

# Exploring the pulvinar path to visual cortex

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**Abstract:** The primary pathway for visual signals from the retina to cerebral cortex is through the lateral geniculate nucleus of the thalamus to primary visual cortex. A second visual pathway has been postulated to pass through the thalamic pulvinar nucleus and to project to multiple regions of visual cortex. We have explored this second visual pathway using a method that allows us to identify the inputs and outputs of pulvinar neurons. Specifically, we applied microstimulation in the superficial layers of superior colliculus (SC) to test for orthodromic activation of pulvinar neurons receiving input from SC. We also microstimulated the cortical motion area MT and tested for antidromic activation of pulvinar to identify neurons projecting to MT (and to determine the presence of orthodromic input back to pulvinar). In this initial report, we concentrate on two observations. First, we find that there are clusters of neurons in the pulvinar that receive input from SC along with neurons that project to MT or receive input from MT. Second, we find that neurons with input from SC have characteristics of the SC superficial layers: they respond to visual stimuli but do not discharge before saccadic eye movements. Neurons projecting to MT respond similarly to these SC-input neurons, while those receiving input from MT more frequently show directional selectivity as does MT. These findings indicate the visual nature of the signals conveyed in this pathway and shed light on the functional role of the thalamus in a possible second visual pathway.

**Keywords:** pulvinar; superior colliculus; MT; two visual pathways; monkey visual pathways

## Introduction

The classic visual pathway studied in the primate is that from the retina to the lateral geniculate nucleus (LGN) to the primary visual cortex, V1. Diamond and Hall in 1969 (Diamond and Hall, 1969) postulated that a second pathway from retina to visual cortex may also provide significant visual information. This proposed second pathway extends from the retina to the superficial layers of the superior colliculus (SC) and from there to the pulvinar

nucleus of the thalamus. Through this second pathway the pulvinar could provide information to multiple cortical visual areas.

The idea of a second visual pathway has had considerable influence since it was first introduced. For example, in cases of damage to the primary visual cortex, the second pathway has been regarded as a possible path for residual visual input, particularly in dorsal stream areas such as the motion area MT (Rodman et al., 1990; Girard et al., 1992). The residual visual abilities of blindsight patients might depend on the input from the pulvinar pathway, particularly for detection of visual motion (Perenin, 1991; Weiskrantz, 2004). Little is known, however, about the existence and functional properties of this

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pathway in the primate brain. The exploration of the pulvinar nucleus with single-neuron recording (Bender, 1981, 1988; Petersen et al., 1985; Robinson, 1993) have encountered two major problems. One is the delineation of regions within the pulvinar through which the pathway to cortex passes. This difficulty has been partly alleviated by improved identification of the subdivisions using neurochemical methods (Gray et al., 1999; Adams et al., 2000; Kaas and Lyon, 2007). The second problem is knowing the connectivity of a given neuron recorded in the pulvinar. Even if a neuron can be localized to a neurochemical subdivision of the pulvinar, that alone does not indicate what input it receives or where it projects.

As a first step to understanding this pathway, we took a new approach to characterize pulvinar function in the awake, behaving monkey. We recorded neurons in the thalamus of monkeys trained to do simple visual motor tasks. But we did not sample neurons at random; we studied only those for which we had some information about their input and/or output. To do this we combined microstimulation and single-neuron recording to identify pulvinar neurons that received input from outside the pulvinar and those that projected to visual cortex. To determine input, we placed stimulating electrodes in the lower superficial layers of the SC, the presumed source of input to the pulvinar neurons that we concentrated on, those in the inferior pulvinar. To test for projections to visual cortex, we placed electrodes in the visual motion area, MT, because there is clear evidence that inferior pulvinar projects to MT and that MT also projects back to pulvinar (Adams et al., 2000; Kaas and Lyon, 2007). Our long term goal is to identify the relay neurons that lie in the pathway, that is, those neurons that receive from the SC and project to MT, to find where these neurons lie, and to ascertain what information they convey along this second visual pathway. In this initial report, however, we concentrate on the first steps toward this goal. We address two aims: to determine whether there is a subregion of pulvinar that contains clusters of neurons either receiving input from SC or projecting to MT, and to describe the functional characteristics of neurons lying in these clusters.

