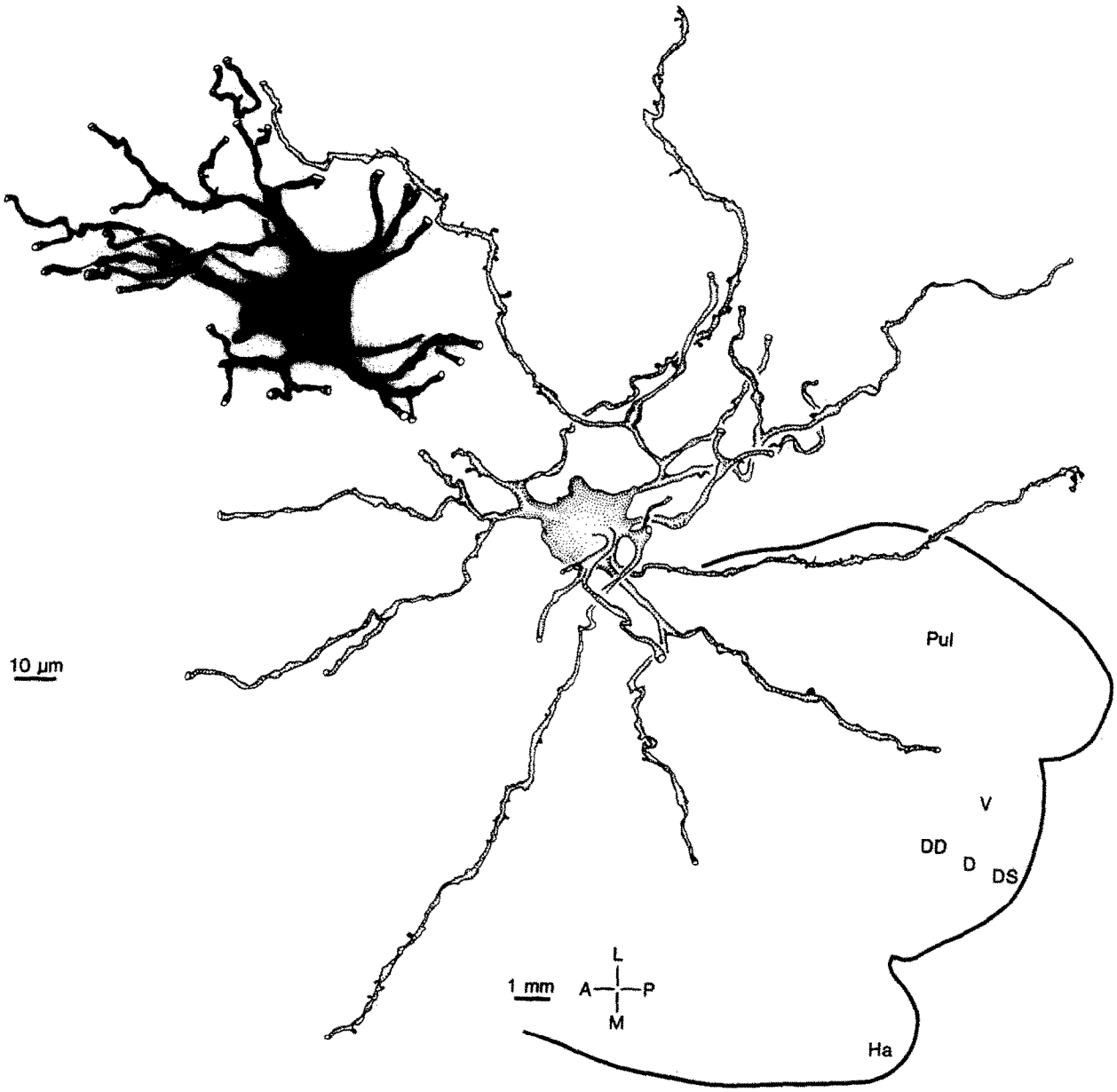


Fig. 8. Small stellate neuron (stippled) with a radiating dendritic field from the ventral nucleus; a larger soma with tufted dendritic branches (hatched) is nearby. Semi-apochromat, N.A. 1.32, ×1250.

neurons were the largest cells in the dorsal division, and only a few small somata were apparent in Nissl preparations (Figs. 3, 4B: SG). The large, deeply staining multipolar cells had centrally placed nuclei and were dispersed in a variegated axonal plexus. Posterior limitans nucleus cells were a slender strip along the dorsomedial wall of the suprageniculate nucleus. They had piriform somata whose long axis was aligned dorsolaterally-to-ventromedially.

