Advances in Anatomy, Embryology and Cell Biology

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

Springer

Chapter 4
Visual Map Representations in the Primate Pulvinar

It has long been suspected that the pulvinar participates in visual functions because it receives direct projections from the retina (Campos-Ortega et al. 1970) and from the SC (Benevento and Fallon 1975; Lin and Kaas 1979). Additionally, the pulvinar is connected with several visual cortical areas (Campos-Ortega and Hayhow 1972; Ogren and Hendrickson 1976; Benevento and Davis 1977). The retinotopic organization of the pulvinar was studied using electrophysiological techniques in the owl (Allman et al. 1972), capuchin (Gattass et al. 1978a), and macaque monkeys (Bender 1981).

In owl monkeys, Allman et al. (1972) found a single topographic representation of the contralateral visual field in PI, where the central 10° of the visual field was represented dorsally and rostrally and more peripheral parts of the visual field were represented ventrally. The lines of isoeccentricity extended caudomedially and corresponded to the small fiber bundle input that also courses caudomedially through PI. The horizontal meridian divides the nucleus into a rostromedial portion, in which the lower visual quadrant is represented, and a caudolateral portion, in which the upper visual quadrant is represented.

Gattass et al. (1978a) described two retinotopic maps in the pulvinar of the capuchin monkey. The map located in the ventrolateral portion (P_{LV} or P1), which comprises PI and the ventral portion of PL, has a greater representation of the central part of the visual field. The projection of the vertical meridian runs along its lateral border, while that of the horizontal one extends from the dorsal third of the hilus of the LGN to the medial border of PI. The lower quadrant is represented dorsally, while the upper quadrant is represented ventrally. The second map, called Pμ (equivalent to P4), located in the dorsomedial portion of PL, is rotated 90° clockwise around the rostrocaudal axis. The vertical meridian is found at the ventromedial border of this nucleus, and the lower quadrant is represented laterally and the upper quadrant medially. Both projections are restricted to contralateral visual hemifield (Fig. 4.1).

R. Gattass et al., *The Pulvinar Thalamic Nucleus of Non-Human Primates: Architectonic and Functional Subdivisions*, Advances in Anatomy, Embryology and Cell Biology 225, https://doi.org/10.1007/978-3-319-70046-5_4

