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Connectional and neurochemical subdivisions of the pulvinar in *Cebus* monkeys

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Abstract

Based on cytoarchitectonic criteria, the primate pulvinar nucleus has been subdivided into medial (PM), lateral (PL), and inferior (PI) regions. However, these subdivisions show no correlation with those established by electrophysiological, immunocytochemical, or neuroanatomical tracer studies. In this work, we studied the connections of the pulvinar nucleus of *Cebus* monkey with visual areas V1, V2, V4, MT, and PO by means of retrograde fluorescent tracers injected into these areas. Based on the projection zones to cortical visual areas, the visual portion of the pulvinar of *Cebus* monkey was subdivided into three subregions: P1, P2, and P3, similar to those described in the macaque (Ungerleider et al., 1984). In *Cebus*, P1 includes the centrolateral portion of traditionally defined PI and adjacent portion of PL. P2 is located in the dorsal portion of PL and P3 includes the medial portion of PI and extends dorsally into adjacent PL and PM. In addition, we studied the histology of the pulvinar using multiple criteria, such as cytoarchitecture and myeloarchitecture; histochemistry for cytochrome oxidase, NADPH-diaphorase, and acetylcholinesterase; and immunocytochemistry for two calcium-binding proteins, calbindin and parvalbumin, and for a neurofilament recognized by the SMI-32 antibody. Some of these stains, mainly calbindin, showed additional subdivisions of the *Cebus* pulvinar, beyond the traditional PI, PL, and PM. Based on this immunohistochemical staining, the border of PI is moved dorsally above the brachium of the superior colliculus and PI can be subdivided in five regions (PI_P, PI_M, PI_C, PI_L, and PI_{LS}). Regions P1, P2, and P3 defined based on efferent connections with cortical visual areas are not architectonically/neurochemically homogeneous. Rather they appear to consist of further chemoarchitectonic subdivisions. These distinct histochemical regions might be related to different functional modules of visual processing within one connectional area.

Keywords: Primate, Visual system, Thalamus, Connections, Calcium-binding proteins

Introduction

The pulvinar nucleus of primates has been studied in various species, with different methods. Walker (1938) subdivided the pulvinar of the *Macaca* into medial (PM), lateral (PL), and inferior (PI) regions based on topographic and cytoarchitectonic criteria. In *Cebus* monkey, Gattass et al. (1978) described two retinotopic maps in the pulvinar based on electrophysiological studies: the ventrolateral group, which comprises PI and the ventral portion of PL; and Pμ, located in the dorsomedial portion of PL. By recording from clusters of neurons in the pulvinar of the *Macaca*, Bender (1981) also found two representations of the visual hemifield, named PI and PL. Whereas the macaque's PI is roughly similar to the ventrolateral map of *Cebus*, the macaque PL and the *Cebus* Pμ are different in terms of extent and visuotopy (Gattass et al., 1978; Bender, 1981).

Based on myeloarchitecture and connections with area MT, Lin and Kaas (1979) distinguished three separate nuclei in PI of owl monkeys and showed that at least some of the subdivisions of PI extend dorsally across the brachium of the superior colliculus (SC). These findings have been confirmed and extended by Cusick et al. (1993) and Stepniewska and Kaas (1997). In addition, Stepniewska et al. (1999) established that the subdivisions of PI which receive ascending connections from the superior colliculus are distinct from the nucleus that projects to area MT. In the macaque, a crescent-shaped region which traverses the brachium of the SC, including parts of PI and the ventral portion of PL, also showed reciprocal and topographic connections with MT (Standage & Benevento, 1983). Ungerleider et al. (1984), studying the corticothalamic projections of area MT in the macaque, found three areas in the pulvinar named P1, P2, and P3. They stated that P1 and P2 correspond to the two visuotopic maps, PI and PL, described by Bender (1981), while P3 is located medially in the inferior pulvinar

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and includes a small portion of the lateral and of the medial pulvinar, located dorsally to the brachium of the SC, similar to the crescent-shaped, MT-projecting region described by Standage and Benevento (1983).

In addition, immunocytochemical studies in macaque and squirrel monkeys (Cusick et al., 1993; Gutierrez et al., 1995; Gray et al., 1999) revealed five subdivisions of the inferior pulvinar, which include all of the traditional inferior pulvinar, but which also extend to encompass parts of the lateral and the medial pulvinar, named PI_P, PI_M, PI_C, PI_L, and PI_{LS}. Whereas the immunocytochemical methods reveal details of the pulvinar architecture that are not apparent from Nissl and myelin stains, their application has not been without controversy. For example, in macaques, Stepniewska and Kaas (1997), based essentially on the same techniques used by Cusick and collaborators (1993), proposed a different immunocytochemical subdivision for PI, which does not include part of the cytoarchitectonic PL, and used a different nomenclature (see Fig. 15).

In spite of the large number of studies, few correlations have been shown among the subdivisions proposed for the various species, on the basis of different criteria. Searching for a scheme of subdivision that could clarify the correlation between these criteria, we studied the pulvinar nucleus of *Cebus apella* with several methods. First, we studied the connections of the pulvinar complex with visual areas V1, V2, V4, MT, and PO by means of retrograde fluorescent tracers injected into these areas. The subdivisions revealed by connections were then correlated with multiple architectural methods. The results based on the projection zones to cortical visual areas demonstrate that the visual portion of the pulvinar can be subdivided into three subregions: P1, P2, and P3, similar to those described in the macaque (Ungerleider et al., 1984). P1 includes the centrolateral portion of traditionally defined PI and adjacent portion of PL. P2 is located in the dorsal portion of PL, and P3 includes the medial portion of PI and extends dorsally into adjacent PL and PM. Furthermore, immunohistochemical staining showed additional subdivisions of the *Cebus* pulvinar, beyond the traditional PI, PL, and PM. Based on this study, the border of PI is moved dorsally above the brachium of the superior colliculus and PI can be subdivided in five regions (PI_P, PI_M, PI_C, PI_L, and PI_{LS}), as described by Cusick and collaborators (1993) in macaques. A partial account of these data was presented elsewhere (Soares et al., 1997).

Materials and methods

Twenty-three adult male *Cebus apella* monkeys weighing between 1.2 and 2.6 kg were used. Seventeen of these monkeys were also used in other studies. In 15 animals, injections of two fluorescent tracers, Fast Blue (FB) and Diamidino Yellow (DY), were made into visual areas V1, V2, V4, MT, and PO (Table 1). The remaining eight monkeys, used for neurochemical studies, did not receive fluorescent tracer injections. All experimental protocols were conducted following the NIH guidelines for animal research and they were approved by the committee for animal care and use of the Instituto de Biofísica Carlos Chagas Filho, UFRJ.

Injections of fluorescent tracers

For three consecutive days prior to surgery, the animals received a daily dose of 0.5 ml of dexamethasone (4 mg/ml, IM), to prevent brain edema. For surgery, the animals were anesthetized with intramuscular injections of ketamine (30 mg/kg) and diazepam (0.8 mg/kg), and were treated with atropine (0.15 mg/kg, IM) to inhibit tracheobronchic secretions. The animals were then maintained under artificial ventilation with halothane (2%) and a mixture of N_2O/O_2 (7:3). Expired CO_2, electrocardiogram, and rectal temperature were continuously monitored and kept within normal physiological ranges.

Table 1. *Summary of injected cortical areas, fluorescent tracers, and plane of section used for each animal*[a]

Case	Cortical Area	Tracer	Plane of Section
1, 2, 3	MT	FB	SAGITTAL
4, 5	MT	FB	SAGITTAL
	V2	DY	
6	MT	FB	SAGITTAL
	PO	DY	
7	MT	FB	CORONAL
	PO	DY	
8	V2	FB	CORONAL
	V4	DY	
9, 10	V2c	FB	CORONAL
	V2p	DY	
11	PO	DY	CORONAL
12	PO	FB	CORONAL
	V1	DY	
13	V1c	FB	CORONAL
	V1p	DY	
14	V1	FB	CORONAL
15	V4c	DY	CORONAL
	V4p	FB	

[a]c: central; p: periphery.

With the exception of four cases, in which injections in MT were made under electrophysiological guidance (Fiorani et al., 1989), all other injections were made under visual guidance. In these cases, we used previously published visuotopic maps (Gattass et al., 1987; Rosa et al., 1988; Piñon et al., 1998; Neuenschwander et al., 1993) to locate the injection sites. The injections of FB (5%) and DY (5%) were made by means of a short beveled 1-μl Hamilton syringe with a 27-gauge needle. In all cases 0.2–0.5 μl of FB or 0.5–1.0 μl of DY were injected.

Histological processing

After variable survival times (14–21 days), the animals were deeply anesthetized with sodium pentobarbital (30 mg/kg) and perfused with normal saline followed by 2% paraformaldehyde in phosphate-buffered saline (PBS); 2% paraformaldehyde in PBS + 2.5% glycerol; PBS + 5% glycerol; and PBS + 10% glycerol. Serial 40-μm-thick sections were obtained using a cryostat. Series of unstained sections, 400 μm apart, were mounted onto double-gelatinized slides, quickly dried, and stored in light-tight boxes. In addition, adjacent series were stained for cell bodies with cresyl violet and for myelin with the Gallyas' method (1979), for acetylcholinesterase (AChE) by the method of Karnovsky and Roots (1964) modified by Hedreen (1985) (five animals), for NADPH-diaphorase following the method of Sagar (1985) (four animals), for cytochrome oxidase by the method of Silverman and Tootell

(1987) (four animals), and for immunocytochemistry for calbindin and parvalbumin (eight animals) and SMI-32 (four animals).

For immunocytochemical reactions, sections were incubated overnight with calbindin-D28K (Swant-Swin Antibodies, Bellinzona, Switzerland), parvalbumin (Swant-Swin Antibodies, Bellinzona, Switzerland), or SMI-32 (Sternberger Monoclonals, Inc., Bethesda, MD) monoclonal antibodies at dilutions of 1:2500, 1:3000, and 1:5000, respectively, in a solution containing 0.05% of bovine albumin and 0.3% of triton X-100 in 0.001M phosphate-buffered saline, pH 7.4. They were then incubated for an additional hour in biotinylated anti-mouse secondary antibody, and then processed by the avidin-biotin method with ABC kits (Vector Labs, Burlingame, CA) and diaminobenzidine. Control sections were prepared by omitting the primary antibody in the incubation solution. These sections showed no specific staining. Sections were examined under brightfield microscopy and photographed.

Cell plotting and assessment of the extent of the injection sites

Unstained sections were scanned with a Zeiss Axioplan fluorescence microscope interfaced to an IBM-AT microcomputer using custom-developed morphometric software. The histological extent of each injection site was estimated following criteria defined by Conde (1987). The visuotopic extent of the injection sites for all areas, except V4, was estimated by examining the location of retrogradely labeled cells in V1 and comparing the position of the patches with the visuotopic map described by Gattass et al. (1987). The extent of the injection site in V4 was estimated by examining the location of labeled cells in area V2, using the visuotopic map described by Rosa et al. (1988). In animals with no electrophysiological recordings, areal boundaries were defined based on differences in myeloarchitectonic patterns, following the criteria previously described by Rosa et al. (1993).