Medial division

The precise limits of this territory were rather difficult to define, particularly on its ventromedial border, where the scattered cells of the interstitial nucleus of the brachium of the inferior colliculus, the brachium of the inferior colliculus itself, and the medial division neurons merged insensibly (Figs. 1A, 2A). Medial division cells could be distinguished by their larger somata and distinctive multipolar branching pattern. These hallmarks also separated them from the fusiform somata of the suprapeduncular nucleus (Fig. 3: SPN) and the smaller, elongated perikarya of the subparafascicular nucleus (Fig. 4C: SPF). There was no apparent or systematic regional variation in medial division cytoarchitecture, and the conspicuous, larger neurons were blended throughout the nucleus, though they were more numerous rostrally. Medium-sized somata (about 250 μm^2 in area) predominated (Fig. 6E) but smaller ones (less than 200 μm^2 in area) were also numerous (Fig. 6F), and the various perikarya had heterogeneous shapes.

Neuronal architecture

The architectonic patterns in Nissl and fiber stained preparations were compared with the results from Golgi impregnated material. In the latter, the criteria for classifying neurons included somatic size, shape, and orientation, as well as the dendritic configuration and branching pattern. The three-dimensional shape of a dendritic field was defined as radiate if it filled a sphere rather evenly; as bushy if it approximated a cylinder whose poles contained or gave rise to most of the dendritic branches; and as intermediate if it had elements of both. Dendritic branching pattern refers to how dendrites divided, for example, if they branched more or less dichotomously, acutely, and sparsely, like stellate neurons; or if they divided obliquely, like sheaves, repeatedly issuing from one stem and with a bushy configuration like tufted cells; or if they branched in an intermediate way. Similar criteria have been used for many years to classify neurons [53,54].

Ventral nucleus

A large neuron with a bushy dendritic field and a tufted branching pattern was often stained. Its elongated perikaryon was about 20×15 μm in diameter, and the main dendrites arose from the somatic poles, usually as 2–3 large trunks and a few thinner ones (Fig. 7B). Less than 10 μm away from the cell body the trunks form tufted branches, some trident-shaped, others T-shaped, but all more or less confined to a cylindrical domain some 250 μm long and 100–150 μm wide. The dendrites tapered, the second-, third- and higher-order branches remaining about equally thick except near their ends, where they tapered further (Fig. 7C). On their primary trunks the dendrites were relatively smooth, but on their third- and higher-order branches they sometimes had diverse appendages ranging from tiny buds to medium-sized pedunculated spines to large smooth ones (Fig. 7C, stippled). Their bushy dendritic fields had the long, medio-lateral axis parallel to the fibers ascending from the brachium of the inferior colliculus (Fig. 2A, B). The more laterally they lay in the ventral nucleus, the more acutely they fanned out rostrally or caudally, although their medial dendritic branches were always aligned with the brachial axons facing the medial division. In 160 μm thick sections most dendrites lay within the plane of the section, and their long axis was consistently dorsolateral-to-ventromedial (Fig. 7; Fig. 8, hatched). In the adult material of the present study axons were unstained beyond their initial few micrometers.

A smaller neuron also occurred in the ventral nucleus (Fig. 8, stippled). Its oval perikaryon was about 15 μm or smaller along its largest dimension, and the thin dendritic branches radiated from nearly anywhere on the soma without obvious orientation and filled a spherical field. The intermediate segments criss-crossed but the distal ones filled an irregular sphere and were often truncated at their extremities, so that rather few actually

ended in any single section. Primary dendrites often branched dichotomously in Y-shapes. Their dendritic field was about two-thirds or less the size of that of the bushy neurons, among whose tufted dendrites single branches of stellate cell dendrites ramified (Fig. 8). Bushy and stellate cell distal dendrites were equally thick, about 2 μm in diameter, but could be distinguished by the relative rarity of dendritic appendages on the latter and their comparative shortness. Appendages were more common on stellate cell middle and distal dendrites.

