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

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Chapter 5

Connectivity of the Pulvinar

Pulvinar connectivity has been studied using a variety of neuroanatomical tracing techniques in both New and Old World monkeys.

PM, for example, has been shown to be interconnected with vast regions of the brain, including the frontal, parietal, and temporal cortices. Several authors have thereby suggested that the PM can be considered a multimodal integrative center (Trojanowski and Jacobson 1974, 1976; Asanuma et al. 1985; Baleyrier and Morel 1992). Despite its importance, we will not address PM in depth in the present work. Instead, we will focus on PI and PL due to their important and direct relation to visual function, as evidenced by their visuotopic organization and their connectivity with several visual areas.

As we suggested above, the differentiation of the pulvinar along primate evolution took place upon a relatively rigid chemoarchitectonic scaffold. With increasing cortical size, we argue that the pulvinar developed new functional subdivisions in order to effectively interconnect and interact with the cortex. Therefore, a fully developed chemoarchitectonic scaffold is readily observed in smaller primate species. However, limited neocortical growth and specialization also limited cortical-pulvinar connectivity. This, in turn, hindered pulvinar functional specialization, including the development of visual maps.

Figure 5.1 illustrates the capuchin pulvinar organization and subdivisions based on chemoarchitectural (left) or connectivity/visuotopy (right) criteria. Several cytoarchitectonic subdivisions have been proposed by different authors (Friedmann 1912; Walker 1938; Olszewski 1952). Some of them, as the one originally proposed by Friedmann (1912), have a good correspondence with the chemoarchitectonic subdivisions observed in small and large nonhuman primates. However, their borders do not correlate with the P1–P4 fields described by Ungerleider et al. (1983, 1984, 2014) and by Adams et al. (2000).

In Fig. 5.2 we present a summary of the reciprocal pulvinar-cortical connections based primarily on our own work (Adams et al. 2000; Soares et al. 2001; Ungerleider et al. 2014; Gattass et al. 2014, 2015) but also on Gutierrez et al.

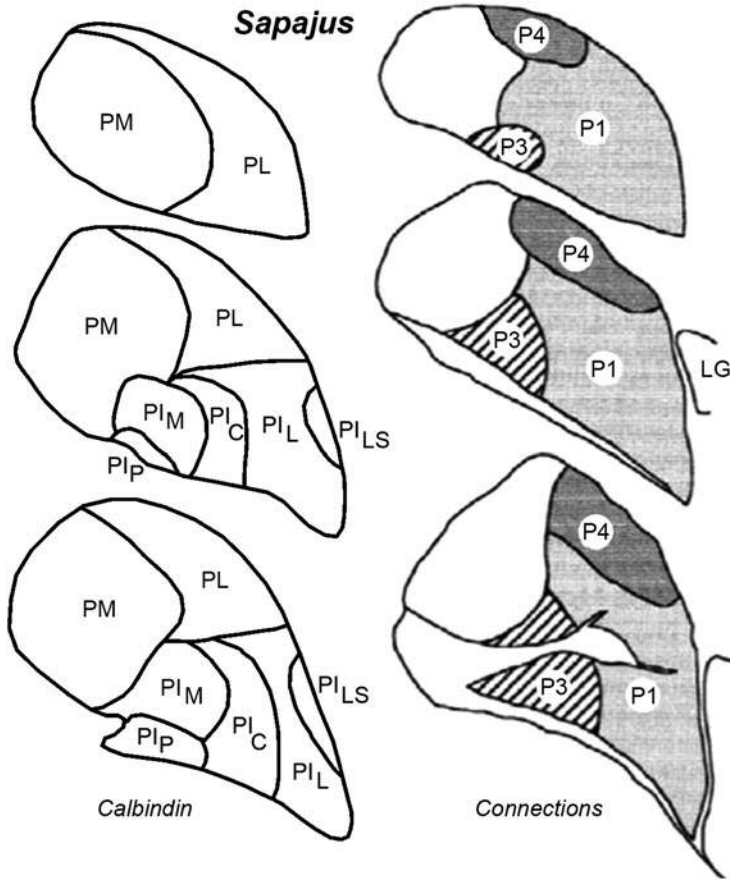


Fig. 5.1 Correspondence between chemoarchitecture and connectivity in the capuchin monkey pulvinar (right hemisphere). Chemoarchitectural subdivisions are based on calbindin immunoreactivity, while the P1–P4 subdivisions are based on the projection fields between the pulvinar and other brain regions, including the cortex. See text for details

