

## Pattern–motion selectivity in the human pulvinar

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On the basis of anatomical and physiological data obtained on animal models, we recently proposed that neurons in the main visual extrageniculate nuclei complex, the pulvinar, are actively involved in higher-order visual processing. Pulvinar neurons have been shown to integrate the component signals of a plaid pattern into a coherent global percept (pattern–motion selectivity). Using positron emission tomography (PET), we have investigated the possibility that the human pulvinar is also involved in plaid-defined higher-order motion integration. Plaid patterns were presented to normal observers in two conditions (coherent vs. transparent) created by varying the relative spatial frequency of the two gratings comprising the plaid. Regions of interest analysis revealed a significant activation of the pulvinar in the coherent condition supporting the notion that the human pulvinar nucleus is involved in higher-order motion processing. Plaid pattern activation was also observed in the medial temporal gyrus (area MT/V5), a motion area with strong anatomical connections to the pulvinar. These data provide the first direct evidence that the human pulvinar is involved in complex motion integration, as previously shown in animal models, and further support the existence of cortico–thalamo–cortical computational networks involved in higher-order visual processing.

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### Introduction

The perception of moving objects requires that local motion cues analyzed in first-order cortical areas (e.g., primary visual cortex) be combined and integrated in higher-order cortical areas (e.g., middle temporal area or MT/V5; Adelson and Movshon, 1982; Movshon and Newsome, 1996). Evidence of a two-stage cortical processing has been demonstrated in animal models (cat and monkey) and in humans using plaid patterns, a stimulus that

can reveal the capacity of neurons to combine incongruent visual components into a coherent moving percept (pattern–motion selectivity; Adelson and Movshon, 1982). Pattern–motion selective neurons have been found in areas V3 and MT/V5 of monkeys (Movshon et al., 1985, 1986; Rodman and Albright, 1989; Gegenfurtner et al., 1997) and in regions of the lateral suprasylvian (AMLS) and ectosylvian cortices (AEV) of the cat (Scannell et al., 1996; Merabet et al., 1998; Zabouri et al., 2003; Ouellette et al., 2004). Neuroimaging studies in humans confirmed the existence of pattern–motion activity in primate areas V3 and MT/V5 (Wenderoth et al., 1999; Castelo-Branco et al., 2002; Huk and Heeger, 2002).

In recent years, our laboratory has shown that higher-order motion processing was not restricted to cortical areas. Higher-order motion selective neurons, including pattern–motion selective cells, have been found in a sub-region of the pulvinar complex in cats (Merabet et al., 1998; Casanova et al., 2001; Dumbrava et al., 2001). This discovery gives great support to the notion that the role of the thalamus goes beyond the mere relaying of sensory information depending upon the state of vigilance, and to the proposal that thalamic nuclei could be actively involved in higher-order visual processing in close collaboration with neocortical areas (Mumford, 1991; Sherman and Guillery, 1996, 2002; Merabet et al., 1998; Casanova et al., 2001; Shipp, 2003; Casanova, 2004). The pulvinar is in an exceptional position to influence cortical processing given its extensive reciprocal connections with virtually all visual cortical areas. For example, the medial nucleus of the pulvinar is primarily connected to association cortices, such as the prefrontal cortex and area 7, involved in attentional processing (Baleydier and Mauguier, 1985; Hardy and Lynch, 1992). More relevant perhaps in the context of this study is the extensive connectivity between the inferior subregion of pulvinar and area MT/V5, known to be involved in higher-order motion analysis (Ungerleider et al., 1984; Shipp, 2001; Lyon et al., 2003; for review, see Casanova, 2004).

Based on the fact that the primate pulvinar is reciprocally connected to areas MT/V5 and V3 and that these areas are known to process complex motion, it is reasonable to propose that, in humans, pulvinar neurons would be involved in higher-order processing in interaction with the cortex, as demonstrated in an animal model. The aim of this study was to investigate the

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possibility that the human pulvinar contributes to higher-order motion processing using plaid pattern stimuli in collaboration with area MT/V5. Parts of these results have been presented in abstract form (Villeneuve et al., 2004).

## Materials and methods

### Subjects

We collected positron emission tomography (PET) data in eight healthy adult volunteers (3F; 5M, aged between 23 and 28 years) who gave their written informed consent. The experimental protocol was approved by the Aarhus University Ethics Committee (Denmark).

