

# The primate pulvinar nuclei: vision and action

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**The pulvinar nuclei of the thalamus are proportionately larger in higher mammals, particularly in primates, and account for a quarter of the total mass. Traditionally, these nuclei have been divided into oral (somatosensory), superior and inferior (both visual) and medial (visual, multi-sensory) divisions. With reciprocal connections to vast areas of cerebral cortex, and input from the colliculus and retina, they occupy an analogous position in the extra-striate visual system to the lateral geniculate nucleus in the primary visual pathway, but deal with higher-order visual and visuomotor transduction. With a renewed recent interest in this thalamic nuclear collection, and growth in our knowledge of the cortex with which it communicates, perhaps the time is right to look to new dimensions in the pulvinar code.**

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THE PULVINAR NUCLEI of the thalamus lie posterior, medial and dorsal to their much better known cousin, the lateral geniculate nucleus, and ‘cover’ the underlying superior colliculus (SC). In the same way as the lateral geniculate (‘knee-like’) nucleus curves around the rising optic tract, the pulvinar (‘cushion’) forms a larger and more-diffuse, but recognizable, mass around the axonal tract that arises from the SC, the brachium of the SC (see Fig. 1). The original four nuclei of the macaque pulvinar were defined in early studies on purely anatomical grounds<sup>1,2</sup>. New and more-exact studies continue to delineate more subdivisions by using more-refined techniques and strategies (for example, see Refs 3 and 4). The most-rostral nucleus, the oral pulvinar, is most heavily connected with somatosensory brain areas and parietal area 5 (Refs 5,6), and is often ignored in reviews of pulvinar function. A recent review has focussed on visual salience as portrayed in responses of cells that are mainly within the inferior and lateral nuclei, and this article is intended to progress that information<sup>7</sup>. While this article will also focus on the three ‘visual’ nuclei, it will also make reference to the oral pulvinar and, wherever possible, restrict itself to the macaque family of Old-World monkeys, which are considered by most to be the best-available animal model for the human visual system.

## Structure

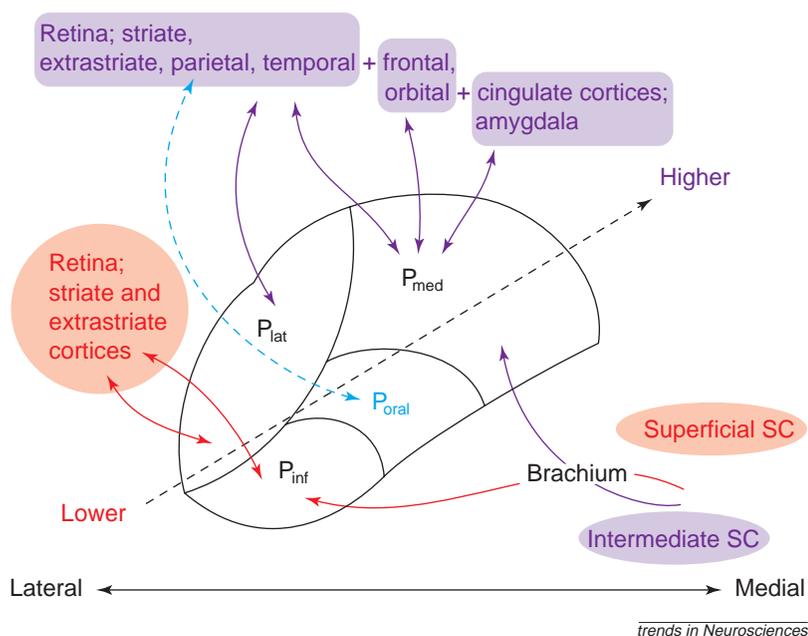
The major inputs to the original three visual pulvinar nuclei, (inferior, lateral and medial) are illustrated in Fig. 1. This diagram should not be regarded as an encyclopaedic list, but it rather suggests that there is a topography in the inputs and outputs associated with these nuclei, which run from ventrolateral to dorso-medial; from early vision [retina, primary visual cortex and low-medium-level extra-striate visual cortex, up to visual area 5 (V5) (also known as the middle temporal area, MT)] to higher cortices, for example, the parietal, frontal, orbital and cingulate cortices; this is paralleled by a shift in sub-cortical inputs from the superficial SC to the intermediate SC. An unmarked subdivision that lies at the border of the lateral and medial nuclei has been termed the dorsomedial area (Pdm), which has inputs from both the superficial and intermediate SC, and the retina<sup>14–16</sup>. A recent anterograde study has con-