(2000), Bridge et al. (2016), and Bourne and Morrone (2017). PI and PL are reciprocally connected with the ventral and dorsal streams of information processing. PI_M receives direct input from the retina and the SC and projects to several areas of the dorsal stream, namely, areas MT, MST, and FST. PI_C and PI_P are also connected with these areas and also with the crescent of MT (MTc). PI_L and PL_V are strongly interconnected with cortical areas of the ventral stream. PL_D projects to the inferior parietal cortex (IPC) and the dorsolateral prefrontal cortex (DLPF). Gutierrez et al. (2000) were able to define PL_D by tracer injections in the IPC and DLPF, but not with injections in the superior temporal gyrus (STG). PM_M and PM_L project to the temporal and parietal cortices, while PM_M also projects to DLPF, orbitofrontal cortex (OFC), and the amygdala. PM_L labeling was found after

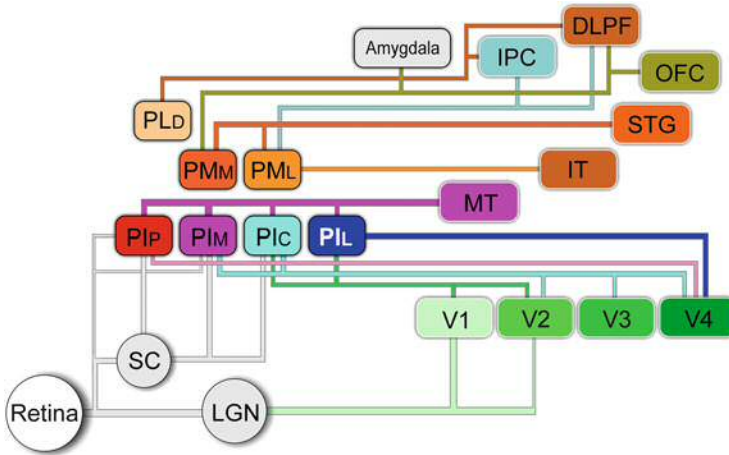


Fig. 5.2 Different cortical areas are richly interconnected with specific subregions of the pulvinar. Rectangles representing cortical regions are depicted on the right, whereas subcortical structures are represented by rectangles and circles on the left of the figure. Colored lines illustrate bidirectional anatomical connections. Projections originating in the retina and SC (grey lines) are unidirectional. *PI_P*, *PI_M*, *PI_C*, and *PI_L* posterior, medial, caudal, and lateral subdivisions of the inferior pulvinar, respectively. *PM_M*, *PM_L* medial and lateral subdivisions of the medial pulvinar, respectively. *PL_D* dorsal subdivision of the lateral pulvinar. *LGN* lateral geniculate nucleus, *SC* superior colliculus, *STG* superior temporal gyrus, *IT* inferotemporal, *IPC* inferior parietal cortex, *OFC* orbitofrontal cortex, *DLPF* dorsal–lateral prefrontal cortex

injections in the prefrontal and IPC and, to a lesser extent, after injections in the STG. *PM_M*, on the other hand, was labeled after tracer injections in IPC and STG but only sparsely following tracer injections in the prefrontal cortex (Gutierrez et al. 2000). *PM_L* and *PL_D* showed overlapping labeling following paired IPC/prefrontal injections, but not following paired IPC/STG injections. Based on their connectivity data, Gutierrez et al. (2000) conclude that *PL_D* may be related to visuospatial functions, whereas *PM* may also be involved in auditory processing.

