J. Anat., Lond. (1964), 98, 4, pp. 611–630
With 1 plate and 10 text-figures
Printed in Great Britain

The neuronal architecture of the medial geniculate body of the cat

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The medial geniculate body is a topographical term for a knee-shaped eminence of the thalamus that, in the cat, lies ventral and posterior to the lateral geniculate body. This paper gives its general internal architecture, based on an analysis of neuronal morphology with Golgi methods. The discordances of the cytoarchitectonic literature are reviewed in the light of the new findings, which are discussed with reference to the connexions and functions of the medial geniculate body.

MATERIALS AND METHODS

The analysis was made on the brains of thirty-five cats, ranging in age from the new-born to a 2·4 kg. adult. Comparative material was prepared from thirty-eight brains of rabbits, chinchillas, rats, mice, opossums, a woodchuck, and a squirrel monkey. Since the analysis depends primarily on the morphology of neuronal processes, close attention was paid to the method of fixation.

For the *Golgi–Cox method*, a schedule from Ramon-Moliner (1961), but with a lithium hydroxide concentration of 0·5%, gave excellent results. Good impregnations were also obtained if, instead of sodium tungstate, enough sodium hydroxide were added to the fixative to give a final pH of 6·0–6·5. The brains were removed as carefully as possible under pentobarbitone anaesthesia and immersed in fixative. They were then cut into slices 6 mm. thick either with scissors or, after mounting in an elastic impression material, with a macrotome (Rasmussen, 1931). It is recognized that the brains may have undergone pre- and post-mortem traumatization and hypoxic periods before fixation. Attempts to use the Golgi–Cox method after perfusion with Cox fixative, 5% potassium dichromate, or a glutaraldehyde fixative were not especially rewarding. When the brain was taken from a living anaesthetized animal in hypothermia (rectal temperature of 21° C.), impregnations of rare delicacy occurred, in which dendritic spines and entire axons with their collaterals were clearly seen more often than with other procedures.

Variants of the osmic acid modification of the *rapid Golgi method* (Golgi, 1903), usually with double or triple impregnation (Ramón y Cajal & de Castro, 1933) of slices 3 mm. thick, were used after immersion or perfusion fixation. Best results were obtained with a perfusion fluid consisting of 0·5% osmium tetroxide, 0·5% methyl cellulose, and 3% potassium dichromate, buffered at pH 7·0 with sodium

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hydroxide. In the resulting preparations the fine details of the delicate dendritic spines and appendages and the fibre plexuses in the brain stem and thalamus were more clearly and consistently preserved than in immersion-fixed material. These preparations were the standard by which the observations of all other Golgi materials were evaluated.

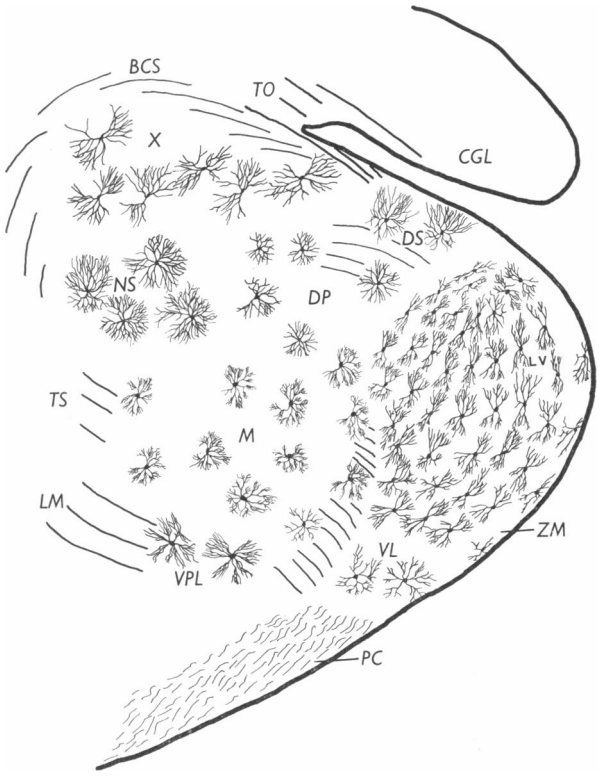
Unbroken series were made in all the standard planes and parallel to the brachium of the inferior colliculus. Moreover, the distribution of all the neurons impregnated in one entire geniculate body of a 15-day-old cat was reconstructed from serial sections onto transparent sheets. From cell counts in thionin-stained sections of an 18-day-old cat, it was estimated that 5–10% of the neurons were impregnated in the Golgi–Cox preparation used. Actually this preparation was chosen because of the remarkable uniformity, i.e. apparent randomness, of the impregnation (Pl. 1, fig. 2). Occasional variations in the uniformity of impregnation were corrected when all the outline drawings on the sheets were superimposed in registration. The boundaries so determined should be accurate within less than one dendritic field radius, which compares with the dendritic overlap between some nuclei. The outlines of Text-fig. 1–5 were made with a projection apparatus or photomicrographs, the cells being filled in under microscopic control. This report deals primarily with qualitative distinctions; presentation of some simple measurements does not imply that the drawings are fit for quantitative or statistical analyses. Perikaryal diameters were measured with an ocular micrometer and expressed as the average of two measurements, one parallel, one perpendicular to the longest axis of the cell body. The observations were compared with preparations stained by the thionin, Klüver or Sudan black methods, or impregnated by a protargol technique or by the silver methods of Richardson (1960) or Rasmussen (1957).

RESULTS

Since the medial geniculate body is a gross topographical formation, its internal boundaries are less well defined than its external limits. The region of the medial geniculate body considered in this report is bordered internally by the myelinated fibre field (Pl. 1, fig. 1) and anteriorly (orally) at a level corresponding to a line passing transversely through the junction of the posterior (caudal) and middle thirds of the lateral geniculate body. The anterior boundary of this region is poorly defined in Nissl and myelin sheath stained preparations.

