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

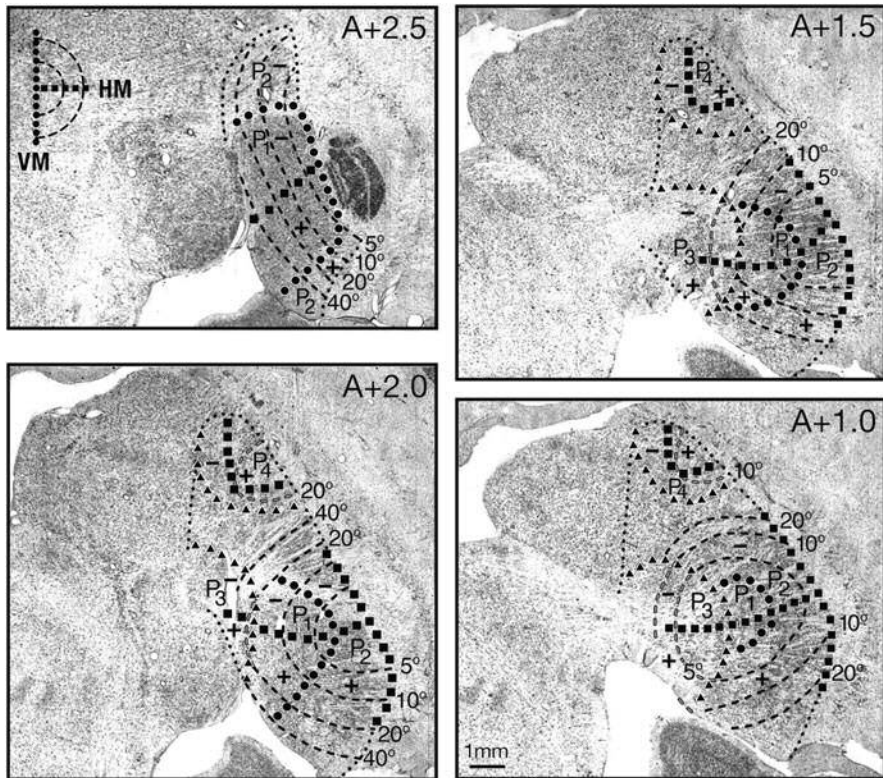
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## Chapter 7

# Visual Topography of the Pulvinar Projection Zones

Injection of tritiated amino acids in V2 revealed topographically organized projections targeting the P1, P2, and P4 regions of the pulvinar. The topographic map in P1 was originally described by Gattass et al. (1978a) in the capuchin monkey and subsequently by Bender (1981) in the macaque monkey. According to these authors, P1 is located in the PI but also includes a small portion of the immediately adjacent PL. The peripheral visual field is represented anteriorly in the medial portion of PI, while the central visual field is represented more posteriorly in the medial portion of PL. The vertical meridian is represented on the lateral edge of the nucleus, while the horizontal meridian is represented obliquely from lateral to medial across the nucleus and tilted slightly downward. The upper field is represented ventrally, while the lower field is represented dorsally.

The P1 map resembles a first-order transformation of the visual field (Allman and Kaas 1971). In the macaque monkey, the lateral portion of P1 seems to follow the P2 organization. It contains a representation of the peripheral visual field, which is located in the anterior portion of the nucleus, and a representation of the central visual field, which is located in the posterior portion of PL (Bender 1981). P2 and P1 share the representation of the vertical meridian, while P2's horizontal meridian representation is a continuation of P1's, in a way that the foveal region is represented at the lateral border of the pulvinar. Thus, the P2 map resembles a second-order transformation of the visual field (Allman and Kaas 1971). Gattass et al. (1978a) described a topographically organized region in dorsal pulvinar that seems to be equivalent to the P4 field described by Adams et al. (2000). P4 has a complex topographic arrangement. The representation of the vertical meridian is located on the dorsal edge of P4, while the representation of the horizontal meridian exits the dorsal edge and divides P4 into dorsal and ventral portions. The representation of the upper visual field occupies the dorsal and anterior P4, while the representation of the lower visual field is located ventral and posterior, adjacent to the lower field representation of P2. The P4 map resembles a distorted first-order transformation of the visual field (Allman and Kaas 1971).



**Fig. 7.1** Visual topography of the pulvinar P1, P2, P3, and P4 fields in the macaque monkey. Representative coronal sections stained for Nissl through the rostral (top left)-to-caudal (bottom right) extent of the pulvinar showing the visual topography of each of the four fields. The visual maps are shown superimposed on each section. Solid circles indicate the representation of the vertical meridian, solid squares indicate the representation of the horizontal meridian, heavy dashes indicate isoecentricity lines, gray colored dashes indicate isoecentricity lines in areas of coarse topography, small solid triangles indicate the borders of P3 and P4, and small dotted lines indicate the borders of the pulvinar fields. The plus sign indicates the upper visual field representation and the minus sign indicates the lower visual field representation. The sections are spaced 0.5 mm apart, and they do not reach the caudal extent of the pulvinar. Abbreviations as in Fig. 2.1. Scale bars = 1 mm. (Modified from Gattass et al. 2014)

Figure 7.1 shows the visuotopic maps of the macaque monkey pulvinar (P1–P4) charted onto Nissl-stained sections. The P1 and P2 maps are based on the work by Bender (1981) and Ungerleider et al. (1983, 1984). The estimate of P3's borders was guided by the work of Ungerleider et al. (1984) and Gattass et al. (2014). The dorsal border of P3 (i.e., the portion above the brachium of the SC) was adjusted to be compatible with the distribution of calbindin immunoreactive neurons presented in previous work (Adams et al. 2000; Gattass et al. 2014). The estimate of P4's border was also guided by the works of Adams et al. (2000) and Gattass et al. (2014).

# 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
- Baleyrier 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

- 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, Scriptor JL, Darensbourg JG, Weber JT (1993) Chemoarchitectonic subdivisions of the visual pulvinar in monkeys and their connective 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 cytoarchitektonik des Zwischenhirns der Cercopitheken mit besonderer Berücksichtigung 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 connective 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