5.1 Pulvinar Connectivity with the Retina and Pretectal Nuclei

The evidence regarding the existence of direct retinal projections to the pulvinar is conflicting. However, some studies in macaque monkeys and baboons indicate a weak direct retinal projection to the PI subdivision (Campos-Ortega et al. 1970; O’Brien et al. 2001). Cowey et al. (1994) showed that HRP injections in the retinorecipient region of the PI of macaque monkeys were able to retrogradely label P α and P β ganglion cells and an even larger number of P γ cells in the retina. Recently, Warner et al. (2010) showed the existence of direct retinal synaptic projections to MT relay cells in *PI_M*.

Regarding the projections from the pretectal nuclei, Benevento et al. (1977) described projections from the retinorecipient zone of this region to PL, to the border between PL and PM, and to PO in the macaque monkey.

5.2 Pulvinar Connectivity with the Superior Colliculus

Projections from the superficial layers of the SC to the pulvinar were described in squirrel (Mathers 1972), macaque (Benevento and Fallon 1975; Trojanowski and Jacobson 1975; Benevento and Standage 1983), and owl (Lin and Kaas 1979) monkeys. In the squirrel monkey, the SC projections were found in the ventral-medial two thirds of the PI (Mathers 1971). In the macaque, Benevento and Fallon (1975) found projections to the medial portion of PI and, more rostrally, to the dorsolateral portions of PI. Partlow et al. (1977) found topographically organized projections to most of the PI, with the lower visual field being represented dorsomedially, and the upper visual field being represented ventrolaterally. The peripheral representation was located along the medial border, and the fovea representation was found to be at the dorsolateral angle, adjacent to the LGN.

Lin and Kaas (1979), based on connectivity and architectonic criteria, subdivided the PI complex of owl monkeys into three distinct regions: the central inferior pulvinar (IPc), the medial inferior pulvinar (IPm), and the posterior inferior pulvinar (IPp). Both IPp and IPc receive projections from the SC, but the terminations in IPp are denser than those in IPc (Lin and Kaas 1979). Terminations in IPm from MT are also particularly dense. None of these visual structures project to IPp. Rather, input to IPp appears to originate from the cortex rostral to MT in the temporal lobe.

Benevento and Standage (1983), in addition to the projections to PI, also described projections from the retinorecipient SC layers to three zones in PL. One of the projections lie mainly along the dorsoventral lateral border of subdivisions $PL\gamma$ and $PL\beta$, extending ventrally to $PL\alpha$. A second projection occupies the lateral portion of $PL\alpha$, and the last one is located medially in $PL\gamma$ and $PL\beta$. These PL subdivisions were described by Rezak and Benevento (1979) when studying the organization of pulvinar projections to the primary visual cortex (V1) of the macaque monkey. They found that projections from PL are restricted to the rostral lateral portion immediately adjacent to and cupping PI ($PL\alpha$). This portion was distinguished from the $PL\beta$, which lies above and adjacent to $PL\alpha$, and from the caudal portion ($PL\gamma$) which did not project to V1.

In addition to the cortico-pulvino-cortical route, there is a pathway that connects the superficial layers of the SC to the dorsal visual cortices MT and V3, through PI_p and PI_M (Berman and Wurtz 2010; Glendenning et al. 1975; Lyon et al. 2010). Because the superficial SC layers receive direct retinal input, this pathway probably represents a second route from the retina to the visual cortex that bypasses the LGN. The fast transmission time estimated between the SC and MT (Berman and Wurtz 2010) suggests that this brainstem-pulvinar-cortical pathway may be well suited to

mediate motion detection, saliency processing, and saccadic suppression and thereby reveal the contribution of the pulvinar to cortical visual processing, perception, and action (Berman and Wurtz 2011).

Inasmuch as brainstem cholinergic inputs suppress zona incerta activity (Trageser et al. 2006), increased vigilance may result in the disinhibition of pulvinar neurons, including the facilitation of transmission along the colliculo-cortical pathway (Trageser and Keller 2004). Trojanowski and Jacobson (1975) also showed direct projection from the LGN to PI and PL in the macaque monkey. Therefore, due to the overall connectivity pattern, the pulvinar may be important to regulate cortico-cortical transmission according to behavioral context.

