Advances in Anatomy, Embryology and Cell Biology

Ricardo Gattass
Juliana G.M. Soares
Bruss Lima

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

Springer

Chapter 9
Response Properties of Pulvinar Neurons Studied with Single-Unit Electrophysiological Recordings

Mathers and Rapisardi (1973) studied the visual and somatosensory responses of the squirrel monkey pulvinar, where they described visual neurons in subregions PL, PI, and PM. Most neurons exhibited a definable receptive field, while only a few responded to diffuse illumination. Approximately twice as many neurons in PI were responsive to light compared to neurons in PL or PM. Nearly all neurons with identifiable receptive fields responded to visual stimulation within 25° of the fovea, on the hemifield contralateral to the recording electrode. The majority of the visual units were responsive to some form of moving stimulus, and some exhibited direction or orientation selectivity. Most visual neurons were monocularly driven and exhibited receptive fields of at least 100 square degrees in area. Mathers and Rapisardi (1973) also found somatosensory neurons in PL. Most of these units exhibited continuous peripheral receptive fields, though a few of these neurons could be bilaterally activated.

In order to systematize our electrophysiological findings and to enable a coherent presentation of the data, we have classified the neurons recorded in the pulvinar according to their functional properties (Gattass et al. 1978a, b). The units were thereby assigned to eight different categories or groups, as summarized in Fig. 9.1.

The first tier of this classification segregates the pulvinar neurons into either static or dynamic units. Neurons classified as static showed a brisk response to stationary stimuli presented over their receptive fields and a similar or weaker response to moving stimulus. In contrast, dynamic units showed poor or no response to stationary stimuli but a brisk response to moving stimuli. Dynamic units predominated (75%) over static ones (25%). About 15% of the units could not be categorized as either static or dynamic and were thereby designated as "unclassified."

Generally, the dynamic units were tuned for stimulus velocity. Static units responded tonically (58%) or, less frequently, phasically (42%) to stimulus onset or offset. In contrast, dynamic units always responded phasically to such stimulus transients.

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_9

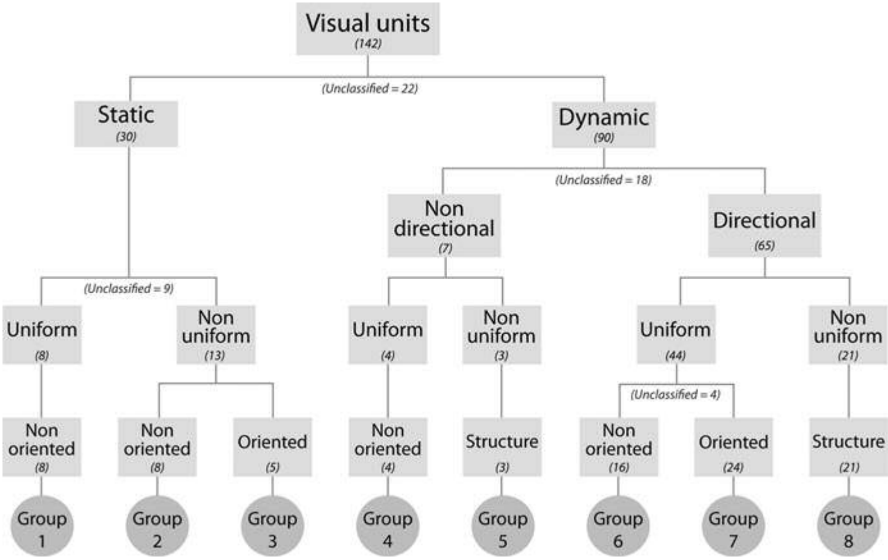

Fig. 9.1 Classification of pulvinar neurons based on their functional response properties measured with electrophysiological recordings. When the data available did not permit a reliable classification of a unit, it was included under a separate heading (i.e. 'unclassified'). The number of units classified under each heading is shown in parenthesis [modified from Gattass et al. (1979)]

9.1 Neurons Classified as "Static"

Static units can be further subdivided on the basis of their receptive field organization. Units classified as "uniform" showed similar response properties throughout the extent of their receptive fields. In contrast, units classified as "nonuniform" exhibited more complex receptive field structure, as outlined below.