Divisions

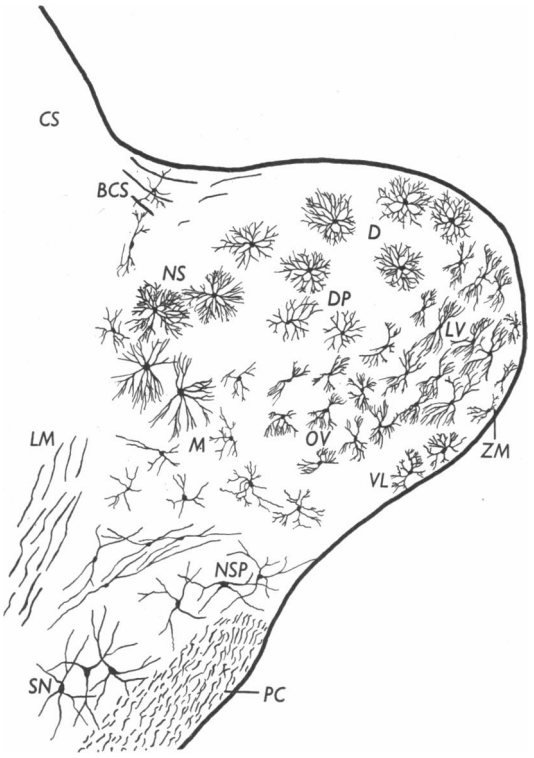
The region displays considerable structural heterogeneity with respect to neuronal types, the fibre architecture, and the form of the afferent telodendria. Two main types occur: the neuron with a short axon, so-called Golgi type II, and the principal neuron with a long axon projecting beyond the nucleus of origin. The major divisions of the medial geniculate body may be delineated solely on the basis of the dendritic branching patterns of the principal neurons. Golgi II neurons are not considered here. The branching pattern of the ventral division (Text-fig. 1, LV) is formed by slender side-branches in arrays resembling sheaves, brushes, or tufts—



Text-fig. 1. Typical distribution of principal neuron types at the junction of the anterior and middle thirds of the medial geniculate body. Transverse section, Golgi–Cox. 15-day-old cat.

the tufted pattern. The dorsal division (Text-fig. 1, DP) is typified by freely radiating, dichotomously branched dendrites. The pattern is formed by consecutive bifurcations into more or less equally slender daughter branches—the radiate pattern. In the medial division (Text-fig. 2, M) both tufted and radiate patterns occur.

Topography and cyto-myeloarchitectonics. The ventral division begins midway in the posterior third of the medial geniculate, forms a ventro-lateral crescentic area, and reaches its greatest development more anteriorly (Text-fig. 1). It is rich in myelinated fibres, and in thionin preparations its perikarya are smaller than the large ones of the medial division. The dorsal division fills all but the medial edge of the posterior tip (Text-fig. 3, D). More anteriorly it adjoins dorso-medially the lateral thalamic nucleus (Text-fig. 1). In myelin stains it is pale. Horizontal fascicles mark the ventral border, which often coincides with a dimple on the dorso-lateral surface that may correspond to the human lateral incisure (Niessl v. Mayendorf, 1922). In thionin stains the perikarya compare in size to those of the ventral division but are slightly larger antero-medially and more scattered. The medial division occupies the ventro-medial quadrant of the medial geniculate. It appears posteriorly among

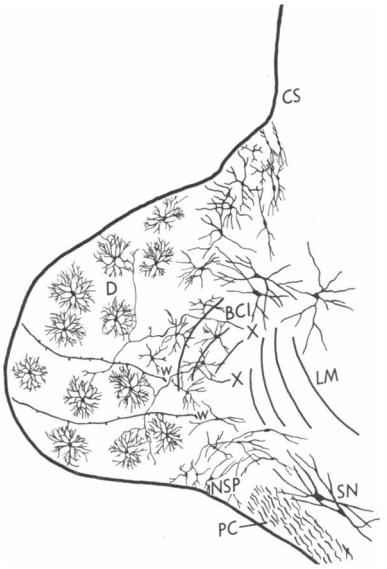


Text-fig. 2. Typical distribution of principal neuron types at the junction of the posterior and middle thirds of the medial geniculate body. Transverse section, Golgi–Cox. 15-day-old cat.

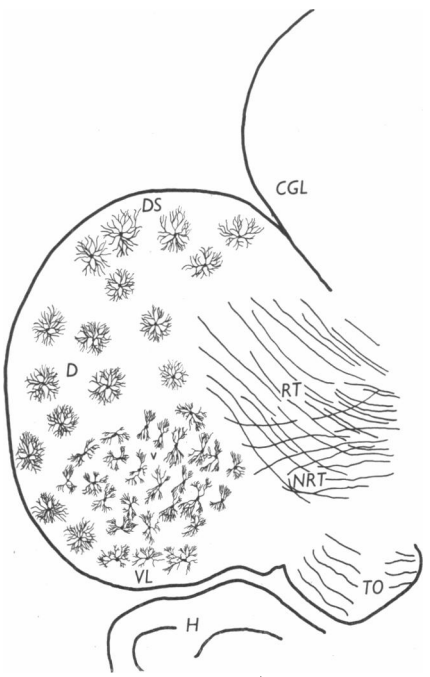
fibres from the brachium of the inferior colliculus and adjoins the ventral thalamic nucleus antero-medially. It is the most heavily myelinated division and contains the largest perikarya.

Fibre architecture. In Richardson silver preparations of the adult cat the fibre plexus of the ventral division appears as a lattice on which the entering brachium of the inferior colliculus is imposed. Most of the neuraxes are 1–2·5 μ in diameter, although some extremely fine ones weave through the lattice. The dorsal division contains an extremely dense tangle of very fine processes less than 0·5 μ in diameter. In these preparations the fibre density greatly exceeds that of the other divisions. In the medial division the fibre architecture is dominated by the longitudinal bundles traversing it lateral to the medial lemniscus. The thickest neuraxes, up to 4·5 μ in diameter, are most numerous here.

Delineation of neuronal groups with myelin stains or reduced silver impregnations of normal material is not necessarily reliable, since it is usually impossible to distinguish the extrinsic plexus and fibres of passage from the true, intrinsic plexus, i.e. the endogenous and exogenous fibres that arborize terminally. Sometimes the rapid Golgi impregnation appears limited exclusively to the intrinsic fibre plexus



Text-fig. 3. Typical distribution of principal neuron types in the posterior tip of the medial geniculate body. *w*, Ascending fibres with hook-like processes entering the capsule of the medial geniculate from the brachium of the inferior colliculus; *x*, afferent fibres ascending from the midbrain tegmentum with collateral twigs in the interstitial nucleus of the brachium of the inferior colliculus. Transverse section, Golgi–Cox. 28-day-old cat.

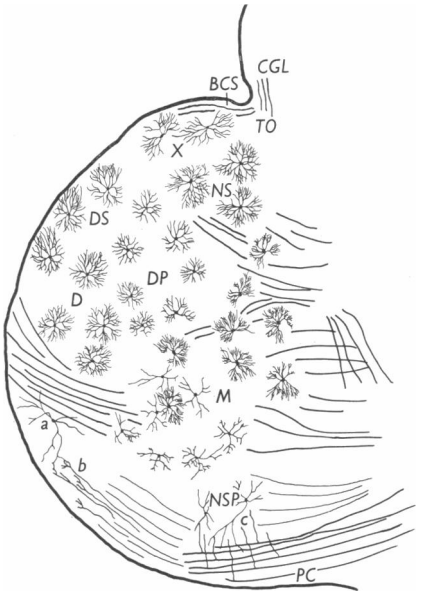


Text-fig. 4. Typical distribution of principal neuron types at the junction of the lateral and middle thirds of the medial geniculate body. Parasagittal section, Golgi–Cox. 28-day-old cat.

or to its exogenous, afferent components. In such preparations the divisions of the medial geniculate are clearly delineated (Text-fig. 6). The ventral division stands out by reason of its dense nests of fibres surrounding faintly chromated perikarya. Laterally a dorso-ventral fibre orientation is seen. In the dorsal division the intrinsic plexus consists of extremely fine fibres, diffusely arranged; nest-like formations are rare. An impregnation limited exclusively to the intrinsic plexus of the medial division is not available.