5.3 Cortical-Pulvinar Connectivity

Large parts of the primate visual cortex exhibit precise visuotopic organization (Gattass et al. 2005, 2015). There are reciprocal and topographically organized visual projections from PI and PL to the striate, prestriate, inferotemporal, and parietal cortices. These projections are observed mainly in cortical layers I, II, and III of area 17 and layers I, III, and IV of areas 18 and 19 (Campos-Ortega and Hayhow 1972; Ogren and Hendrickson 1975, 1976, 1977; Benevento and Rezak 1975, 1976; Trojanowski and Jacobson 1976; Rezak and Benevento 1979). In area 18, the labeling intensity was heavier than that observed for area 17. Pulvinar terminals were found in layer IV, in the lower portion of layer III, and in layer I as alternating zones of densely and sparsely labeled patches (Ogren and Hendrickson 1977; Rezak and Benevento 1979; Wong-Riley 1977). In the dense regions, grains extended vertically from layer IV to layer I in a manner previously reported for somatosensory cortex by Jones et al. (1978). The mean center-to-center distance between the dense zones is greater and more variable than that seen in layer II of area 17 (Ogren and Hendrickson 1977).

The cortico-pulvinar neurons were pyramidal in shape and ranged in size from small to large. In heterotypical cortex, they were found in layers V and VI, whereas in area 17, they were found mainly in layer Vb (Lund and Boothe 1975; Trojanowski and Jacobson 1976; Ogren and Hendrickson 1977).

The topographical organization of the V1-pulvinar projections were described in the marmoset (Spatz and Erdmann 1974), macaque (Campos-Ortega and Hayhow 1972; Ogren and Hendrickson 1976; Ogren 1977), and squirrel (Holländer 1974; Ogren 1977) monkeys. Two regions of the pulvinar receive fibers from V1: PL and PI. Tracer injection within the central visuotopic representation resulted in the labeling of the lateral halves of PI and PL, while peripheral injections showed more medial labeling. The vertical meridian is represented in the architectonical boundary between these two pulvinar regions, consistent with previous electrophysiological recordings (Allman et al. 1972; Bender 1981).

Lin et al. (1974), using horseradish peroxidase (HRP), showed that projections from the pulvinar to MT in the owl monkey were originating mainly from the

medial portion of the PI. In the macaque monkey, Standage and Benevento (1983) found overlapping retrogradely filled cells and anterogradely transported terminal grains located exclusively within a crescent-shaped region, which traverses the brachium of the SC to include the PI and PL. The connections between MT and the pulvinar crescent are reciprocal and topographically organized, with the lower visual field represented dorsally and the upper visual field represented ventrally (Soares et al. 2001). There is an expanded representation of central vision located caudally within the crescent, while peripheral vision is represented rostrally (Standage and Benevento 1983).

Using HRP and ^3H leucine in combination, Trojanowski and Jacobson (1975) demonstrated that the connections between the superior temporal gyrus (STG) and the pulvinar are topographical and reciprocal. STG projects to and receives projections from the ventromedial PM, while the posterior third is reciprocally connected mainly to ventromedial PL and medial PI. More recently, the connections of the pulvinar with the visual cortex were studied in macaque monkey with tracer injections in areas V1, V2, V4, MT, and PO (Adams et al. 2000; Gattass et al. 2014; Ungerleider et al. 2014). The connectivity of the pulvinar with area V2 was studied by Ungerleider et al. (2014) in macaque monkeys using multiple tracer injections in different eccentricities in V2. Figure 5.3 shows the regions of the pulvinar containing the corresponding labeled summary of seven selected cases. It is possible to observe well-defined topographic maps in P1 and P2, and a cruder map in P4, which may exhibit some degree of segregation between the upper and lower visual field representations. The projections from V2 in these seven cases encompass almost the entire extent of the P1, P2, and P4 fields of the pulvinar. The injection sites in Cases 2, 6, and 10, which were located in the upper visual field representation of V2, led to ventral patches in P1 (Fig. 5.3, A +2.5–A+2.0) and P2 (Fig. 5.3, A +2.0–A+1.0) and to a central patch in P4 (Fig. 5.3, A +2.0–A+1.0). The injections in the lower visual field representation of V2 led to dorsal patches in P1 (Fig. 5.3, A +2.5–A+2.0) and P2 (Fig. 5.3, A +2.0–A+1.0) and to both dorsal and ventral patches in P4 (Fig. 5.3, A +2.0–A+1.0). The patches revealed by the V2 injections show a considerable overlap in all pulvinar fields, suggesting coarser topographic organizations in these fields as a result of convergent input and/or larger receptive fields in the pulvinar, when compared to those in V2 (Ungerleider et al. 2014).