## Methods

The general techniques used in these experiments, including those for antidromic and orthodromic stimulation, have been described previously (Sommer and Wurtz, 2004). Briefly, the monkey sat in a primate chair and faced a tangent screen on which visual stimuli and saccade targets were projected. The monkey's tasks were either to fixate while the receptive field characteristics of an isolated neuron were examined or to make saccades from one target to another to determine the relation of the neuron's activity to saccades.

Our recordings were concentrated in the visual pulvinar, spanning the inferior and lateral divisions. The data described here were obtained in a single hemisphere from more than 60 recording sites in a zone that extended up to 7 mm medial-lateral and up to 10 mm anterior–posterior. Within this zone, penetrations were typically made at 1 mm spacing, and at 0.5 mm in areas of interest. Once we isolated a single pulvinar neuron, we used microstimulation to determine whether it was connected to either MT or SC. For example, if microstimulation in MT evokes a spike from the pulvinar neuron under study, it indicates that the pulvinar neuron is connected to MT. The nature of the connection is indicated by the kind of activation, *antidromic* (backward-going) or *orthodromic* (forward-going). If microstimulation in SC or MT antidromically activates or backfires the pulvinar cell, this tells us that the pulvinar cell sends output to that structure. By contrast, if microstimulation orthodromically activates or synaptically drives the pulvinar cell, this tells us that the pulvinar cell receives input from that structure. Three features of the evoked spike distinguish between antidromic and orthodromic activation: the reliability of evoking the spike, the electrical latency, and whether it passes the collision test (Lemon, 1984). See Fig. 1 for an outline of the procedure.

## Results

In this initial survey, we identified a total of 101 pulvinar neurons with connections to either SC or MT. These neurons fell into three categories: (1) neurons

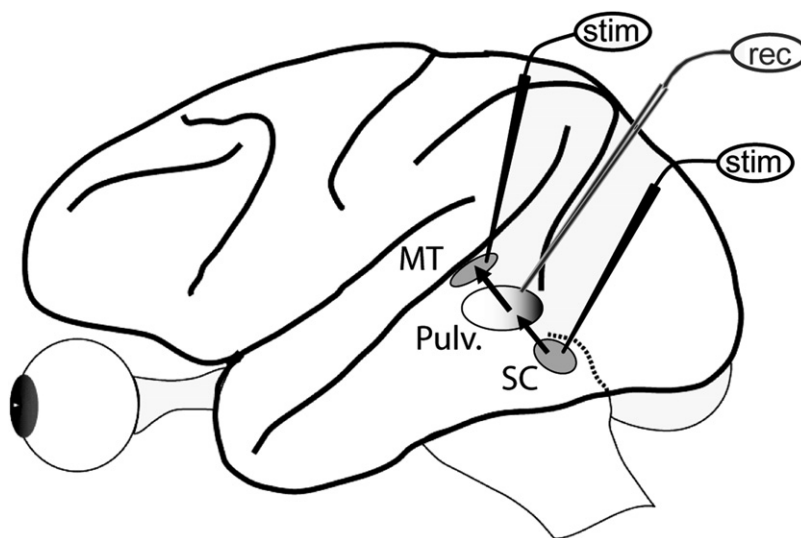


Fig. 1. Studying the second visual pathway by identifying connected neurons in the pulvinar. A sagittal view of the macaque brain shows the configuration of recording and stimulating electrodes used to identify pulvinar neurons with connections to superior colliculus (SC) or area MT. A recording microelectrode is lowered into the pulvinar nucleus (Pulv.). Once a single neuron is isolated, microstimulation is used to determine whether the cell receives input or sends output to either SC or MT (see Methods).

with input from the SC ( $n = 56$ ), (2) neurons with output to area MT ( $n = 21$ ), (3) neurons with input from area MT ( $n = 24$ ). A fourth possible group, neurons with output to SC, were exceedingly rare ( $n = 2$ ) and will not be considered further. We first describe the localization of these connected neurons within the pulvinar, and then turn to the characterization of their functional properties.

