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The Pulvinar Thalamic Nucleus of Non-Human Primates: Architectonic and Functional Subdivisions

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Chapter 3
Chemoarchitecture of the Pulvinar

Cytochemical and immunocytochemical methods reveal details of the pulvinar architecture that are not apparent from Nissl and myelin staining. However, the results of these techniques have been interpreted in different ways by different investigators, each adopting different sets of nomenclature for the various pulvinar subdivisions.

3.1 Chemoarchitecture in the Macaque Monkey

In the macaque, Lysakowski et al. (1986) described a dense acetylcholinesterase (AChE) reactivity in regions of PI and PL that coincide with the projections zones of the SC described by Benevento and Standage (1983). Studies of the chemoarchitecture of the pulvinar in macaque monkeys using histochemical reactivity for the cytochrome oxidase (CO) and AChE enzymes and immunostaining for calbindin (Cb), parvalbumin (Pv), SMI-32, Cat-301, and Wisteria floribunda agglutinin (WFA) (Cusick et al. 1993; Gutierrez et al. 1995; Gray et al. 1999) revealed five subdivisions of PI, which include all of the traditional PI but which also encompass parts of PL and PM. Two of these subdivisions match those described by Lin and Kaas (1979), namely, the posterior (PI_P) and medial (PI_M) subdivisions. However, the central or "classic" portion was subdivided into central (PI_C) and lateral (PI_L) subdivisions. PI_M, a calbindin-poor zone located between PI_P and PI_C (regions with intense staining for calbindin) presented elevated CO and AChE activity, elevated SMI-32 and parvalbumin immunostaining, and dense patches of WFA and Cat-301 immunostaining. The intense patches of AChE staining within PI_M closely resemble the dense AChE-positive bands that overlap zones of tectal input, as described by Lysakowski et al. (1986). PI_C was characterized by a moderate AChE and a light CO activity, lightly stained for parvalbumin, very lightly stained for WFA, and with only few SMI-32 labeled neurons. PI_P, a small region located more rostrally, exhibited light AChE activity, was very lightly stained for WFA and was unstained for SMI-32.

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In addition, PI_P, in the sections stained for CO or parvalbumin, was distinctly paler than the adjacent PI_M. PI_L adjoins the LGN and lightly stains for calbindin, parvalbumin, and CO. Gutierrez et al. (1995) described yet in macaque monkeys a most lateral portion, termed the shell of PI_L (PI_{LS}), which appeared to contain many dendrites intensely stained for calbindin, in addition to numerous WFA-stained neurons, when compared to more medially adjacent portions of PI_L. The medial border of PI_{LS} is often characterized by large calbindin stained cells.

Stepniewska and Kaas (1997), based on the same techniques used by Cusick and collaborators (Cusick et al. 1993; Gutierrez et al. 1995; Gray et al. 1999), proposed a new subdivision for PI where PI_C, which does not include part of the cytoarchitectonic PL subregion, was subdivided in PI_{CL} and PI_{CM} (Table 1.1).

Figure 3.1 shows enlarged micrographs of calbindin immunoreactive cells in the pulvinar of the macaque monkey (Adams et al. 2000). PI_P and PI_{CM} were the