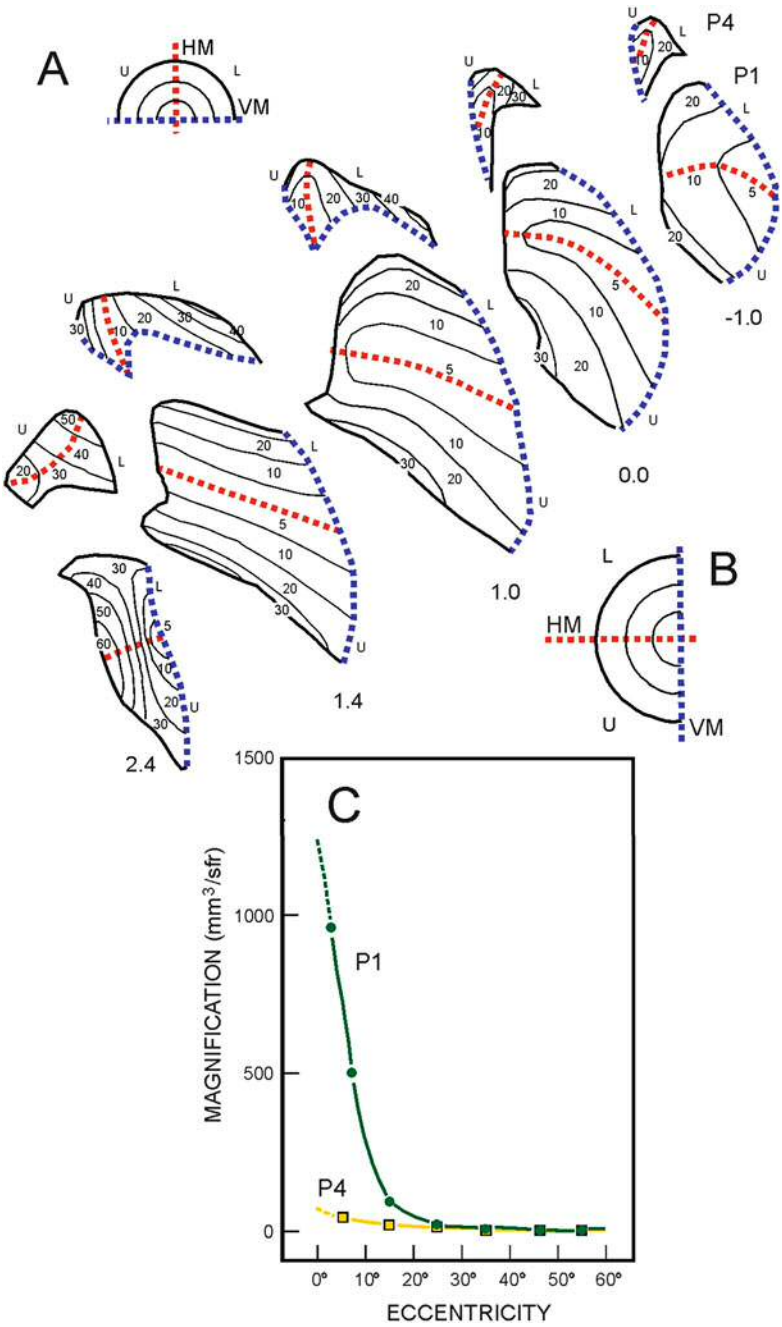

Fig. 4.1 Visual topography of the P4 (Pμ, A) and P1 (P_{LV}, B) sub-regions of the capuchin monkey pulvinar (right hemisphere). The visuotopic organization of the pulvinar is represented in polar coordinates, corresponding to the visual hemifield representations also shown in Panels (**a**) and (**b**).

By recording from clusters of neurons in the pulvinar of the macaque monkey, Bender (1981) also found two representations of the contralateral hemifield. One representation lies mainly within PI but extend into the adjacent PL. The vertical meridian lies in the dorsal and lateral margins of the PI, while the representation of the periphery is found in the medial margin adjacent to the MGN. Central vision is represented laterally and posteriorly. The second representation lies within the PL. The lower quadrant representation lies at its dorsal portion, while the upper quadrant is represented at the ventral half. The horizontal meridian lies in the external margin of the pulvinar. The two maps share a common representation of the vertical meridian.

The visuotopic organization of PI is similar in all three primate species. The vertical meridian and central vision representation are found at the border with LGN, while the peripheral vision representation is found adjacent to the MGN. However, in capuchin and macaque monkeys, this map extends into the adjacent PL. A second visuotopic map has been described in both capuchin and macaque monkeys. However, the lateral map of the macaque monkey is different in extent and visuotopic organization from that of the capuchin Pμ, which is smaller in size and is located more dorsally in the pulvinar.

Petersen et al. (1985), in a behavioral study with macaque monkeys were able to describe, in addition to PI and PL as proposed by Bender (1981), a dorsomedial region (Pdm) of PL, which has a crude retinotopic organization. Other regions exhibiting visual responses, but without clear retinotopic organization, were described in PL by Benevento and Miller (1981). They found neurons in the caudal part of PL, called PLɣ, with large, bilateral receptive fields that were sensitive to changes in luminance levels, were selective to various types of stimulus motion, and exhibited complex binocular interactions. This area seems homologous in location and visual properties to area Pμ of the capuchin monkey described by Gattass et al. (1978a).

Subsequently, Ungerleider et al. (1983, 1984), based on the pulvinar connectivity with V1 and MT, termed the PI and PL maps of the macaque monkey, respectively, the "P1" and "P2" fields. The second map in the capuchin monkey, named Pμ by Gattass et al. (1978a), was located dorsally to PI and was subsequently named "P4" by Adams et al. (2000). P4 may be at least in part coextensive with Pdm (Petersen et al. 1985). Ungerleider et al. (1984) described a third field, "P3," in the pulvinar characterized by rich connectivity with area MT. It is located

Fig. 4.1 (continued) U and L denote upper and lower visual fields, respectively. The antero-posterior plane is indicated in millimeters at the bottom of the sections. (**c**) The magnification factor (in cubic millimeter per stereoradian, mm^3/str) of P1 and P4 as a function of eccentricity. Note that P1 has a much larger representation of the central visual field as compared to P4 [modified from Gattass et al. (1978a)]

posteromedially in PI but also includes small adjacent portions of PL and PM that lie dorsal to the brachium of the SC (see also Standage and Benevento 1983). P3 does not seem to have a well-defined visuotopic map like its neighbor P1, although it has yet to be mapped electrophysiologically.