### **Location**

Connected neurons were located within a zone of the pulvinar just adjacent to the LGN. The posterior pole of the LGN, where neurons represent parafoveal locations, served as our primary landmark. We found connected pulvinar neurons immediately medial and posterior to this part of LGN, in a zone that extended approximately 4 mm medial and 3 mm posterior. A schematic of the area just posterior to the LGN is shown in Fig. 2. We found the greatest concentration of connected pulvinar neurons in a smaller zone centred about 3 mm medial and 2 mm posterior to the LGN landmark. Throughout the general zone in which connected neurons were located, we encountered them at depths spanning up to 6 mm; the majority were

located at a depth comparable or dorsal to the LGN landmark, though some were located more ventrally. We did not find strong evidence for a segregation of the three classes of connected neurons in any dimension; rather the three classes of pulvinar neurons were largely intermingled. The localization of these connected cells indicates that there exists a region of the pulvinar in which there may be a convergence of signals travelling from SC to MT, as well as signals returning from MT.

### **Neuronal responses of pulvinar neurons in the pathway**

Our examination of neural activity focused on two questions regarding the salient properties of pulvinar neurons that received input from SC and those that projected to or received input from MT. We first asked: do pulvinar neurons with input from the SC have functional properties similar to neurons in the superficial layers of SC, which have clear visual responses to spots of light over a region of the contralateral visual field? Or do they have properties similar to neurons in the intermediate layers, which have visual responses but also have activity before the onset of the saccade? Our stimulating

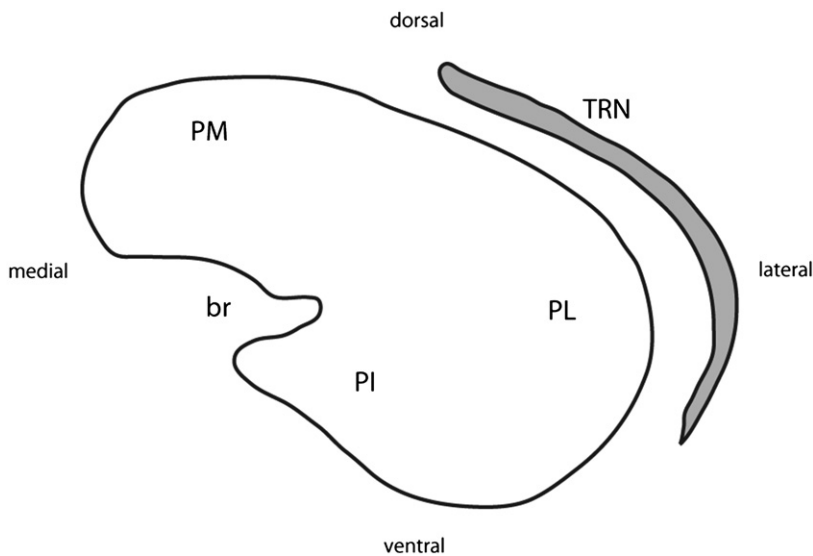


Fig. 2. Regions of the pulvinar with neurons receiving input from SC and neurons projecting to MT. Schematic shows a coronal cross-section through the pulvinar at the level where single-unit recording was concentrated, just posterior to the LGN. The visual subdivisions, PI and PL, are of greatest interest for connected cells. PM = medial pulvinar; PL = lateral pulvinar, PI = inferior pulvinar, br = brachium of the superior colliculus, TRN = thalamic reticular nucleus.