Dorsal nucleus

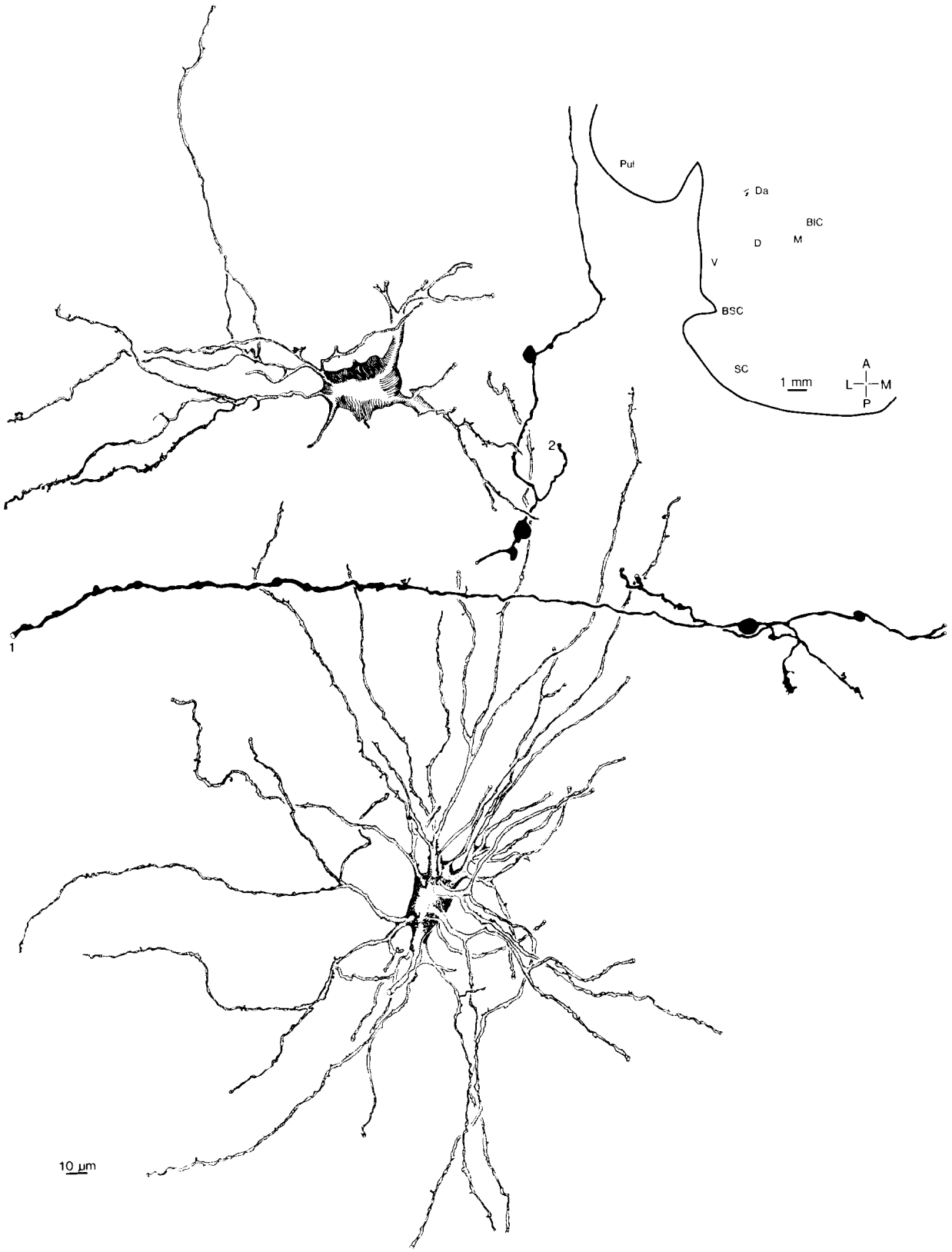
These neurons were somewhat more diverse in structure than cells in the ventral nucleus, and lacked the laminar arrangement characteristic of the latter. Three main types of cells were distinguished: large radiate neurons with a stellate branching pattern, large bushy cells with tufted dendritic branches, and smaller neurons which may have a tufted, stellate, or even intermediate dendritic configuration.

The large radiate neurons were common, occurring throughout the dorsal nuclei, including the rostral pole (Fig. 9: Da). Their oval or slightly elongated somata (Fig. 10, stippled; Fig. 11, lightly hatched) had 6–10 primary dendrites, each dividing dichotomously usually twice or sometimes three times, and their distal segments projected from the plane of section (Fig. 9, stippled). The dendritic field was about 300 μm in diameter and spherical in shape. Primary trunks were 4–5 μm thick, secondary and higher-order branches about half as thick. Intermediate dendritic segments overlapped to form a web-like mass, but there was little in the way of any preferential orientation to the spherical dendritic domain, nor did the axonal plexus (Fig. 2C) have a dominant orientation; axons believed to be extrinsic by their size, trajectory, and terminal branching pattern assumed diverse positions with reference to dendrites. Similar axons sometimes coursed at right angles to dendrites (Fig. 9: 1) or paralleled them while emitting collaterals or *boutons de passage* (Fig. 9: 2). Large stellate cell dendrites were sinuous and of uniform thickness between their second branch point and just before their terminal, where they tapered. Their sparse dendritic appendages lay here and on segments remote from the primary branches.