Gattass et al. (2014) studied the connectivity of the pulvinar with V4 in the macaque monkey. Figure 5.4 illustrates the distribution of labeled cells and terminals in the pulvinar and surrounding regions after injections of anterograde and retrograde tracers (HRP, Bis, and ^3H) in V4 in one macaque monkey (Case 5 from Gattass et al. 2014). Several clusters of labeled cells and terminals were found in P1 (sections 1–5), P2 (sections 2–6), P3 (sections 3–5), and P4 (sections 3–6).

Figure 5.5 shows projecting cells and terminals in a montage of parasagittal sections after an injection in the upper visual field representation of V4. Note the four patches with labeled cells and terminals, corresponding to the P1, P2, P3, and P4 fields. Note also that the patches corresponding to the projections originating

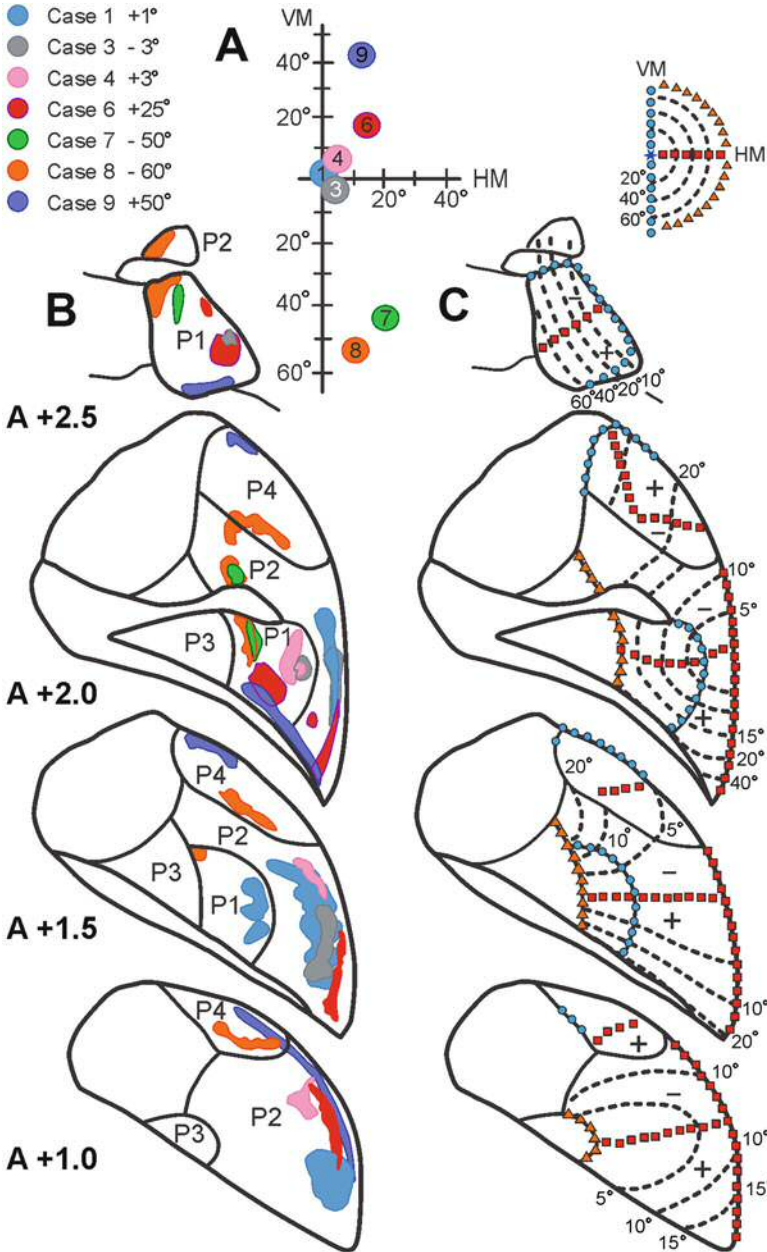


Fig. 5.3 Projections from V2 to the pulvular. Three topographically organized projection zones (P1, P2, and P4) of the macaque monkey pulvular revealed by anterograde tracer injections into V2 at different eccentricities for seven selected cases (upper left). The list of the cases and the locations of the receptive field centers in V2 are shown in (a). (b) Reconstructions of the projection zones shown on coronal sections of the pulvular from anterior (+2.5) to posterior (+1.0) section planes. (c) Representation of the topographical maps in the projection zones P1, P2, and P4 of the pulvular plotted on the corresponding sections shown in (b) [modified from Ungerleider et al. (2014)]

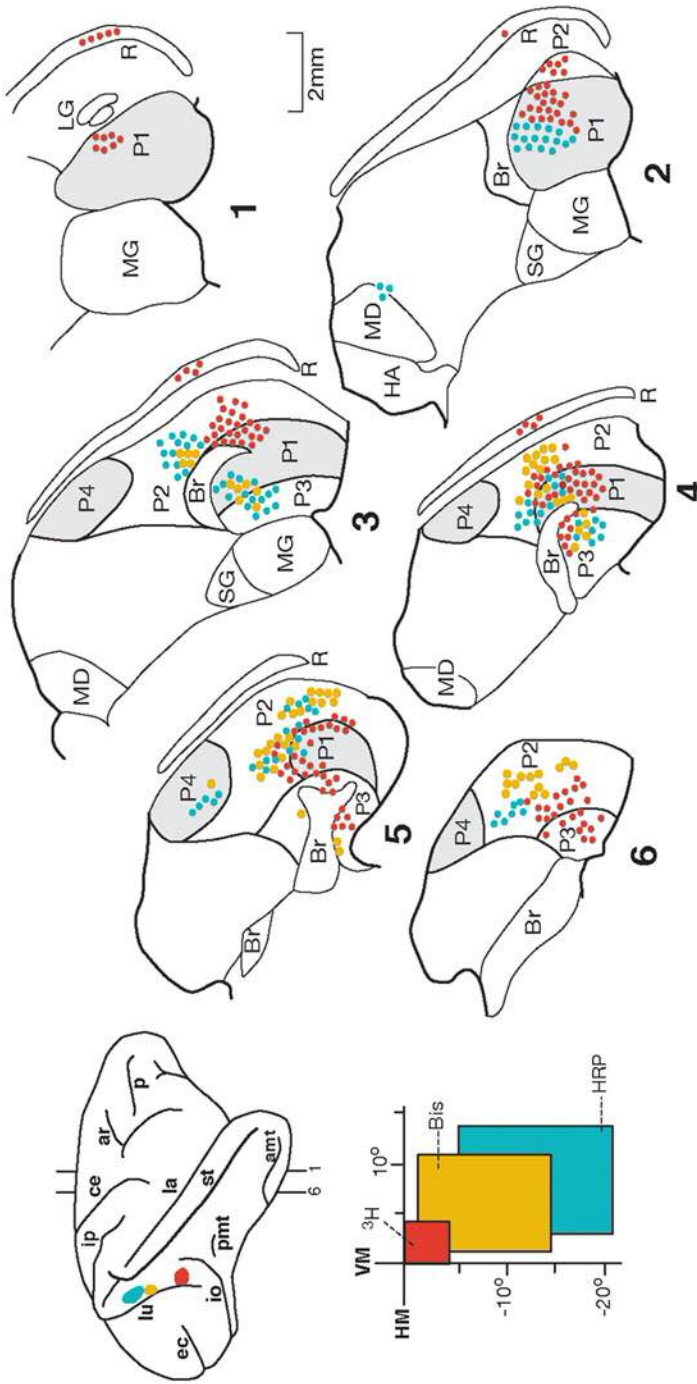
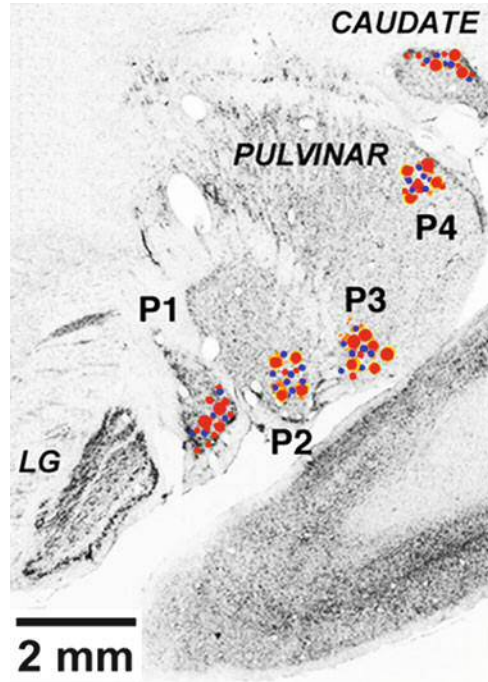