Specific neuronal populations

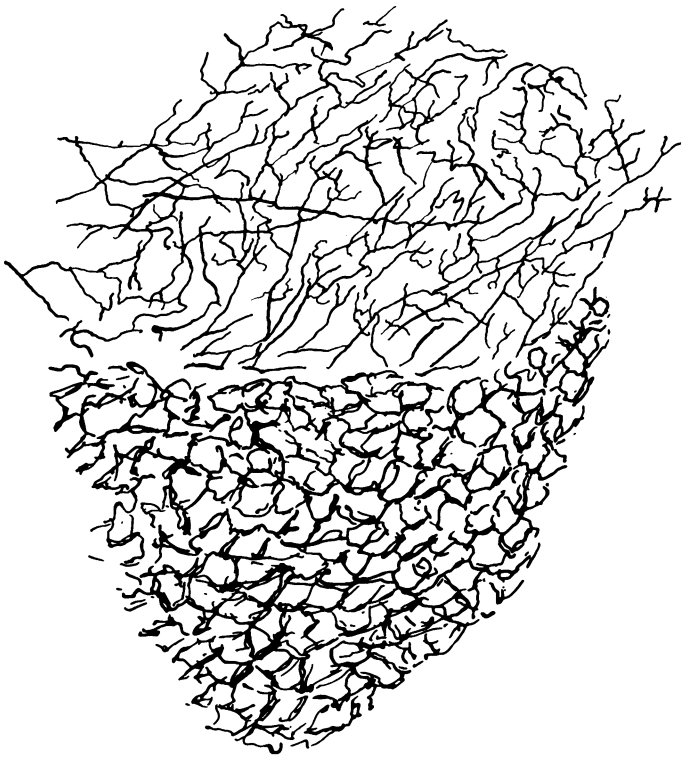
Specific neuronal types are differentiated and mapped according to the number, size, distribution, and branching pattern of the dendrites and the forms of the axons and the dendritic appendages. A neuronal population, or nucleus, may then be identified as a spatial distribution of neurons of a specific morphological type. The forms of the afferent telodendria consistently associated with each population are also given. The following records the most frequent types of principal neurons but is not exhaustive.



Text-fig. 5. Principal neuron types at the junction of the medial and middle thirds of the medial geniculate body. *a*, Neuron associated with ventral edge of the brachium of the inferior colliculus; *b*, descending axons to this neuron; *c*, collaterals of the cerebral peduncle. Parasagittal section, Golgi-Cox. 28-day-old cat.

Ventral division. The *ventral nucleus* is typified by strongly tufted dendrites (Text-fig. 7). Each neuron has 6–8 dendrites and about forty branching points. The dendritic field is discoid with long dorso-ventral and antero-posterior axes of 200–300 μ, closer to 200 μ on the average. The mean perikaryal diameter of 100 principal neurons is 17·2 $\mu \pm 1{\cdot}1$. The neurons are arranged in parallel laminae, well seen in transverse or horizontal sections of the pars lateralis (Text-fig. 2, LV). A

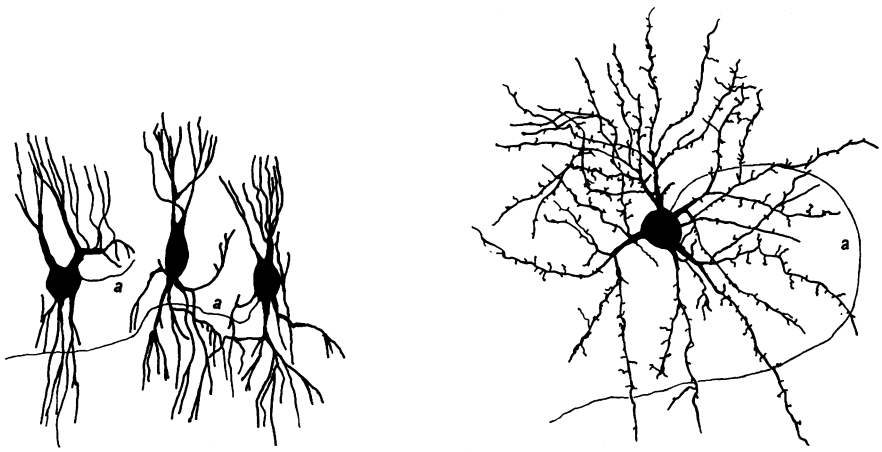
pars ovoidea (OV) is distinguished ventro-medially, but its structure is essentially the same. Its laminae are coiled but none the less continuous with those of the pars lateralis. A histological demonstration of this, with a more detailed account of the ventral division, is presented in a later paper. The dendritic surfaces are formed into swellings or folds, stubby thorns, and knobby spines (Text-fig. 8). Most of the spines and thorns are approximately 1–2 μ in diameter, but thinner spines are also seen on the distal dendrites. The robust efferent axons run anteriorly after emitting an occasional collateral. The *preterminal* fibres ascending from the brachium of the inferior colliculus course parallel to the laminae (Text-fig. 9) and contact perikarya and dendrites in dense clusters of knobby branches.



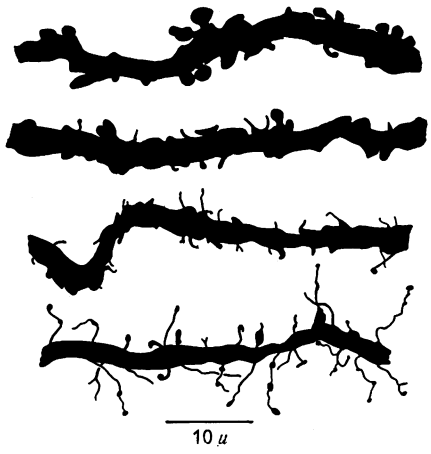
Text-fig. 6. The patterns of the intrinsic afferent fibre plexuses of the dorsal (top) and ventral (OV) nuclei of the medial geniculate body. Transverse section, rapid Golgi, chrome-osmium perfusion. Free-hand drawing. 41-day-old cat.