Results

Cytoarchitectonic analysis

Based on cytoarchitecture, we can subdivide the pulvinar of *Cebus* into three major regions, which we named following the terminology proposed by Walker (1938). Fig. 1 shows a series of coronal sections through the pulvinar of *Cebus*, at different A-P levels, stained by the Nissl method. The medial pulvinar (PM) is a large, homogeneous, and compact nucleus, while the lateral pulvinar (PL) contains cells that are separated into clumps by many fibers passing horizontally through this nucleus. The inferior pulvinar (PI) is a compact and darkly stained nucleus, separated from the remainder of the pulvinar by the brachium of the superior colliculus (see also Fig. 10A).

Analysis of connectional data

Projections to MT

Seven animals received fluorescent tracer injections in MT. The injections involved the region of representation of 5–25 deg of the visual field, both in the upper and lower quadrants. In all cases, the pattern of distribution of labeled cells in the pulvinar was similar to the cases illustrated in Figs. 2, 3, and 4. Figs. 2 and 3 show cases studied in the parasagittal plane, while Fig. 4 illustrates one case studied in the coronal plane. All injections resulted in

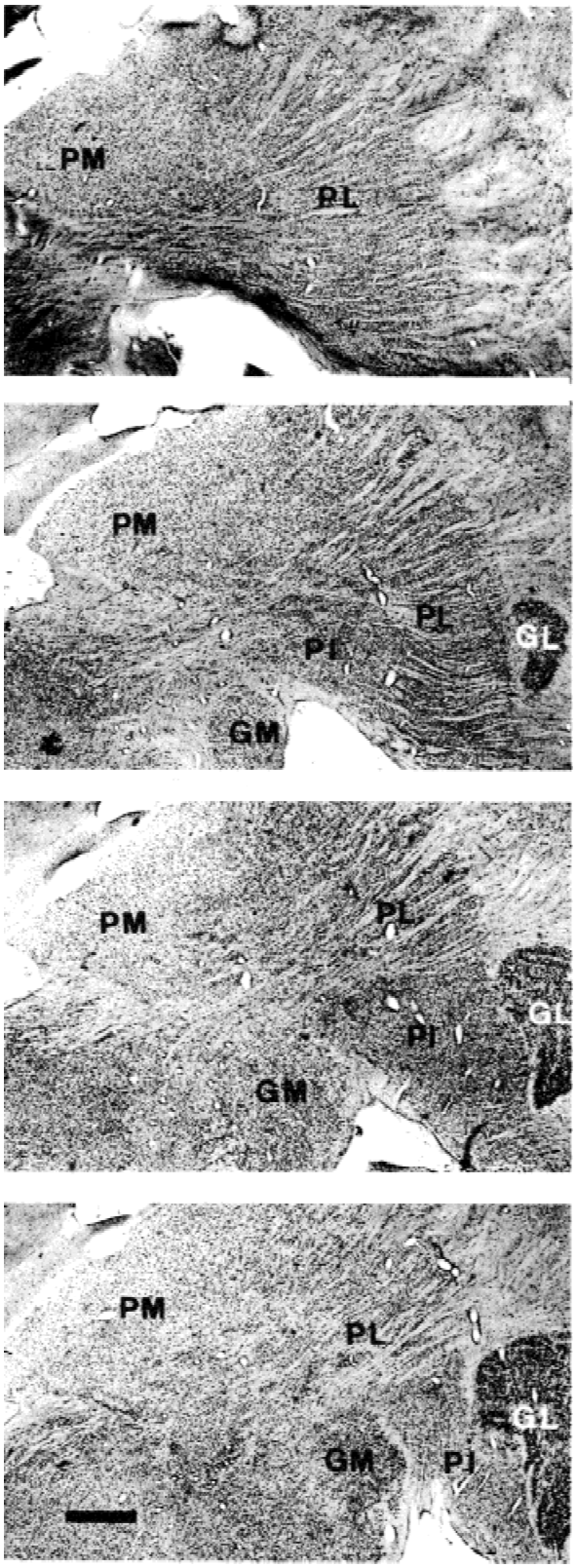

Fig. 1. Photomicrographs of Nissl-stained serial coronal sections (caudal-to-rostral) through the *Cebus* pulvinar spaced 400 μm apart illustrating the subdivisions; PM: medial pulvinar; PL: lateral pulvinar, and PI: inferior pulvinar using the nomenclature proposed by Walker (1938). GL: lateral geniculate nucleus, and GM: medial geniculate nucleus. Scale bar = 1 mm.

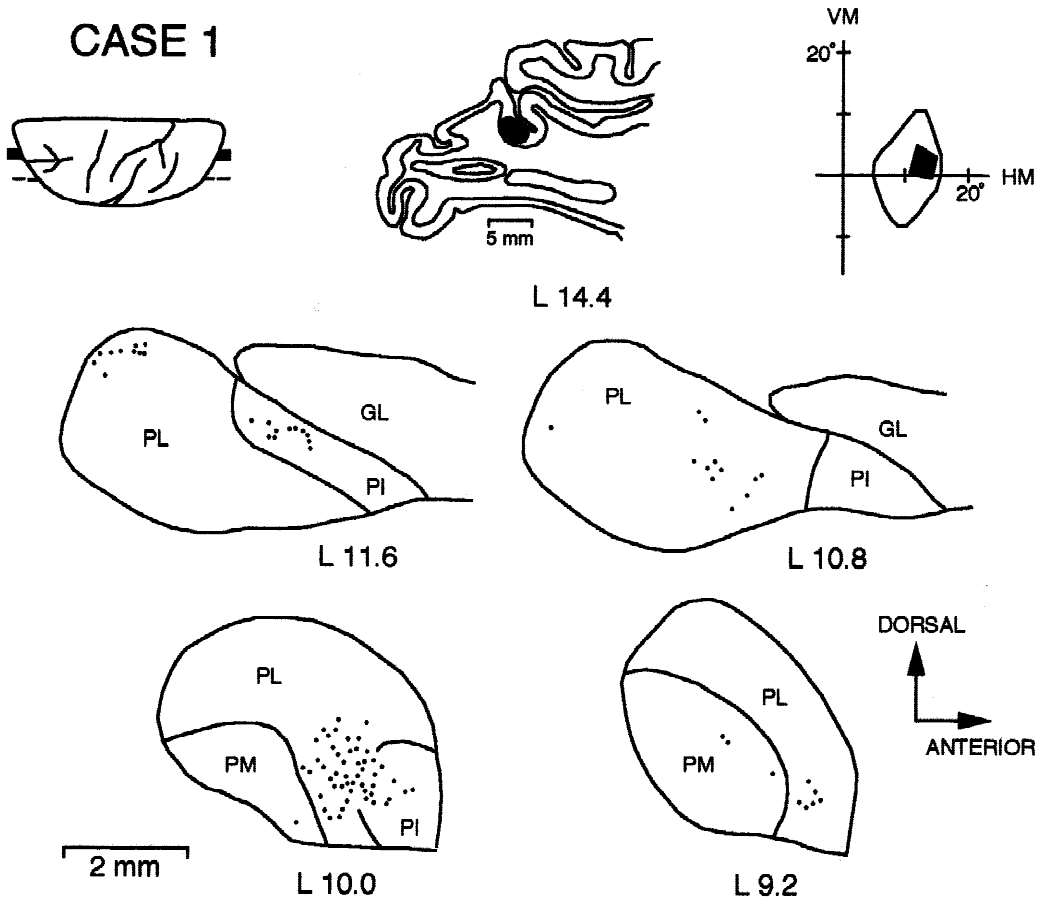

Fig. 2. Summary of data from a case with injection of FB in MT. Upper left: dorsal reconstruction of the left hemisphere showing the levels of the parasagittal sections through the pulvinar illustrated below. Upper middle: parasagittal section to illustrate the extent of the injection site. Upper right: representation of the visual field with the estimated visuotopic extent of the injection site (outline), and the receptive field recorded at the injection site (black). Lower: parasagittal sections through the pulvinar with the labeled cells indicated by dots.

three regions of labeling in the pulvinar: one in the dorsal portion of PL; a second region located laterally in PI; and a third, more densely labeled region, located medially. The latter region, which is more easily identifiable in the coronal plane (Fig. 4), includes parts of traditional PI but extends dorsally across the brachium of the SC into adjacent PL and PM.

Projections to V2

Fluorescent tracers were injected into V2 in five cases. In three of these cases, we injected only one tracer in the region of representation of the central lower visual field. In the remaining two cases, injections of two different tracers were made: one in the region of representation of the central and another in the region of the representation of the intermediate portion of the visual field (5–10 deg). Figs. 3 and 5 illustrate cases of central injections in V2. In all cases of central injections, labeled cells were only found in the centrolateral portion of PL (see also Fig. 6).

Fig. 6 illustrates two cases in which FB was injected in the region of the representation of the central visual field, in the lower (Fig. 6A) and upper (Fig. 6B) quadrants, while DY was injected in the region of the representation of the intermediate (5–10 deg) inferior visual field. Comparison of the data shown in the cases of Figs. 6A–6B shows that centrally located injections labeled cells in a more ventral and posterior portion of PL, while intermediate injections labeled cells in a patch located more dorsally and anteriorly.

Projections to V4

Two animals received fluorescent tracer injections in V4. One of the animals received a single injection of DY that extended to the region of representation of the central 8 deg of the visual field in the lower quadrant (Fig. 5). The second animal received one injection of DY in the region of representation of the central visual field (5 deg) and a more peripherally (15 deg) located injection of FB (not illustrated). All injections labeled cells in the central portion of PL and, similar to V2, peripherally located injections in V4 labeled cells placed more dorsally than central injections.