firmed the previous suggestion that the inferior pulvinar and elements of lateral pulvinar receive major cortical inputs from the early extra-striate cortex, while lateral and medial pulvinar receive input from higher cortices such as the parietal cortex<sup>17</sup>. Interestingly, in the same study, injections in inferior parietal cortex area 7 also labelled the oral pulvinar<sup>17</sup>. Further subdivisions of the pulvinar nuclei have been made on the basis of many criteria (see Ref. 18 for a comprehensive review) and the most-recent suggestions posit the division of the inferior pulvinar into four components that are defined by chemoarchitecture [in the macaque, these divisions are made on the basis of calbindin, AChE and SMI-32 (an antibody against a non-phosphorylated neurofilament epitope) localization], which include some elements of the classically defined lateral and medial pulvinar nuclei, but still confines these areas to a ventral position<sup>3,19</sup>, with the subdivisions appearing as blocks running dorso-ventrally. Similarly, Kaas and co-workers have divided this nucleus into four sub-nuclei, in three species (including the macaque), on the basis of Nissl, cytochrome oxidase, calbindin, AChE and CAT-301 staining<sup>4</sup> – a mapping that is in reasonable agreement with that of Cusick and co-workers<sup>3,19</sup>. While the original lateral pulvinar is generally left as a single entity, it should be remembered that the more-recent findings that concern the inferior and mediodorsal components have each encroached upon the original cytoarchitectonic lateral division. Even the apparently homogeneous medial nucleus can be subdivided, with AChE staining revealing an AChE-dense dorsomedial area that is connected closely with the orbito-frontal cortex<sup>20</sup>. Thus, the pulvinar complex expands to include approximately eight to ten anatomically defined subdivisions! The physiological properties and inter-relationships of these multiple regions are as yet unclear, and it seems likely that future studies should be directed towards a more-detailed examination of this complex organization (see Ref. 18 for a recent review).

## Infrastructure

The pulvinar, like many other thalamic nuclei, has long been known to comprise both projection neurones and intrinsic interneurones (for a review see Ref. 18). Within the medial and lateral pulvinar, cells that project

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**Fig. 1.** The major cortical and sub-cortical inputs to the inferior, lateral and medial pulvinar nuclei. The diagram should not be taken as anatomically correct. For much of the anterior–posterior extent of the pulvinar only a subset of the four main nuclei are visible; the outline has, therefore, been flattened to allow the trend expressed in mediolateral and dorsoventral axes to be visualized more easily. Cortical connections are reciprocal (double-headed arrows), although the degree of overlap of such connections within the various nuclei is still a matter of debate. ‘Lower’ vision, V1 and near-striate visual cortices are labelled in red, while ‘higher’ cortices, visual association such as parietal and prefrontal and non-sensory or association cortices such as frontal and cingulate, are labelled in purple. Thus, the underlying trend from V1 to cingulate is clearly seen moving from ventro–lateral to dorso–medial, following the broken black arrow. The cortical input to oral pulvinar (blue broken line) is suggested to be of mainly parietal origin (area 5a) and is located anterior to the majority of the rest of the pulvinar. Within the areas outlined here, several sub-areas in inferior and lateral pulvinar are retinotopically organized. There might be a number of retinotopic maps in these areas, and visually driven cells are found here and in other non-retinotopically organized parts of the pulvinar, such as the dorsomedial region. Input from the colliculus enters the nucleus from the ventral surface via the large fibre tract known as the brachium of the SC, ‘fanning’ out to target input to the appropriate pulvinar nuclei. Abbreviations:  $P_{inf}$ , inferior pulvinar;  $P_{lat}$ , lateral pulvinar;  $P_{med}$ , medial pulvinar;  $P_{oral}$ , oral pulvinar; SC, superior colliculus.