References

Adams MM, Webster MJ, Gattass R, Hof PR, Ungerleider LG (2000) Visual cortical projections and chemoarchitecture of macaque monkey pulvinar. J Comp Neurol 419:377–393

Allman JM, Kaas JH (1971) Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). Brain Res 35:89–106

Allman JM, Kaas JH, Lane RH, Miezin FM (1972) A representation of the visual field in the inferior nucleus of the pulvinar in the owl monkey. Brain Res 40:291–302

Andersen RA, Snyder LH, Li CS, Stricanne B (1993) Coordinate transformations in the representation of spatial information. Curr Opin Neurobiol 3:171–176

Asanuma C, Andersen RA, Cowan WM (1985) The thalamic relations of the caudal inferior parietal lobule and the lateral prefrontal cortex in monkeys: divergent cortical projections from cell clusters in the medial pulvinar nucleus. J Comp Neurol 241:357–381

Baimbridge KG, Celio MR, Rogers JH (1992) Calcium-binding proteins in the nervous system. Trends Neurosci 15:303–308

Baleydier C, Morel A (1992) Segregated thalamocortical pathways to inferior parietal and inferotemporal cortex in macaque monkey. Vis Neurosci 8:391–405

Beck PD, Kaas JH (1998) Thalamic connections of the dorsomedial visual area in primates. J Comp Neurol 396:381–398

Bender DB (1981) Retinotopic organization of macaque pulvinar. J Neurophysiol 46:672–693

Bender DB, Youakim M (2001) Effect of attentive fixation in macaque thalamus and cortex. J Neurophysiol 85:219–234

Benevento LA, Davis B (1977) Topographical projections of the prestriate cortex to the pulvinar nuclei in the macaque monkey: an autoradiographic study. Exp Brain Res 30:405–424

Benevento LA, Fallon JH (1975) The ascending projections of the superior colliculus in the rhesus monkey (*Macaca mulatta*). J Comp Neurol 160:339–361

Benevento LA, Miller J (1981) Visual responses of single neurons in the caudal lateral pulvinar of the macaque monkey. J Neurosci 11:1268–1278

Benevento LA, Rezak M (1975) Extrageniculate projections to layers VI and I of striate cortex (area 17) in the rhesus monkey (*Macaca mulatta*). Brain Res 96:51–55

Benevento LA, Rezak M (1976) The cortical projections of the inferior pulvinar and adjacent lateral pulvinar in the rhesus monkey (*Macaca mulatta*): an autoradiographic study. Brain Res 108:1–24

Benevento LA, Standage GP (1983) The organization of projections of the retinorecipient and nonretinorecipient nuclei of the pretectal complex and layers of the superior colliculus to the lateral pulvinar and medial pulvinar in the macaque monkey. J Comp Neurol 217:307–336

R. Gattass et al., *The Pulvinar Thalamic Nucleus of Non-Human Primates: Architectonic and Functional Subdivisions*, Advances in Anatomy, Embryology and Cell Biology 225, https://doi.org/10.1007/978-3-319-70046-5

Benevento LA, Rezak M, Santos-Anderson R (1977) An autoradiographic study of the projections of the pretectum in the rhesus monkey (*Macaca mulatta*): evidence for sensorimotor links to the thalamus and oculomotor nuclei. Brain Res 127:197–218

Berman RA, Wurtz RH (2010) Functional identification of a pulvinar path from superior colliculus to cortical area MT. J Neurosci 30:6342–6354

Berman RA, Wurtz RH (2011) Signals conveyed in the pulvinar pathway from superior colliculus to cortical area MT. J Neurosci 31:373–384. https://doi.org/10.1523/JNEUROSCI.4738-10.2011

Bourne JA, Morrone MC (2017) Plasticity of visual pathways and function in the developing brain: is the pulvinar a crucial player? Frontier of system. Neuroscience 11:3. https://doi.org/10.3389/fnsys.2017.00003

Bridge H, Leopold DA, Bourne JA (2016) Adaptive pulvinar circuitry supports visual cognition. Trends Cogn Sci 20:146–157

Campos-Ortega JA, Hayhow WR (1972) On the organization of the visual cortical projection to the pulvinar in *Macaca mulatta*. Brain Behav Evol 6:394–423

Campos-Ortega JK, Hayhow WR, de V Clover PF (1970) A note on the problem of retinal projections to the inferior nucleus of primates. Brain Res 22:126–130