### Visual stimulation

Plaid patterns were used to investigate the contribution of pulvinar cells in motion integration mechanisms. The plaid pattern was composed of two superimposed identical drifting sine wave gratings (0.3 contrast), differing only in orientation by  $120^\circ$ . In this condition, the two component gratings are integrated into a single percept that moves in an intermediate direction to the motion directions of the component gratings. By modifying specific parameters of the plaid, it is possible to alter its perception (coherent vs. non-coherent). One of the parameters that greatly affect the mechanisms of integration of the plaids is the relative spatial frequency (SF) of its comprising gratings (Adelson and Movshon, 1982; Clifford and Vaina, 1999). Coherence is perceived when the spatial frequencies of the two gratings are identical, but transparency (non-coherence) is perceived when the spatial frequencies are different, i.e., component gratings appear to slide one on top of the other and no integration occurs.

Four different forms of plaid patterns were used to isolate integration mechanisms. The baseline stimulus (*baseline*, Fig. 1, panel A) was a plaid composed of two gratings of the same spatial frequency (0.2 c/deg) and temporal frequency (0 Hz, i.e., no motion). The second stimulus was a coherent plaid composed of two drifting gratings of the same low spatial frequency (0.2 c/deg) drifted at a temporal frequency of 4 Hz (*low SF coherent*, Fig. 1, panel B). This stimulus would activate three different populations of pulvinar cells: two assemblies of neurons would be driven by the motion of the two components of the plaid (one population for each component; component–motion selective cells), and a third assembly would be driven by the integrated direction of motion of the plaid (pattern–motion selective cells). The third plaid pattern was composed of two gratings of different spatial frequency (0.2 and 0.5 c/deg) drifting at the same temporal frequency of 4 Hz. The latter plaid is typically known as *transparent* (Fig. 1, panel C) since the two gratings appear to slide one on top of the other. Consequently, only two populations of cells coding for the direction of the components of the plaid would be activated by this stimulus (component selective cells). Subtraction of regional cerebral blood flow (rCBF) changes induced by the *coherent* (three populations of cells) and *transparent* plaids (two populations of cells) should reflect the activity of the cells involved in the binding of local elements into a single coherent pattern. The fourth type of plaid (Fig. 1, panel D) was coherent and was composed of two gratings of 0.5 c/deg spatial frequency (the same spatial frequency

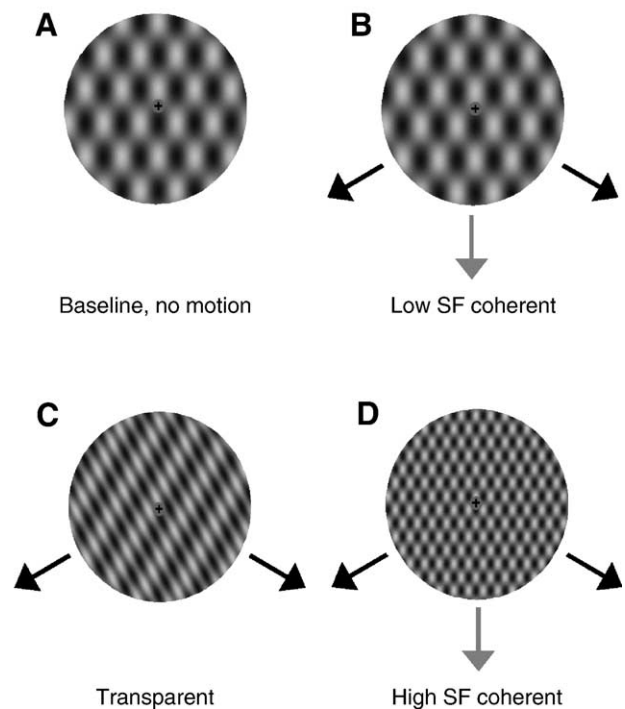


Fig. 1. The four types of plaids used in the experimental paradigm. In panels B–D, the black arrows represent the direction of motion of each component while the grey arrow represents the integrated direction, when applicable. (A) *Baseline* stimulus, there is no motion in this pattern. (B) *Low SF coherence* condition composed of two superimposed drifting gratings of the same spatial frequency and temporal frequency that strongly activated integration processing. (C) *Transparent* condition made of two superimposed drifting gratings of different spatial frequency but identical temporal frequency. This stimulus does not trigger integration processing as both gratings appear to drift one on top of each other and only the motion of the components is therefore perceived. (D) *High SF coherent* condition made of two drifting gratings of the same spatial and temporal frequency. Brain activation related to this stimulus was made to prevent any reduction of responsiveness caused by the use of different grating spatial frequencies.

of the second grating in the *transparent* condition) with the same temporal frequency of 4 Hz (*high SF coherent*). This stimulus was used as a control to rule out the possibility that differences between the *coherent* and *transparent* conditions were due to a weaker response to the spatial frequencies used in one of the conditions.