The *marginal zone* is an external strip associated with the capsule of the medial geniculate body. As Cajal (1955) observed, the dendrites are usually arranged parallel to the surface, and the axons project into the capsule. In the present material the dendritic fields usually contain four primary trunks and are less branched and tufted than those of the ventral nucleus. The lateral half of the field is pierced at right angles by the capsular fibres; the medial half is embraced by the ascending and descending branches of fibres from the capsule (Text-fig. 9). The dendritic spines are short, rod-shaped spicules about 1·5 μ thick.

The *ventro-lateral nucleus* is a small group ventro-lateral to the ventral nucleus and dorso-lateral to the suprapeduncular nucleus. The dendrites are the least tufted of the ventral division, but they are distinguishable from those of the dorsal division (Text-figs. 4, 10). The neurons have six primary dendrites and about forty-five branching points in a spheroidal field. The dendritic spines, 0·5–1·0 μ thick and 1–2 μ long, are the finest and longest of the principal neurons of the ventral division but not as long or as delicate as those of the dorsal division (Text-fig. 8). Afferent fibres contact both somata and dendrites. The axons pass from the nucleus ventro-medially or medially through the ventral nucleus where some of these end.

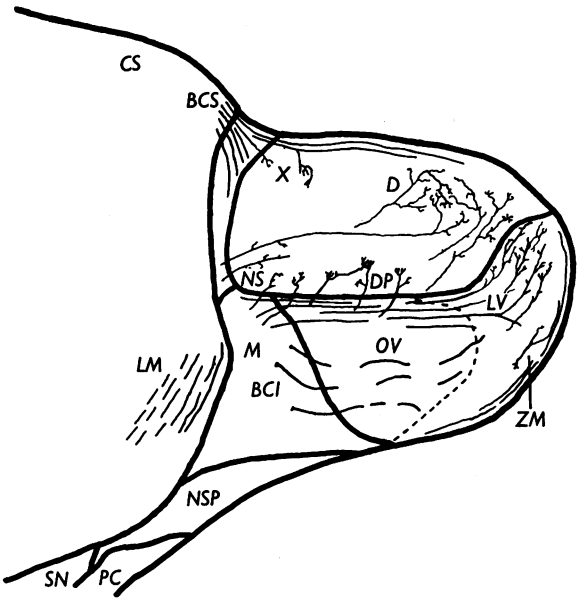


Text-fig. 7. *Left:* three tufted principal neurons, ventral nucleus (pars lateralis) of the medial geniculate body; transverse section, Golgi–Cox. The dendritic fields of such cells appear the same in horizontal sections. *Right:* radiate principal neuron, dorsal nucleus of the medial geniculate; transverse section, rapid Golgi, chrome-osmium perfusion. The dendritic fields of such cells appear the same in any plane of section. *a*, Axon. Camera lucida, × 200.



Text.-fig. 8. Dendritic segments of principal neurons (top to bottom): ventral nucleus (pars ovoidea), medial division (tufted zone), ventro-lateral nucleus, dorsal nucleus. Rapid Golgi, chrome-osmium perfusion. Camera lucida, × 1140.

Dorsal division. The *dorsal nucleus* extends from the posterior tip of the medial geniculate antero-laterally as far as the posterior end of the lateral geniculate body. Each neuron has six evenly spaced, radiating dendrites, each with 8–9 bifurcations. The branches are arranged diffusely in a spherical field of relatively constant dimensions, 300–320 μ in diameter (Text-fig. 7). The mean perikaryal diameter of 100 principal neurons is 18·4 $\mu \pm 1{\cdot}9$. The dendritic appendages are finer than those of the ventral division. The shorter ones resemble the tiny knobbed spines found elsewhere, e.g. in the cerebellar cortex. The longer ones are probably dendritic branchlets (Text-fig. 8). Not all the neurons have branchlets, even in perfused



Text-fig. 9. Transverse scheme of different patterns of preterminal plexus of the ascending fibres to various parts of the dorsal and ventral divisions of the medial geniculate body of the cat. The laminar distribution of the brachium of the inferior colliculus is coiled in the pars ovoidea (OV) and cannot be illustrated here (see text). Rapid Golgi methods.

specimens. Whether or not their absence was artifactual is uncertain. However, when present, they occur on all the dendrites of a given neuron. They are rarely clearly seen in immersion-fixed material or elsewhere in the medial geniculate. The axons often describe an arc of 180° within the dendritic field before leaving the nucleus anteriorly. Many emit extensive collaterals in the dorsal nucleus. The afferent fibres to the dorsal nucleus are diffuse and extremely fine, 0·5 μ or less in diameter. Each fibre contacts the dendrites of many neurons, supplying a few terminals to each, as if at random. Axo-somatic contacts are rarely identified.

In the anterior half of the dorsal division the most dorsal neurons form a *superficial tier*, described by Cajal (1955). In the present series this tier has radiating dendrites resembling those of the underlying dorsal nucleus (Text-fig. 5). The perikarya and dendritic fields, however, are larger and more widely spaced. The dorsal dendrites have more branches than the others. This feature may be related to the

afferent fibres emerging from the overlying capsule, from the brachium of the superior colliculus posteriorly and the optic tract anteriorly, as Cajal noted. These neurons also send their axons into the capsule. Since it probably differs in its connexions from the dorsal nucleus, it may be regarded as a *superficial dorsal* nucleus.

The *deep dorsal nucleus* is situated between the dorsal and the ventral nucleus. It extends from the middle of the posterior third to the anterior third of the medial geniculate (Text-fig. 5). It resembles the dorsal nucleus, except that its dendritic fields are smaller, less branched, and have no long branchlets. The mean perikaryal diameter of 100 principal neurons is $18{\cdot}0\ \mu \pm 1{\cdot}8$. The axons are directed anteriorly. The intrinsic afferent plexus is generally diffuse and very fine, and effects predominantly axo-dendritic contacts. Additional, stouter elements form sparse, cup-like formations about the ventral-most neuronal perikarya (Text-fig. 9).