9.1.1 Uniform Non-oriented (Group 1)

The "uniform non-oriented" units were nonselective to stimulus orientation and displayed somewhat homogeneous response properties across their receptive field. However, their receptive field borders were not always definable, and some units responded to diffuse illumination. Figure 9.2 illustrates an example of such a unit, which responds with a tonic *on* discharge during stimulus presentation. Note that the response to a 7° spot varies in magnitude depending on the stimulation site within the receptive field.

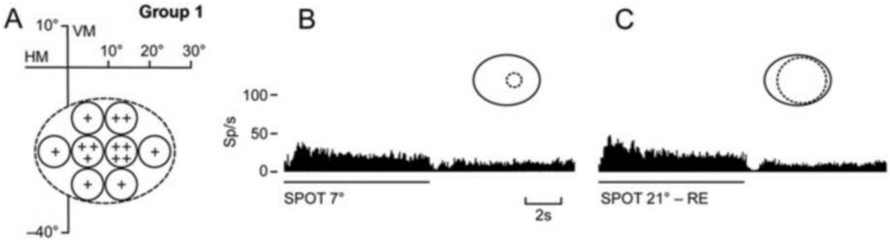

Fig. 9.2 Group 1 unit isolated in P1. This unit gives an *on*-tonic response to stimuli presented anywhere within its RF. In (**a**), the number of crosses indicates the relative magnitude of the response to a 7° spot. Note that the response magnitude does not vary appreciably when either a 7° spot (**b**), a 21° spot (**c**) or diffuse light (not shown) is presented to the RF. The continuous line below the post-stimulus time histograms (*psth*) indicates stimulus duration. (**b**) and (**c**) represent two *on-off psths* of the cumulative number of events that occurred in each of 256 bins following the onset (*on*) and interruption (*off*) of the stimulus presentation. The time span covered by each bin is adjustable. Each histogram represents the cumulative acquisition of 30 trials. Abbreviations used in this and in the other figures: *VM* vertical meridian, *HM* horizontal meridian, *Sp/s* discharge rate in spikes per second [modified from Gattass et al. (1979)]

9.1.2 Nonuniform Non-oriented (Group 2)

Neurons classified as "nonuniform non-oriented" were similar to Group 1, except that their receptive field subregions exhibited distinct functional properties. Namely, these neurons responded with either excitation or inhibition depending on the portion of the receptive field being stimulated. For the subset of pulvinar neurons studied in Gattass et al. (1979), responses to stimulus onset or offset could always be evoked by stimulating the receptive field center. Interestingly, visual stimulation on the receptive field periphery was always phasic, regardless if the response to receptive field center stimulation was tonic or phasic.

9.1.3 Nonuniform Oriented (Group 3)

The Group 3 "nonuniform oriented" neurons distinguish themselves from Group 2 by their selectivity to visually oriented stimuli presented within their receptive field. The responses to static stimuli presented to the receptive field center were predominately excitatory and tonic, even though inhibitory or phasic responses could also be observed, especially when stimulating the receptive field surround. Indeed, we observed nonuniformities in the functional organization of these receptive fields. The responses reflected different degrees of center vs. surround interaction, where center-surround antagonism was usually predominant. An example of a Group 3 unit is illustrated in Fig. 9.3. Note the tonic sustained response when stimulating the receptive field center (Fig. 9.3-A_2) and the phasic response when