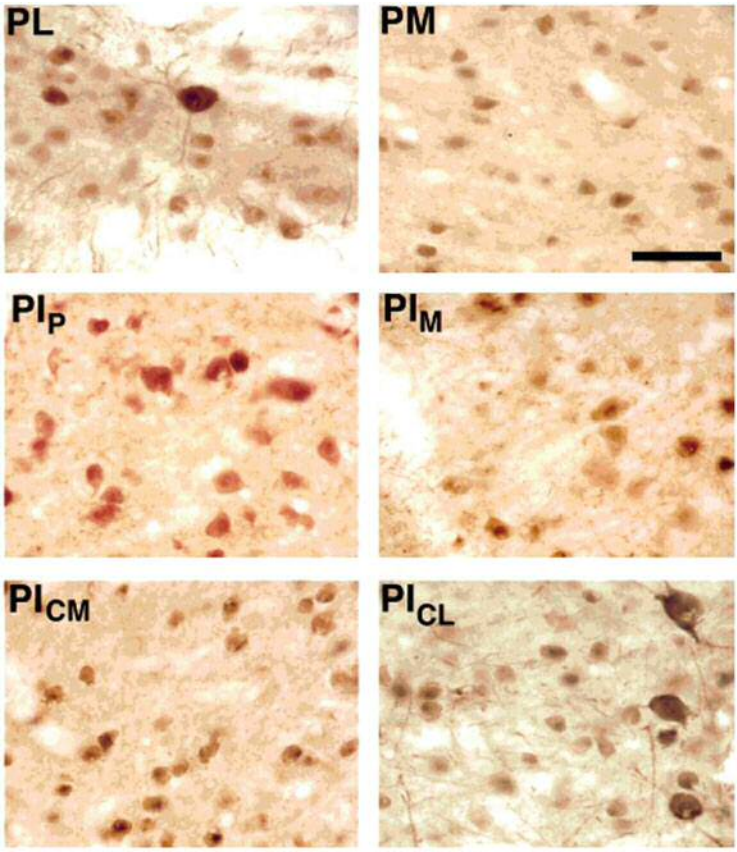

Fig. 3.1 Chemoarchitecture of the macaque monkey pulvinar. High magnification photomicrographs of calbindin-positive cells in the different subdivisions of the pulvinar. Each photomicrographs shows calbindin immunoreactive cells in PL, PM, PI_P, PI_M, PI_{CM}, and PI_{CL}. See text for details. Scale bar = 200 μm [modified from Adams et al. (2000)]

regions showing the strongest calbindin immunoreactivity (note the darkly stained small cells and dense neuropil that are revealed by the reaction). The difference between the two regions was that the PI_{CM} zone contained a few large cells (not shown in figure), which were absent in PI_P. The PI_M subdivision, the calbindin-poor PI region located between PI_P and PI_{CM}, contained very little neuropil staining and only a few faintly labeled cells. The PI_{CL} zone showed moderate calbindin staining. Within the latter, there was a dense population of small calbindin-containing neurons and moderate neuropil staining, as well as a small number of large stained neurons. The small calbindin-containing neurons had a clear stained soma with a few visible dendrites, while the larger immunoreactive neurons had a darkly stained soma with radiating dendrites. Relative to PI_M, PI_{CL} had denser neuropil staining and more darkly stained calbindin immunoreactive neurons, but the staining was not as intense as in PI_P and PI_{CM}. The distinguishing feature of PI_{CL} was the numerous large cells that were scattered throughout this subdivision. The ventral portion of the cytoarchitectonic PL was similar to PI_{CL} in that both of these regions had a large number of small calbindin-containing neurons and a few scattered large cells. Although Cusick et al. (1993) and Gutierrez et al. (1995) considered this subdivision as part of PI_{CL} (PI_L in their terminology), PI_{CL} and PL could be distinguished by the presence of horizontally oriented fiber bundles in the latter. Dorsally in the pulvinar, cytoarchitectonic PM also contained many small calbindin-positive neurons and a few scattered large neurons (not shown in figure). However, the neuropil in PM was more intensely stained than in PL.

Gutierrez et al. (2000) described a region in the dorsal portion of PL, named PL_D, which stained dark and uniform for AChE and parvalbumin, but appeared pale with calbindin immunostaining. The ventromedial border between the neurochemical subdivision PL_D and the rest of the dorsal pulvinar, termed the medial pulvinar (PM), could be sharply defined. AChE and parvalbumin reactivities were weaker for PM compared to PL_D and displayed both lateral (PM_L) and medial (PM_M) histochemical divisions. PM_M contained a central "oval" region ($PM_{M\text{-}C}$) that stained darker for AChE and parvalbumin than the surrounding region.

3.2 Chemoarchitecture in New World Monkeys

Steele and Weller (1993), based on AChE activity, divided PL of the squirrel monkey into a lateral, darker staining subdivision, denominated PL_L, and a medial one, PL_M. Additionally, in accordance with Lin and Kaas (1979), they subdivided PI into a "classic" lateral region (PI_C), a "middle" region (PI_M), and a posterior region (PI_P). PI_M is located between PI_C and PI_P, with the former displaying a weak staining and the latter two subregions exhibiting a relatively strong staining for AChE. This AChE staining pattern for PI_M is opposite to the PI_M staining pattern described for the squirrel monkey by Gray et al. (1999) and Stepniewska and Kaas (1997). These authors, however, found in PI of the squirrel and owl monkeys a pattern similar to the one described for the macaque, with small variations. Squirrel