Projections to V1

Fluorescent tracers were injected into central V1 (0–5 deg) in three animals. In addition, one of these animals received a second,

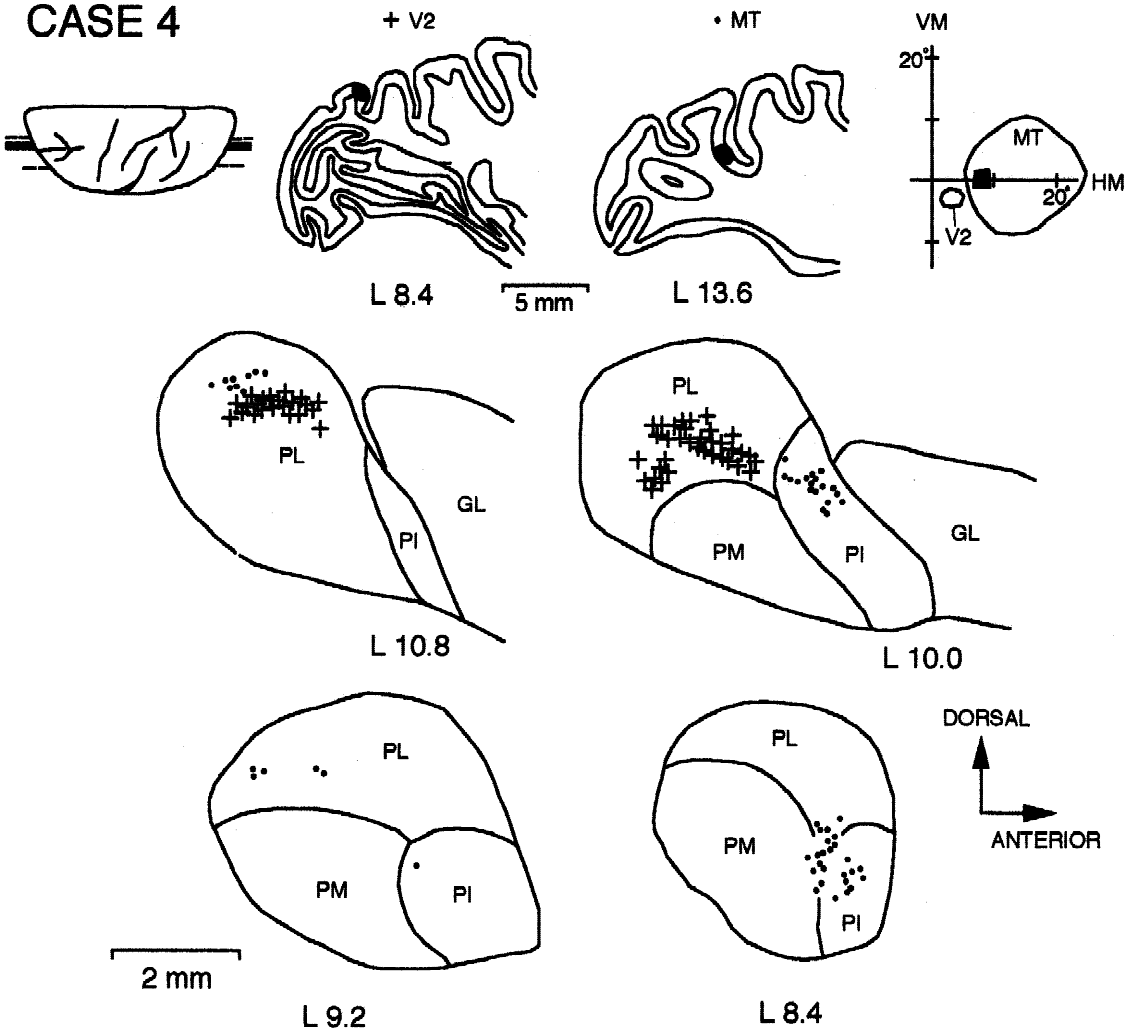

Fig. 3. Summary of data from a case with injections of FB in MT and DY in V2. Lower: parasagittal sections through the pulvinar with the labeled cells indicated by dots for MT injection and by crosses for V2 injection. Conventions are as in Fig. 2.

more peripheral, injection of a different tracer. After V1 injections, we observed two patches of labeled cells: one, posteriorly, in the lateral portion of PL, and a second one, which includes adjacent portions of PI and PL, at more anterior levels. A case of a central injection is illustrated in Fig. 7. Similar to V2 and V4 connections, cells labeled after the peripheral injection in V1 were located more dorsally than those labeled following a central injection (not illustrated).

Projections to PO

Four animals received fluorescent tracer injections in PO. Three cases included the representation of both quadrants, while in one of the cases the injection was restricted to the region of representation of the upper quadrant. In the first three cases, we observed labeled cells in the dorsolateral portion of PL and in the centromedial portion of PI (Figs. 4 and 7), while in the last case labeled cells were only observed in the dorsolateral portion of PL.

Connectional subdivisions of the pulvinar

Analysis of the efferent projections of the pulvinar to cortical visual areas shows that the visual pulvinar complex of *Cebus* monkey can be subdivided into three regions. This subdivision was based primarily on the three projection zones to area MT. However, we also took into account the projection zones to areas V1, V2, V4, and PO to draw the limits between these projection zones. To avoid introducing a new nomenclature, we have named these regions P1, P2, and P3 following the terminology proposed by Ungerleider et al. (1984) for macaques, in spite of being defined on the basis of efferent projections. Inasmuch as the key criterion to define P3 in this paper was the connectivity with area MT, we found it appropriate to use Ungerleider et al.'s terminology for all of the connectional data. However, the amount and extent of the labeling in the pulvinar in all cases is restricted, allowing us to draw only arbitrary borders. The limits of P3 and P2 with P1 were defined by the projections to areas V2 and V4, that are restricted

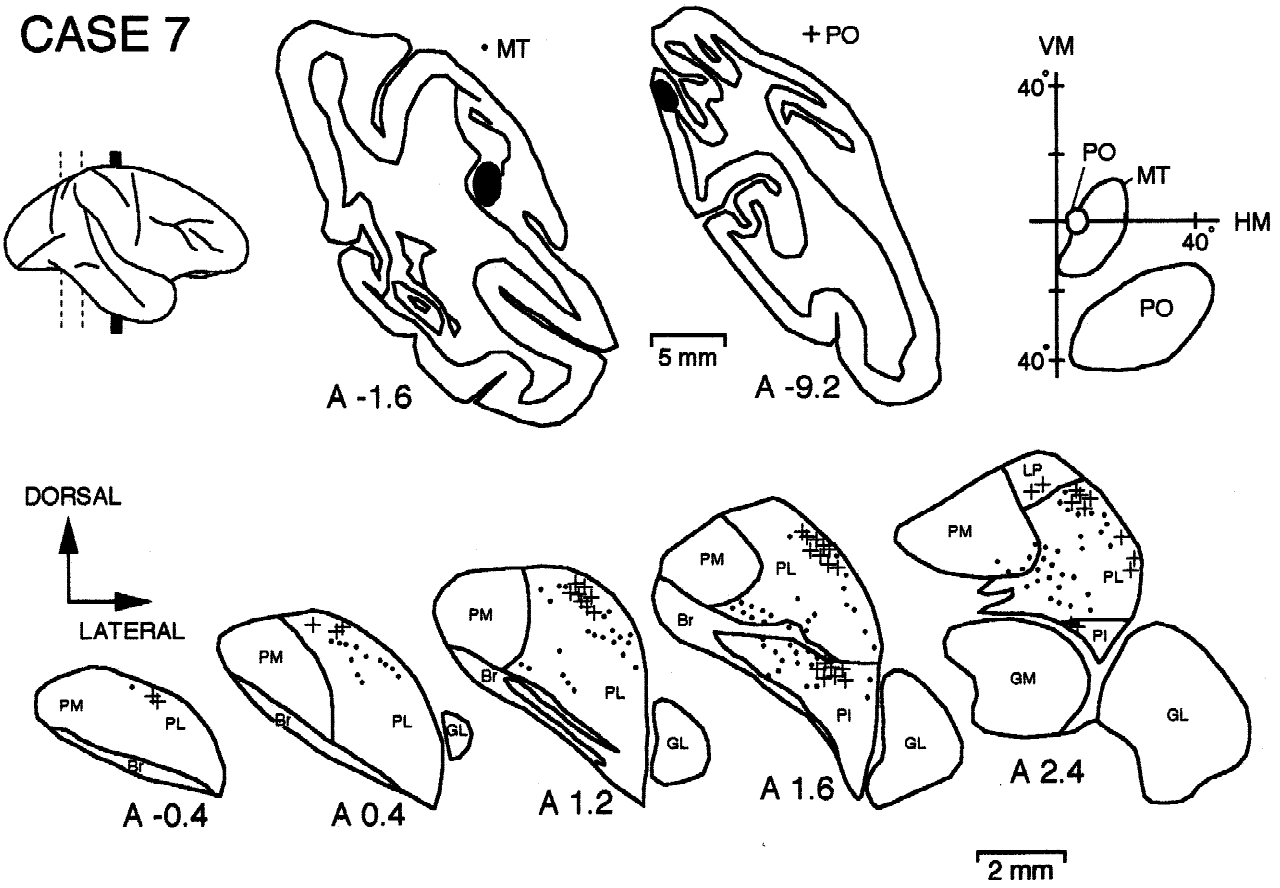

Fig. 4. Summary of data from a case with injections of FB in MT and DY in PO. Upper left: lateral view of the right hemisphere showing the levels of the coronal sections through the pulvinar (dark bar), and through the injection sites (dashed lines). Upper right: representation of the visual field showing the estimated visuotopic extents of the injection sites (outlines). Lower: coronal sections through the pulvinar with the labeled cells indicated by dots for MT injection and by crosses for PO injection.

to P1. Fig. 8 shows a summary of the pulvinar regions containing labeled cells after injections in cortical visual areas of all animals studied. P1, which includes the centrolateral portion of traditional PI and the adjacent portion of PL, projects heavily to V1, V2, and V4 and lightly to MT and PO. P2, located in the dorsal portion of PL, has heavy projections to MT and PO and a light projection to V1. P3 includes the medial portion of traditional PI and adjacent portions of PL and PM, and projects mainly to MT, but also has a light projection to PO. A schematic diagram of these projections is illustrated in Fig. 9. Based on the amount of labeled cells in each of the pulvinar regions after injections in a single cortical area, we divided the projections into light (dashed) and heavy (continuous) lines. This representation is not absolute, inasmuch as no attempt was made to compare the density of projections to different cortical areas. The lack of comparison is related to the different sizes of injection sites in different areas.

Chemoarchitectonic analysis

The chemoarchitectonic pattern of the pulvinar was studied with cytochrome oxidase and NADPH-diaphorase. These enzymes have been used as histochemical activity markers and show similar topographic distribution in the cortex (Wong-Riley, 1979; Sandell, 1986). The staining for these enzymes in the pulvinar nucleus of *Cebus*, like in the lateral geniculate nucleus (GL), is restricted to the neuropil, and does not include cell bodies (Figs. 10C,D and Figs. 11A,B). Traditionally defined PI is easily identifiable by its nonhomogeneous heavy stain. A lighter strip separates its medial from its lateral heavily stained portions. PL stains moderately and PM shows a weak reaction, being lightly stained. Myeloarchitectonically PI can also be clearly identified, in parasagittal sections, as a pale region separated from the remainder of the pulvinar which is rich in fiber bundles (Fig. 10B).