Stimuli were displayed in a circular window of  $30^\circ$  diameter on a 21-inch monitor (Tektronix; luminance of  $40 \text{ cd/m}^2$ ) positioned 57 cm from the subject's eyes in a dark room. Each stimulus was presented in an ON/OFF ratio of 7 s/3 s for the full length of the recording time (Fig. 2A). A central fixation cross in a grey circular patch ( $2^\circ$  in diameter) was present in all stimulus presentations to prevent eye movements and optokinetic nystagmus. Since ocular motion is known to induce MT/V5 and pulvinar activation (Newsome et al., 1988; Galati et al., 1999), eye movements were monitored for each subject in the scanner using an eye tracking system (Quick Glance 1, EyeTech Digital Systems, USA). Scans in which ocular displacement occurred were rejected from the analysis.

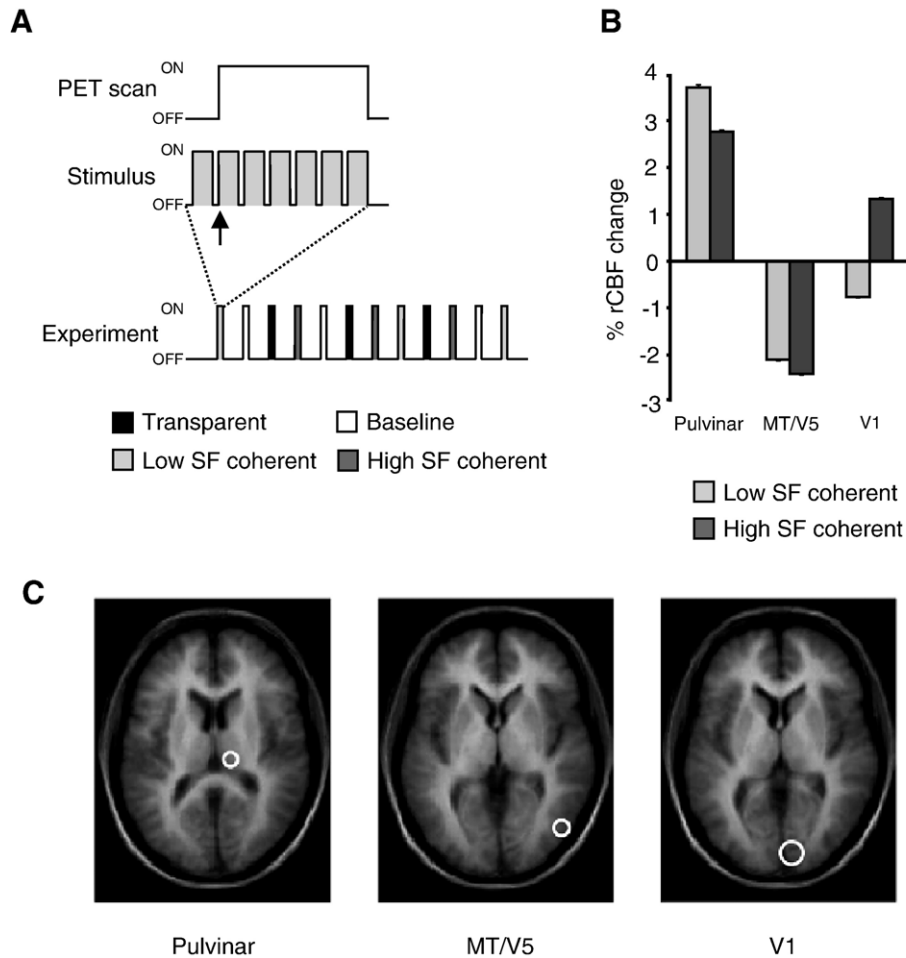


Fig. 2. (A) Schematic representation of the experimental paradigm. The bottom trace represents the four stimulus conditions in a pseudo-randomized order, each repeated three times. Each condition lasted 70 s during which the stimulus presentation was made in an ON/OFF ratio of 7 s/3 s (middle trace). The arrow represents injection time and the onset of scanning (upper trace). In all cases, the stimulus presentation started 10 s before tracer injection. Consequently, the scan lasted 60 s. (B) Bar charts representing percent rCBF changes in the low and high SF coherent conditions with respect to the transparent condition. (C) A schematic representation of the location of the ROI analysis. The white circles delimit the areas of interests, namely, the pulvinar ( $z = 12$ ), MT/V5 ( $z = 6$ ) and V1 ( $z = 5$ ).