Fig. 5.4 Connections of the pulvinar with area V4 in the macaque monkey. Three anterograde and retrograde tracers were injected at topographically defined locations in V4, as depicted in a lateral view of the right hemisphere (left). Labeled cells and terminals are shown in coronal sections of the pulvinar and surrounding areas (right). See text for details [modified from Gattass et al. (2014)]

Fig. 5.5 Connections of the pulvinar with area V4 (parasagittal sections of the left hemisphere). Retrograde labeled cells (red-orange concentric icons) and anterograde labeled terminals (blue dots) were found at the topographically corresponding locations of the P1–P4 projection zones of the pulvinar after HRP injection in V4. Note also the projections to and from the caudate to V4 [modified from Gattass et al. (2014)]



from a tracer injection site in the upper visual field representation of V4 are located ventrally in fields P1–P3 and dorsally in P4 (Gattass et al. 2014).

Adams et al. (2000) showed that projections from the pulvinar to V1 and V2 in macaque monkeys overlap in two separate fields that are in register with the visual field maps of P1 and P2. In some, but not all, cases, an additional projection field was found from P3 to V2. However, we did not observe reciprocal projections from V2 to P3 in all cases. MT projecting cells were also found in P1 and P2 but were mainly concentrated in the medial portion of P3. Adams et al. (2000) also showed extensive projections from P2 to V4 but sparser projections from P1 and still sparser from P3. Our current scheme shows that V2 projecting neurons terminate in P2, P3, and P4, similar to the projection field of area V4.

Immunohistochemical studies in macaque, capuchin, and squirrel monkeys have revealed five similar subdivisions of the pulvinar, which include all of PI but which also encompass parts of PL and PM. These regions have been named PI_P, PI_M, PI_C, PI_L, and PI_{L,S} (Cusick et al. 1993; Gutierrez et al. 1995; Gray et al. 1999; Adams et al. 2000; Soares et al. 2001). The similarities in the chemoarchitectonic subdivisions contrast with the distinct connectivity and the different visuotopic organizations found in the pulvinar among these species.