The immunocytochemical localization of calbindin in the pulvinar of *Cebus* is illustrated in Fig. 12. When reacted for calbindin, the pulvinar shows regions with distinct staining patterns similar to those found by Cusick et al. (1993) in macaque. The medial portions of traditional PI, PL, and adjacent PM are poorly stained for calbindin. This area was termed PI_M by Cusick et al. (1993) and separates two heavily stained areas named PI_P and PI_C. PI_L, which includes the ventral portion of PL and the lateral portion of traditional PI, shows a less intense reaction in the neuropil depicting however some large dispersed and well-stained cells (Fig. 14C). The border between PI_L and PL was determined solely by the

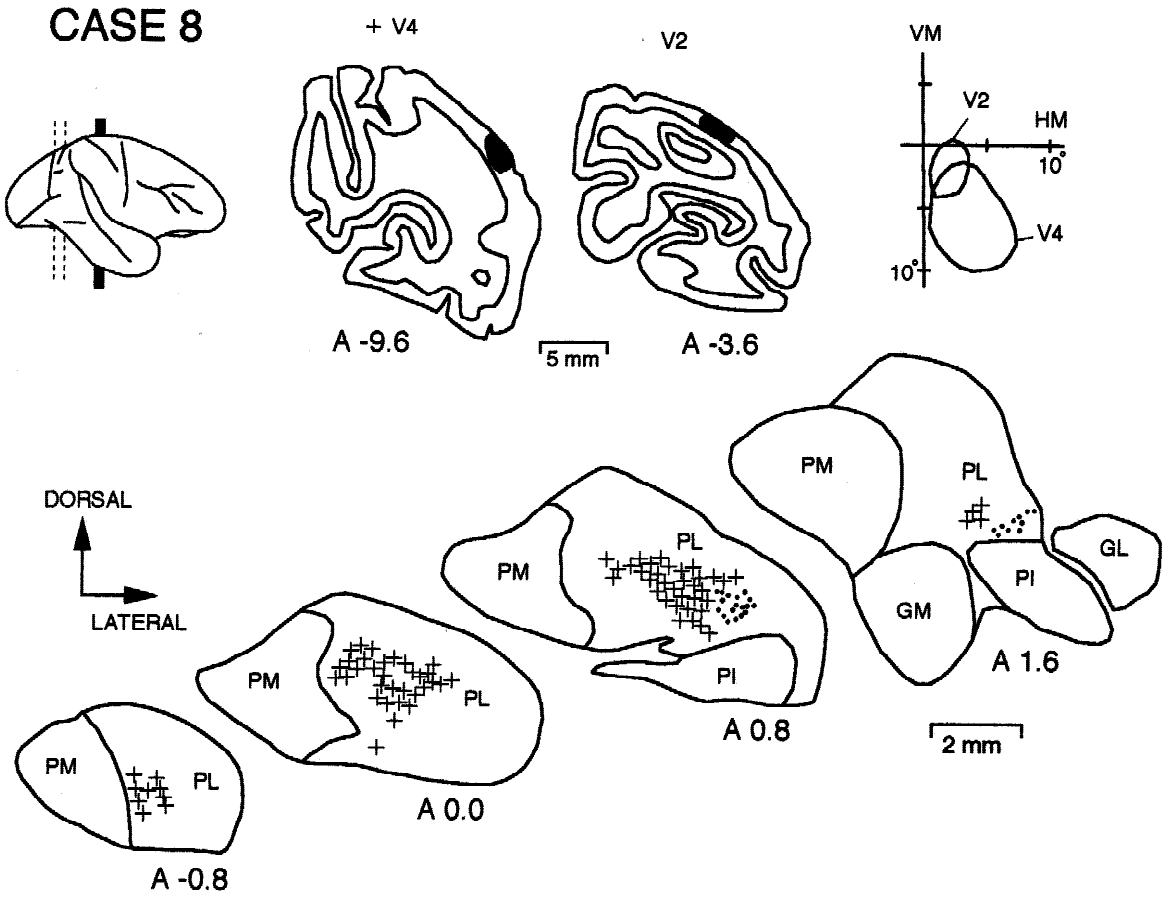

Fig. 5. Summary of data from a case with injections of FB in V2 and DY in V4. Labeled cells for V2 injection are indicated by dots and for V4 injection by crosses. Conventions are as in Fig. 4.

presence of these large calbindin stained neurons, which are rare in the dorsal portion of PL. Laterally in PI_L, at the border of the GL, we also observe a darker narrow band similar to PI_{LS} as described by Gutierrez et al. (1995). The stain for parvalbumin shows a more homogeneous pattern throughout the pulvinar (Fig. 13F), depicting however a heavier stain in the intermediate region of PI.

SMI-32, a monoclonal antibody that recognizes a nonphosphorylated epitope of neurofilament proteins (Sternberger & Sternberger, 1983), has recently been used to define regional patterns of cortical organization in the visual system (Hof & Morrison, 1995). The pulvinar shows a light staining pattern for SMI-32 (Fig. 13E), with the presence of a small population of large, heavily labeled neurons scattered throughout the nucleus, being more conspicuous in PL (Figs. 14B and 14D). These cells have a distribution similar to that of the large calbindin-positive cells. In addition, the intermediate portion of PI shows a darker staining pattern and a concentration of moderately labeled medium-sized cells (Fig. 14A). This pattern is similar to that described in macaque by Gutierrez et al. (1995).

Analysis of adjacent sections reacted with different methods (Fig. 13) does not allow us to propose a single scheme for the subdivision of the pulvinar. However, in addition to the three major subdivisions already described based on the cytoarchitecture and myeloarchitecture, PM, PL, and PI (Figs. 13A, 13G, and 13H), one can easily identify a calbindin-poor region (Fig. 13D), which includes the dorsal portion of PI and parts of adjacent PL and PM. This calbindin-poor region exhibits a darker staining for cytochrome oxidase (Fig. 13C) and for SMI-32 (Fig. 13E), which however are not exactly coextensive.

The pulvinar shows a heavy reaction for AChE (Fig. 13B) with the intermediate and posterior portions of PI as well as the lateral portion of PL exhibiting slightly heavier staining. This pattern of AChE staining resembles that described in *Macaca* (Lysakowski et al., 1986) and in squirrel monkeys (Steele & Weller, 1993), but it is different from that shown by Gray et al. (1999), with PI_M stained darkly for AChE.

We did not observe a homogeneous chemoarchitectonic pattern within subdivisions P1, P2, and P3. P1, for example, shows a darker reaction for calbindin in its medial and inferior portions and a less intense reaction in its lateral portion.

Discussion

The pulvinar nucleus of several primate species has been investigated by various groups, using different methods of study. However, the classic architectural subdivisions of the pulvinar into medial, lateral, and inferior pulvinar (Walker, 1938) do not correspond to the subdivisions described based on connectional patterns

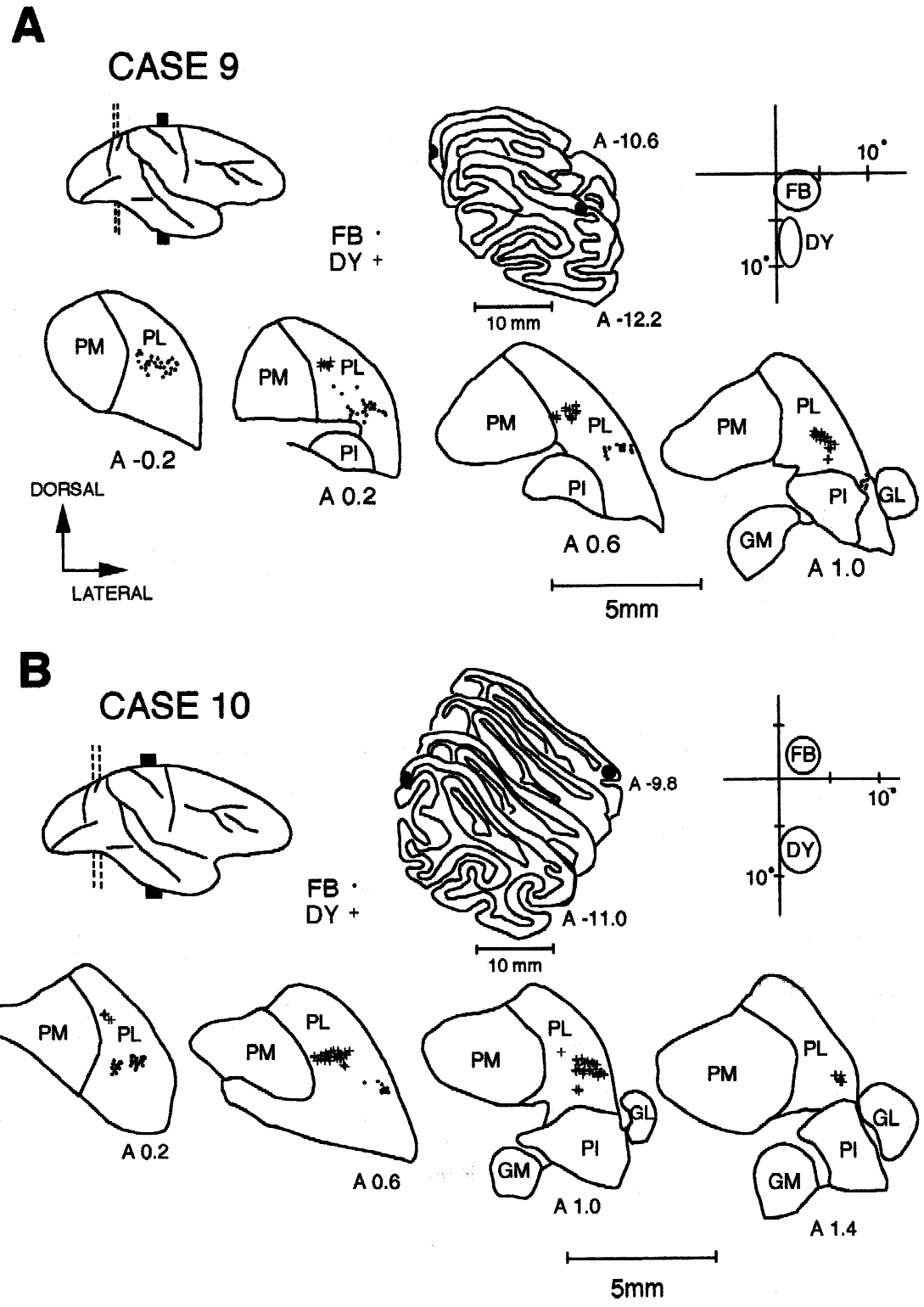

Fig. 6. Data from two cases with injections of FB in central and DY in peripheral V2, showing the projection fields in the pulvinar. Conventions are as in Fig. 4.

(e.g. Lin & Kaas, 1979; Ungerleider et al., 1984), electrophysiological recordings (Allman et al., 1972; Gattass et al., 1978; Bender, 1981), or chemoarchitecture (Cusick et al., 1993; Steele & Weller, 1993; Gutierrez et al., 1995; Stepniewska & Kaas, 1997; Gray et al., 1999; Adams et al., 2000). As a consequence, various schemes of subdivision have been proposed for this nucleus. A comparison of the subdivisions of the pulvinar from various studies is illustrated in Fig. 15.