A second type of large neuron, but with a bushy mode of dendritic branching, was also found in the dorsal nuclei. These cells had oblate (Fig. 9, hatched; Fig. 11, stippled soma) or elongated (Fig. 10, hatched) perikarya from whose poles 3–5 primary dendrites extended and, in about 50 μm, branched several times in tightly coiled bushes like tufts. Single tufts may have a dozen or more branchlets, although sparser tufts occurred too. Each tuft fanned out to colonize a truncated cone of neuropil, single branches ramifying and terminating together (Fig. 10, hatched, upper left) or leaving the section ensemble (Fig. 10, hatched, lower right). The texture of the dendrites was much more crenated, lumpy, and irregular than that of other dorsal nucleus dendrites, and their shafts had few appendages. While the shape of their dendritic field was elongated, it did not have a consistent orientation, as did ventral nucleus bushy cells. This principle applied except in the superficial dorsal nucleus (Fig. 1A), where the slender, lamellar configuration of the nucleus imposed a more flattened orientation to the neurons (Figs. 3, 4B).

The abundant small neurons of the dorsal nuclei were evident also in Golgi preparations. Their oval or drumstick-shaped somata had 6–8 thin dendrites some 2–3 μm in diameter. These arose irregularly (Fig. 11, stippled and hatched cells) and, after branching once or twice, many dendrites ended near the cell. The size of the dendritic field was usually less than 200 μm in diameter, and was often half that size. Dendritic branching was usually dichotomous and the same neuron may have both stellate and tufted patterns on adjacent segments (for example, see Fig. 11, bottom). The shape of the dendritic domain embodied this complexity of branching, sometimes being more stellate and radiate (Fig. 11, top) and, at other times, more bushy and tufted (Fig. 11, bottom). Perhaps these somewhat different patterns signify different populations of small cells in the dorsal nuclei, for