Chalupa LM, Coyle RS, Lindsley DB (1976) Effect of pulvinar lesions on visual pattern discrimination in monkeys. J Neurophysiol 39:354–369

Colby CL, Gattass R, Olson CR, Gross CG (1988) Topographical organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. J Comp Neurol 269:392–413

Cowey A, Stoerig P, Bannister M (1994) Retinal ganglion cells labelled from the pulvinar nucleus in macaque monkeys. Neuroscience 61:691–705

Crick FC (1984) Function of the thalamic reticular complex: the search light hypothesis. Proc Natl Acad Sci U S A 81:4586–4590

Cusick CG, Scripter JL, Darensbourg JG, Weber JT (1993) Chemoarchitectonic subdivisions of the visual pulvinar in monkeys and their connectional relations with the middle temporal and rostral dorsolateral visual areas, MT and DLr. J Comp Neurol 336:1–30

Danziger S, Ward R, Owen V, Rafal R (2001–2002) The effects of unilateral pulvinar damage in humans on reflexive orienting and filtering of irrelevant information. Behav Neurol 13:95–104

DeFelipe J (1997) Types of neurons, synaptic connections and chemical characteristics of cells immunoreactive for calbindin-D28K, parvalbumin and calretinin in the neocortex. J Chem Neuroanat 14:1–19

Desimone R, Wessinger M, Thomas L, Schneider W (1990) Attentional control of visual perception: cortical and subcortical mechanisms. Cold Spring Harb Symp Quant Biol 55:963–971

Eidelberg E, Saldias CA (1960) A stereotaxic atlas for Cebus monkeys. J Comp Neurol 115:103–123

Federer F, Ichida JM, Jeffs J, Schiessl I, McLoughlin N, Angelucci A (2009) Four projection streams from primate V1 to the cytochrome oxidase stripes of V2. J Neurosci 29:15455–15471

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47

Friedmann M (1912) Die cytoarchitektonic des zwischenhirns der Cercopitheken mit bersonderer berucksichtigung des thalamus opticus. J Psychol Neurol 18:308–378

Fries P (2005) A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn Sci 9:474–480

Fries P (2015) Rhythms for cognition: communication through coherence. Neuron 88:220–235

Fries P, Reynolds JH, Rorie AE, Desimone R (2001) Modulation of oscillatory neuronal synchronization by selective visual attention. Science 291:1560–1563

Gattass R, Desimone R (1996) Responses of cells in the superior colliculus during performance of a spatial attention task in the macaque. Rev Bras Biol 56(Su 2):257–279

Gattass R, Desimone R (2014) Effect of microstimulation of the superior colliculus on visual space attention. J Cogn Neurosci 26:1208–1219