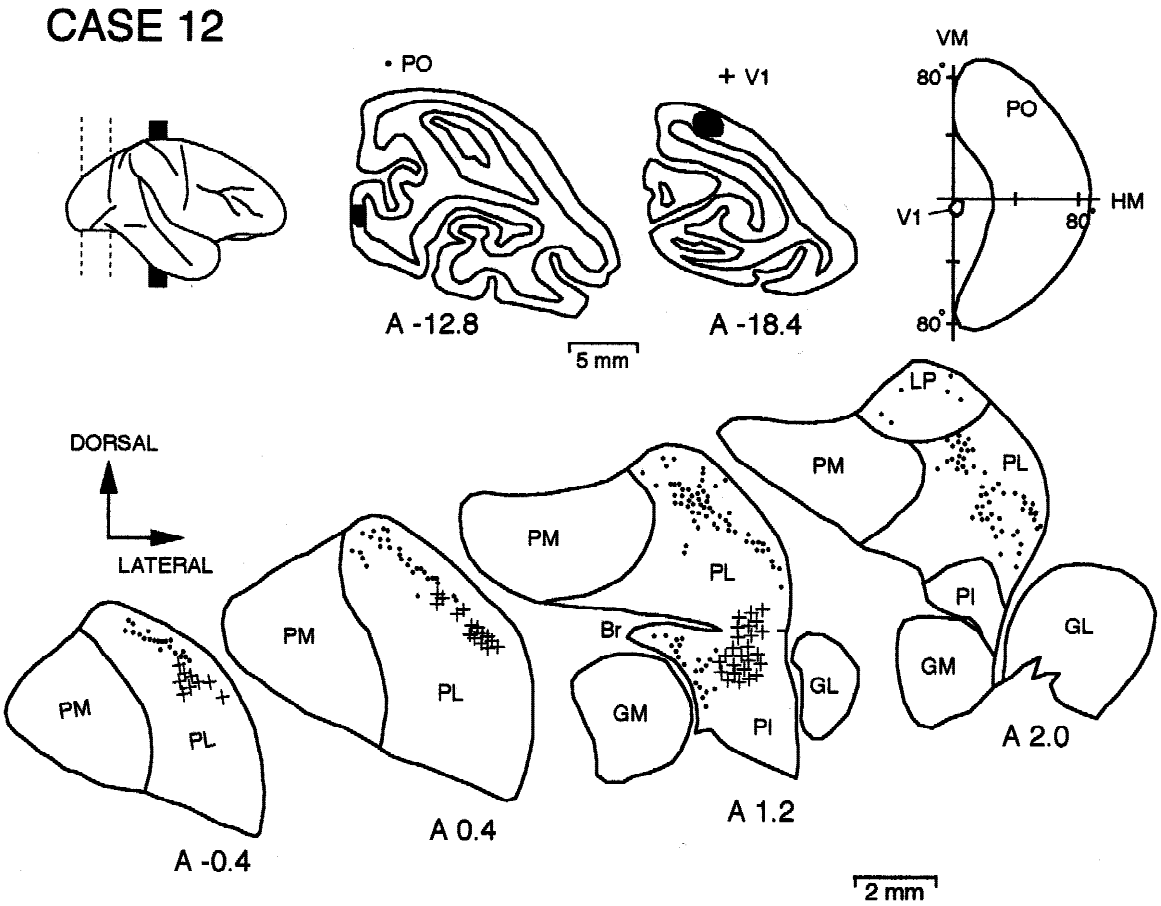

Fig. 7. Summary of data from a case with an injection of FB in PO and an injection of DY in V1. Dots and crosses indicate labeled cells for PO injection and V1 injection, respectively. Conventions are as in Fig. 4.

Electrophysiological subdivisions

The retinotopic organization of the pulvinar was studied using electrophysiological techniques in *Aotus* (Allman et al., 1972), *Cebus* (Gattass et al., 1978), and *Macaca* (Bender, 1981). In the original study of the organization of the pulvinar in owl monkeys, a single visuotopic map was shown in the inferior pulvinar (Allman et al., 1972). More recently, Stepniewska and Kaas (1997) proposed a scheme, in which most of the representation of the contralateral hemifield would be located in the lateral portion of traditional PI, in the region defined PI_{CL} by these authors. In *Cebus* and *Macaca*, two retinotopic maps were found; however, these maps are not in similar topographical locations in both monkeys. The present data suggest that P1 in *Cebus* is comparable to the ventrolateral group described by Gattass et al. (1978), which has a retinotopic organization similar to that defined as PI in rhesus (Bender, 1981). Nonetheless P1 differs from PI described by Bender (1981) inasmuch as it extends into the ventrolateral portion of cytoarchitectonic PL. In addition, the visuotopic map PL in rhesus is not comparable to that of area Pμ defined in *Cebus*, which is smaller and located more dorsally (Gattass et al., 1978). We also believe that in *Cebus* the topographical subdivision Pμ corresponds to part of the connectional subdivision P2 described in this paper.

In a comparative study of the representation of the visual field in the pulvinar of *Macaca* (Old World) and of *Callithrix* (New World), Dick and collaborators (1991) concluded that the two animals have the same number of areas, with similar maps, but their maps seem to be rotated approximately 90 deg, in relation to one another. The horizontal meridian is represented ventrodorsally in *Callithrix*, while in rhesus it is represented mediolaterally. The location and orientation of the visual maps of the pulvinar described in *Cebus* (Gattass et al., 1978) are similar to those described in *Callithrix* (Dick et al., 1991).

Connectional subdivisions

Ungerleider and collaborators (1983), in a study of the topography of the projections from V1 to the pulvinar of the *Macaca*, described two topographical representations of the contralateral visual field (P1 and P2). In this study, in *Cebus*, we also found two projection zones to V1 from the pulvinar, which we named P1 and P2, following the nomenclature proposed by Ungerleider and collaborators (1983). It is worth noting that the subdivisions described in this paper are based on efferent connections of the pulvinar, while those described by Ungerleider and collaborators are based on projections to the pulvinar. P1 in *Cebus* is located in the region that comprises P1 and P2 in macaques, and P2 in *Cebus* is located more dorsal and posterior than P2 in macaques (Fig. 16).

Gutierrez and Cusick (1997), using anterograde tracers, showed that the striate cortex projects to four of the histochemically dis-

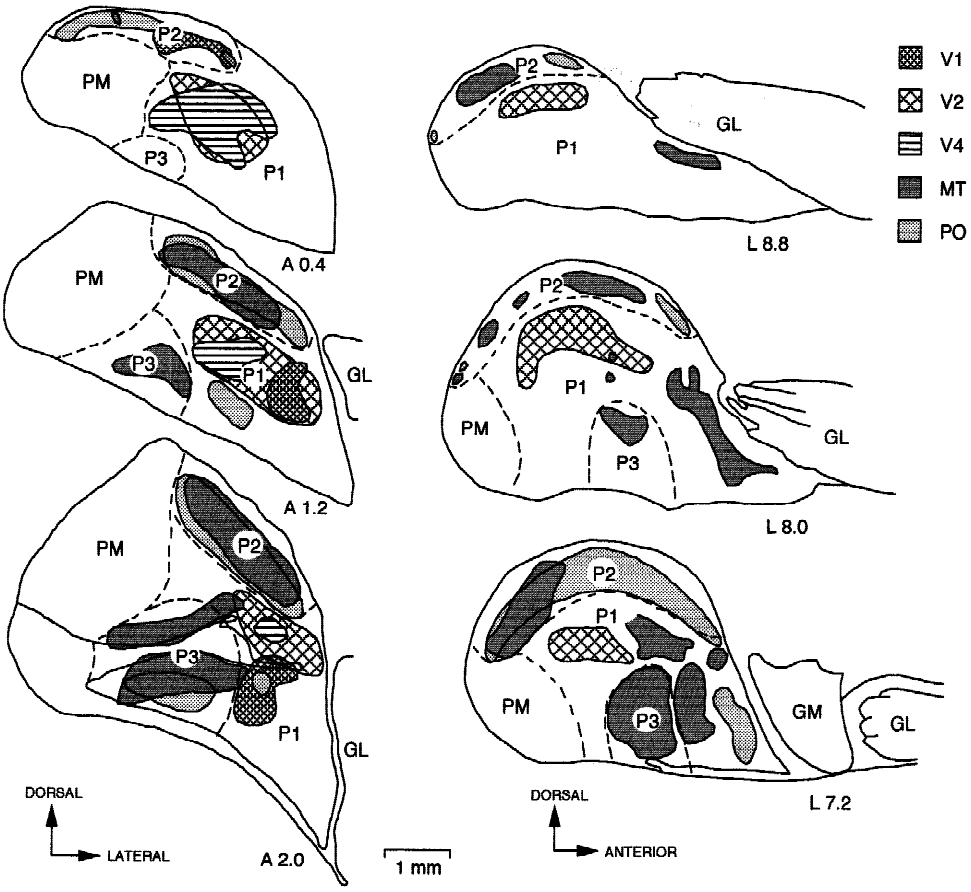

Fig. 8. Summary diagram of the pulvinar of *Cebus* to illustrate the regions containing labeled cells after injections in cortical areas V1, V2, V4, MT, and PO, with corresponding symbols. This figure is based on data pooled from all animals studied in the coronal (left) and in the parasagittal (right) planes. Dashed lines delimit the projection zones P1, P2, and P3. For details, see text.

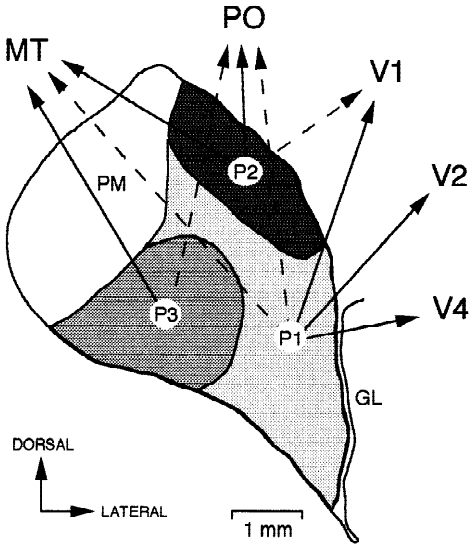

Fig. 9. Schematic diagram of a coronal pulvinar section showing the efferent projections of the pulvinar to cortical visual areas V1, V2, V4, MT, and PO. Continuous arrows—heavier projections; dashed arrows—lighter projections.

tinct zones in PI: PI_M, PI_C, PI_L, and PI_{LS}. The largest labeled zone was found within PI_L. However, after retrograde tracer injections labeled neurons were only observed in PI_L and PI_{LS}, suggesting that only these subdivisions project back to V1.

Studies of the efferent connections of V2 in macaque (Campos-Ortega & Hayhow, 1972; Benevento & Davis, 1977) using tritiated amino acids revealed two zones of projections in the pulvinar: one in the inferior pulvinar and another in the adjacent lateral pulvinar that are coincident with the two visuotopic maps described for this species. Our data in *Cebus* showed, however, that the projection zone to V2 is limited to the centrolateral portion of the lateral pulvinar. These apparently conflicting results could be explained either by the fact that V2 injections in the present study are located in dorsal or central V2 or by the use of different tracers in these studies, or also by species' differences.

