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

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Chapter 6

Reestablishing the Chemoarchitectural Borders Based on Electrophysiological and Connectivity Data

The neurons projecting from the P1 and P2 regions of the pulvinar to area V2 overlapped those neurons projecting to area V1 in all cases studied by Ungerleider et al. (2014). Interestingly, in the two animals with retrograde tracer injections in areas V2, MT, and V4, the neurons in the pulvinar projecting to area V2 overlapped more extensively with those projecting to area V4 than with those projecting to area MT. The region with the most extensive overlap of cells projecting to areas V2 and V4 occurred in PI_{CL} of the P1 and P2 fields. There was minimal overlap between the projection zones from the pulvinar to V2 and MT. This was due to the fact that after retrograde tracer injection in area MT, the labeling found in P1 and P2 was sparse. In the P1 and P2 fields, neurons were found to project to both V1 and V2. However, in these cases, we did not observe any double-labeled pulvinar neuron projecting both to V2 and V4 or to both V2 and MT.

The P3 field was found to send projections to visual areas V2, V4, and MT, but not to V1. Each chemoarchitectonic region within the P3 field was observed to project differentially to each of these cortical areas. In all cases, projections to V2 arose from PI_{CM}, and in three of these cases, projection neurons were also seen in PI_M. Projections to area V4 arose from PI_P and PI_{CM} in all cases, while area MT received projections from all P3 subdivisions. In the two monkeys with retrograde tracer injections in V2, MT, and V4, we observed dense overlapping projection zones from within P3's PI_{CM} subdivision to areas V2 and V4. The overlap between pulvinar fields projecting to MT and V2 was minimal mainly because the neurons projecting to area MT were quite few. Unlike the overlapping pulvinar projection fields to areas V1 and V2, in all of the monkeys studied with retrograde tracer injections in MT and V4, there was a clear interdigitation of labeled neurons. This was because the strongest pulvinar projections to MT and V4 seemed to originate, respectively, from subregions PI_M and PI_P/PI_{CM} (Fig. 6.1). Adams et al. (2000) suggested that the pulvinar integration of cortical afferents and efferents could take advantage of the lamellar organization of the chemoarchitectonic divisions, where superimposed concentric shells are aligned through their visuotopic organization.

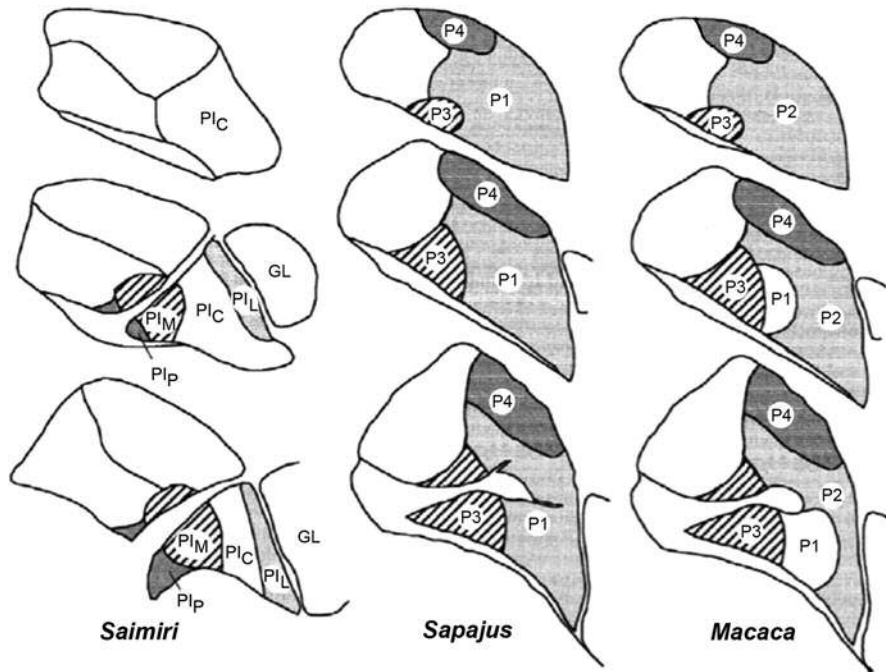


Fig. 6.1 A comparison of the projection fields of the pulvinar (right hemisphere representation) in squirrel, capuchin, and rhesus monkeys. See text for details

This concentric shell structure would allow local topographic integration necessary for spatial visual enhancement or suppression of specific visual information.