to parietal<sup>11,21</sup>, frontal<sup>21</sup> and temporal<sup>12,22</sup> cortices form ‘disc-like aggregates’ running, interestingly, from the ventrolateral to dorsomedial aspect. Each cortical field has a separate set of projection neurones, even when these fields are adjacent and interconnected cortico-cortically<sup>11</sup>. This is illustrated in Fig. 2, which shows the distribution of two sets of pulvinar cells that project to adjacent parietal areas 7a and the lateral intra-parietal sulcus (area LIP). More recently, a similar distribution was reported for cells in medial pulvinar that project to the prefrontal cortex<sup>22</sup>, and in cells projecting from the lateral and parts of inferior pulvinar to the dorsomedial visual cortical area, DM (Ref. 23), although cells that project to the temporal lobe are found more ventrally and seem less well organized<sup>12</sup>. It is interesting to note that the anatomical organization of the inferior nucleus outlined above suggests a block or slab-like organization running dorso–ventrally, which, in this highly curved region, might well be a continuation of the slab-like structures described in lateral and medial pulvinar (perhaps forming sheets or slabs running orthogonally to fibre tracks entering from the brachium?). This slab-like unit of organization, noted particularly in medial and lateral pulvinar might account for the difficulty in defining fields physiologically, as the strata clearly run orthogonally to the most-obvious route by which the

area can be examined electrophysiologically, by using electrodes passing in a vertical or near vertical track. Future studies could well require an extremely oblique track to be able to assess directly the similarities between adjacent cells in these ‘slabs’, where crude retinotopic organization might even exist (given that such rough retinotopy is known to exist in many of the cortical areas providing input).

A recent study in medial pulvinar also examined its internal structural organization and found that cells in this area included two types of projection cells, as well as three types of local interneurons, suggesting that the circuitry to allow considerable integration of cortical inputs by means of local connections exists within this nucleus<sup>22</sup>. Cortical inputs to the pulvinar in macaque and squirrel monkeys have recently been shown to be of two distinct types<sup>24–26</sup>: E-type (‘elongate’ or type 1, which is putatively derived from small to medium cortical-layer-V pyramidal cells) and R-type (‘round’ or type 2, which is suggested to be from giant cortical-layer-V pyramidal cells). In a rather broad generalization that compares known geniculate and cortical structure and function with this pulvinar information, it has been suggested that the E-type afferents are modulatory in nature and that the R-type afferents are directly excitatory (or ‘driving’)<sup>27</sup>. E-type axons are highly divergent in their pulvinar connectivity and frequently synapse in several nuclei, while R-type axons form denser and more-focussed synaptic arrays. Interestingly, it has been suggested that the proportion of E- to R-type axons might vary from cortical area to cortical area, such that, for example, the input from the striate cortex is predominantly E-type, while that from V5 (MT) is predominantly R-type. Thus the suggestion is that the receptive-field properties of cells in the pulvinar area receiving input from MT will reflect the properties of MT cells more accurately, while those receiving input from V1 might reflect the other non-V1 inputs more accurately, perhaps sub-cortical inputs, which are modulated by activity that arises in V1. It is also interesting to note that R-type axons often project beyond the pulvinar to other brain structures, including the SC (Ref. 26), whereby the information provided to the pulvinar nuclei in this driving stream will be duplicated in lower structures such as the colliculus, perhaps providing a top-down control of coherent activities. For future studies, it will be of great importance to examine the nature of the synaptic inputs from other cortical regions, such as area 7, LIP of the parietal cortex, and frontal and orbital cortices, in order to characterize more fully the rules governing connectivity between individual cortical fields and their pulvinar counterparts.