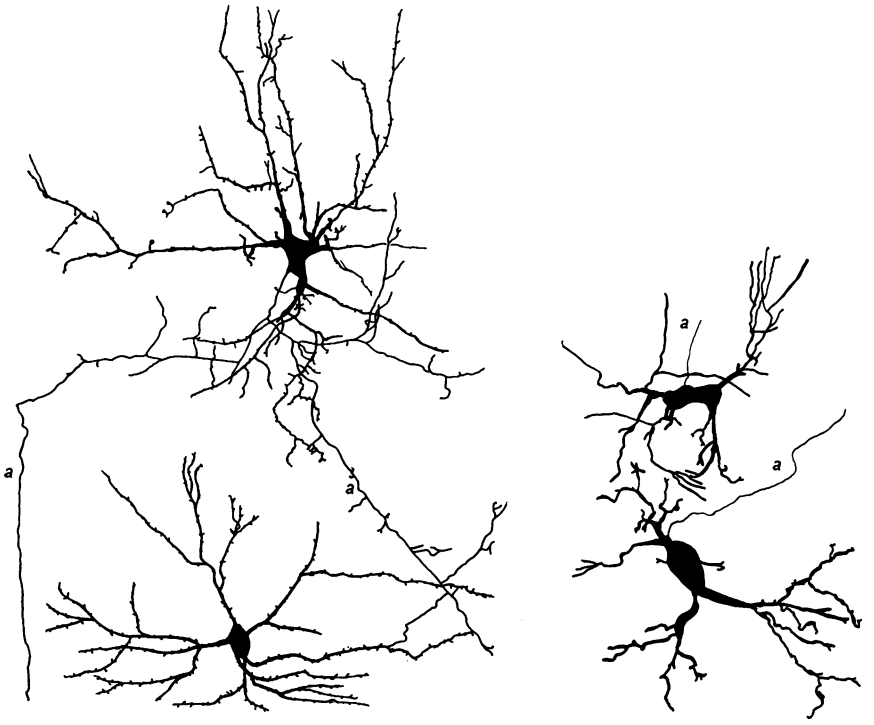
The *suprageniculate nucleus* occupies the ventro-medial part of the dorsal division, reaches its greatest extent at the level of Text-fig. 1, and disappears anteriorly beneath the lateral thalamic nucleus. The dendrites are radiate with eight primary trunks and 70–80 branching points in an irregularly spherical field of some 350 μ in diameter. The fine dendritic spines resemble the short spines of the dorsal nucleus. The mean perikaryal diameter of 100 principal neurons is $20{\cdot}3\ \mu \pm 1{\cdot}7$. The axons leave the nucleus to enter the thalamo-cortical radiations. The intrinsic afferent plexus has the fine, diffuse character of the dorsal division in general, but coarser elements occur, too.

Medial division. The *radiate neurons* are numerous posteriorly among the fibres of the brachium of the inferior colliculus and infrequent anteriorly. The dendritic branches, unlike those of the dorsal division, occur at irregular intervals, often at wide angles, and are arranged in oval, discoid fields pierced at right angles by longitudinal fibres. The neurons have four to eight primary dendrites and eight to thirty branching points. The perikaryal diameters are 13–18 μ, 15 μ on the average. The dendrites, sometimes more than 300 μ long, are, on the average, the longest in the medial geniculate body. The spines are sparse and very fine. The axons project to adjacent groups, especially to the dorsal, suprageniculate, and ventral nuclei and to the tufted zone of the medial division. The afferents effect mainly axo-dendritic, fewer axo-somatic contacts.

The *tufted neurons* first appear posteriorly in the dorsal region of the medial division, where they mingle with radiate neurons (Text-fig. 2). Anteriorly they fill the whole division. They are sharply demarcated dorsally from the radiate neurons of the suprageniculate nucleus. The dendrites are distinct from those of the ventral thalamic nucleus anteriorly and the ventral nucleus of the medial geniculate laterally. They are less strongly tufted, arise at more even intervals, branch more acutely, and appear less bushy with perhaps less overlap between individual dendritic trees. The perikaryal diameters measure 20–25 μ. The ovoid dendritic fields have eight primary trunks and about forty branching points. The average dendritic length is about 160 μ, but one or two dendrites are often longer, up to 250 μ. There are many short spines and fewer thick, clavate appendages, generally smaller than those of the ventral nucleus (Text-fig. 8). The axons project anteriorly. The afferents often contact the dendrites at right angles and also form a perisomal terminal plexus.

Quantitative data

Unless otherwise stated, all quantitative data, uncorrected for shrinkage, apply to a 15-day-old cat's brain impregnated by the Golgi–Cox method. Data from older brains suggest that the *relative* values for the different populations remain essentially the same, but a definitive quantitative, developmental analysis would exceed the scope of this study. Measurements of perikaryal diameters in thionin or Golgi series do not provide a sensitive enough tool, in this study, to delineate the major divisions. But the relative dimensions of the dendritic field and perikaryon do.



Text-fig. 10. *Left:* principal neurons, ventro-lateral nucleus, one with extensive axon collaterals (*a*, *a*); rapid Golgi, chrome-osmium perfusion; 41-day-old cat. *Right:* principal neurons, dorsal nucleus, 2-day-old cat: many dendrites end in forks or 'sprouts', not seen in adults; the perikarya and dendritic trunks seem disproportionately large compared to the branches; *a*, axon; Golgi-Cox. Camera lucida, ×200.

Differences of neuronal packing density in the medial geniculate are probably significant. Counts of cells with single prominent nucleoli in adult thionin preparations indicate that the densities of neurons maintain the following ratios: medial division, 1·0; ventro-lateral nucleus, 1·5; suprageniculate nucleus, 1·5; dorsal nucleus, 2·0; ventral nucleus (pars lateralis), 3·0. Although packing density was not used to delineate the populations originally, it may facilitate their identification with perikaryal stains. The packing densities in the Golgi preparations are not a constant function of the densities in thionin stains.

Development

In the new-born cat the tufted dendrites of the ventral nucleus are distinct from the radiate ones of the dorsal nucleus, but finer distinctions are hindered by the fact that the dendritic pattern may not be fully presented (Text-fig. 10). Moreover, the neurons tend to appear in clusters, so that demarcation of nuclear borders is difficult. Nor does the intrinsic fibre plexus appear evenly impregnated, especially in the dorsal half of the dorsal division (see Cajal's fig. 183, 1955). This is achieved in the present series after the first post-natal week, when few 'incomplete' dendrites are seen, except in the dorsal division. This division presents its typical appearance later than the ventral. By 2 weeks 'incomplete' dendrites are rare, the typical features are clearly represented, and population boundaries are as sharp as in older animals. Since no changes in the relative extents or contents of the neuronal populations are detected after this time, the distinguishing features reported should apply to the mature cat. This is not to say that no developmental changes, especially quantitative ones, occur in the cat after 2 weeks of age.

Comparative anatomy

Three major divisions of the medial geniculate body, with dendritic patterns similar to those of the cat, occur in all the species examined. The relative positions and extents of the specific neuronal populations and their morphological complexities vary by species. It need only be noted here that the kind of analysis used for the cat may prove useful for determining homologous neuronal populations.

DISCUSSION

Published observations with the Golgi methods on the medial geniculate body are known only from the work of Cajal (1955), which the reader should consult by way of introduction to the present, more detailed study. Other studies depend on perikaryal or fibre stains. A review of the anatomical literature on the medial geniculate body is not available, but most of the important references are cited here.

Parcellation. Clark (1932, 1933), in his comparative studies of the thalamus, distinguished a 'pars ventralis' of the medial geniculate, derived from the subthalamus, and a dorsal, main mass, from the dorsal thalamus. The distinction was supported by Kuhlenbeck (1935) in an ontogenetic, and by Papez (1936) in a comparative study. This structural organization was questioned by Bodian (1939) and Rose (1942*a*) on architectonic and ontogenetic grounds.