### Procedure

Subjects were shown samples of the stimuli and were asked to identify the coherent and transparent conditions. They were then prepared for scanning (insertion of a fine needle catheter into the brachial vein) and positioned in the scanner. Subjects were instructed to maintain fixation during each stimulus presentation and to report verbally their percept after each scan (down = coherent; down right and/or down left = transparent). The experiment involved 12 sequential measurements (four conditions in a pseudo-randomized order, each repeated three times) of regional cerebral blood flow (rCBF) during the presentation of the different visual stimuli (Fig. 2A).

### Data acquisition and analysis

rCBF was measured with an ECAT Exact HR47 PET camera (Siemens/CT, Knoxville, TN) in 3-D mode following intravenous bolus injections of 500 MBq of  $H_2^{15}O$ . A single 60-s frame was acquired (voxel size:  $4.6 \times 4.6 \times 5 \text{ mm}^3$ ), starting at 60,000 true counts/s. Successive scans were separated by at least 10 min.

Visual stimulus presentation was started 10 s before tracer injection and was continued throughout the rest of the scanning time (Fig. 2A). Images were reconstructed with a measured attenuation correction and filtered to 12-mm full-width half-maximum (FWHM) isotropic *Gaussian kernel* with a Hanning filter of cut-off frequency 0.15 cycles/s. PET volumes were realigned using the Automated Image Registration (AIR 3.0) method to correct for head movements between the scans. The first PET image was co-registered with the subject's T1-weighted MRI (GE Sigma, Milwaukee, WI, 1.5T) brain volume (Collins et al., 1994) and mapped into standardized stereotaxic space (Talairach and Tournoux, 1988) using a nine-parameter affine transformation.

Given our specific hypothesis and the nature of the experimental protocol, global search would have been insensitive after being corrected for multiple comparisons (Friston et al., 1996; Ingavir, 1999). Consequently, analysis was restricted to targeted circumscribed areas. The pulvinar coordinates were identified using anatomical landmarks and Talairach coordinates and its location corresponded to the coordinates found in the literature (Morel et al., 1997; Ptito et al., 1999; Sperling et al., 2001; Beer et al., 2002; Kastner et al., 2004). A circular region of interest (ROI)

Table 1  
ROI analysis of area involved in motion processing

ROI ( $x, y, z, r$ )	Contrasts	$P$ value	Pair-wise comparison
Pulvinar (8, -25, 12, 5)	Low SF coherent–transparent	0.001	Low SF coherent $\uparrow$
	High SF coherent–transparent	0.01	High SF coherent $\uparrow$
MT/V5 (50, -70, 2, 6)	Low SF coherent–transparent	0.03	Transparent $\uparrow$
	High SF coherent–transparent	0.007	Transparent $\uparrow$
V1 (5, -87, 5, 10)	Low SF coherent–transparent	0.358	–
	High SF coherent–transparent	0.07	–

Results of ROI analyses computed in the pulvinar nucleus, area MT/V5 and V1. Both pulvinar and MT/V5 present significantly different levels of activation in relation to the coherent/transparent conditions. The rightward column illustrates the conditions which rCBF is increased.

of 5 mm radius was centered over the pulvinar nucleus coordinates (8, -25, 12;  $x, y, z$ ). The small ROI was used to minimize the potential contributing effects of neighboring thalamic nuclei. ROI analyses were also performed in area MT/V5 and V1. Location of area MT/V5 was possible by contrasting motion conditions and *baseline* (no motion) and it corresponded to coordinates reported in previous studies (50, -70, -2; Tootell et al., 1995; Dumoulin et al., 2000; Beer et al., 2002; Fortin et al., 2003; Ptilo et al., 2003). Six millimeter radius ROI was performed to investigate the contribution of area MT/V5 in complex motion processing. ROI at coordinates 5, -87 and 5 ( $x, y, z$ , radius 10 mm) was also carried out to evaluate the contribution of area V1 in integration mechanisms (Fig. 2C). The size of the ROI varied according to the targeted regions to reflect their different sizes and to be in accordance with the above studies. ROI values represent the mean rCBF and the standard deviation of the voxels within each ROI. For a single region and for each subject, 12 values were obtained, one for each scan (3 scans per condition, 4 conditions). For each condition, the ROI values were averaged. A paired-sample  $t$  test was used to evaluate rCBF changes between conditions. Analyses were carried out with DOT software (MNI).

## Results

In order to isolate brain areas involved in pattern–motion processing, we carried out ROI analysis in which the *low SF coherent* condition was contrasted with the *transparent* condition. This test revealed significant rCBF increases in the right pulvinar, corresponding to a higher activation for the *low SF coherent* condition in comparison to the *transparent* condition ( $P < 0.001$ ). This subtraction also revealed significant implication of the right area MT/V5 ( $P = 0.03$ ), the *transparent* stimulus yielding a higher level of activation in comparison to the *low SF coherent* condition.