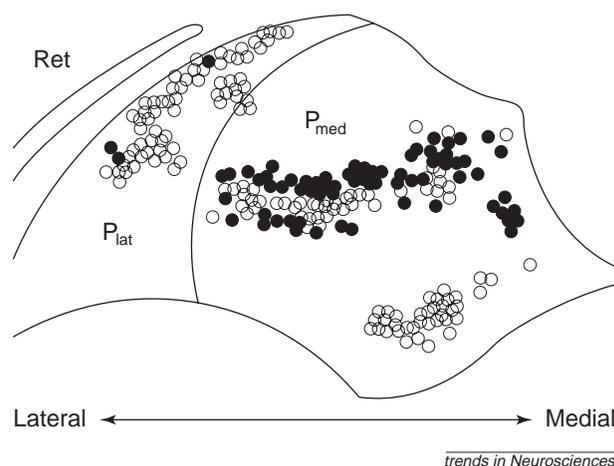
### Vision

It is without doubt that the majority of the pulvinar nucleus is involved in vision (see Refs 18 and 28). The traditional view is that its inferior and lateral components are primarily associated with the striate and near-striate cortices, while elements of the lateral and the medial component are associated with ‘higher’ cortices, as has been outlined above. The suggestion that has been most widely accepted over the years is that of visual ‘saliency’ or ‘attention’, in which cells in the ventral and lateral compartments (inferior and the ventral part of the lateral, but up to and perhaps including Pdm) signal the importance or relevance of stimuli that fall inside classically defined visual receptive fields, which are often

binocular and can be orientation- or even colour-specific, but are spread heterogeneously throughout the region, which is probably an accurate reflection of the heterogeneous cortical (and sub-cortical) inputs<sup>7,29–32</sup>. Such ‘salience’ can be signalled by an increase or decrease (that is, the suppression of non-salient cues) in visual responses when an attended target is within the receptive field. However, the attended target need not necessarily be the subject of an intended behavioural response, but merely the subject of attention *per se*<sup>16,32</sup>. Furthermore, it has been hypothesized that the activity of pulvinar cells might be enhanced when multiple targets are present (a visually enriched environment?) although these ideas await investigation using appropriate animal studies<sup>18</sup>. Thus, the basic model suggests that the visual cells in the pulvinar signal salience in a retinotopic framework, represented in inferior, lateral and Pdm pulvinar nuclei. However, visual responses alone (modulated or otherwise) are not the whole repertoire of pulvinar neurones.

### Action

A proportion of cells in the inferior and lateral pulvinar have responses (retinotopically organized) that are modulated by the position of the eye in the orbit (while also signalling ‘salience’)<sup>33</sup>. Thus, the activity of these cells requires an action (shift of eye position) for this modulation to become evident. This is remarkably reminiscent of the responses of cells in the inferior parietal lobule<sup>8</sup>, whose activities are considered to mark attendance to a visual cue, in particular when this cue will become the target for a saccadic eye-movement<sup>34</sup>. Eye-movement-related responses (action) are also found widely within pulvinar<sup>16</sup>. In a very recent study, evidence has shown that binocular eye-movement-signalling depth is transmitted to the SC from parietal cortical area LIP (Ref. 35), perhaps via fibres that also synapse within the lateral or medial pulvinar<sup>24–26</sup>. Responses produced during and following saccadic eye-movements have also recently been reported in the non-retinotopic region Pdm, in which some cells also showed colour- and form-specific responses<sup>32</sup>. While the eye-movement-related responses are again similar to responses in the inferior parietal cortex, the colour and form specificities are less similar, and the distribution of these cells within Pdm (perhaps the ventral Pdm) is not stated<sup>32</sup>. Such eye position and eye-movement-related signals transform the information represented in the neural code from a strictly retinotopic reference frame to some higher order, perhaps a head- or body-centred reference frame. It is this type of information shift that is currently of great interest in studies of cortical function<sup>8,10</sup>. In all pulvinar cases, however, the experiments have been performed in the absence of head movements; that is to say, with a restriction placed on the ability of the animal to move its head (head-fixed), and constraining movements to be expressed only by movements of the eyes, regardless of whether or not the natural expression of such a behavioural response would combine head and eye movements. This is an issue of paramount importance: it will be of utmost interest to re-examine such responses in a head-free paradigm, such as that used successfully in cortical experiments that show gaze-dependent modification of parietal-cell firing, which encodes either the eye or head movement (and presumably a sum of the two) required to fixate a target of interest<sup>35</sup>. Perhaps surprisingly, there are no available studies of possible