The 'pars ventralis' probably corresponds to groups described by Jacobsohn (1909) in the human as the nucleus peripeduncularis lateralis, by Přecechtěl (1925) in the elephant as the nucleus transversus infrageniculatus, and by Cajal (1955) as the nucleus suprapeduncularis. The latter term may be preferable for historical reasons. Its dendritic morphology and connexions with the cerebral peduncle (Text-figs. 2, 5) suggest that it may be profitably studied with the other peripeduncular groups which it adjoins and resembles.

Parcellations of the medial geniculate body dorsal to the suprapeduncular nucleus fall into three categories: dorsal and ventral divisions, medial and lateral,

or none. Among those not finding definite divisions were Bianchi (1909) in the rabbit, Clark (1928, 1929) and Campbell & Ryzen (1953) in insectivores, Clark (1930) in the tarsier, Feremutsch (1962) in the chimpanzee, and Kölliker (1896) in the human. Bianchi (1909), Campbell & Ryzen (1953), and Clark (1930) did distinguish 'suprageniculate nuclei, which are probably included in the present dorsal division.

In 1881 Gudden clearly figured dorsal and ventral divisions of the medial geniculate body of the rabbit. Nissl (1913) documented this, and Münzer & Wiener (1902) added a medial nucleus. Nearly all investigators recognized at least these basic divisions in the rabbit (cf. Rose, 1935; Rose, 1942*b*). Cajal's (1955) account of the medial geniculate body of the rabbit, guinea-pig, kitten, and puppy was well founded on fibro-cellular studies. He recognized a 'superior lobe' of widely, evenly spaced neurons, an 'inferior lobe' of more closely packed neurons, and a 'medial or large-celled nucleus'. He divided the 'inferior lobe' into an 'ovoid subnucleus' and a marginal layer with long, variably oriented dendrites. Winkler & Potter (1911, 1914) described 'a-, b-, and c-nuclei', corresponding partially to the 'subnucleus ovoideus', the 'superior lobe', and the external-marginal and suprapeduncular regions, respectively. Schemes similar to Cajal's, with more or less subdivisions, were proposed by Müller (1921), Marburg (1923), Hornet (1933), Rose (1942*b*), and Sychowa (1962) in several mammals, including man. Malone (1910) and Winkler (1921) did not distinguish the medial nucleus.

Monakow (1895) was perhaps the first to divide the medial geniculate body into lateral 'principal' and medial 'magnocellular' parts, while ignoring the dorsal division that his own figures (1882) clearly depict. Gurdjian's (1927) distinction of lateral, dense-celled and medial, sparse-celled parts may be similar. In 1929 Rioch published a study that dominated subsequent investigation of the medial geniculate body, at least in the English-speaking world. He described a ventro-medial 'pars magnocellularis' of large neurons and designated the rest of the medial geniculate the 'pars principalis' without representing the dorsal division. This simplified scheme was applied to various species by many investigators, including Ingram, Hannet & Ranson (1932), Walker (1938), Krieg (1948), Olszewski (1952), and Kuhlenbeck (1954). In the opossum, Bodian (1939) found central and marginal groups, but these may not correspond to Rioch's divisions. In elaborating Vogt's (1909) myeloarchitectonic scheme, Friedemann (1911) described a 'pars caudoventralis' of small scattered cells and a 'pars orodorsalis' of large, densely packed cells forming the main part of the medial geniculate and containing a lateral marginal zone of still larger cells. A ventro-medial magnocellular group was identified with the ventral thalamic nucleus, although Friedemann could not show continuity between the two. Clark (1933) suggested that the 'pars caudoventralis' corresponds to his 'pars ventralis' and that the medial nucleus does not belong to the medial geniculate body.

The present findings agree with Cajal (1955). The 'pars principalis', or 'pars parvocellularis', of later authors contains parts of two different structures, the dorsal and ventral divisions. The dorsal division corresponds to Cajal's 'superior lobe'. In the cat it is an integral part of the medial geniculate that includes the posterior tip of this body. The suggestion that Cajal's 'superior lobe is really the caudal end of the pars posterior of the lateral nucleus' of the thalamus (Clark,

1933) is not consistent with the present observations. Cajal did not distinguish a suprageniculate nucleus, but this cannot be equated with the dorsal division in the cat, as some observations in the tarsier (Clark, 1930) may imply. In the ventral division (Cajal's 'inferior lobe') the pars ovoidea of the ventral nucleus and the marginal zone correspond to his 'subnucleus ovoideus' and marginal cells, respectively. Between them are the lateral part of the ventral nucleus and the ventro-lateral nucleus. The principal neurons of the latter nucleus resemble those of Cajal's external region. In the medial division, the zone of tufted neurons, corresponding to Cajal's 'medial nucleus', should not be identified with the ventral thalamic nucleus or the suprageniculate nucleus, since their dendritic morphology is different. The tufted neurons are included in the 'pars magnocellularis', 'nucleus parageniculatus', or 'medial accessory' medial geniculate body of other authors, which, however, often apply to a larger region. This discrepancy may reflect the well-known difficulty of analysing this region with Nissl body stains (e.g. see Rioch 1929), as well as the need to extend the present analysis more anteriorly.

Subcortical connexions. The findings of Jeleńska-Macieszyna (1911), Woollard & Harpman (1940), and Moore & Goldberg (1963) suggest that the inferior colliculus projects to the medial and ventral, but not to the dorsal division of the medial geniculate body. Comparison of the present scheme with a reconstruction of the inferior collicular projections (Rasmussen, 1961) establishes this conclusion in the cat. Pathways to the medial, but not the ventral division, are thought to come from the spinal lemniscus (Nauta & Kuypers, 1958), the fastigial nucleus (Carpenter, 1960), the superior colliculus (Altman & Carpenter, 1961), and possibly the vestibular system (Mickle & Ades, 1954). They are said to project to the 'pars magnocellularis' in the cat, but their relationships to tufted and radiate cells are uncertain. The subcortical projections from the medial geniculate body (Glorieux, 1929; Ades, 1941) are not sufficiently clarified to identify their sources. The only subcortical projections described in the present study, besides those of axon collaterals, are short ones from the medial division.

Cortical connexions. Cajal (1903) observed descending, possibly cortical, fibres to the ventral, but not to the dorsal division of the medial geniculate body. Sachs (1909) traced Marchi granules in the cat from lesions involving the suprasylvian gyrus to the antero-dorsal medial geniculate, as Meyjes (1934) did in the rabbit from auditory cortex to all but the postero-dorsal medial geniculate. Walther & Rasmussen (1960) have given additional evidence of differences in the cortical projections to the dorsal and ventral divisions. The medial division probably receives from several cortical regions, including insular (Desmedt & Mechelse, 1959*a*) and ectosylvian (Walther & Rasmussen, 1960) regions.