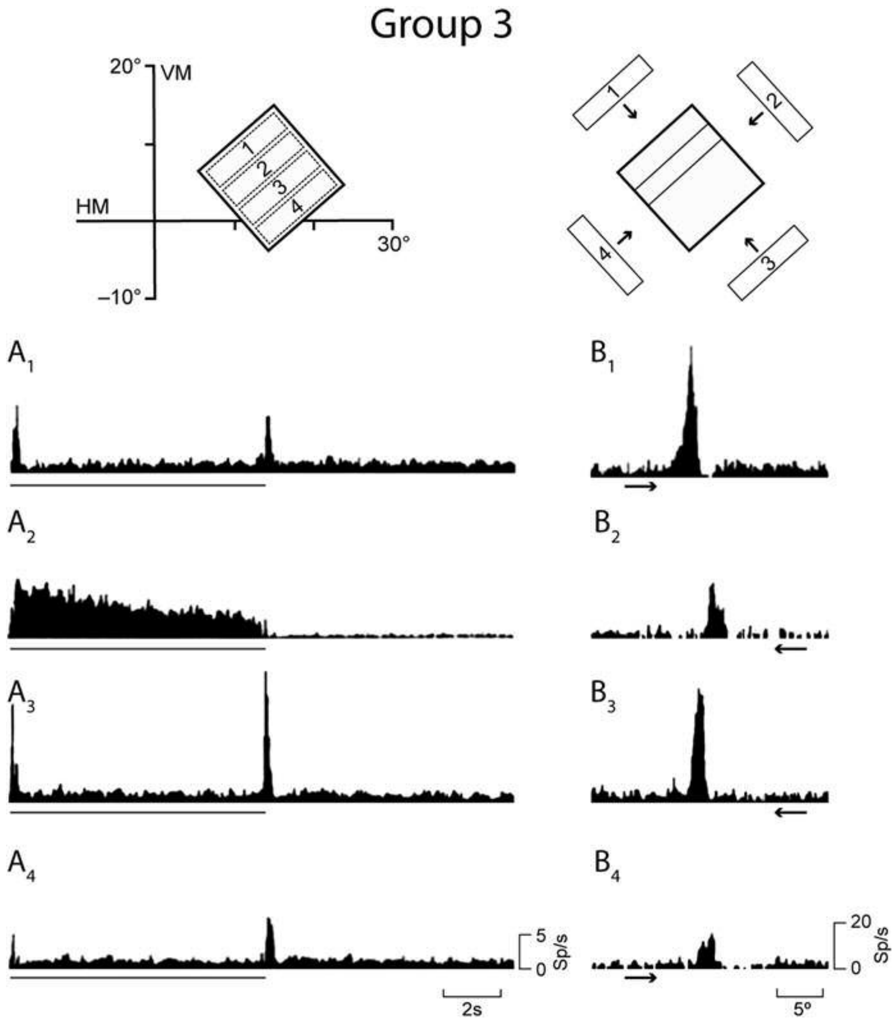

Fig. 9.3 Response characteristics of a P1 single unit (Group 3). (A_1), (A_2), (A_3) and (A_4) illustrate *on-off psths* corresponding to neuronal responses to a stopped slit (2.5° wide) presented in four distinct regions of the RF (top left panel). Note the tonic *on*-response in (A_2) contrasting with the phasic *on-off* response to stimulation in other regions of the receptive field. Panels B_1, B_2, B_3 and B_4 illustrate *psths* of the cumulative number of spike events for each direction of stimulus displacement across the screen (top right panel). The plots in (B) correlate neuronal firing with stimulus displacement in the directions indicated by the arrows. Note that the neuron exhibits a preferred stimulus orientation (see Panels B_1 and B_3), but does not show direction selectivity. Stimulus velocity = 13°/s. Data was gathered for 30 trials (Panels A_1–A_4) and for 15 trials (Panels B_1–B_4) [modified from Gattass et al. (1979)]

stimulating the receptive field flanks (Fig. 9.3-A_1, A_3 and A_4). Panels $B_{1\text{-}4}$ illustrate the orientation selectivity of this particular unit.

9.2 Neurons Classified as "Dynamic"

The main criterion for pulvinar neurons to be classified as "dynamic" constituted their poor response to static stimuli being presented over their receptive fields. Dynamic units could be additionally subdivided based on their sensitivity to stimulus motion direction. Within the "dynamic" group, the majority of the units were direction selective. Units that were nondirection selective usually responded to a luminous spot moving along any axis within their receptive field. Interestingly, units classified as "dynamic" were predominately binocularly driven.