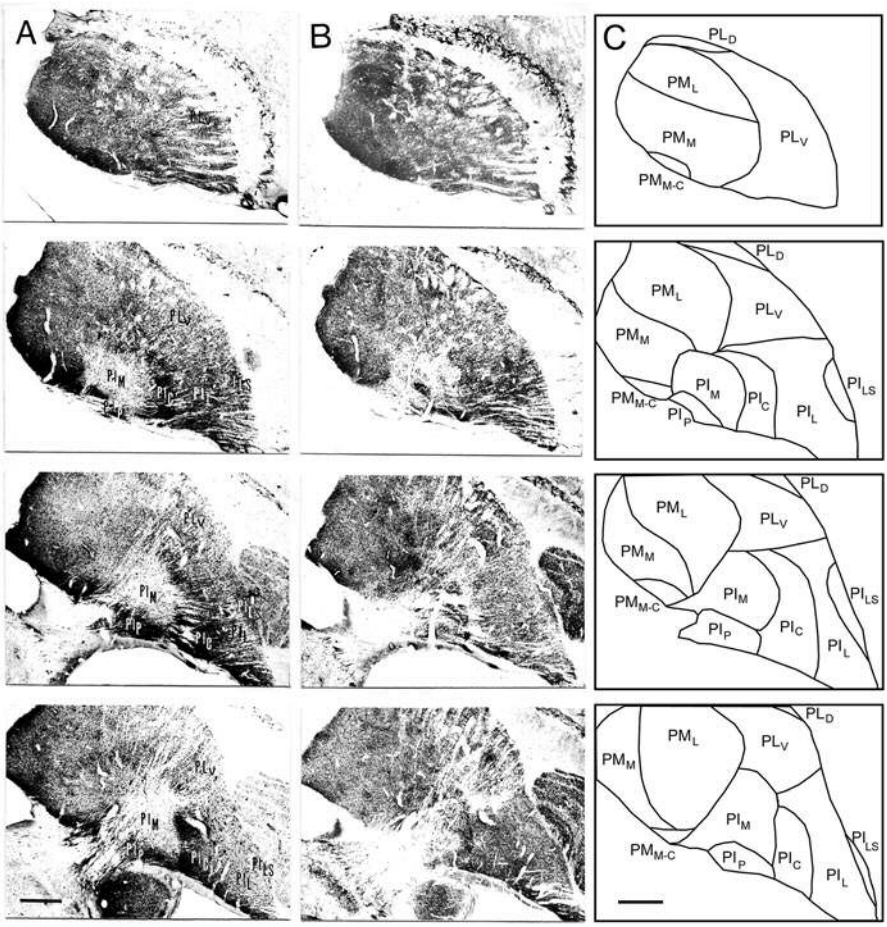

Fig. 3.2 Subdivisions of the capuchin monkey pulvinar (**c**) based on calbindin (**a**) and parvalbumin (**b**) immunostaining. Note that we adopted the nomenclature proposed by Cusick et al. (1993) and Gutierrez et al. (2000). Additionally, we here subdivide PL into ventral (PL_V) and dorsal (PL_D) portions. Histological sections are spaced 400 μm apart. Scale bar = 1 mm [modified from Soares et al. (2001)]

and macaque monkeys showed opposite staining patterns within PI_C and PI_M for the Cat-301 antibody.

In the pulvinar of the capuchin monkey, Soares et al. (2001) described a chemoarchitectonic pattern similar to the one described in the macaque monkey by Cusick and collaborators (Cusick et al. 1993; Gutierrez et al. 1995). The immunohistochemical staining for calbindin and parvalbumin in the pulvinar of the capuchin monkey is illustrated in Fig. 3.2. Based on immunohistochemical staining, mainly for calbindin, the border of PI was shifted dorsally, above the brachium of the SC. Additionally, PI was subdivided into five regions (PI_P, PI_M,

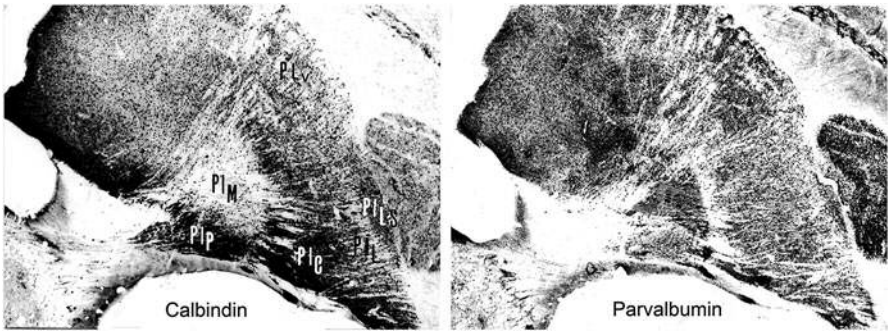

Fig. 3.3 Chemoarchitecture of the capuchin monkey pulvinar. Enlarged photomicrographs of adjacent coronal sections of the pulvinar (shown in Fig. 3.2) reacted for the calcium-binding proteins calbindin and parvalbumin [modified from Soares et al. (2001)]