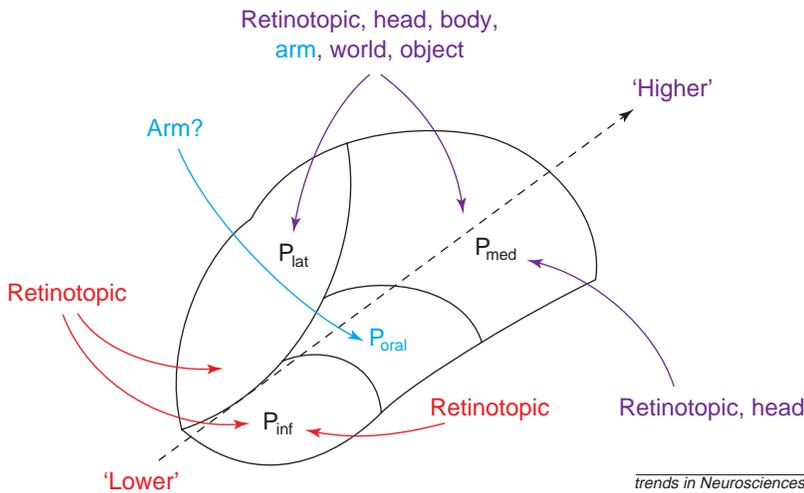


**Fig. 2.** The cells that project from lateral and medial pulvinar nuclei ( $P_{lat}$  and  $P_{med}$ ) to two adjacent cortical areas: the lateral intraparietal area (LIP) and area 7a. While both inferior and lateral nuclei project to LIP (open circles), only the medial nucleus projects to 7a (closed circles). Both cortical areas are part of the inferior parietal lobule and the neurones in these two adjacent areas share some visual or visuomotor properties (for reviews see Refs 8,9). However, the frame of reference in which their information is encoded differs between the two areas: cells in LIP have retinotopic and head-centred frames of reference, and cells in 7a have retinotopic and body-centred (or world-centred) frames of reference<sup>10</sup>. Note the slab-like organization of the cell groups, inter-digitating in the medial nucleus essentially without overlap. This organization is also seen for projection cells to some areas of frontal cortex and the superior temporal sulcus<sup>11</sup>, and for cells in the oral pulvinar projecting to parietal area 5a (Ref. 12); it might represent a common feature throughout at least lateral and medial pulvinar. ‘Ret’ is the reticular nucleus overlying the thalamus. Modified, with permission, from Ref. 13.

head-movement-related responses in macaque pulvinar (admittedly, a difficult experimental paradigm), despite the fact that both the parietal cortex and the intermediate layers of the SC are involved in such movements, and have been studied in this way<sup>10,36–38</sup>. It is hypothesized that this type of experiment will take the first steps towards exposing underlying organizing principles within the enigmatic medial pulvinar, where gaze signals from cortex and colliculus can be combined with signals marking salience in a supra-retinotopic frame or frames of reference (see Fig. 3).