Fig. 9. Stellate neuron (stippled) with radiating dendrites and a → tufted cell (hatched) with sparse dendritic tufts from the dorsal nucleus. Afferent axons (1, 2) with prominent *boutons de passage* have varied orientations and may represent ascending or descending inputs. Planapochromat, N.A. 1.32, ×2000.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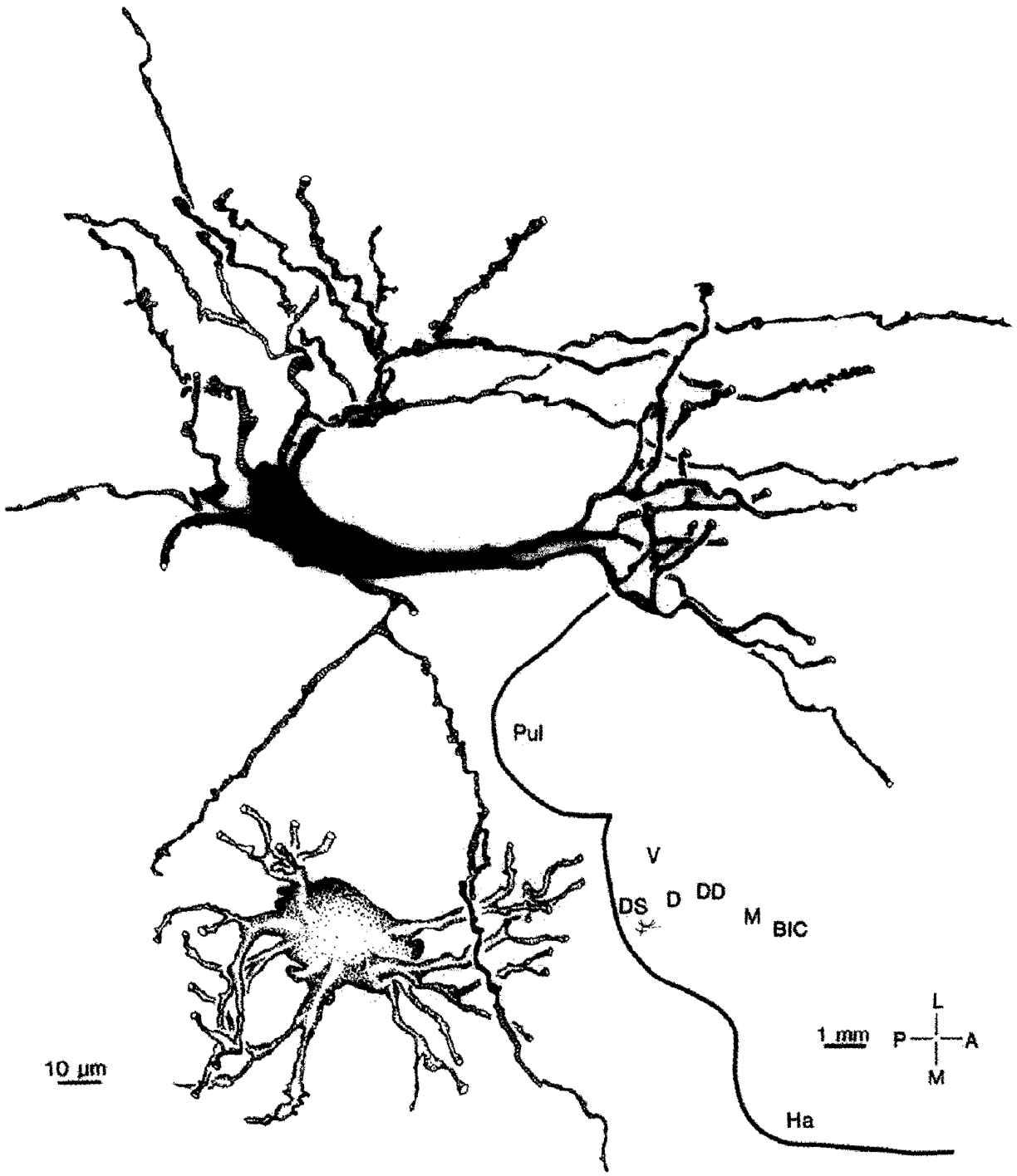
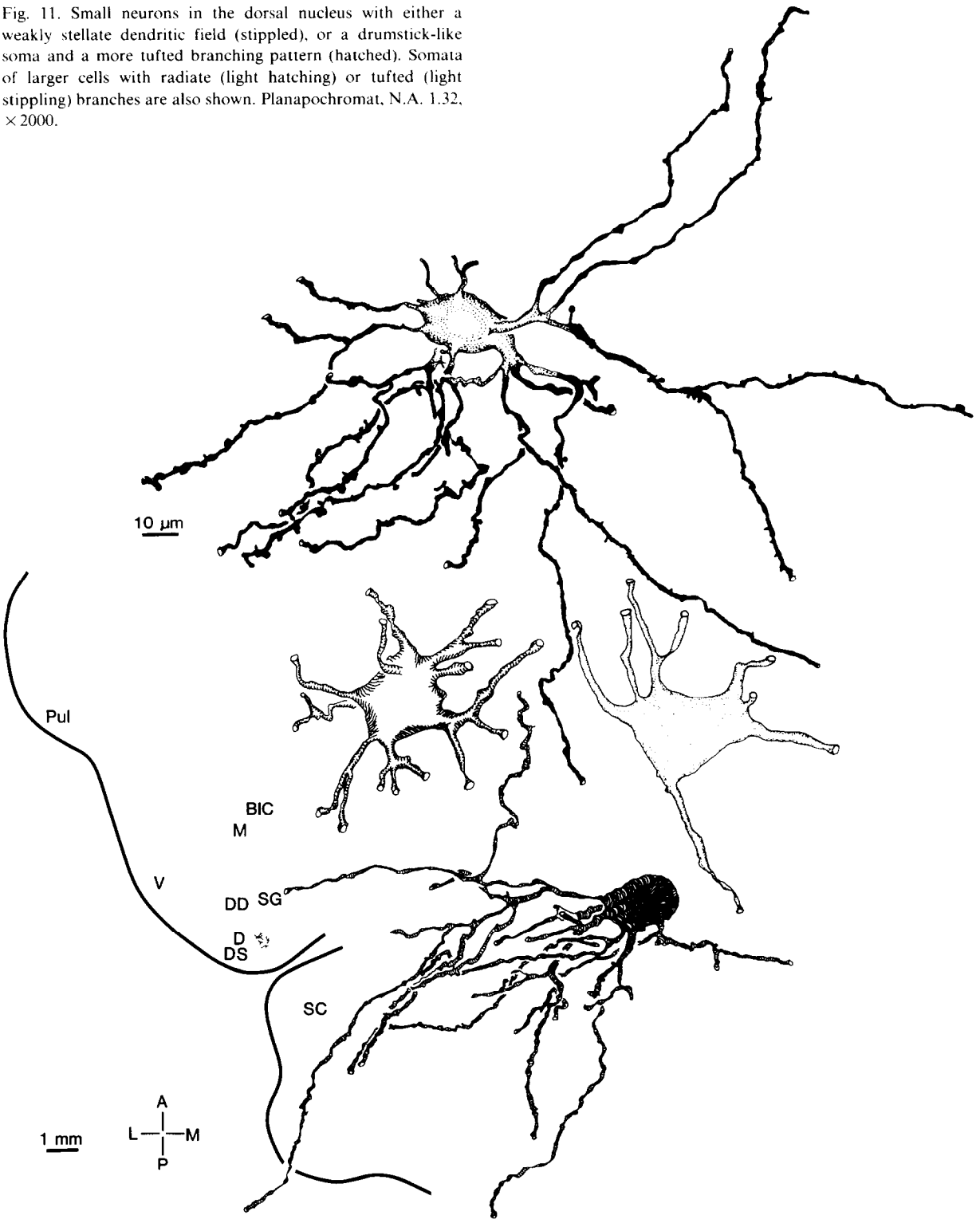