In the capuchin monkey, Soares et al. (2001) were unable to clearly segregate P1 from P2 based on their connectivity pattern with areas V1, V2, MT, and V4, in spite of the great chemoarchitectonic similarities between macaque and capuchin monkeys. Areas V2 and V4 in the capuchin monkey have preferential connections with

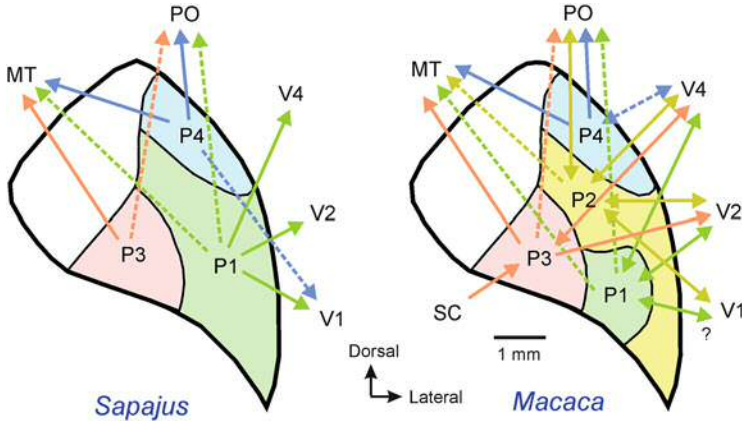


Fig. 5.6 The three projection fields (P1, P3, and P4) of the capuchin pulvinar and the four projection fields (P1, P2, P3, and P4) of the macaque pulvinar revealed after tracer injections in cortical areas V1, V2, V4, PO, and MT. Strong and weak projections between the pulvinar and these five regions are represented by arrows (continuous and dashed, respectively) [Left—modified from Soares et al. (2001) and right based on Colby et al. (1988) and Gattass et al. (2014)]

P1, which may correspond to the ventrolateral complex described in this species by Gattass et al. (1978a) and could correspond to both P1 and P2 described in the macaque monkey. A similar segregation was described by Cusick et al. (1993) and Stepniewska and Kaas (1997), who established that the subdivisions of PI that receive ascending projections from the SC are distinct from the portion of the nucleus that projects to area MT.

Figure 5.6 compares the three projection fields (P1, P3, and P4) of the capuchin monkey pulvinar with the four projection fields (P1, P2, P3, and P4) of the macaque monkey pulvinar, focusing on their projections to and from visual areas V1, V2, V4, PO, and MT. Projections from the SC are also illustrated in this figure.

Kaas and Lyon (2007) have further proposed that the pulvinar nuclei could be segregated into two groups related to the two streams of visual information processing, namely, the ventral and dorsal streams for object and spatial vision, respectively (Mishkin and Ungerleider 1982). According to this proposal, the pulvinar nuclei would provide cortico-pulvinar-cortical interactions that would enable the spread and integration of information both within each visual stream and across streams, in addition to relaying visual information from the SC, via P3, to the dorsal stream cortical areas (Ungerleider and Christensen, 1977).

There are two feedforward projections to V2: one from the lateral/inferior pulvinar and the other from V1. Inasmuch as neither the pulvinar nor V2 can be visually activated following V1 removal, either or both of these inputs could serve as a neuronal driving source to V2 (Marion et al. 2013). Reversibly inactivating the PL in the galago (a prosimian primate) was found to prevent supra-granular V1 neurons from responding to visual stimulation (Purushothaman et al. 2012). Conversely, reversible, focal excitations of the lateral pulvinar were found to increase

fourfold the visual responses in coincident V1 receptive fields and shift partially overlapping V1 receptive fields toward the topographic representation of the excitation site (Purushothaman et al. 2012). Excitation of PL after LGN lesions activated supra-granular layer V1 neurons. If these results also hold in other primates, then PL would be in a strategic position to control and gate information outflow from V1 during changes of state or attention (Purushothaman et al. 2012; Sherman and Guillery 2002). Consistent with this potential role of the pulvinar in regulating the effects of spatial attention, deactivation of PL causes spatial attention deficits in monkeys (Desimone et al. 1990). Finally, joint recordings in V4 and PL of macaque monkeys performing a visual attention task show synchronized activity between the two structures (Saalmann and Kastner 2011).

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