To rule out the possibility that the differences might be related to the different spatial frequencies used in the *transparent* condition, *high SF coherent* stimulus was compared with the *transparent* condition. This subtraction also yielded a significant level of activation within the pulvinar ( $P < 0.01$ ) and area MT/V5 ( $P = 0.007$ ) as for the *low SF coherent* condition. This confirms that the differences between conditions were not due to a weak activation of pulvinar and MT/V5 cells to the spatial frequency used but rather to pattern selective cells involved in integration mechanisms. The rCBF changes in the low and high SF coherent conditions in the two areas are shown in panel B of Fig. 2.

ROI analyses were also performed in area V1 to study the implication of this area in complex motion processing. Comparison

between the *coherent* conditions (*low SF* and *high SF*) and the *transparent* condition did not reveal any significant differences in area V1 (*low SF coherent*:  $P = 0.358$ ; *high SF coherent*:  $P = 0.07$ ; see Table 1 and panel B of Fig. 2).

There were no significant differences between the activation induced by the *low and high SF coherent* conditions in area MT/V5 and pulvinar (pulvinar:  $P = 0.264$ ; MT/V5:  $P = 0.769$ ). The *high SF coherent* condition was more effective in activating V1 neurons ( $P = 0.012$ ; *high SF coherent* > *low SF coherent*), in accordance with the observation that BOLD signal intensity in area V1 varies with gratings' spatial frequency (Mendola et al., 1999).

The limitation in the number of stimuli that could be used with PET did not allow for an accurate delineation of area V3 and the establishment of the correct coordinates necessary to carry out ROI analysis.

## Discussion

Our findings are the first to demonstrate that the human pulvinar is involved in pattern–motion processing, i.e., in binding visual signals from disparate motion components into a coherent percept. It confirms previous findings in the cat model which originally revealed the implication of the pulvinar in higher-order motion processing (Merabet et al., 1998; Dumbava et al., 2001) and further support the notion that the thalamus may actively participate in higher-order visual functions in partnership with cortical areas through cortico-thalamo-cortical pathways (Mumford, 1991; Sherman and Guillery, 1996, 2002; Merabet et al., 1998; Casanova et al., 2001; Shipp, 2003; Casanova, 2004). In this context, it is worth noting that we also observed pattern–motion activity in area MT/V5, as previously reported in humans (Castelo-Branco et al., 2002; Huk and Heeger, 2002). Given that complex stimulus yield activation in the pulvinar and area MT/V5, we propose the existence of computational modules comprising thalamic and cortical entities specifically involved in higher-order processing.

The absence of significant differences in area V1 in relation to complex motion processing was not surprising given the bulk of evidence that neurons in the primary visual cortex in cats and monkeys could not signal the true direction of a plaid pattern (Movshon et al., 1985; Rodman and Albright, 1989; Movshon and Newsome, 1996; Merabet et al., 1998; Dumbava et al., 2001; Villeneuve et al., 2005; but see Guo et al., 2004). In addition, previous brain imaging studies have not reported pattern–motion activation of V1 in humans (Castelo-Branco et al., 2002; Huk and Heeger, 2002).

### Higher-order functions in pulvinar

While the present study showed specifically that pulvinar neurons can be involved in plaid-defined complex motion, a few other studies also suggested a higher-order function of this extrageniculate nuclei complex. Recently, Ward et al. (2002) described spatial coding and feature binding deficits in a patient with unilateral damage to the rostral part of the pulvinar. These authors proposed that the pulvinar is part of a neural network involved in the integration of local elements. In this line of thinking, Beer et al. (2002) reported a pulvinar activation in human observers stimulated with optic flow, a stimulus that also requires integration of local elements moving in different directions (global motion). They interpreted this activation by the sensation of self-motion (vection) produced by optic flow patterns and the state of arousal (autonomic response) associated with it. Given the higher-order properties of pulvinar neurons (Merabet et al., 1998; Dumbrava et al., 2001; the present study), it may well be that this activation comes from motion integration processes per se. Finally, our findings are also in accordance with the observation by Clifford and Vaina (1999) that a patient who suffered a lateral posterior thalamic (pulvinar) infarct accompanied by an occipital lesion (deep white matter ischemia), experienced major impairments in the processing of plaid patterns.