In the cat the anterior 'pars principalis' degenerates after lesions of auditory cortical area A I, but not the posterior tip, unless A II and the temporo-insular cortex are damaged (Rose & Woolsey, 1958; Diamond, Chow & Neff, 1958). In the medial division the large perikarya may degenerate after lesions involving the ectosylvian and the temporo-insular (Neff & Diamond, 1958), second somatic (Rose & Woolsey, 1958), or anterior suprasylvian areas (Locke, 1961). The posterior medial division may not degenerate after nearly complete hemi-decortication (Moore & Goldberg, 1963). These findings suggest that, *at the very least*, the ventral

nucleus projects to A I, the dorsal nucleus to temporo-insular cortex, the medial tufted cells to an area or areas surrounding the ectosylvian cortex, and the medial radiate cells to subcortical loci. Similar interpretations might apply to the retrograde findings of Dantchakoff (1902), Münzer & Wiener (1902), Yoshida (1924), and Meyjes (1934) in the rabbit, of Lashley (1941) in the rat, of Sychowa (1963) in the dog, of Rundles & Papez (1938) in the mangabey and baboon, and of Walker (1936, fig. 16; 1938, expts. 17, 21) and Locke (1961) in the macaque. Further analysis of the cortical connexions from retrograde studies is precluded by the large lesions necessarily used, often involving several cortical areas. It may not be readily pursued until the anatomical bases of the so-called 'sustaining projection' (Rose & Woolsey, 1958) and of retrograde and transneuronal degeneration are better understood.

Neuronal morphology and function. In choosing the criteria to identify a neuronal population, it was assumed that the form of the receptor processes, especially the dendrites, and of the conductor processes, especially the intrinsic afferent plexus, would be likely to have functional significance. The distinction of two basic dendritic patterns corresponding to radiate and tufted was first introduced to the study of the thalamus by Kölliker (1896). Ramon-Moliner (1962) has extended the general analysis of basic dendritic patterns. In the medial geniculate body the three major divisions may be distinguished on the basis of dendritic patterns alone. The anatomical cogency of these distinctions is witnessed by consistent differences of the number of dendrites and branching points, the dimension and shape of the dendritic fields, the size and shape of the dendritic spines and appendages, the packing density and arrangement of the principal neurons, the form and distribution of the intrinsic afferent plexuses, and finally, the typical relationships and contacts of these with the principal neurons. The relative sizes, densities, and patterns of the terminal contacts observed in the Golgi preparations conform with their appearance in Rasmussen's silver technique for demonstrating synaptic endings. The functional significance of the neuronal groups defined is confirmed by differences in neural connexions, *where these are securely established.* When the neuronal morphology is considered in relation to these connexions, the following indications of their functions emerge.

The ventral division of the medial geniculate body is typified by neurons with tufted dendrites, a type thought by Ramon-Moliner (1962) to occur chiefly in 'regions with a relatively homogeneous type of input, i.e. receiving axons from circumscript cell groups often related to specific sense organs'. This proposition is partially exemplified by the ventral nucleus, which projects to the primary auditory cortex and is a terminus of the auditory pathway from the inferior colliculus and its brachium. Many clusters of large terminals convene on a neuron from its afferent fibre. This form of arborization may correspond to that related by Scheibel & Scheibel (1963) to systems maintaining some type of spatial representation. The neurons of the ventral nucleus are arranged in laminae, parallel to the ascending brachial fibres. In this sense the neural elements are highly ordered. Whether the laminae subserve frequency discrimination, as seems likely, remains to be demonstrated. Nevertheless, the structure of the ventral nucleus is suitable for relay of a highly differentiated sensory input or for differentiation, in its own right, of a relatively homogeneous, viz. auditory, modality.

The dorsal division is typified by neurons with radiate dendrites, a common type in the brain stem reticular formation and regions having a multiplicity of dissimilar connexions (Ramon-Moliner, 1962). The connexions of the dorsal division are largely undetermined, but a cortical projection site (Desmedt & Mechelse, 1959*b*) and afferent input (Morest, 1963) may represent more than one sensory modality. The ascending afferents are extremely fine, presumably slowly conducting. Their telodendria are diffusely branched and establish relatively few, isolated fine contacts with any one neuron, chiefly at dendritic loci. In this sense the afferent projections tend to overlap and are not highly ordered. A similar type of arborization in the brain stem reticular formation may be correlated with 'non-representational' systems, presumably involved in integrative functions (Scheibel & Scheibel, 1963). These features suggest that the dorsal division may be involved in the integration of sensory inputs that are heterogeneous with respect to the modality, the parameters, or the temporal or spatial sequence of stimuli.

In the medial division the morphological variation perhaps suggests that more populations occur than are reported at this time. The dendritic length and branching of the radiate neurons resemble those of the nearby lateral mesencephalic tegmentum. Although they are sharply segregated from the latter in Golgi preparations, one is inclined to ascribe to them a mesencephalic, rather than a diencephalic, origin. The geometrical relationship of the dendritic fields to the fibres is typical of many so-called interstitial, or 'bed', nuclei. In fact, elements of the interstitial nucleus of the brachium of the inferior colliculus, described by Cajal (1955), accompany the brachial fibres into the medial division. The other radiate elements may be related to fibres from other than the inferior colliculus. These features and the projections of these neurons to adjacent nuclei suggest that this zone distributes diverse systems to functionally appropriate subcortical nuclei. A more detailed analysis of these neurons and their connexions will be necessary before a more definite hypothesis of their capacities for integrative or other functions may be advanced.

Although the tufted neurons of the medial division present some features analogous to other tufted thalamic groups, such as the ventral thalamic nucleus, an analogous relationship to one specific afferent system is not established. Perhaps they are thalamic vestibular neurons, but there is no critical evidence for it at this time (Mickle & Ades, 1954; Locke, 1961). Of the tufted thalamic patterns, that of the medial division is the most weakly expressed. Its dendritic patterns and other features might be regarded as intermediate between those of the ventral thalamic nucleus and the suprageniculate nucleus. Whether this implies that the input, e.g. vestibular, requires a less specialized apparatus for its mediation, or whether there are less secure synaptic relationships, in the sense of Rose & Mountcastle (1959), with multiple inputs is uncertain. The latter possibility conforms to the anatomical (see p. 624) and electrophysiological (Knighton, 1950; Poggio & Mountcastle, 1960; Carreras & Anderson, 1963) evidence implicating the 'pars magnocellularis' with plurimodal brain stem systems and with the second somatic sensory and so-called 'association' areas of the cortex.

It remains only to note that the error inherent in the application of the highly selective Golgi techniques to samples of unknown numerical significance does not

allow one to exclude the existence of other populations in the medial geniculate body. Indeed, the argument of this inquiry is not the desirability of a particular parcellation or classification but of structurally intelligible hypotheses regarding the functions of the medial geniculate body.