Fig. 10. Bushy neuron with tufted dendrites (hatched) and a stellate cell soma (stippled) in the superficial dorsal nucleus. Planapochromat, N.A. 1.32, ×2000.

Fig. 11. Small neurons in the dorsal nucleus with either a weakly stellate dendritic field (stippled), or a drumstick-like soma and a more tufted branching pattern (hatched). Somata of larger cells with radiate (light hatching) or tufted (light stippling) branches are also shown. Planapochromat, N.A. 1.32, ×2000.



other local variations, for example, the form and concentration of dendritic appendages, were evident. However, in view of the limited number of small neurons impregnated in this material, any firm distinction would be premature. The dendritic appendages were diverse in form and concentrated along the middle dendrites of small stellate cells, where they often nested among lumpy, irregular dendritic swellings and dilatations.

Discussion

Previous studies of the human central auditory pathways

There has been a recent renewal of interest in the structure of auditory areas in the human brain stem and cerebral cortex. A conspicuous exception to this trend is the medial geniculate body.

The gross structure and the cytology of the human dorsal and ventral *cochlear nuclei* have recently been described. Many of the same cell types or pathways already studied extensively in the cat have been documented in the human material [7,31,39], although systematic Golgi studies usually remain to be done. The structure of the *superior olivary complex* and related fiber tracts has been studied in primates, including man [61,62].

The Golgi and other methods have been applied in the human *inferior colliculus* to define its cell types and architectonic subdivisions. A major finding is that many of the nuclear subdivisions and the various cell types identified in the cat inferior colliculus can also be recognized in humans. Certain subdivisions are proportionally expanded or reduced in size, or their location is altered because of brain stem flexures or the expansion of adjacent structures. However, the relative correspondence between the neuronal architecture of the species is significant [25]. The studies pertinent to the human medial geniculate body are reviewed below. Much of the older literature was reviewed by Morest [40].

The location of the human *auditory cortex* has been determined by electrophysiological methods to lie across the transverse temporal gyrus [10,11,50]. Although the structure and postnatal development of its neurons have been described in humans [12,56], too little is known of its structure in non-human species to permit systematic comparisons.

Older studies of the human medial geniculate body are often difficult to interpret because of methodological vagaries in fixation and staining. Another problem is inconsistent morphological standards for defining subdivisions, and the relative neglect of the Golgi method as a tool in the study of neuronal structure. The staining properties of Nissl substance may permit distinctions among certain cells and some cytoarchitectonic areas to be made, but the information in these and fiber stained preparations, alone, cannot adequately define different subdivisions, or describe these differences in much detail in the human [24,28,46]. Some workers [46] have described as many as five subdivisions in human medial geniculate material. However, the basis for such a classification is unclear and these schemes have not been generally adopted by later workers. Their correspondence with the three divisions and thirteen subdivisions described in the cat medial geniculate body is uncertain [40,41,53,70,72–74]. For example, no part of the human medial geniculate body in Müller's [46] scheme is defined as exclusively auditory.