Gattass R, Oswaldo-Cruz E, Sousa APB (1978a) Visuotopic organization of the Cebus pulvinar: a double representation of the contralateral hemifield. Brain Res 152:1–16
Gattass R, Sousa AP, Oswaldo-Cruz E (1978b) Single unit response types in the pulvinar of the *Cebus* monkey to multisensory stimulation. Brain Res 158:75–87
Gattass R, Sousa APB, Oswaldo-Cruz E (1979) Visual receptive fields of units in the pulvinar of *Cebus* monkey. Brain Res 160:413–430
Gattass R, Nascimento-Silva S, Soares JGM, Lima B, Jansen AK, Diogo ACM, Farias MF, Marcondes M, Botelho EP, Mariani OS, Azzi J, Fiorani M (2005) Cortical visual areas in monkeys: location, topography, connections, columns, plasticity and cortical dynamics. Philos Trans R Soc Lond Ser B Biol Sci 360:709–731
Gattass R, Galkin TW, Desimone R, Ungerleider L (2014) Subcortical connections of area V4 in the macaque. J Comp Neurol 522:1941–1965
Gattass R, Lima B, Soares JGM, Ungerleider LG (2015) Controversies about the visual areas located at the anterior border of area V2 in primates. Vis Neurosci 32:E019. https://doi.org/10.1017/S0952523815000188
Glendenning KK, Hall JA, Diamond IT, Hall WC (1975) The pulvinar nucleus of *Galago senegalensis*. J Comp Neurol 161:419–458
Goldberg ME, Wurst RH (1972) Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. J Neurophysiol 35:560–574
Gray D, Gutierrez C, Cusick CG (1999) Neurochemical organization of inferior pulvinar complex in squirrel monkeys and macaques revealed by acetylcholinesterase histochemistry, calbindin and CAT-301 immunostaining, and Wisteria floribunda agglutinin binding. J Comp Neurol 409:452–468
Gross CG (1991) Contribution of striate cortex and the superior colliculus to visual function in area MT, the superior temporal polysensory area and the inferior temporal cortex. Neuropsychologia 29:497–515
Gutierrez C, Cusick CG (1997) Area V1 in macaque monkeys projects to multiple histochemically defined subdivisions of the inferior pulvinar complex. Brain Res 765:349–356
Gutierrez C, Yaun A, Cusick CG (1995) Neurochemical subdivisions of the inferior pulvinar in macaque monkeys. J Comp Neurol 363:545–562
Gutierrez C, Cola MG, Seltzer B, Cusick CG (2000) Neurochemical and connectional organization of the dorsal pulvinar complex in monkeys. J Comp Neurol 419:61–86
Harting JK, Hall WC, Diamond IT (1972) Evolution of the pulvinar. Brain Behav Evol 6:424–452
Hashikawa T, Rausell E, Molinari M, Jones EG (1991) Parvalbumin- and calbindin-containing neurons in the monkey medial geniculate complex differential distribution and cortical layer specific projections. Brain Res 544:335–341
Hof PR, Morrison JH (1995) Neurofilament protein defines regional patterns of cortical organization in the macaque monkey visual system: a quantitative immunohistochemical analysis. J Comp Neurol 352:161–186
Hof PR, Glezer II, Condé F, Flagg RA, Rubin MB, Nimchinsky EA, Vogt Weisenhorn DM (1999) Cellular distribution of the calcium-binding proteins parvalbumin, calbindin, calretinin in the neocortex of mammals: phylogenetic and developmental patterns. J Chem Neuroanat 16:77–116
Holländer H (1974) Projections from the striate cortex to the diencephalon in the squirrel monkey (*Saimiri sciureus*). A light microscopic radioautographic study following intracortical injection of H^3 leucine. J Comp Neurol 155:425–440
Jones EG, Hendry SHC (1989) Differential calcium binding protein immunoreactivity distinguishes classes of relay neurons in monkey thalamic nuclei. Eur J Neurosci 1:222–246
Jones EG, Coulter JD, Hendry SH (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. J Comp Neurol 181:291–347
Kaas JH, Lyon DC (2007) Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. Brain Res Rev 55:285–296

LaBerge D, Buchsbaum MS (1990) Positron emission tomography measurements of pulvinar activity during an attention task. J Neurosci 10:613–619
Levitt JB, Yoshioka T, Lund JS (1995) Connections between the pulvinar complex and cytochrome oxidase-defined compartments in visual area V2 of macaque monkey. Exp Brain Res 104:419–430
Lima B, Singer W, Neuenschwander S (2011) Gamma responses correlate with temporal expectation in monkey primary visual cortex. J Neurosci 31:15919–15931
Lin CS, Kaas JH (1979) The inferior pulvinar complex in owl monkeys: architectonic subdivisions and patterns of input from the superior colliculus and subdivisions of visual cortex. J Comp Neurol 187:655–678
Lin CS, Wagor E, Kaas JH (1974) Projections from the pulvinar to the middle temporal visual area (MT) in the owl monkey, Aotus trivirgatus. Brain Res 76:145–149
Lund JS, Boothe RG (1975) Interlaminar connections and pyramidal neuron organization in the visual cortex, area 17 of the Macaque monkey. J Comp Neurol 159:305–344
Lyon DC, Nassi JJ, Callaway EM (2010) A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. Neuron 65:270–279
Lysakowski A, Standage GP, Benevento LA (1986) Histochemical and architectonic differentiation of zones of pretectal and collicular inputs to the pulvinar and dorsal lateral geniculate nuclei in the macaque. J Comp Neurol 250:431–448
Marion R, Li K, Purushothaman G, Jiang Y, Casagrande VA (2013) Morphological and neurochemical comparisons between pulvinar and V1 projections to V2. J Comp Neurol 521:813–832
Mathers LH (1971) Tectal projection to the posterior thalamus of the squirrel monkey. Brain Res 35:295–298
Mathers LH (1972) Ultrastructure of the pulvinar of the squirrel monkey. J Comp Neurol 146:15–42
Mathers LH, Rapisardi SC (1973) Visual and somatosensory receptive fields of neurons in the squirrel monkey pulvinar. Brain Res 64:65–83
Mishkin M, Ungerleider LG (1982) Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. Behav Brain Res 6:57–77
Nakamura RK, Mishkin M (1986) Chronic 'blindness' following lesions of nonvisual cortex in the monkey. Exp Brain Res 63:173–184
O'Brien BJ, Abel PL, Olavarria JF (2001) The retinal input to calbindin-D28k-defined subdivisions in macaque inferior pulvinar. Neurosci Lett 312:145–148
Ogren MP (1977) Evidence for a projection from pulvinar to striate cortex in the squirrel monkey (*Saimiri sciureus*). Exp Neurol 54:622–625
Ogren MP, Hendrickson AE (1975) Afferent and efferent pathways of striate cortex in squirrel and rhesus monkey. Anat Rec 181:439
Ogren MP, Hendrickson AE (1976) Pathways between striate cortex and subcortical regions in *Macaca mulatta* and *Saimiri sciureus*: evidence for a reciprocal pulvinar connection. Exp Neurol 53:780–800
Ogren MP, Hendrickson AE (1977) The distribution of pulvinar terminals in visual areas 17 and 18 of the monkey. Brain Res 137:343–350
Ogren MP, Hendrickson AE (1979) The structural organization of the inferior and lateral subdivisions of the Macaca monkey pulvinar. J Comp Neurol 188:147–178
Olshausen BA, Anderson CH, Van Essen DC (1993) A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. J Neurosci 13:4700–4719
Olszewski J (1952) The thalamus of the *Macaca mulatta* – an Atlas for use with the stereotaxic instrument. S. Karger, Basel, 93 p
Partlow GD, Colonnier M, Szabo J (1977) Thalamic projections of the superior colliculus in the rhesus monkey, *Macaca mulatta*: a light and electron microscopic study. J Comp Neurol 171:285–318