Investigating the calbindin immunoreactivity in the macaque monkey pulvinar, Adams et al. (2000) extended the original cytoarchitectonic subdivisions previously described by Olszewski (1952) and offered new insight into pulvinar delimitation and connectivity pattern. PM was easily distinguished from PL by its distribution pattern of both large and small calbindin-containing neurons and by its neuropil disposition and staining. In addition, calbindin staining suggested further partitioning of PI that was not evident in previous studies using only the Nissl stain. The original PI could thereby be further subdivided into PI_P , PI_M , PI_{CM} , and PI_{CL} . Both the PI_P and PI_C zones displayed the strongest calbindin immunoreactivity. The PI_{CL} zone was moderately reactive for calbindin staining, while PI_M was almost devoid of calbindin immunoreactivity. The border between P1 and P2, and the lateral border of P3 with P1 and P2, could be defined using calbindin immunoreactivity. Nissl staining, while being able to identify these borders, revealed an otherwise fairly homogenous staining pattern, which was only interrupted by the brachium of the SC.

The neurons that project to area V1 in New and Old World monkeys were found in the dorsal portion of PI_{CL} , and they overlapped the pulvinar field projecting to area V2 in all animals studied (Stepniewska and Kaas 1997). Additionally, the

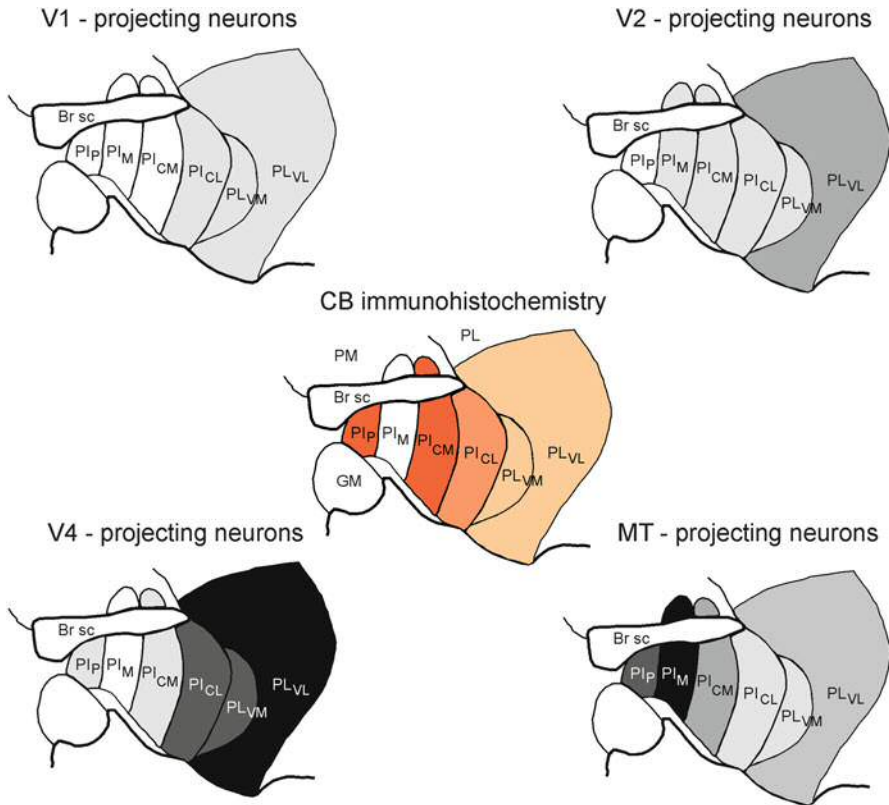


Fig. 6.2 Subdivisions of the pulvinar based on chemoarchitecture (calbindin immunocytochemistry) and its relationship with pulvinar-cortical connectivity. The illustration allows direct correlation of calbindin immunoreactivity with the density of pulvinar-cortical connectivity (gray scale) with visual areas V1, V2, V4, and MT. Areas PL_{VM} and PL_{VL} are labeled PI_L in Figs. 3.2 and 5.2. For details, see text (modified from Adams et al. (2000))