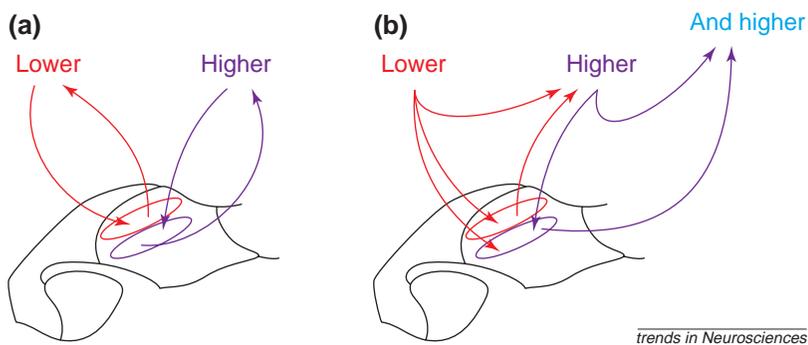
With this in mind, it is interesting to note that another action signalled by cells of the pulvinar nuclei is that of a reach by an arm to a target. Cells that are active during such activity are found in essentially all of the pulvinar nuclei, although they have been reported to be more concentrated in oral and lateral nuclei (in the *Cebus appella* monkey<sup>39</sup> and in the macaque<sup>13,40</sup>). Reaching responses in pulvinar are also attention gated; passive limb movements are not signalled. Both goal-directed and pan-directional limb-movement responses have been described. It is therefore of interest to note the recent rise of interest in reaching activities in the macaque parietal (superior and inferior) and related cortices<sup>41</sup> (for reviews see Refs 9,42,43) and to note that, like a number of pulvinar cells<sup>39</sup>, some parietal cells reveal reaching responses only in complex tasks that involve concomitant saccadic eye-movement tasks<sup>41</sup>.

These action-related responses pose a further set of currently unanswered questions. As outlined above, while retinotopically organized receptive fields can be measured only in the framework of a retinal measurement system (eccentricity), the addition of eye (or head) position or arm-related responses, questions the frame



**Fig. 3.** A possible set of reference frames in which information could be signalled to the pulvinar from cortical and sub-cortical inputs. Inputs from a number of cortical fields and two compartments of the superior colliculus to the various pulvinar nuclei are shown as arrows with red to purple used to denote the range of complexity of reference frame, from retinotopic up to object centred with blue indicating somatosensory or polysensory. The colour scheme is the same as that used in Fig. 1, and the cortical and subcortical areas denoted in Fig. 1 probably send data encoded in the references frames (which are indicated in this figure by the text). Individual reference frames, for example retinotopic, can be found at different levels (that is, both red and purple), but are sent from regions of cortex with more or less complexity in their ‘visual’ responses. Thus, for example, red retinotopic information to the inferior pulvinar will come from striate and near extra-striate cortex, while purple retinotopic information to lateral pulvinar might come from parietal cortex. The frames of reference described require that retinally based information be supplemented by additional information (for example, on the position of the eye in the orbit, which provides head-centred information) so that the cell responses can be modulated by the change in position of a target with respect to the head rather than the retina. In ascending order of complexity, information on the position of the head on the body provides information in a body- or world-centred coordinate system, and this can be extended further, up to and including an object-centred reference frame, where cell responses depend upon the position of a selected object within the world. Such information is known to be available from the cortical fields known to associate with the pulvinar as shown in Fig. 1. Abbreviations: P<sub>inf</sub>, inferior pulvinar; P<sub>lat</sub>, lateral pulvinar; P<sub>med</sub>, medial pulvinar; P<sub>oral</sub>, oral pulvinar.

of reference in which such responses are expressed: a retinotopic receptive field combined with an input that signals eye position within the orbit will code information in a head-centred reference frame. Indeed, with appropriate information on the relevant position of the head on the body, or the arm with respect to the body,



**Fig. 4.** Cortico–thalamo–cortical loops. (a) Information descending to the pulvinar from the various cortical areas can be kept separate, if each ‘slab-like’ unit within the pulvinar projects back to only the same cortex from which it receives input. Thus each pulvinar unit would signal salience to its own cortical field, in a context (reference frame) that is ‘understood’ by that cortical region. (b) Alternatively, a set of open-loop connections could pass information from cortical region to region, which has been postulated by Koch and Crick<sup>27</sup> to be a useful mechanism for passing information from one cortical field to another without the requirement of strong (directed) cortico–cortical loops (considered the route to ‘uncontrolled oscillations’). Thus, information can be passed from lower areas to areas of higher complexity by mixing at the level of the pulvinar. The colour scheme is the same as that used in Figs 1 and 3.