Several studies have shown that area MT projects mainly to the dorsomedial portion of the traditional inferior pulvinar, spreading to the adjacent lateral and medial pulvinar (Lin & Kaas, 1979; Wall et al., 1982; Standage & Benevento, 1983). This zone, in the rhesus monkey, was later named P3 by Ungerleider and collaborators (1984). In addition to P3, these authors also described projections from MT to the two zones previously described, based on the projections from V1, named P1 and P2. A strong connection from

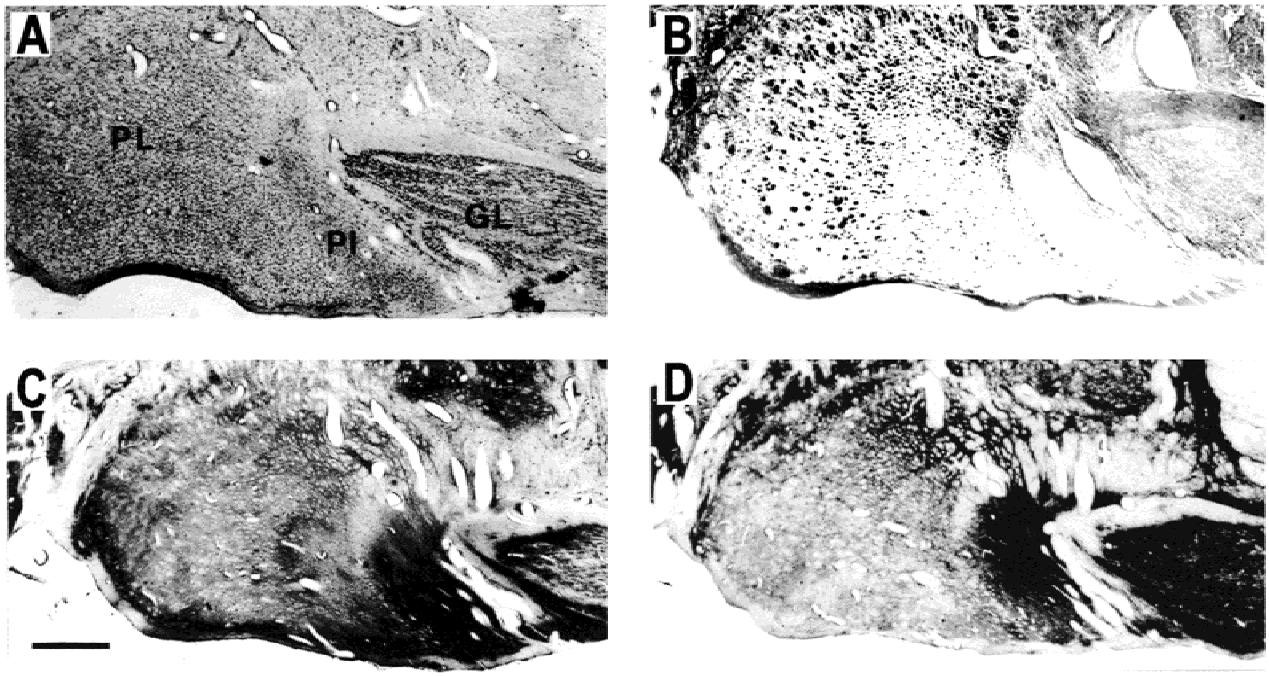

Fig. 10. Photomicrographs of adjacent parasagittal sections of the *Cebus* pulvinar stained with Nissl (A), Gallyas (B), Cytochrome oxidase (C), and NADPH-diaphorase (D) methods. In all cases, the borders of PI are easily identifiable. Scale bar = 1 mm.

MT to a location similar to that of P3 of macaques had already been described in owl monkeys by Lin and Kaas (1979) who named this region as IP_m. Later, Cusick and collaborators (1993) also described a similar projection to the region named PI_M in squirrel and macaque monkeys. In addition, these authors also demonstrated this area to be intensely stained for cytochrome oxidase and for parvalbumin, and lightly stained for calbindin. In the present study, using retrograde tracers, we also found three projection zones from the pulvinar to MT in *Cebus* which we named P1, P2, and P3, in an attempt to make a parallel with the zones previously described by Ungerleider and collaborators (1984) in macaque monkeys with anterograde tracers. As in other studies, P3 is the area with heaviest projections to MT.

Adams et al. (2000) showed that projections from the pulvinar to V1 and V2 in macaque are overlapping. In addition, they showed that these cells are found in two separate fields that are in register with the visual field maps of P1 and P2. In some cases, an additional projection to area V2 was found in P3. MT projecting cells were also found in P1 and P2, but were mainly concentrated in the most medial portion of P3.

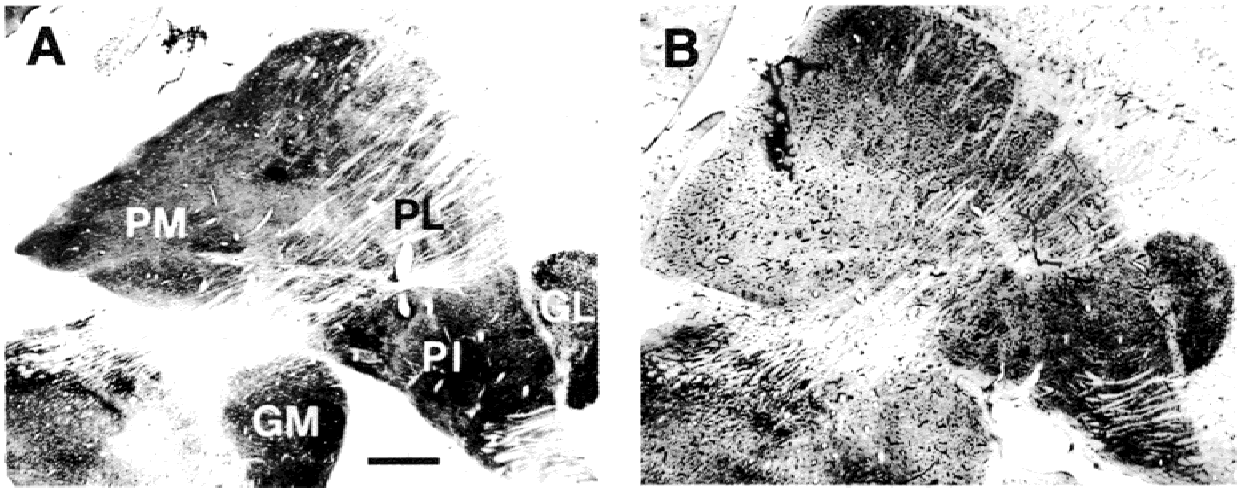

Fig. 11. Photomicrographs of adjacent coronal sections of the pulvinar stained for Cytochrome oxidase (A) and NADPH-diaphorase (B). Scale bar = 1 mm.

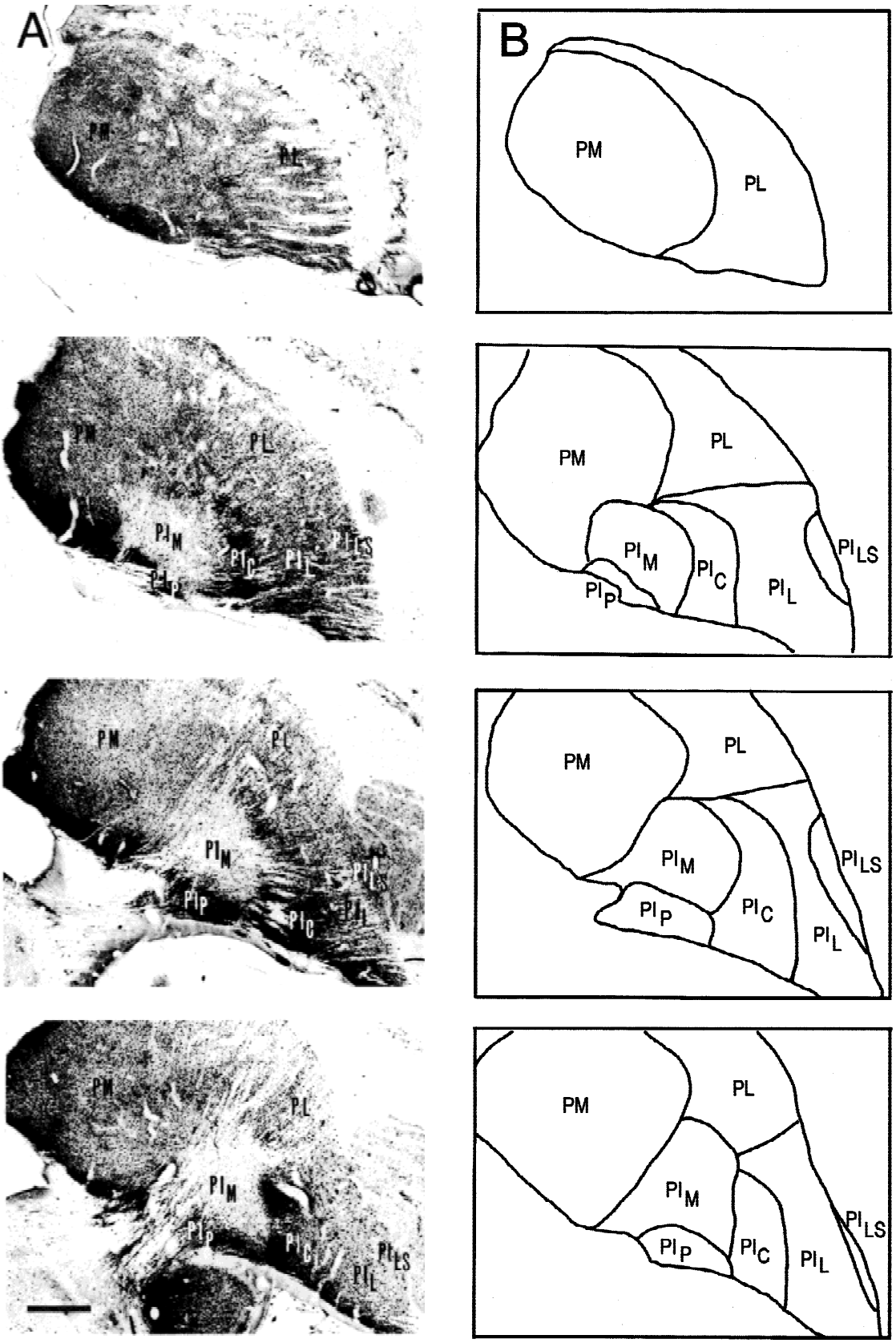

Fig. 12. A: Photomicrographs of a series of caudal-rostral coronal sections (400 μm apart) through the pulvinar reacted for calbindin. B: Outline drawings of the coronal sections showing the subdivisions of the pulvinar revealed by this reaction, using the nomenclature proposed by Cusick et al. (1993). Note that with this method, PI can be subdivided into PI_P (posterior), PI_M (medial), PI_C (central), PI_L (lateral), and PI_{LS} (lateral shell) regions. Scale bar = 1 mm.