9.2.1 Nondirectional Uniform Non-oriented (Group 4)

Only a small proportion of the "dynamic" units were found to be nonselective for either stimulus direction or orientation. Neurons exhibiting these response characteristics were evenly distributed as presenting a uniform (Group 4) or a nonuniform (i.e., structured; see Group 5) receptive field organization. The neurons showing uniform responses discharged briskly when a spot of light crossed the borders of their receptive fields, including when the stimulus swept at high velocities. However, sustained tonic responses could be elicited using "jerky stimulus movements."

9.2.2 Nondirectional Nonuniform with Structure (Group 5)

The pulvinar neurons with nonuniform receptive fields (Group 5) contrast with those having uniform receptive fields (Group 4) in two ways: Group 5 neurons have smaller receptive fields and show a preference for low stimulus velocities, compared to those neurons classified as Group 4. The work of Gattass et al. (1979) reported on only three units belonging to Group 5. Two of them had a receptive field with a center-surround organization, and one had subregions within its receptive field that were selective to different stimulus properties. Figure 9.4 illustrates a Group 5 neuron with center-surround receptive field organization. The presentation of a static stimulus restricted to the receptive field center produced a weak phasic response (Fig. 9.4b). An annular stimulus sparing the receptive center elicited no response, while it also blocked the neuron from discharging during the simultaneous presentation of a center stimulus. Note that the unit exhibits no orientation or direction selectivity (Fig 9.4c). The small difference in response amplitude observed for the vertical (1–6) as compared to the horizontal (3–4) stimuli may

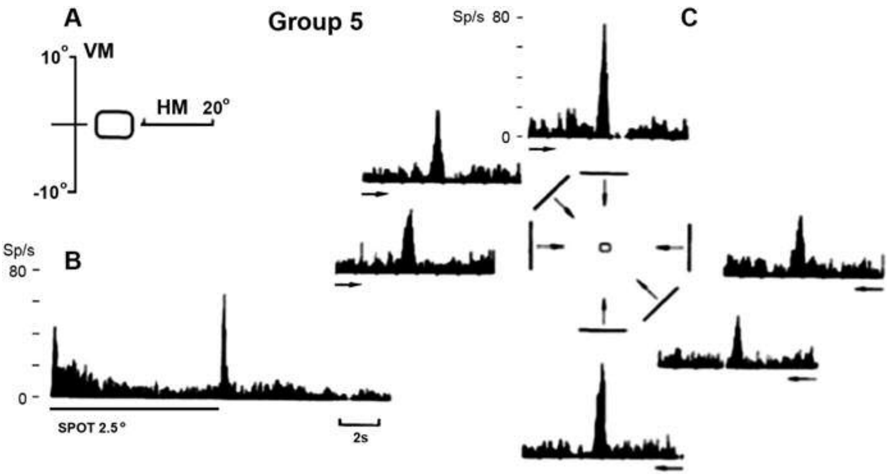

Fig. 9.4 Example of non-directional unit showing surround suppression (Group 5). (**a**) Example unit isolated in P4 and possessing a rectangular receptive field located at the level of the horizontal meridian, near the fovea. (**b**) Phasic ON-OFF response evoked by a 2.5° diameter spot presented at the center of the receptive field. (**c**) PSTHs of the responses of the same unit obtained when a full slit (0.75° wide) is displaced across its receptive field in the directions indicated by the arrows (stimulus velocity = 9°/s, 20 trials) [modified from Gattass et al. (1979)]

be attributed to the larger area of the RF being activated when the slit was oriented parallel to the long horizontal axis of the receptive field.