pulvinar projection zones to areas V1 and V2 fell within the visual field maps of P1 and P2. There was another projection zone to area V2 that was found in P3 of all monkeys studied. The neurons projecting to area MT were found in the ventral part of PM, scattered throughout PL, and in the PI_L, PI_M, PI_{CM}, and PI_{CL} subdivisions. Therefore, in accordance with Ungerleider et al. (1984), the strongest projections to MT originated in P3. Note that the labeled neurons seen in the ventral part of PM could have been the result of an extravasation of the tracer injections into neighboring area FST. The neurons projecting to area V4 were observed in PI_{CL}, PI_{CM}, and PI_P and occupied portions of all three visual field maps (P1, P3, and P4).

Figure 6.2 offers an integrated perspective of pulvinar partitioning based on calbindin immunostaining and the connectivity strength of each of the corresponding pulvinar subdivisions with visual areas V1, V2, V4, and MT. Note the PI partitioning into posterior (PI_P), medial (PI_M), central medial (PI_{CM}), and

central lateral (PI_{CL}) regions. The P1 field, as described by Ungerleider et al. (1983), includes PI_{CL} and the ventromedial portion of PL (i.e., PL_{VM}). The P2 field corresponds to the ventrolateral portion of PL (i.e., PL_{VL}), while the P3 field corresponds to PI_P, PI_M, and PI_{CM}. Projection fields to areas V1 and V2 were found to be overlapping in P1 and P2, but the projections from P2 to V2 were found to be denser than those to V1. V2 also received light projections from PI_{CM} and, less reliably, from PI_M. Pulvinar projections to V4 and MT were more abundant than projections to V1 and V2. Neurons projecting to V4 were observed in P1, P2, and in subdivisions PI_P and PI_{CM} of P3. Neurons projecting to MT were found in P1 and P2 but mainly in the PI_M subdivision of P3. Note the interdigitated nature of the projection fields from P3 to area V4 and area MT (PI_P and PI_{CM} subfields projecting to V4 and the PI_M subfield projecting to MT).

These subdivisions are comparable to those described by Cusick and colleagues (Cusick et al. 1993; Gutierrez et al. 1995; Gutierrez and Cusick 1997). Using calbindin immunohistochemistry and pulvinar-V1 connectivity pattern, these authors proposed further subdivisions of the PI complex. Additionally, they renamed the ventrolateral portion of PL (i.e., the lateral shell of PI) as PI_L and PI_{L-S}. Their proposed nomenclature change for PI was based on their findings that area V1 projects to all of the subdivisions of the ventral portion of the pulvinar. Our experimental results do not support their new classification, since we find no clear correlation between connectivity patterns or calbindin immunostaining and visuotopic function organization in the pulvinar. However, there is evidence for further PI partitioning based both on calbindin immunostaining and on the projection patterns from PI to areas MT and V4. Notably, these criteria suffice to delineate the ventrolateral border of P3.

Stepniewska and Kaas (1997) used calbindin immunohistochemistry in New World and Old World monkeys to delineate the subdivisions of the pulvinar, particularly to further subdivide the PI (Table 1.1). Their delineation takes into account that a portion of PL is chemoarchitecturally similar to PI and thereby extends the former above the brachium of the SC. Their results fit better with the functional maps described by Gattass et al. (1978a) and Bender (1981) and also with our chemoarchitectonic work (Soares et al. 2001).

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