Since the pulvinar has been shown to be involved in visuospatial attention (LaBerge and Buchsbaum, 1990; Robinson and Petersen, 1992; Bender and Youakim, 2001; Karnath et al., 2002; Ward et al., 2002; Kastner et al., 2004), one may suggest that the activation we reported in the pulvinar might be due to attentional rather than motion mechanisms. Given the difference in activation between the coherent and transparent conditions, this assumption would imply that the coherent condition is attentionally more demanding than the transparent condition. While, to our knowledge, there is no study that directly investigated this issue, there is experimental evidence that goes against this possibility. Indeed, the fact that switching between coherent and transparent occurs automatically without attention and goes equally well in both directions might argue that both conditions are equivalent as far as attentional load is concerned (M. von Grunau, personal communication). It may well be that the coherent condition is somehow attentionally less demanding, because coherence is usually the first percept seen when there is switching between coherent and transparent conditions (von Grunau and Dubé, 1993). Finally, if attention was involved, comparable *coherent* activations would have been found in pulvinar and area MT/V5,<sup>1</sup> and this was not the case as discussed below.

### Pattern-motion processing in pulvinar and area MT/V5

It is worth noting that opposite activity profiles were found in pulvinar and area MT/V5. While highest activity levels in pulvinar were evoked by *coherent* plaid patterns, maximum activation was found in area MT/V5 for the *transparent* one. Data similar to ours were obtained in area MT/V5 by Castelo-Branco et al. (2002). The activity profile in MT/V5 may be explained by Hupé and Rubin (2003) model suggesting an MT/V5 architecture where neural

representations of the coherent and transparent interpretations of the stimulus continually compete for dominance, via inhibitory connections. In the *transparent* condition, the two cell assemblies activated by the two grating components would inhibit pattern-motion neurons. In the *coherent* conditions, the cell assembly activated by the integrated direction of motion would inhibit the two cell assemblies representing grating components. Consequently, activation of area MT/V5 will be higher in the *transparent* condition (two assemblies vs. one; Castelo-Branco et al., 2002). This model of reciprocal inhibition cannot be applied to the pulvinar because a “reverse” profile of activation was found. This would indicate that the pulvinar would have a complete simultaneous representation of both integration and segmentation processing without cross-inhibition between each representation (pattern vs. component). Therefore, the pulvinar could act as a coordinator of the neural representations in area MT/V5 (Shipp, 2003).

### Models of motion integration

As stated in the Introduction, it is generally considered that visual motion processing involves two cortical stages (Adelson and Movshon, 1982; Movshon and Newsome, 1996). The first and second stages would involve direction-selective neurons in V1 and pattern-motion cells in area MT/V5, respectively (Movshon et al., 1985; Rodman and Albright, 1989; Movshon and Newsome, 1996; Castelo-Branco et al., 2002; Huk and Heeger, 2002). Neurons in area V3 are likely to be part of this computational network (Movshon and Newsome, 1996; Gegenfurtner et al., 1997; Wenderoth et al., 1999). Based on the present findings and previous theoretical and experimental studies (Mumford, 1991; Sherman and Guillery, 1996, 2002; Merabet et al., 1998; Casanova et al., 2001; Shipp, 2003; Casanova, 2004), we propose that the thalamus, and in particular the pulvinar, should be considered as a necessary component of the computational network subtending complex motion integration. All levels of motion processing have been described in the pulvinar and, because of its extensive functional relationship with cortical areas, it is likely that this thalamic nuclei complex could actively influence in- and out-going cortical signals within the motion network.

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### References

- Adelson, E.H., Movshon, J.A., 1982. Phenomenal coherence of moving visual patterns. *Nature* 300, 523–525.
- Baleydier, C., Mauguier, F., 1985. Anatomical evidence for medial pulvinar connections with the posterior cingulate cortex, the retrosplenial area, and the posterior parahippocampal gyrus in monkeys. *J. Comp. Neurol.* 232, 219–228.
- Beer, J., Blakemore, C., Previc, F.H., Liotti, M., 2002. Areas of the human brain activated by ambient visual motion, indicating three kinds of self-movement. *Exp. Brain Res.* 143, 78–88.
- Bender, D.B., Youakim, M., 2001. Effect of attentive fixation in macaque thalamus and cortex. *J. Neurophysiol.* 85, 219–234.

<sup>1</sup> PET and fMRI studies have shown that activity is enhanced in MT/V5 when a subject is attending a stimulus rather than viewing it passively (Corbetta et al., 1991; Buechel et al., 1998; O’Craven et al., 1997).