SUMMARY

1. The neuronal structure of the medial geniculate body of the cat has been studied with modifications of the Golgi methods.

2. An analysis of neuronal populations chiefly in terms of their dendrites and afferent plexuses reveals ventral, dorsal, and medial divisions.

3. The ventral division contains neurons with tufted dendrites, a laminar arrangement, and orderly contacts with clustered terminals of the brachium of the inferior colliculus. These elements are probably concerned with a spatially localized, differential auditory function, e.g. frequency discrimination.

4. The dorsal division, including the posterior tip of the medial geniculate, contains neurons with radiate dendrites, a scattered arrangement, and diffuse axo-dendritic afferent contacts. These elements are probably concerned with the integration of heterogeneous, perhaps plurimodal, inputs.

5. In the medial division the neurons with radiate dendrites have properties of an interstitial nucleus suitable for the relay of multiple fibre systems. The neurons with tufted dendrites have features in common with the dorsal and ventral divisions.

6. Some of the constituent populations of each division, including the supra-geniculate nucleus, are characterized.

7. Certain quantitative, developmental, and comparative aspects of the analysis are considered, and the literature of the architectonics and connexions of the medial geniculate reviewed.

This investigation was carried out in the laboratory of Dr G. L. Rasmussen. His advice and encouragement, and the technical aid of Miss E. P. McCrane and Mr F. D. Nolan are gratefully acknowledged. The painstaking preparation of nearly 10,000 of the Golgi sections is the handiwork of Mrs R. R. Morest.

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LIST OF ABBREVIATIONS

BCI	Brachium colliculi inferioris
BCS	Brachium colliculi superioris
CGL	Corpus geniculatum laterale
CGM	Corpus geniculatum mediale
CS	Colliculus superior
D	Nucleus dorsalis, CGM
DP	Nucleus dorsalis profundus, CGM
DS	Nucleus dorsalis superficialis, CGM
H	Hippocampus
IL	Incisura lateralis, CGM
LM	Lemniscus medialis
LV	Pars lateralis (V)
M	Divisio medialis, CGM
NRT	Nucleus reticularis thalami
NS	Nucleus suprageniculatus
NSP	Nucleus suprapeduncularis
OV	Pars ovoidea (V)
PC	Pedunculus cerebri
RT	Radiationes thalami
SN	Substantia nigra
TO	Tractus opticus
TS	Tracti spinothalamici
V	Nucleus ventralis, CGM
VL	Nucleus ventro-lateralis, CGM
VPL	Nucleus ventralis postero-lateralis thalami
X	Subnucleus, nucleus lateralis posterior thalami
ZM	Zona marginalis, CGM

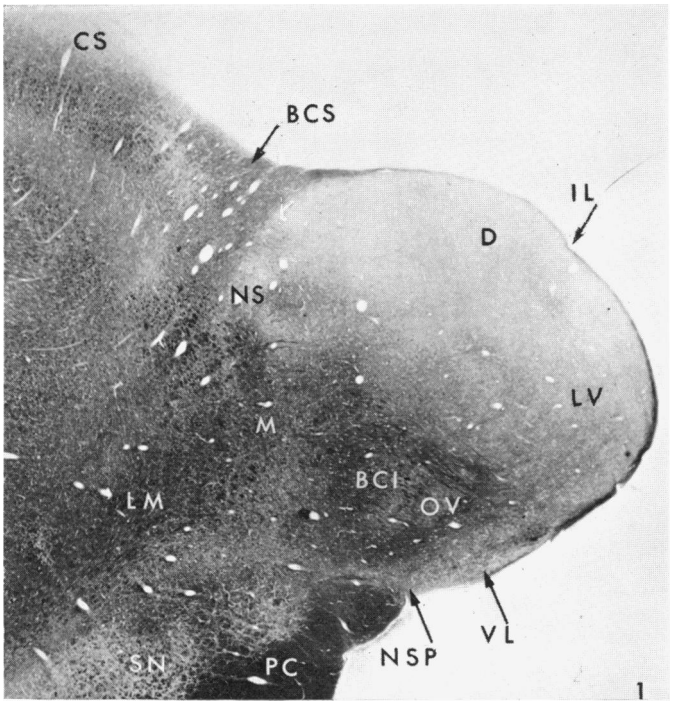
EXPLANATION OF PLATE

These transverse sections are perpendicular to the horizontal axis of the brain stem.

PLATE 1

Fig. 1. Transverse section through the middle third of the medial geniculate body of an adult cat. Frozen section stained with Sudan Black B; ×9.

Fig. 2. Golgi–Cox preparation from the medial geniculate body of a 15-day-old cat. At this magnification (×87·5) and section thickness (120 μ) cell types are not distinguished, but the uniformity of the impregnation used for the total reconstruction (see p. 2) is exemplified. A sparsely impregnated periphery, limited here to the marginal zone and fibre capsule, often occurs in Golgi–Cox, but not in the rapid Golgi preparations.


CS
BCS
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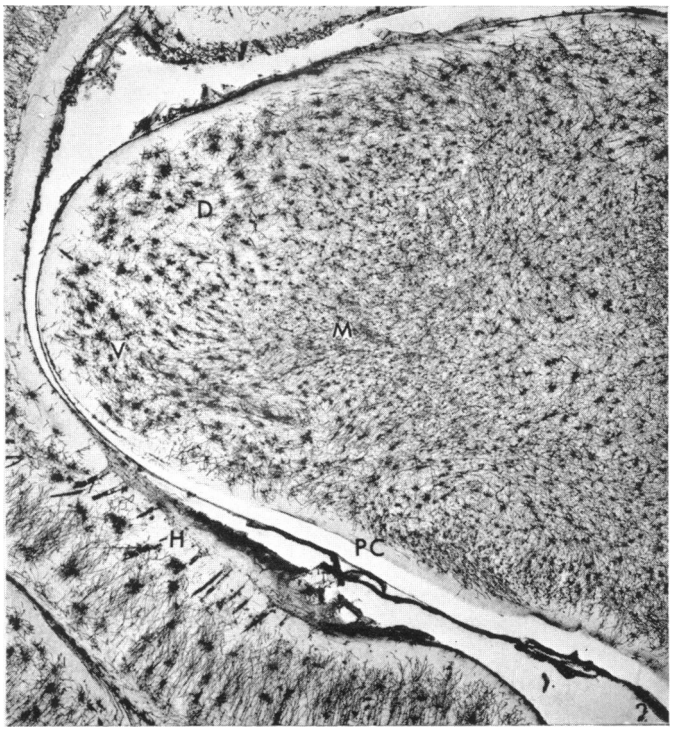
PC
1


D
M
V
H
PC
2