Petersen SE, Robinson DL, Keys W (1985) Pulvinar nuclei of the behaving rhesus monkey: visual response and their modulation. J Neurophysiol 54:867–885
Petersen SE, Robinson DL, Morris JD (1987) Contributions of the pulvinar to visual spatial attention. Neuropsychologia 25:97–105
Posner MI, Petersen SE (1990) The attention system of the human brain. Annu Rev Neurosci 13:25–42
Purushothaman G, Marion R, Li K, Casagrande VA (2012) Gating and control of primary visual cortex by pulvinar. Nat Neurosci 15:905–912
Rafal RD, Posner MI (1987) Deficits in human visual spatial attention following thalamic lesions. Proc Natl Acad Sci U S A 84:7349–7353
Rakic P (1974) Embryonic development of the pulvinar – LP complex in man. In: Cooper IS, Riklan M, Rakic P (eds) The pulvinar – LP complex. Charles C. Thomas, Springfield, IL, pp 3–35
Rezak M, Benevento LA (1979) A comparison of the organization of the projections of the dorsal lateral geniculate nucleus, the inferior pulvinar and the adjacent lateral pulvinar to primary visual cortex (area 17) in the macaque monkey. Brain Res 167:19–40
Robinson DL, Petersen SE (1992) The pulvinar and visual salience. Trends Neurosci 15:127–132
Rockland KS, Pandya DN (1979) Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Res 179:3–20
Saalmann YB, Kastner S (2011) Cognitive and perceptual functions of the visual thalamus. Neuron 71:209–223
Saalmann YB, Pinsk MA, Wang L, Li X, Kastner S (2012) The pulvinar regulates information transmission between cortical areas based on attention demands. Science 337(6095):753–756
Sherman SM, Guillery RW (2002) The role of the thalamus in the flow of information to the cortex. Philos Trans R Soc Lond Ser B Biol Sci 357:1695–1708
Shipp S (2000) A new anatomical basis for 'spotlight' metaphors of attention. Eur J Neurosci 12 (Suppl 11):196
Shipp S (2003) The functional logic of cortico-pulvinar connections. Philos Trans R Soc Lond Ser B Biol Sci 358:1605–1624
Sincich LC, Horton JC (2002) Pale cytochrome oxidase stripes in V2 receive the richest projection from macaque striate cortex. J Comp Neurol 447:18–33
Siqueira EB (1971) The cortical connections of the nucleus pulvinaris of the dorsal thalamus in the rhesus monkey. Int J Neurol 8:139–154
Soares JGM, Gattass R, Souza APB, Rosa MGP, Fiorani M Jr, Brandão BL (2001) Connectional and neurochemical subdivisions of the pulvinar in Cebus monkeys. Vis Neurosci 18:25–41
Soares JGM, Diogo ACM, Fiorani M, Souza APB, Gattass R (2004) Effects of inactivation of the lateral pulvinar on response properties of second visual area cells in Cebus monkeys. Clin Exp Pharmacol Physiol 31:580–590
Spatz WB, Erdmann G (1974) Striate cortex projections to the lateral geniculate and other thalamic nuclei; a study using degeneration and autoradiographic tracing methods in the marmoset Callithrix. Brain Res 82:91–108
Standage GP, Benevento LA (1983) The organization of connections between the pulvinar and visual area MT in the macaque monkey. Brain Res 262:288–294
Steele GE, Weller RE (1993) Subcortical connections of subdivisions of inferior temporal cortex in squirrel monkeys. Vis Neurosci 10:563–583
Stepniewska I, Kaas JH (1997) Architectonic subdivisions of the inferior pulvinar in NewWorld and OldWorld monkeys. Vis Neurosci 14:1043–1060
Sternberger LA, Sternberger NH (1983) Monoclonal antibodies distinguish phosphorylated and nonphosphorylated forms of neurofilaments in situ. Neurobiology 80:6126–6130
Trageser JC, Keller A (2004) Reducing the uncertainty: gating of peripheral inputs by zona incerta. J Neurosci 24:8911–8915
Trageser JC, Burke KA, Masri R, Li Y, Sellers L, Keller A (2006) State-dependent gating of sensory inputs by zona incerta. J Neurophysiol 96:1456–1463