- Buechel, C., Josephs, O., Rees, G., Turner, R., Frith, C.D., Friston, K.J., 1998. The functional anatomy of attention to visual motion: a functional MRI study. *Brain* 121, 1281–1294.
- Casanova, C., 2004. The visual functions of the pulvinar. In: Chalupa, L.M., Werner, J.S. (Eds.), *The Visual Neurosciences*. The MIT Press, Cambridge, USA, pp. 592–608.
- Casanova, C., Merabet, L., Desautels, A., Minville, K., 2001. Higher-order motion processing in the pulvinar. *Prog. Brain Res.* 134, 71–82.
- Castelo-Branco, M., Formisano, E., Backes, W., Zanella, F., Neuenschwander, S., Singer, W., Goebel, R., 2002. Activity patterns in human motion-sensitive areas depend on the interpretation of global motion. *Proc. Natl. Acad. Sci. U. S. A.* 99, 13914–13919.
- Clifford, C.W.G., Vaina, L.M., 1999. Anomalous perception of coherence and transparency in moving plaid patterns. *Brain Res. Cogn. Brain Res.* 8, 345–353.
- Collins, D.L., Neelin, P., Peters, T.M., Evans, A.C., 1994. Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *J. Comput. Assist. Tomogr.* 18, 192–205.
- Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., Petersen, S.E., 1991. Selective and divided attention during visual discrimination of shape, color and speed: functional anatomy by positron emission tomography. *J. Neurosci.* 11, 2383–2402.
- Dumbrava, D., Faubert, J., Casanova, C., 2001. Global motion integration in the cat's lateral posterior–pulvinar complex. *Eur. J. Neurol.* 13, 2218–2226.
- Dumoulin, S.O., Bittar, R.G., Kabani, N.J., Baker Jr., C.L., Le Goualher, G., Pike, B.G., Evans, A.C., 2000. A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. *Cereb. Cortex* 10, 454–463.
- Fortin, A., Faubert, J., Ptito, A., Gjedde, A., Kupers, R., Ptito, M., 2003. Stereoscopic processing in the human brain as a function of binocular luminance rivalry. *NeuroReport* 14, 1163–1166.
- Friston, K.J., Price, C.J., Fletcher, P., Moore, C., Frackowiack, R.S., Dolan, R., 1996. The trouble with cognitive subtraction. *Neuroimage* 4, 97–114.
- Galati, G., Pappata, S., Pantano, P., Lenzi, G.L., Samson, Y., Pizzamiglio, L., 1999. Cortical control of optokinetic nystagmus in humans: a positron emission tomography study. *Exp. Brain Res.* 126, 149–159.
- Gegenfurtner, K.R., Kiper, D.C., Levitt, J.B., 1997. Functional properties of neurons in macaque V3. *J. Neurophysiol.* 77, 1906–1923.
- Guo, K., Benson, P.J., Blakemore, C., 2004. Pattern motion is present in V1 of awake but not anaesthetized monkeys. *Eur. J. Neurosci.* 19, 1055–1066.
- Hardy, S.G., Lynch, J.C., 1992. The spatial distribution of pulvinar neurons that project to two subregions of the inferior parietal lobule in the macaque. *Cereb. Cortex* 2, 217–230.
- Huk, A.C., Heeger, D.J., 2002. Pattern–motion responses in human visual cortex. *Nat. Neurosci.* 5, 72–75.
- Hupé, J.M., Rubin, N., 2003. The dynamics of bi-stable alternation in ambiguous motion displays: a fresh look at plaids. *Vision Res.* 43, 531–548.
- Ingavir, M., 1999. Pain and functional imaging. *Philos. Trans. R. Soc. London* 354, 1347–1358.
- Karnath, H.O., Himmelbach, M., Rorden, C., 2002. The subcortical anatomy of human spatial neglect: putamen, caudate nucleus and pulvinar. *Brain* 125, 350–360.
- Kastner, S., O'Connor, D.H., Fukui, M.M., Fehd, H.M., Herwig, U., Pinski, M.A., 2004. Functional imaging of the human lateral geniculate nucleus and pulvinar. *J. Neurophysiol.* 91, 438–448.
- LaBerge, D., Buchsbaum, M.S., 1990. Positron emission tomographic measurements of pulvinar activity during an attention task. *J. Neurosci.* 10, 613–619.
- Lyon, D.C., Jain, N., Kaas, J.H., 2003. The visual pulvinar in tree shrews: II. Projections of four nuclei to areas of visual cortex. *J. Comp. Neurol.* 467, 607–627.
- Mendola, J.D., Dale, A.M., Fischl, B., Liu, A.K., Tootell, R.B., 1999. The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *J. Neurosci.* 19, 8560–8572.
- Merabet, L., Desautels, A., Minville, K., Casanova, C., 1998. Motion integration in a thalamic visual nucleus. *Nature* 396, 265–268.
- Morel, A., Magnin, M., Jeanmonod, D., 1997. Multiarchitectonic and stereotactic atlas of the human thalamus. *J. Comp. Neurol.* 387, 588–630.