9.2.3 Directional Uniform Non-oriented (Group 6)

Neurons exhibiting direction selectivity were the most abundant visual units found in the pulvinar. These neurons usually preferred slow stimulus velocities. They could be subdivided into two broad categories: units exhibiting uniform receptive fields either with (Group 7) or without (Group 6) orientation selectivity, as well as units exhibiting nonuniform receptive fields (Group 8). Group 6 neurons were characterized by the fact that they responded equally well to either a spot of light or to a broad set of oriented stimuli displaced across their receptive fields (Fig. 9.5).

9.2.4 Directional Uniform Oriented (Group 7)

Group 7 neurons distinguished themselves from Group 6 units by the presence of orientation selectivity. The vast majority of these cells actually exhibited bidirectional responses. They thereby elicited only weak responses to a spot of light displaced across their receptive field. Accordingly, they were much more narrowly

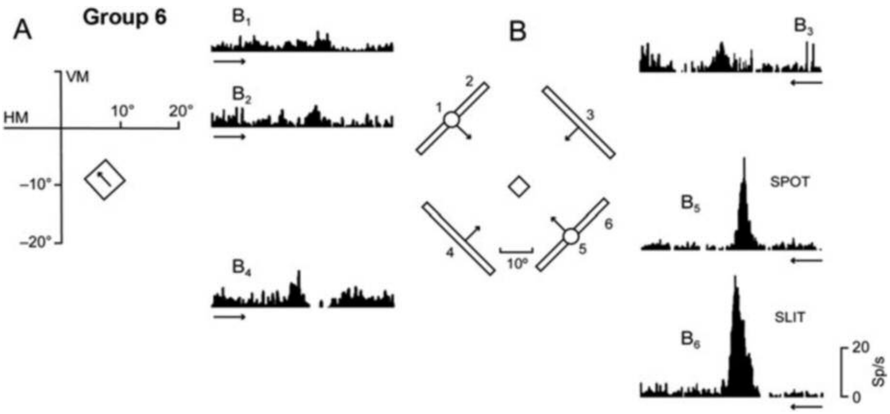

Fig. 9.5 Directional uniform non-oriented unit (Group 6). (**a**) Receptive field of the unit isolated in P1. (**b**) The PSTHs illustrate the unidirectional response of the unit to a 1° wide full slit (stimulus velocity = 7°/s, 20 trials). Similar results were obtained when the slit was substituted by a spot [modified from Gattass et al. (1979)]

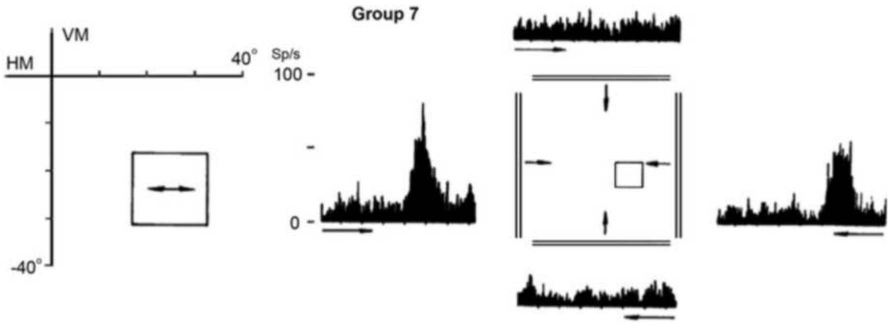

Fig. 9.6 Unit isolated in P2 and assigned to Group 7. The receptive field of the isolated single unit, located in the lower contralateral visual hemifield, shows bidirectional response to a full 2.5° wide slit. Each PSTH was obtained from 15 trials. Arrows indicate the direction of stimulus displacement (modified from Gattass et al. (1979)]

tuned to a preferred orientation compared to the previous group. Some units showed responses suppression for visual stimuli orthogonal to the preferred orientation. An example of a Group 7 unit is illustrated in Fig. 9.6.