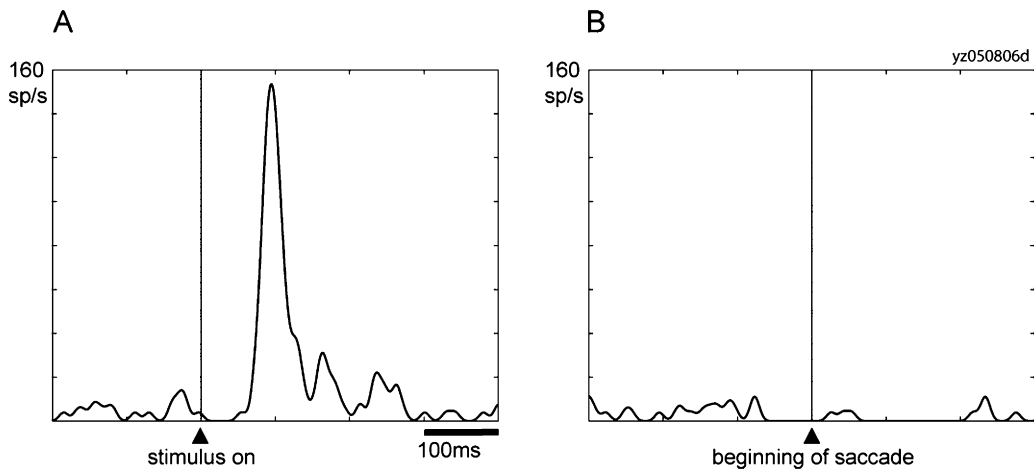


Fig. 3. Pulvinar neurons with input from SC have visual but not presaccadic activity. The activity of a single example neuron with input from SC during the memory-guided saccade task. (A) Activity is aligned on the appearance of the stimulus. The pulvinar neuron gives a brisk visual response. (B) Activity is aligned on the beginning of the eye movement. The neuron has no significant presaccadic build-up or burst activity. In each panel, the spike density function is smoothed with an 8 ms Gaussian.

electrodes targeted the lower superficial layers, but we considered the possibility that the intermediate layers might also be activated by microstimulation. We found that pulvinar neurons with input from the SC had activity profiles that resembled those of

neurons in the superficial layers of SC: they had visual responses but no presaccadic activity. These properties are illustrated for an example pulvinar neuron with SC input in Fig. 3. This pulvinar neuron had a restricted receptive field located

parafoveally in the contralateral visual field, at an eccentricity of  $3.5^\circ$ . When a small target ( $1^\circ$ ) appeared in the receptive field, the neuron gave a brisk response. When the monkey made a memory-guided saccade to the same target location, the neuron's activity was not modulated (Fig. 3B). We observed the same pattern in the vast majority of the pulvinar neurons with input from SC. The only deviations from this pattern were neurons for which we were unable to identify a clear visual receptive field; we have not observed presaccadic activity in any of the sampled cells. These findings demonstrate that the properties of pulvinar cells in this pathway reflect input from the superficial but not the intermediate layers of SC.

Second, we asked: do pulvinar neurons with input from or output to MT show evidence of the directional tuning observed in MT itself? Here we found that the functional properties of the pulvinar neurons reflected their relationship to MT. Specifically, directional tuning was prominent in pulvinar neurons with input from MT but not in those that projected to MT. An example of a directionally tuned neuron with *input* from MT is shown in Fig. 4A. Its activity is shown for eight directions of random dot motion, which moved at an optimal speed of  $40^\circ/\text{s}$  at 100% coherence in a  $10^\circ$  diameter window centred on its receptive field ( $40^\circ$  eccentricity). The neuron fired strongly when motion was up and to the right (preferred direction), but gave little response to motion in the opposite (null) direction. As a measure of its directional selectivity, we computed a directional index (DI) using the formula where  $\text{DI} = 1 - \text{null}/\text{pref}$ , where *null* and *pref* are the average firing rates in the null and preferred conditions, respectively, after subtraction of spontaneous activity. DI values greater than 1 indicate directional selectivity, and values greater than 0.6 indicate directional bias. The DI for this pulvinar neuron was 1.07, comparable to values observed in area MT. An example pulvinar neuron with *output* to MT is shown in Fig. 4B. This neuron gave a brisk transient response to the random dot motion in its receptive field, irrespective of the direction of motion (motion parameters as above;  $30^\circ$  eccentricity). Its activity was not strongly tuned for direction, as indicated by its DI of 0.08. We found a similar trend in the population of pulvinar

neurons connected to area MT in which we were able to obtain data for the directional series ( $n = 22$ ). Neurons that received input from MT were likely to be directionally tuned (6/8) and typically had weak responses to stationary stimuli. Neurons that projected to MT were less likely to be directionally tuned, although we did observe directional selectivity or bias in some of these neurons as well (6/14). Overall, these neurons with projections to MT tended to resemble the pulvinar cells with input from SC, in that they often had a brisk visual response to stationary stimuli.