PI_C, PI_L, and PI_{LS}). Figure 3.3 shows two enlarged sequential coronal sections of the capuchin monkey pulvinar stained for calbindin and parvalbumin. Under calbindin staining, the original inferior pulvinar can be further subdivided into PI_P, PI_M, and PI_C. Both the PI_P and PI_C zones display the heaviest calbindin immunoreactivity. The PI_M is almost devoid of calbindin immunoreactivity. On the other hand, the staining for parvalbumin shows a heavily labeled PI_M and a homogenous staining for PI_C, PI_L and PI_{LS}. PI_P is only lightly labeled by parvalbumin.

The capuchin pulvinar, specially the intermediate and posterior portions of PI and the lateral portion of PL, also react strongly for AChE. This pattern of AChE staining resembles that described in the macaque (Lysakowski et al. 1986) and squirrel (Steele and Weller 1993) monkeys, but it differed from the pattern described by Gray et al. (1999), where PI_M stained strongly for AChE.

Figure 3.4 shows enlarged photomicrographs of portions of PI stained for the SMI-32 antibody. SMI-32, a monoclonal antibody that recognizes a nonphosphorylated epitope on neurofilament proteins (Sternberger and Sternberger 1983), has been used to define regional patterns of cortical organization in the visual system (Hof and Morrison 1995). In the pulvinar as a whole, the immunocytochemistry for SMI-32 shows a light staining pattern. However, we find some large, heavily labeled neurons scattered throughout PM and PI but mainly throughout PL (Fig. 3.4b). These cells are similar to the large calbindin-positive neurons that are present in similar locations of the pulvinar but that are fewer in number. The medial portion of PI shows a darker staining as well as some moderately labeled medium-sized SMI-32 cells (Fig. 3.4a).

In spite of the differences in nomenclature that have been proposed by the various authors, a similar chemoarchitectonic pattern is revealed by calbindin reactions in all primate species studied so far. There is an agreement relative to the borders of PI_P and PI_M and of the darker adjacent region named PI_C (Gutierrez et al. 1995; Gray et al. 1999; Soares et al. 2001) or PI_{CM} (Stepniewska and Kaas 1997; Beck and Kaas 1998; Adams et al. 2000). In addition, all these authors

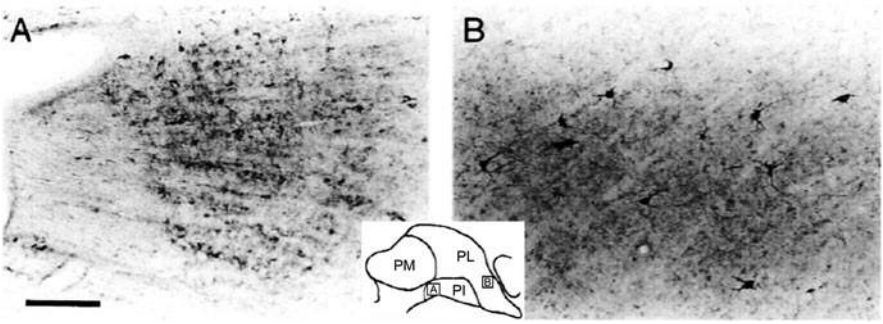

Fig. 3.4 Chemoarchitecture of the capuchin monkey pulvinar. Enlarged photomicrographs of a coronal section of the pulvinar (right hemisphere) reacted with the SMI-32 antibody. Note the very distinct reactivity patterns in the PI (i.e., PI_P) and the PL (i.e., PI_L) subdivisions (panels (**a**) and (**b**), respectively). Scale bar = 30 μm [modified from Soares et al. (2001)]

reinforce the idea that these subdivisions cross the limits of the brachium of the SC, occupying part of the adjacent PM and/or PL. The major controversy is related to the partitioning of the ventrolateral portion of the pulvinar. Cusick and colleagues (Cusick et al. 1993; Gutierrez et al. 1995; Gray et al. 1999), based on the similarity of calbindin staining patterns in the lateral portion of PI and in the ventral portion of PL and by the fact that the V1 projection zone extends dorsal to the brachium of the SC, consider this region as a single subdivision named PI_L. However, other authors (Stepniewska and Kaas 1997; Beck and 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 the traditional PI region of macaque monkeys. 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 connectivity data, argue that ventral PL should not be included as part of the PI, in spite of the fact that PI_{CL} and ventral PL look neurochemically similar.

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