- Movshon, J.A., Newsome, W.T., 1996. Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. *J. Neurosci.* 16, 7733–7741.
- Movshon, J.A., Adelson, E.H., Gizzi, M.S., Newsome, W.T., 1985. The analysis of moving visual patterns. *Pontif. Acad. Sci. Scr. Varia* 54, 117–151.
- Movshon, J.A., Adelson, E.H., Gizzi, M.S., Newsome, W.T., 1986. The analysis of moving visual patterns. In: Chagas, C., Gattas, R., Gross, C. (Eds.), *Pattern Recognition Mechanisms*. Springer Verlag, New York, pp. 148–164.
- Mumford, D., 1991. On the computational architecture of the neo-cortex: I. The role of the thalamo-cortical loop. *Biol. Cybern.* 65, 135–145.
- Newsome, W.T., Wurtz, R.H., Komatsu, H., 1988. Relation of cortical areas MT and MST to pursuit eye movements: II. Differentiation of retinal from extraretinal inputs. *J. Neurophysiol.* 60, 604–620.
- O'Craven, K.M., Rosen, B.R., Kwong, K.K., Treisman, A., Savoy, R.L., 1997. Voluntary attention modulates fMRI activity in human MT–MST. *Neuron* 18, 591–598.
- Ouellette, B.G., Minville, K., Faubert, J., Casanova, C., 2004. Simple and complex visual motion response properties in the anterior medial bank of the lateral suprasylvian cortex. *Neuroscience* 123, 231–245.
- Ptito, M., Johannsen, P., Faubert, J., Gjedde, A., 1999. Activation of human extrageniculostriate pathways after damage to area V1. *Neuroimage* 9, 97–107.
- Ptito, M., Faubert, J., Gjedde, A., Kupers, R., 2003. Separate neural pathways for contour and biological-motion cues in motion-defined animal shapes. *Neuroimage* 19, 246–252.
- Robinson, D.L., Petersen, S.E., 1992. The pulvinar and visual salience. *Trends Neurosci* 15, 127–132.
- Rodman, H.R., Albright, T.D., 1989. Single-unit analysis of pattern–motion selective properties in the middle temporal visual area (MT). *Exp. Brain Res.* 75, 53–64.
- Scannell, J.W., Sengpiel, F., Tovee, M.J., Benson, P.J., Blakemore, C., Young, M.P., 1996. Visual motion processing in the anterior ectosylvian sulcus of the cat. *J. Neurophysiol.* 76, 895–907.
- Sherman, S.M., Guillery, R.W., 1996. Functional organization of thalamo-cortical relays. *J. Neurophysiol.* 76, 1367–1395.
- Sherman, S.M., 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.
- Shipp, S., 2001. Corticopulvinar connections of areas V5, V4, and V3 in the macaque monkey: a dual model of retinal and cortical topographies. *J. Comp. Neurol.* 439, 469–490.
- Shipp, S., 2003. The functional logic of cortico-pulvinar connections. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 358, 1605–1624.
- Sperling, R.A., Bates, J.F., Cocchiarella, A.J., Schacter, D.L., Rosen, B.R., Albert, M.S., 2001. Encoding novel face–name associations: a functional MRI study. *Hum. Brain Mapp.* 14, 129–139.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain*. Georg Thieme Verlag, Stuttgart.
- Tootell, R.B., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., Belliveau, J.W., 1995. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* 15, 3215–3230.
- Ungerleider, J.G., Desimone, R., Galkin, T.W., Mishkin, M., 1984. Subcortical projections of area MT in the macaque. *J. Comp. Neurol.* 223, 368–386.

- Villeneuve, M.Y., Kupers, R., Gjedde, A., Ptito, M., Casanova, C., 2004. Pattern–motion selectivity in the human pulvinar: a PET study. *Neuroimage* 22, S39.
- Villeneuve, M.Y., Ptito, M., Casanova, C., submitted for publication. Global motion integration in the postero-medial part of the lateral suprasylvian cortex in the cat. *Eur. J. Neurosci.*
- von Grünau, M.W., Dubé, S., 1993. Ambiguous plaids: switching between coherence and transparency. *Spat. Vis.* 7, 199–211.
- 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.
- Wenderoth, P., Watson, J.D.G., Egan, G.F., Tochon-Danguy, H.J., O’Keefe, G.J., 1999. Second order components of moving plaids activate extrastriate cortex: a Positron Emission Tomography study. *NeuroImage* 9, 221–234.
- Zabouri, N., Ptito, M., Casanova, C., 2003. Complex motion sensitivity of neurons in the visual part of the anterior ectosylvian cortex. *Neurosci. Abstr.* 29, 179.4.