9.2.5 Directional Nonuniform with Structure (Group 8)

Units classified as "direction nonuniform with structure" (Group 8) had basically two types of receptive field organization. The simplest type of organization exhibited receptive fields with a single responsive region surrounded by inhibitory

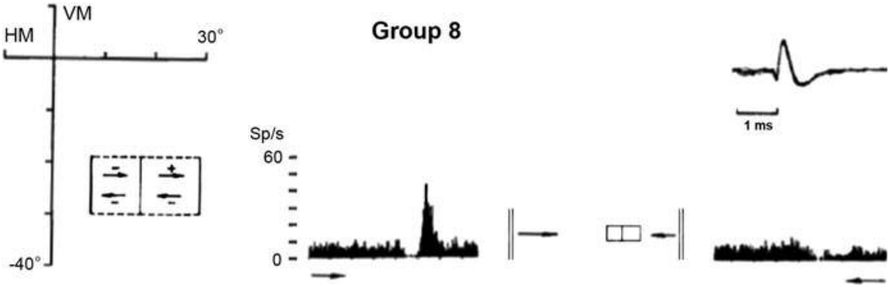

Fig. 9.7 Isolated single unit exhibiting a complex receptive field organization (Group 8) recorded in P1 (spike waveform depicted on the top right). PSTH containing the responses of 20 trials of the isolated single unit displaying a bidirectional inhibitory response in the left portion of the receptive field, while the right portion of the receptive field gave an excitatory response to the stimulus moving in one direction and a inhibitory response to the stimulus moving in the opposite direction. The stimulus was a full 2° wide slit moving at a velocity of 9°/s (modified from Gattass et al. (1979)]

flanks and was usually selective to a single direction of stimulus motion. The more complex type showed receptive fields with multiple subregions interacting with each other in intricate ways to produce a neuronal response. At least one of these subregions was found to have some form of direction selectivity. A representative example of the latter type is illustrated in Fig. 9.7. Note the two identified subregions of its receptive field. The first subregion, closer to the vertical meridian, elicits inhibitory responses to both directions of motion of a vertically oriented stimulus. Stimulation over the second subregion of the receptive field elicits excitatory responses for a rightward moving vertical stimulus but inhibitory responses for the opposite direction.

Other than the classification presented above based on the work of Gattass et al. (1979), few other studies have attempted to systematically study the response properties of pulvinar neurons. Benevento and Miller (1981) investigated the visual properties of neurons in the caudal subdivision of PL (PLɣ) in the macaque monkey and described large, unflanked, bilateral receptive fields, which seemed to be disproportionately representing the central portion of the visual field. Additionally, the majority of the units were sensitive to stimulus motion and responded to binocular visual stimulation. Some neurons exhibited complex response interactions within different subregions of their receptive fields, while others responded to stimuli moving toward or away from the center of gaze.

A comparison of the different types of units found in the pulvinar with those described in the various hierarchical stages of visual processing leads us to an interesting question: what is the functional significance of units in the pulvinar showing properties similar to those described at different levels of the visual processing pathway? If we consider the pulvinar as a link between the geniculostriate and retinotectal systems, the presence of receptive fields showing various degrees of complexity is in accordance with an associative or integrative function and therefore enables this thalamic structure to participate in circuits involved in perceptual selection. This role would also help to explain the preservation of form discrimination in both cats and monkeys after removal of striate and peristriate cortices (Nakamura and Mishkin 1986). The presence of neurons in the pulvinar with complex receptive fields and the dependence of their visual responses on the animal's arousal state (see below) could help to explain the severe deficit produced by pulvinar lesions on discrimination tasks that require a high degree of visual attention (Ward et al. 2002). Patients with pulvinar lesions show deficits in spatial information coding for the contralateral visual hemifield. Specifically, these patients have difficulty localizing stimuli in the affected visual space. These difficulties extend to the binding of visual features that are dependent on spatial information (Ward et al. 2002). Thalamic neglect in humans is rare, and severe attentional deficits that occur due to pulvinar lesions typically do not persist for longer periods. However, a milder cognitive deficit, which consists in slower orienting responses to the contralesional hemifield, is found in some patients and may be a residual form of thalamic neglect (Danziger et al. 2001–2002; Rafal and Posner 1987).

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