Ramón y Cajal [54] described superior, inferior, and medial lobes in the cat medial geniculate body to which, respectively, the dorsal, ventral, and medial divisions of the present account correspond. However, his nomenclature was largely neglected by many English-speaking investigators. The parcellation of the cat thalamus by Rioch [55] achieved wide currency and has been almost universally applied to the cat and human medial geniculate body and to other species, too. The difficulty with such an architectonic scheme is its reliance on Nissl- and fiber-stained preparations alone to define neuronal boundaries. Thus, Rioch's parvocellular division includes parts of both the ventral and dorsal divisions as presently defined; only some of these neurons are actually parvocellular, and these cells mingle among many other types of cells with little in the way of segregation by size. Since the neurons in each of these subdivisions in non-human species have a characteristic dendritic architecture [70,72–74] as well as separate patterns of midbrain afferents [4,42] and cortical targets [71], such a cytoarchitectonic for-

mulation creates a paradox in definition and nomenclature which persists to this day, and with which it is difficult to reconcile much of the subsequent morphological and connectional work. Rioch's classification also obscures any functional distinction between the cells in the ventral division, which are likely to have narrow auditory tuning curves, and the neurons of the dorsal division, whose tuning may be broader and not exclusively auditory. Perhaps these cell types embody parallel pathways [2,30,70]. The same reservations apply to Rioch's definition of the magnocellular division, only a small fraction of whose neurons are magnocellular, and not all of which are functionally or structurally part of the auditory system [40,68,70–72].

Many of the more recent studies of the structure of the human thalamus make no, or only minimal, distinctions between subdivisions of the medial geniculate body [17,60,66]. If a parcellation is attempted, as a rule the nomenclature of Rioch [55] is used and no account of structural differences, except those in cell-stained preparations, is given. Typically, principal (laterodorsal) and magnocellular (medial) subdivisions may be defined [33], but these terms are not used consistently in the literature (e.g., [5,18,47,48]). A case study of the problems in definition and nomenclature appears in a symposium where several experts on thalamic anatomy discussed and drew subdivisions from the same sections of a single human thalamus [18]. Most of the participants recognized no cytoarchitectonic subdivisions of the medial geniculate body; a few defined subdivisions, but primarily within the framework established by Rioch [55]. Only two groups (Feremutsch and Simma, and Krieg) recognized more subdivisions than this, and they, too, largely accepted Rioch's nomenclature [18]. This study and a companion [19] are the first modern investigations to provide any detailed karyometric data on the human thalamus. For the medial geniculate body, however, the data are rather limited and do not bear upon the question of different subdivisions or the distinctions between them.

The most complete and useful modern study, by Van Buren and Borke [67], analyzed the pattern of thalamic retrograde degeneration after auditory (and peri-auditory) cortical lesions, the structure of the nerve cells in Golgi–Cox and Nissl preparations, and variations in the size and location of thalamic nuclei. The nomenclature of Rioch [55] is accepted without qualification and was transferred directly to the human thalamus from the carnivore thalamus. However, the Golgi–Cox data in this study did not differentiate in much detail between the cell types in any of the subdivisions of the human medial geniculate body recognized in the present account. Besides a general description of the neurons in these preparations, there was no systematic, nucleus-by-nucleus description of the morphology of the neurons in the subdivisions, nor was the range of variation within a subdivision described, except in terms of somatic size. Distinctions were not made between principal neurons and Golgi type II cells, either on morphological or connectional grounds, nor was the axonal plexus, the major fiber tracts, or the axons of the medial geniculate body described. Adjoining subdivisions, such as the posterior limitans nucleus, which have been described in the literature [18,60], were not included by Van Buren and Borke [67] as part of the auditory thalamus.

A large body of recent literature has demonstrated that the retrograde degeneration method often does not reveal connections which can be documented by more sensitive axoplasmic transport techniques in infrahuman species [69,71]. Thus, any inferences as to tonotopic organization between human and non-human species based only on retrograde changes in the auditory thalamus after cortical lesions are premature. A recent atlas of the human thalamus makes no regional architectonic distinctions within the medial geniculate complex [5]. This problem is significant since studies of, for example, the human lateral geniculate body reveal considerable variation in the disposition, number, and shape of individual cellular laminae [27]. Many of the types of neurons described here appear to be comparable in their structure to some of the cells in the human lateral geniculate body [15]. Certain cell types, for example, bushy principal neurons and small cells with a stellate dendritic configuration, may be common features of specific thalamic sensory nuclei and possibly homologous in different species [45,49, 70,72].

Functional organization

Experimental work on the cat has shown that not all of the nuclei of the medial geniculate body are equally concerned with hearing. Evidence has accumulated that in humans, as well, certain parts of the medial geniculate body and of the adjacent posterior thalamus are integral in the transmission and processing of somatic sensory, including nociceptive, information. Thus, at least some fibers of the spinothalamic tract terminate in, or give off collaterals to, the medial division [36–38], and somesthetic parasthesias frequently invade the medial division [21]. Warm or hot sensations are evoked from the region of the juncture of the medial and dorsal divisions. Most acoustic responses are referred to the contralateral ear, and polysensory results are common near the dorsal and caudal borders of the medial geniculate body. Little in the way of any systematic organization of best frequency has been described in the human medial geniculate body [64,65].

