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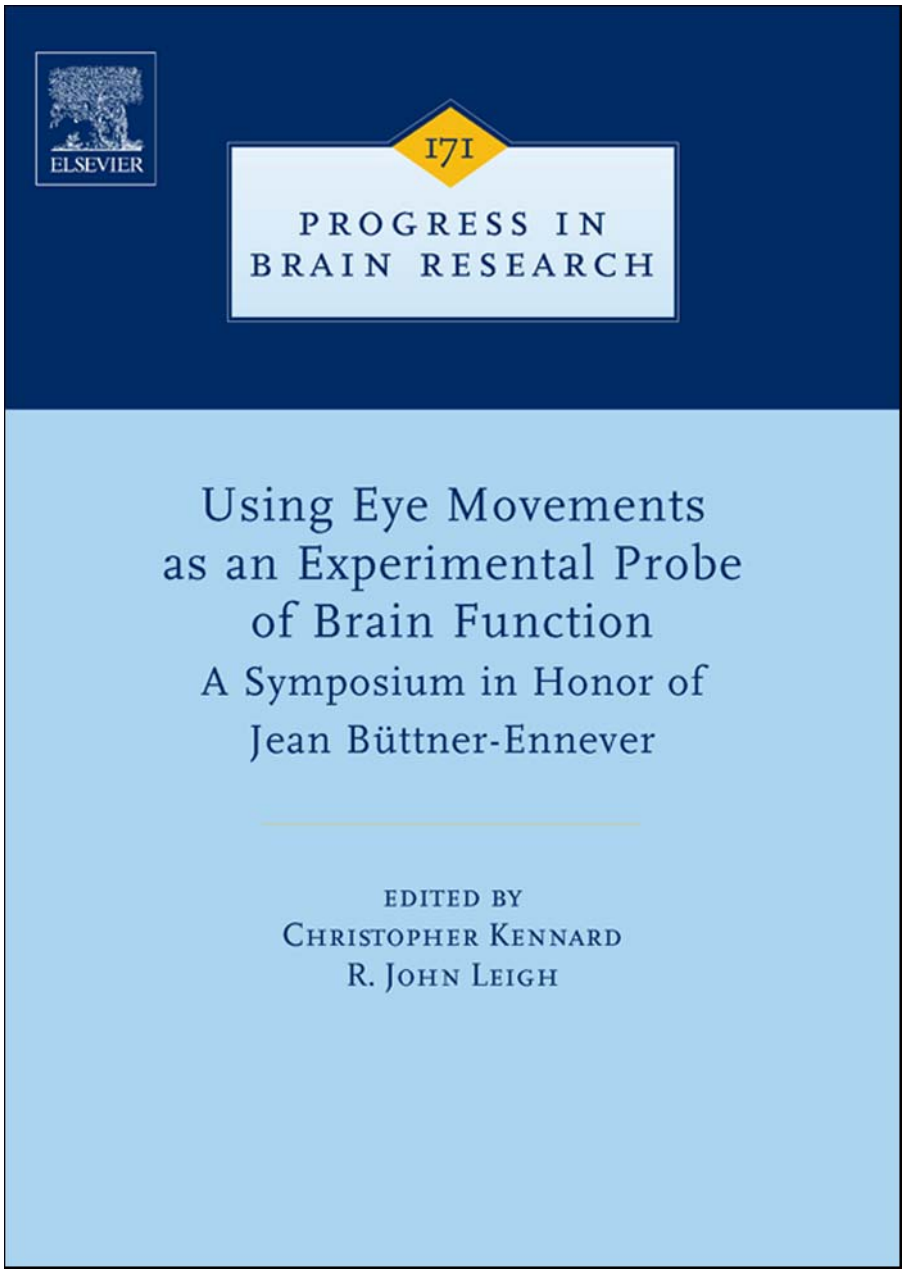

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CHAPTER 5.15

The role of the human pulvinar in visual attention and action: evidence from temporal-order judgment, saccade decision, and antisaccade tasks

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Abstract: The pulvinar nucleus of the thalamus has been considered as a key structure for visual attention functions (Grieve, K.L. et al. (2000). Trends Neurosci., 23: 35–39; Shipp, S. (2003). Philos. Trans. R. Soc. Lond. B Biol. Sci., 358(1438): 1605–1624). During the past several years, we have studied the role of the human pulvinar in visual attention and oculomotor behaviour by testing a small group of patients with unilateral pulvinar lesions. Here we summarize some of these findings, and present new evidence for the role of this structure in both eye movements and visual attention through two versions of a temporal-order judgment task and an antisaccade task. Pulvinar damage induces an ipsilesional bias in perceptual temporal-order judgments and in saccadic decision, and also increases the latency of antisaccades away from contralesional targets. The demonstration that pulvinar damage affects both attention and oculomotor behaviour highlights the role of this structure in the integration of visual and oculomotor signals and, more generally, its role in flexibly linking visual stimuli with context-specific motor responses.