Treue S, Maunsell JH (1996) Attentional modulation of visual motion processing in cortical areas MT and MST. Nature 382:539–541
Trojanowski JQ, Jacobson S (1974) Medial pulvinar afferents to frontal eye fields in rhesus monkey demonstrated by horseradish peroxidase. Brain Res 80:395–411
Trojanowski JQ, Jacobson S (1975) Peroxidase labeled subcortical pulvinar afferents in rhesus monkey. Brain Res 97:144–150
Trojanowski JQ, Jacobson S (1976) Areal and laminar distribution of some pulvinar cortical efferents in rhesus monkey. J Comp Neurol 169:371–392
Ungerleider LG, Christensen CA (1977) Pulvinar lesions in monkeys produce abnormal eye movements during visual discrimination training. Brain Res 136:189–196
Ungerleider LG, Galkin TW, Mishkin M (1983) Visuotopic organization of projections of striate cortex to inferior and lateral pulvinar in rhesus monkey. J Comp Neurol 217:137–157
Ungerleider LG, Desimone R, Galkin TW, Mishkin M (1984) Subcortical projections of area MT in the macaque. J Comp Neurol 223:368–386
Ungerleider LG, Galkin TW, Desimone R, Gattass R (2008) Cortical connections of area V4 in the macaque. Cereb Cortex 18:477–499
Ungerleider LG, Galkin TW, Desimone R, Gattass R (2014) Subcortical projections of area V2 in the macaque. J Cogn Neurosci 26:1220–1233
Walker AE (1938) The primate thalamus. University of Chicago Press, Chicago, IL
Ward R, Danziger S, Owen V, Rafal R (2002) Deficits in spatial coding and feature binding following damage to spatiotopic maps in the human pulvinar. Nat Neurosci 5:99–100
Warner CE, Goldshmit Y, Bourne JA (2010) Retinal afferents synapse with relay cells targeting the middle temporal area in the pulvinar and lateral geniculate nuclei. Front Neuroanat 4:8. https://doi.org/10.3389/neuro.05.008.2010
Womelsdorf T, Schoffelen J-M, Oostenveld R, Singer W, Desimone R, Engel AK, Fries P (2007) Modulation of neuronal interactions through neuronal synchronization. Science 316:1609–1612
Wong-Riley MTT (1977) Connections between the pulvinar nucleus and the prestriate cortex in the squirrel monkey as revealed by peroxidase histochemistry and autoradiography. Brain Res 134:249–267
Zeki S, Shipp S (1989) Modular connections between areas V2 and V4 of macaque monkey visual cortex. Eur J Neurosci 1:494–506
Zhou H, Schafer RJ, Desimone R (2016) Pulvinar-cortex interactions in vision and attention. Neuron 89:209–220