The possibly multisensory nature of the human medial division is consistent with the idea in the cat that the medial division receives a large number of other, non-auditory inputs [1,68], whereas the ventral division is principally, if not exclusively, auditory [3,9]. The physiological properties of dorsal division cells are quite different, and undoubtedly reflect their unique patterns of brain stem (and, perhaps, cortical) afferents [2,4,65]. The subdivisions of the medial geniculate body therefore represent at least three different types of thalamic functional organization: a lemniscal, purely auditory pathway (ventral division), a polysensory pathway (dorsal division), and a plurimodal pathway (medial division). These distinctions are supported by functional, connectional, and structural evidence [70].

Finally, it should be mentioned that in primates there may be direct cochlear nucleus-to-medial geniculate body pathways which do not appear to be present in cats [62,63]. These could provide a route for rapid access of auditory information to the medial geniculate body from various channels.

The bilateral loss of the cortical areas in the temporal lobe in humans, to which the medial geniculate body projects, results in profound deficits in auditory behavior [29,67]. Comparable deficits have been described in monkeys [26] in whom the auditory cortical projection areas [8] had been bilaterally extirpated. The medial geniculate body thus has an important, possibly obligatory, role in human auditory behavior.

Homologous neurons

Can the distinctive neuronal populations described in the present account be considered homologous with those in the cat medial geniculate body? It is impossible to resolve this question with certainty since the issue of which traits are diagnostic of homology differs among various students (see [45]) and because so many of the intermediate or ancestral forms of the various neurons and axons either have not been studied or are extinct. In lieu of a more complete phylogenetic series, criteria of comparable position, connections, development, and structure are often used. The relative positions of the medial geniculate body and of some of the particular nuclei are comparable in cat and human. Too little is known of the midbrain or cortical connections in humans to permit any systematic comparison. The development of the human medial geniculate body [13,14] cannot readily be compared with the cat (or, for that matter, with any other species) since this sequence has never been described with respect to the various nuclei, much less the types of neurons. With regard to structure, the present account provides evidence that some, but not necessarily all, of the types of neurons may be homologous. This assertion must be conditional because the criteria for homology are not completely independent. For example, principal cells are largely defined by their size, shape, and dendritic configuration; however, unless their axons are thalamofugal, these neurons may function as Golgi type II cells, or, conceivably, even share attributes of both types of cells. Hence, while many of the cell types in the present account resemble neurons in the cat medial geniculate body, it is not certain if the concordance is complete in every respect. In any case, with regard to the neuropil, there are striking interspecific differences.

Speculations on neuropil structure

Perhaps the most striking feature of the human medial geniculate body is the relative sparsity of neurons and the corresponding development of the

neuropil. In non-human species the opposite trend appears to prevail [45,53]. These differences imply that, in certain species, characteristic variations in the structural basis for the analysis of acoustic signals might follow. The predominance of small neurons and the extraordinary development of the local fiber plexus attributable to their axons has long been recognized as a distinctive feature differentiating neuronal organization in non-human species [22,30,43,44,52] and humans [32,54]. The present study describes and extends this pattern to the human medial geniculate body. Perhaps these local circuits or somewhat larger anatomical arrangements [59] form a structural basis for temporally extended electrophysiological events, which could be related to highly discriminative aspects of speech and hearing [34,56,57].

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Abbreviations

Aq	cerebral aqueduct
BIC	brachium of the inferior colliculus
BSC	brachium of the superior colliculus
CP	cerebral peduncle
D	dorsal nucleus of the medial geniculate body
Da	anterior dorsal nucleus of the medial geniculate body
DD	deep dorsal nucleus of the medial geniculate body
DS	superficial dorsal nucleus of the medial geniculate body
Ha	habenula
L	posterior limitans nucleus
LGB	lateral geniculate body and perigeniculate nuclei
M	medial division of the medial geniculate body
MZ	marginal zone
OT	optic tract
OV	ovoid nucleus of the medial geniculate body
Pt	pretectum
Pul	pulvinar
SC	superior colliculus
SG	suprageniculate nucleus of the medial geniculate body
SPF	subparafascicular nucleus
SPN	suprapeduncular nucleus
V	ventral nucleus of the medial geniculate body

Orientation of the sections: A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral.

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