Keywords: pulvinar; thalamus; human; attention; saccade decision; antisaccade; temporal order judgment; visuomotor transformation; saccade; eye movements

Introduction

Converging evidence from humans and experimental animals has implicated the central and lateral thalamus in oculomotor control. Saccades can be elicited by electrical stimulation of these nuclei (Schlag and Schlag-Rey, 1971; Crommelinck et al., 1977), and single units are active in relation to saccades (Crommelinck et al., 1977; Schlag-Rey and Schlag, 1977, 1984). Humans with lesions of central thalamus are impaired in using corollary discharge to remap the location of the second target in a double-step saccade paradigm (Bellebaum et al., 2005).

The role of the pulvinar nucleus in eye-movement control, which is the focus of the current research, remains less explored. This largely visual nucleus has direct connections with extrastriate visual cortex and with the superior colliculus and oculomotor cortex of frontal and parietal lobes (Romanski et al., 1997; Grieve et al., 2000; Shipp, 2003). These

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connections position it to play a vital role in controlling visual attention and eye movements.

The involvement of the pulvinar in visual attention has been demonstrated by electrophysiological and lesion studies in monkeys (Chalupa et al., 1976; Bender, 1981; Beneveto and Miller, 1981; Petersen et al., 1985, 1987), and in humans (LaBerge and Buchsbaum, 1990; Ward et al., 2002; Danziger et al., 2004; Michael and Desmedt, 2004; Ward and Arend, 2007; Ward et al., 2007). Recently, we have also found that lesions to the spatial maps of the pulvinar affect object-based location coding (Ward and Arend, 2007). This complex spatial coding within the pulvinar may reflect its role in integrating and maintaining different frames of reference computed in different cortical areas, and could represent a computation supporting visually guided action including eye movements.

Some lesion studies in monkeys reporting prolonged fixation durations and increases in saccade latency were confounded by lesion extension into the brachium of the superior colliculus (Ungerleider and Christensen, 1977, 1979). No impairments in single- and dual-step saccade tasks were observed in monkeys with restricted pulvinar lesions (Bender and Butter, 1987; Bender and Baizer, 1990), leading Bender and Baizer (1990) to suggest that the pulvinar is more likely to be involved in the integration of saccadic eye movements with visual processing, than in saccade generation.

Nevertheless, single-cell recordings in the pulvinar showed response modulation during eye movements (Petersen et al., 1985; Robinson et al., 1986). Robinson et al. (1990) tested the excitability of pulvinar neurons during eye movements and observed modulation in response to a visual stimulus as a function of the position of the eye in the orbit. These findings resemble those found in lateral intraparietal cortex (Andersen et al., 1990).

In humans, focal lesions to the pulvinar are relatively rare, and some studies that have examined the effects of pulvinar lesions on eye movements have been confounded by the fact that the patients also had cortical lesions (Zihl and von Cramon, 1979; Ogren et al., 1984), or had hemispatial neglect (Watson and Heilman 1979; Brigell et al., 1984; Hirose et al., 1985). Rafal et al. (2004) measured saccade latencies for voluntary saccades (initiated by verbal instructions) and visually summoned saccades (toward peripheral targets) in three patients with chronic focal lesions of posterior thalamus (SM, TN, and GJ, all of whom also participated in the current research; see Fig. 2 in the Methods section). They reported that the presence of a fixation point had the normal effect of prolonging the latencies for voluntary saccades, but did not affect latencies for visually summoned saccades. Also, as shown in Fig. 1, the patients had longer latencies to initiate contralesional saccades for both voluntary and visually summoned saccades.

Here, we report the effects of pulvinar lesions on both perceptual judgments and oculomotor performance in a group of patients with chronic, unilateral pulvinar lesions. Three patients were tested in an antisaccade task, and five patients were tested in two temporal-order judgment tasks: a perceptual decision task and a saccade decision task.