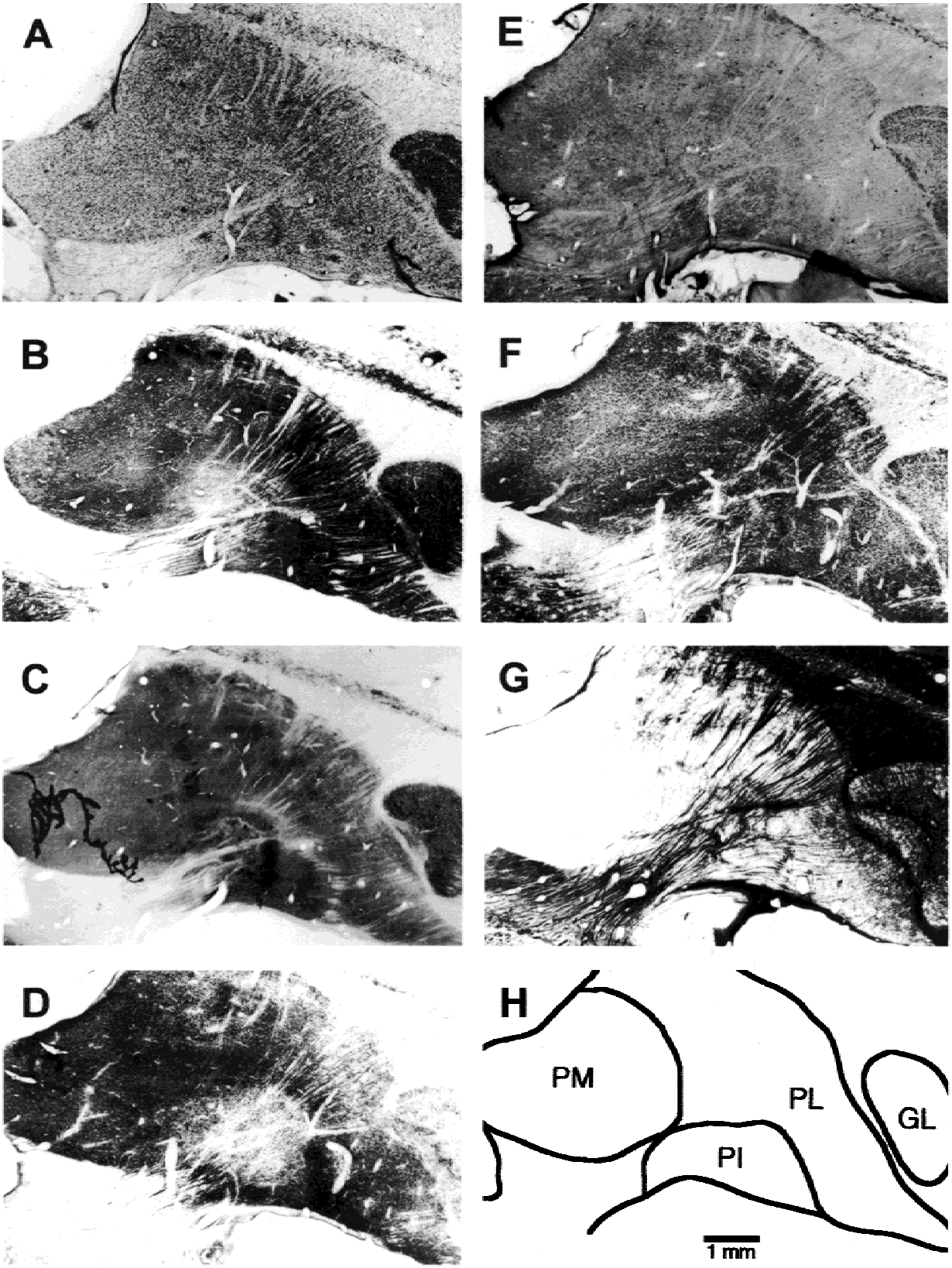

Fig. 13. Photomicrographs of adjacent coronal sections of the pulvinar stained for Nissl (A), acetylcholinesterase (B), Cytochrome oxidase (C), calbindin (D), SMI-32 (E), parvalbumin (F), and Gallyas (G). H: Outline drawing of section D to illustrate the subdivisions of the pulvinar using the nomenclature proposed by Walker (1938).

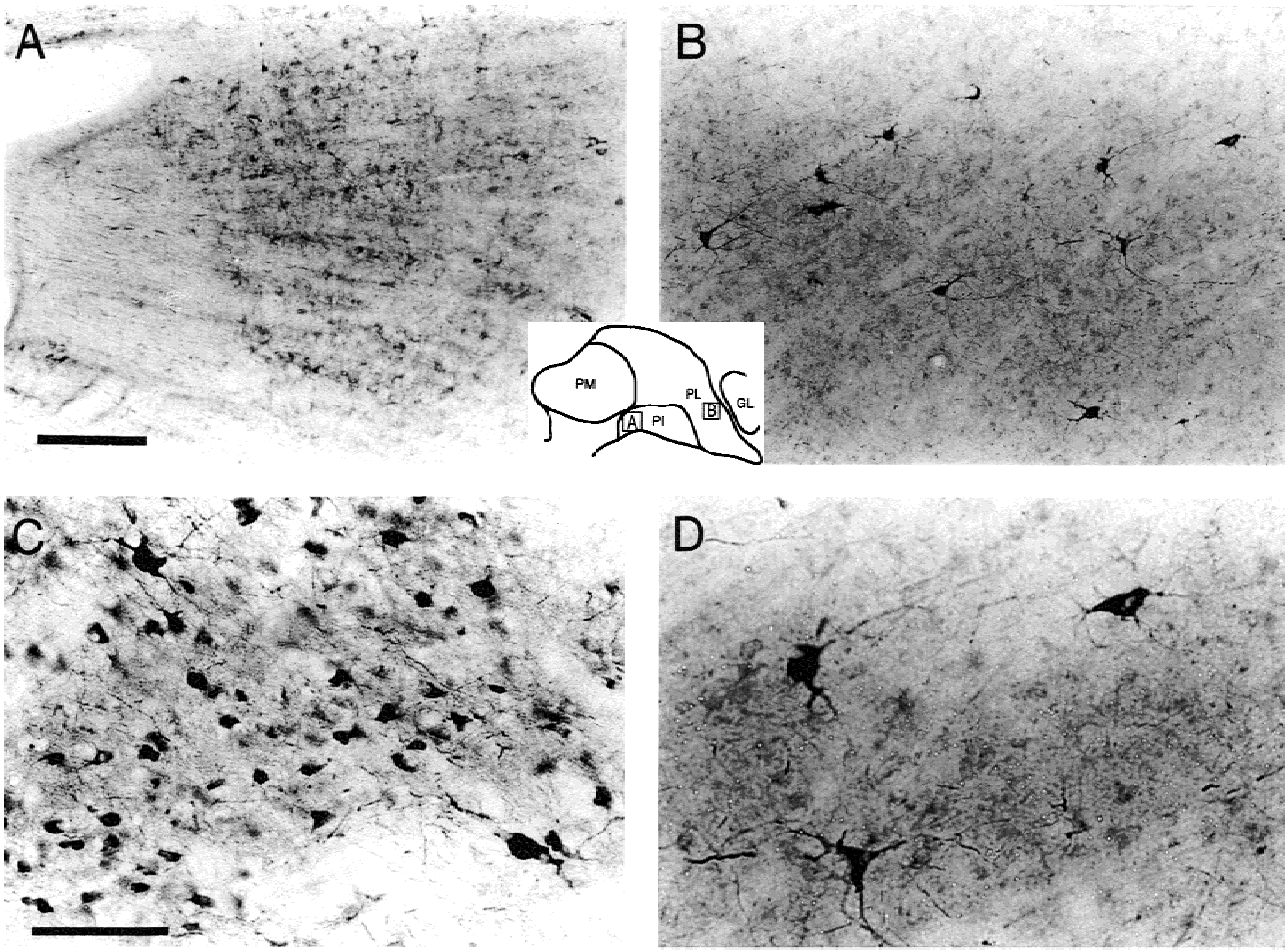

Fig. 14. Photomicrographs of coronal sections through PI (A) and PL (B–D). Two regions (A and B, in insert) of one section stained for SMI-32, at same magnification, show differences in cell type and in density between the medial portion of PI and PL. Calbindin-immunostained section (C) illustrates large and well-stained cells in PL, in the same region and with the same magnification as in the SMI-32 stained section (D). Scale bars = 200 μm (A, B) and 100 μm (C, D).

In *Macaca,* the projections of the pulvinar to V4 were found in the ventral portion of the lateral pulvinar and less intensely in the caudal portion of the inferior pulvinar (Baleydier & Morel, 1992). Adams et al. (2000) showed an extensive projection zone to V4 from the region named P2, with sparser projections from P1 and still sparser from P3. Our results in *Cebus* showed that V4 projecting neurons are located in the central portion of the lateral pulvinar, similar to the projections to V2 described above. It is worth noticing, however, that the injections in V4 in this study are restricted to the central representation of the visual field, occupying up to 8 deg in the inferior quadrant. Thus, we cannot rule out the possibility that the other projection zones described in previous works could be due to more evenly distributed injections in V4.

We observed a great similarity between our results in *Cebus* and those described in marmoset by Dick and collaborators (1991), inasmuch as we observed a concentric arrangement of the cortical projection zones (see Figs. 3 and 5). This arrangement supports the theory of concentric zones proposed by these authors, where the projection zone to area 18 constitutes a central core region beginning ventro-laterally in PL, where the pulvinar is in contact with the GL. It is surrounded by the projection zone of area 19, and this in turn is surrounded medially and dorsally by zones projecting to the temporal and parietal association cortices. This concentric arrangement may be related to the ontogenesis of the thalamus and of the cortex (Brysch et al., 1990).