### Discussion and conclusion

We draw two conclusions from these initial exploratory experiments. First, the use of orthodromic and antidromic stimulation demonstrates the clear existence of a subregion in pulvinar in which there are neurons that receive input from the SC, neurons that project from pulvinar to MT, and neurons that receive input from MT. The second conclusion is that these neurons are conveying visual information to and from cortex, not saccadic premotor activity. This is reasonable given previous anatomical evidence that the ascending pathway through the inferior pulvinar originates primarily in the superficial layers (Benevento and Fallon, 1975). It is also intriguing to see direct evidence that there are neurons in this subregion of the pulvinar that project to MT, as well as those that receive input from MT. This observation is of particular interest given the argument that communication between cortical areas benefits from pathways through higher-order thalamic structures as well as the direct connections from one cortical area to the next (Sherman and Guillery, 2002).

The next steps in these investigations require the positive identification of relay neurons (those that receive from SC and project to MT) in order to demonstrate unequivocally that a second visual pathway does indeed pass through pulvinar, despite doubts based on neuroanatomical studies (Stepniewska et al., 2000). More important will be to determine the contribution of this pathway to visual processing in cortex and to such functions as

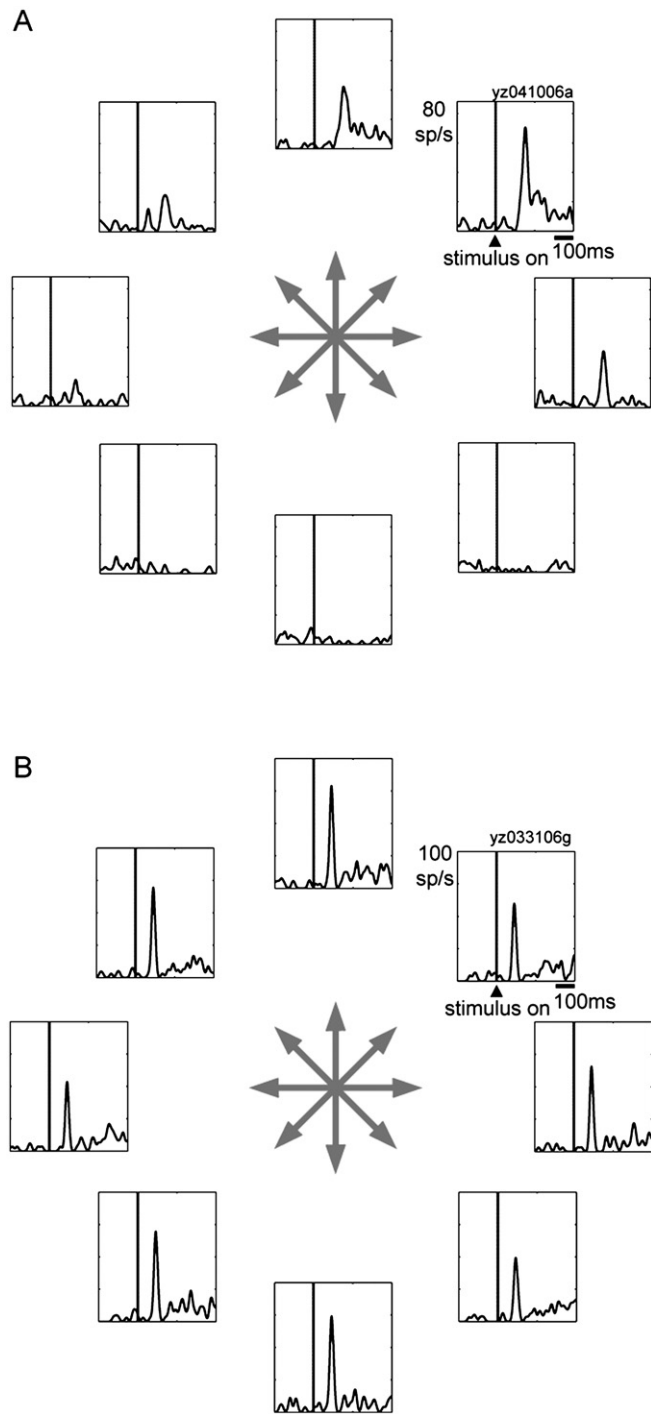


Fig. 4. Pulvina neurons with input from MT are more likely to be directionally selective than are pulvina neurons with output to MT. The visual responses to eight different directions of motion are shown for (A) an example pulvina neuron receiving input from MT and (B) an example pulvina neuron sending output to MT. Activity is aligned on the appearance of the stimulus.

visual attention already demonstrated in the pulvinar (Petersen et al., 1985, 1987).

## References

- Adams, M.M., Hof, P.R., Gattass, R., Webster, M.J. and Ungerleider, L.G. (2000) Visual cortical projections and chemo-architecture of macaque monkey pulvinar. *J. Comp. Neurol.*, 419: 377–393.
- Bender, D.B. (1981) Retinotopic organization of macaque pulvinar. *J. Neurophysiol.*, 46: 672–693.