head or target, a number of possible reference frames can be identified, which include world-centred or even object-centred frames (as recently found in the macaque supplementary eye fields<sup>42</sup>). Figure 3 suggests some possible reference frames with tentative pulvinar locations. These reference frames have now been shown to be used by a number of relevant cortical areas in order to express the locations of attended objects or objects that are the intended target of a saccadic eye-movement, or head or arm movement (for reviews see Ref. 8). Until appropriate experiments are carried out, the ‘measurement system’ for salience in the less-understood elements of the pulvinar is unlikely to be revealed.

**The future**

While there is overwhelming evidence that the pulvinar has a role in visual salience, it is clear that the addition of other modalities, such as those expressed by goal-seeking arm movements, add additional dimensions to the puzzle. Perhaps there is a role in directing attention or intention in eye and limb movements in the general frame of reference of personal space, where such goal-directed movement might encompass more than one sensory modality. While the two anatomical descriptions can, on further study, be found to be different facets of the same coin, current evidence suggests that individual sub-nuclei, as described for the inferior and parts of the lateral nucleus, and the ‘slabs’ seen most clearly in inferior and medial nuclei, might participate in direct reciprocal connection with the appropriate cortical fields extending from V1 to areas such as the parietal and frontal, and orbital and cingulate cortices (Fig. 4a). It is in these higher cortical areas where there has recently been an explosion of interest in the processing of visual and personal space using the awake macaque model<sup>8,9,43</sup>. Thus, the hypothesis now proposed is that new studies of pulvinar function should address the known properties of the input stream from cortical cells and their likely influence on cells within appropriate pulvinar regions, by using paradigms that are known to activate the cortical cells projecting to, and perhaps directly driving, pulvinar cells. These should include visual and visuomotor tasks such as saccadic and smooth-pursuit eye-movement tasks, but integrated with tasks that use different frames of reference, which include reaching tasks to visual or even auditory targets, in enriched sensory environments.

However, another intriguing suggestion<sup>27</sup> that has recently been made, to account for the cortico–thalamo–cortical loops that are possible within the anatomy reviewed in this article, is that a series of open-loop connections (Fig. 4b) can transfer information up a chain of cortical areas by looping ‘through’ thalamus to reinforce a direct (one way) cortico–cortical connection. Such an intriguing mechanism could, of course, still signal salience; indeed, this would be the reinforcing signal itself: a signal that passes from cortical field to cortical field, reinforced within the pulvinar. The underlying suggestion here is that, should a particular cortical field project into another using strong, driving inputs, the presence of cortico–cortical feedback (perhaps involving a third field) would result in uncontrolled oscillation (note there are a number of underlying anatomical assumptions that are too complex for this brief article). If, however, strong driving connections were fed forward through the driving connections both cortico–cortically and via the thalamus (pulvinar, R-type connection)

while feedback was of a modulatory type, either cortico-cortical or cortico-thalamic (pulvinar, E-type connection), then the circuitry would allow a stable hierarchical process that involves feedback. These strong connections are illustrated in Fig. 4b. However, like many aspects of pulvinar function, it remains to be put to the test, and it is possible that a combination of both direct reciprocal and open-loop connections exists, which is dependent upon the relative strengths of R- and E-type inputs from given cortical fields.

With the rapid approach of the new millennium, it is hoped that novel experimental approaches coupled with fresh points of view (perhaps from a different frame of reference) will see an amalgamation occurring, when, at the very least, work on colliculus and cortex will together provide an insight into the true function of the enigmatic pulvinar.

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### Erratum

Rod pathways: the importance of seeing nothing, by Lindsay T. Sharpe and Andrew Stockman, Vol. 22, pp. 497–504.

In the legend to Fig. 1, there was a small error in line 11 that referred to the colour in the figure. It should read 'Only the parasol ON (light blue) and OFF (beige) pathways, which transmit the latest rod signals, are shown.'

We apologize to the authors and readers for this mistake.

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