Chemoarchitectonic subdivisions of the pulvinar

Studies of the chemoarchitecture of the pulvinar in *Saimiri* and in *Macaca* using calbindin, parvalbumin, and cytochrome oxidase (Cusick et al., 1993; Gutierrez et al., 1995; Gray et al., 1999) suggested a subdivision of the inferior pulvinar of these species in five portions: posterior (PI_P), medial (PI_M), central (PI_C), lateral (PI_L), and lateral shell (PI_{LS}). In the pulvinar of *Cebus*, we found a similar chemoarchitectonic pattern. In addition, we found that PI_M, the region with dense connections with MT, poor in calbindin staining and with a dark stain for SMI-32 and for cytochrome oxidase is included in P3, as defined by MT projections. In *Cebus*, P3 includes PI_P in addition to PI_M. Despite their distinct chemoarchitectonic patterns, PI_L and PI_C in *Cebus* were considered as a single region, named P1, based on the projections to cortical visual area V2. In addition, in owl monkeys, squirrel monkeys, and macaques, both V2 and DM have dense connections with PI_{CM} and

ANIMAL	METHODS	PULVINAR SUBDIVISIONS							SOURCE
Macaca	Cytoarchitecture	PM	PI			PL			Walker, 1938
	Electrophysiology				PI	PL			Bender, 1981
	Connectivity		P3		P1	P2			Ungerleider et al., 1984
	Immunocyto-chemistry	PM	PI_P	PI_M	PI_C	PI_L	PI_{LS}	PL	Cusick et al., 1993 Gutierrez et al.,1995 Gray et al., 1999
		PM	PI_P	PI_M	PI_{CM}	PI_{CL}	PL		Stepniewska & Kaas, 1997
		PM	PI_P	PI_M	PI_{CM}	PI_{CL}	PL_{VM} PL_{VL}		Adams et al., 2000
Cebus	Electrophysiology			P_{LV}			$P\mu$		Gattass et al., 1978
	Connectivity		P3	P1			P2		Present work
	Immunocyto-chemistry	PM	PI_P	PI_M	PI_C	PI_L	PI_{LS}	PL	
Saimiri	Cytochemistry	PM PL_M	PI_P	PI_M	PI_C			PL_L	Steele & Weller,1993
	Immunocyto-chemistry	PM	PI_P	PI_M	PI_C		PI_L	PL	Cusick et al., 1993
		PM	PI_P	PI_M	PI_C	PI_L	PI_{LS}	PL	Gray et al., 1999
Aotus	Electrophysiology		PI						Allman et al., 1972
	Cytoarchitecture + Connectivity		IP_P	IP_M	IP_C				Lin & Kaas, 1979
	Immunocyto-chemistry	PM	PI_P	PI_M	PI_{CM}	PI_{CL}	PL		Stepniewska & Kaas, 1997

Fig. 15. Rough parallel of the subdivisions of the pulvinar of four primate species defined by means of different methods of study by different authors.

PI_{CL} (P1), whereas PI_M (P3) is densely interconnected with MT (Lin & Kaas, 1979; Cusick et al., 1993; Stepniewska & Kaas, 1997; Beck & Kaas, 1998). The neurochemical subdivision of the inferior pulvinar resembles the cytoarchitectonic subdivision proposed by Friedmann (1912) in *Cercopithecus*, where $P\gamma_1$, $P\gamma_2$, $P\eta$, P_δ, and $P_{\delta 1}$ correspond respectively to PI_P, PI_M, PI_C, PI_L, and PI_{LS}.

These distinct histochemical regions might be related to different functional modules or different aspects of visual processing within one area. Gray et al. (1999) suggested the existence of a modular organization within one of the subdivisions of PI, PI_M, based on its patchy appearance in all neurochemical methods used.

Comparison of the organization of pulvinar in the New World and Old World monkeys

Among Simiiformes primates one can distinguish two main groups, based on anatomical characteristics and on biogeographical aspects: the platyrrhines, or New World monkeys, with a distribution restricted to the neotropic area; and the catarrhines, or Old World monkeys, whose original distribution included Africa, Europe, and Asia. The nature of the ancestral group common to all Simiiformes is still subject to discussion. It is known, however, that there was a long isolation period, of at least 35 million years, among the simians of the New and of the Old World (Fleagle, 1988). In spite of that long isolation period, the study of *Cebus apella*, a primate with similar brain size, sulcal pattern, and ecological niche to those of *Macaca*, revealed the existence of a visual cortex with basically the same areas, similar connectivity, and similar visuotopic organizations (Gattass et al., 1981*a*,*b*, 1987, 1988, 1990; Rosa et al., 1988; Fiorani et al., 1989). However, anatomical and electrophysiological studies of the pulvinar complex in these species (Gattass et al., 1978; Bender, 1981; Ungerleider et al., 1983; Dick et al., 1991) have demonstrated differences in the organization of this thalamic nucleus in these monkeys.

Comparisons of the subdivisions P1, P2, and P3 of the pulvinar in *Cebus* and *Macaca* show strong similarities, as well as small differences. Both species have a very similar connective pattern, where V1 has strong connections with P1 and P2, while MT has, in addition to connections with P1 and P2, strong connections with P3. However, there are some differences in their relative positions within the pulvinar. In *Cebus*, P2 is located more dorsally in PL, and P1 extends more laterally. In addition, the location of P2 in *Cebus* resembles that of Pdm described in the macaque by Petersen and collaborators (1985) in a behavioral study. This nucleus is located in a dorsomedial region of the lateral pulvinar and has a crude retinotopic organization with attentional modulation. However, P2 in *Cebus* extends to more lateral portions of PL. Gutierrez et al. (2000), based on histochemical criteria, defined the dorsal lateral pulvinar nucleus (PLd) located along the dorsolateral edge of the pulvinar in macaques. This region may correspond to the projection field P2 in *Cebus*.

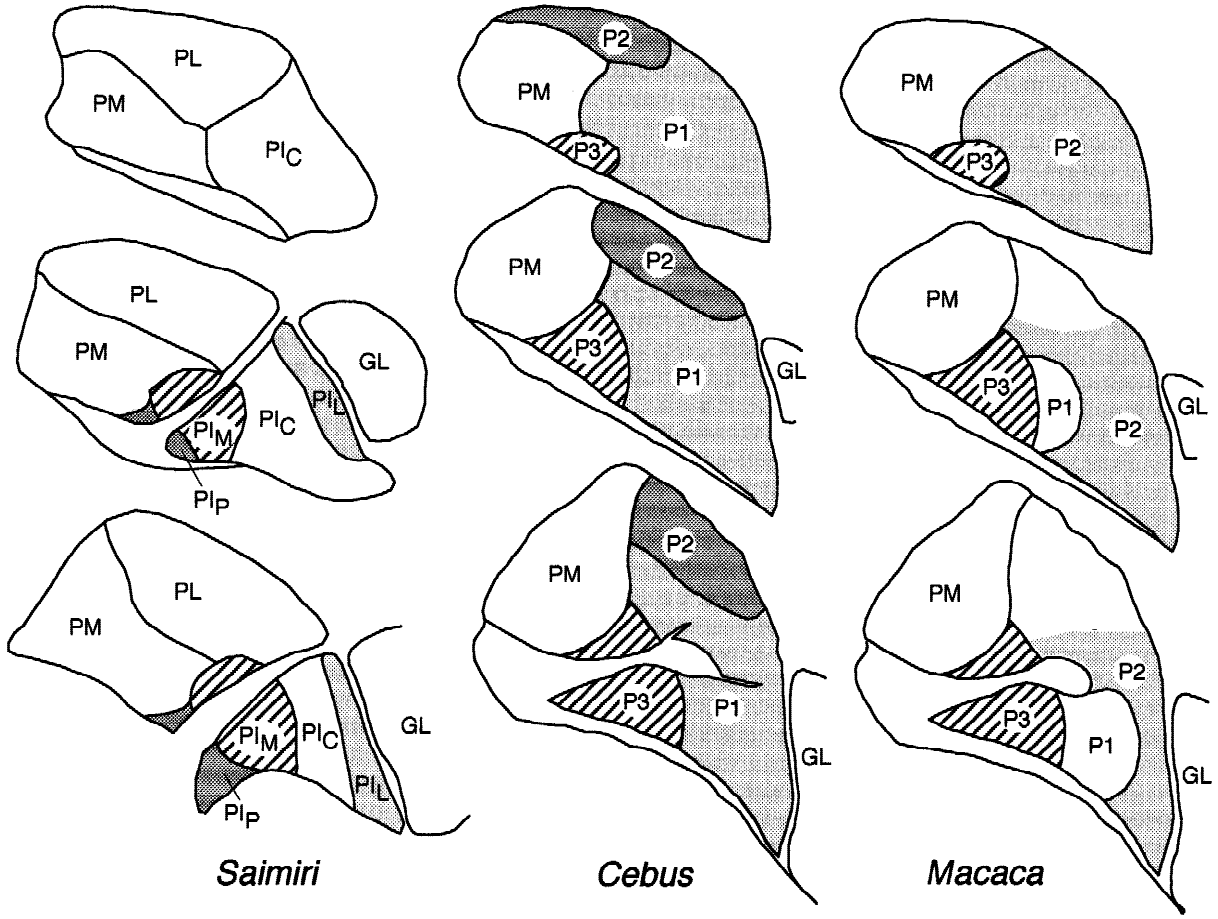

Fig. 16. Schematic diagrams comparing the pulvinar subdivisions of *Cebus* (this study), Saimiri (Cusick et al., 1993), and *Macaca* (Ungerleider et al., 1984). For details, see text.

In spite of the differences in nomenclature used, a similar chemoarchitectonic pattern is revealed by calbindin reactions in all primates studied. There is an agreement relative to the borders of PI_P, PI_M, and of the darker adjacent region named PI_C (Gutierrez et al., 1995; Gray et al., 1999; and present study) or PI_{CM} (Stepniewska & Kaas, 1997; Beck & Kaas, 1998; Adams et al., 2000). In addition, all these authors reinforce the idea that these subdivisions cross the limits of the brachium of the SC occupying part of adjacent PM and/or PL. The major controversy is related to the subdivision of the ventrolateral portion of the pulvinar. Cusick and colleagues (Cusick et al., 1993; Gutierrez et al., 1995; Gray et al., 1999) based on similar patterns of calbindin staining observed in the lateral portion of PI and in the ventral portion of PL, and by the fact that V1 projection zone extends dorsal to the brachium of the SC, consider this region as a single subdivision named PI_L. However, some authors (Stepniewska & Kaas, 1997; Beck & Kaas, 1998; Adams et al., 2000) prefer to maintain the original subdivisions proposed by Lin and Kaas (1979), and subdivide PI_C into PI_{CM} and PI_{CL}. Although these authors recognize that PI_{CM} extends above the brachium of the SC, they assume PI_{CL} to be restricted to the lateral portion of traditional PI of macaques. However, they accept the possibility that part of the region defined as PL may be part of PI_{CL}, as suggested by Gutierrez et al. (1995). Adams et al. (2000) based on their connectional data argue that ventral PL should not be included as part of the inferior pulvinar, in spite of the fact that PI_{CL} and ventral PL look similar neurochemically. Our present connectional data support the subdivision of Cusick and colleagues where the lateral portion of PI and the ventral portion of PL form a single subdivision. However, a more detailed mapping study is necessary to delimit this region dorsally.

The amazing similarities of the chemoarchitecture of the pulvinar in *Aotus*, *Saimiri*, *Cebus*, and *Macaca* contrast with the different subdivisions based on cortical connectivity and electrophysiological mapping. Thus, further comparative studies involving cortical connections and detailed mapping and chemoarchitecture of the pulvinar in the same animals and in different species are necessary to elucidate real differences.

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