- Bender, D.B. (1988) Electrophysiological and behavioral experiments on the primate pulvinar. *Prog. Brain Res.*, 75: 55–65.
- Benevento, L.A. and Fallon, J.H. (1975) The ascending projections of the superior colliculus in the rhesus monkey (*Macaca mulatta*). *J. Comp. Neurol.*, 160: 339–361.
- Diamond, I.T. and Hall, W.C. (1969) Evolution of neocortex. *Science*, 164: 251–262.
- Girard, P., Salin, P.A. and Bullier, J. (1992) Response selectivity of neurons in area MT of the macaque monkey during reversible inactivation of area V1. *J. Neurophysiol.*, 67: 1437–1446.
- Gray, D., Gutierrez, C. and Cusick, C.G. (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.
- Kaas, J.H. and Lyon, D.C. (2007) Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res. Rev.*, 55: 285–296.
- Lemon, R. (1984). Methods for neuronal recording in conscious animals. In: Smith A.D. (Ed.), *IBRO Handbook Series: Methods in the Neurosciences*. Vol. 4. J. Wiley & Sons, New York, pp. 95–102.
- Perenin, M.T. (1991) Discrimination of motion direction in perimetrically blind fields. *NeuroReport*, 2: 397–400.
- Petersen, S.E., Robinson, D.L. and Keys, W. (1985) Pulvinar nuclei of the behaving rhesus monkey: visual responses and their modulation. *J. Neurophysiol.*, 54: 867–886.
- Petersen, S.E., Robinson, D.L. and Morris, J.D. (1987) Contributions of the pulvinar to visual spatial attention. *Neuropsychologia*, 25: 97–105.
- Robinson, D.L. (1993) Functional contributions of the primate pulvinar. *Prog. Brain Res.*, 95: 371–380.
- Rodman, H.R., Gross, C.G. and Albright, T.D. (1990) Afferent basis of visual response properties in area MT of the macaque. II. Effects of superior colliculus removal. *J. Neurosci.*, 10: 1154–1164.
- Sherman, S.M. and Guillery, R.W. (2002) The role of the thalamus in the flow of information to the cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 357: 1695–1708.
- Sommer, M.A. and Wurtz, R.H. (2004) What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. *J. Neurophysiol.*, 91: 1381–1402.
- Stepniewska, I., Qi, H.X. and Kaas, J.H. (2000) Projections of the superior colliculus to subdivisions of the inferior pulvinar in New World and Old World monkeys. *Vis. Neurosci.*, 17: 529–549.
- Weiskrantz, L. (2004) Roots of blindsight. *Prog. Brain Res.*, 144: 229–241.