Methods

Patients

All patients had chronic (10–24 months post ictus), unilateral lesions affecting the posterior thalamus (Fig. 2) due to hypertensive intracerebral haematoma, except for CR who had sustained a haemorrhagic contusion avulsing the pole of the pulvinar from closed head injury. In one patient (a woman), the lesion was in the right hemisphere and in the other four (all men) it was on the left. Lesion analyses for these patients have been reported previously (Ward et al., 2002; Danziger et al., 2004; Ward and Arend, 2007). Except CR, all patients had contralesional motor and/or sensory deficits. None had any evidence of cognitive impairment and all were living independently. They all had intact visual fields and normal contrast sensitivity, and had no signs of visual neglect or visual extinction. All five patients were tested in the saccade decision and perceptual temporal-order judgment tasks. SM, TN, and GJ were tested in the antisaccade task.

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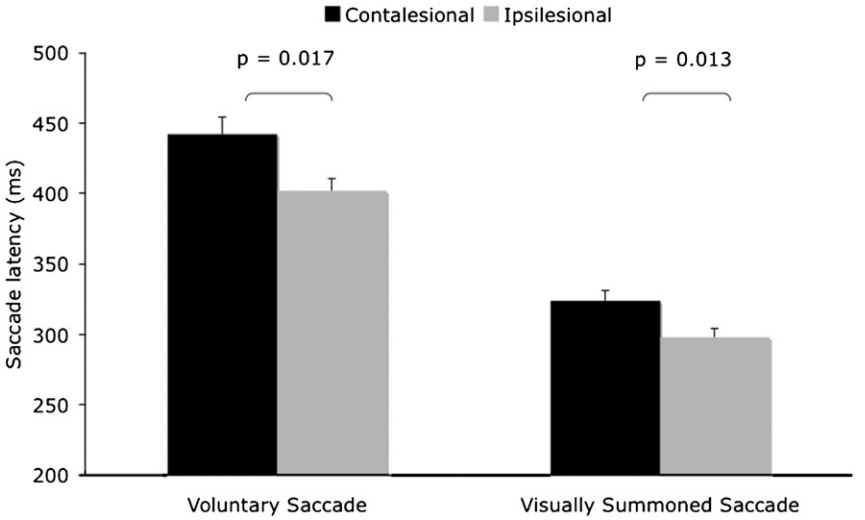

Fig. 1. Mean saccade latency (error bars denote standard error of the mean) for voluntary saccades and visually summoned saccades towards ipsilesional and contralesional fields.

Temporal-order judgment tasks

Patients were instructed to fixate on a 1° dark filled circle at the centre of a white monitor screen for 2 s before the onset of the left and right targets. The targets consisted of grey 1° filled circles that appeared at 10° to the left and to the right of the fixation point on every trial. There were three different stimulus onset asynchronies (SOAs) between presentation of the first target on one side of the screen and the second target on the opposite side of the screen: simultaneously, left or right target first at 17 ms SOA, and left or right target first at 150 ms SOA. The first stimulus event was presented for 1000 ms and the second for 1000 ms minus the asynchrony.

Saccade and perceptual decision tasks were tested in separate blocks. In the saccade task, patients were instructed to make an eye movement towards the target that appeared first. In the perceptual decision task, patients were instructed to maintain fixation and to indicate which target appeared first by pressing the left or right button on the keypad of a Gravis joystick using the index and middle fingers of the ipsilesional hand. Each block consisted of 150 trials taking about 10 min. CR and DG each completed four blocks of both tasks. GJ and SM each completed four blocks of the saccade decision task and three blocks of the perceptual decision task. TN completed three blocks of each task.

Antisaccade task

After an inter-trial interval of 2500 ms, each trial began with a display consisting of a black background on which there were a white fixation point and two unfilled 2.4° white squares each located 10° to the right and left, respectively. Patients maintained their gaze on the fixation point (a white filled circle measuring 0.7°) for a variable interval ranging between 700–1300 ms, after which a target (a white 1.8° asterisk that appeared randomly in the left or right box and remained visible until response) was presented. The instructions were to move the eyes away from the target towards the box in the opposite visual field. In half the trials, the fixation point offset simultaneously with target presentation, and in the other random half of the trials, the fixation point remained visible. Experimental sessions consisted of one block of 80 trials. Patient SM completed seven blocks and the other two patients completed five blocks each.

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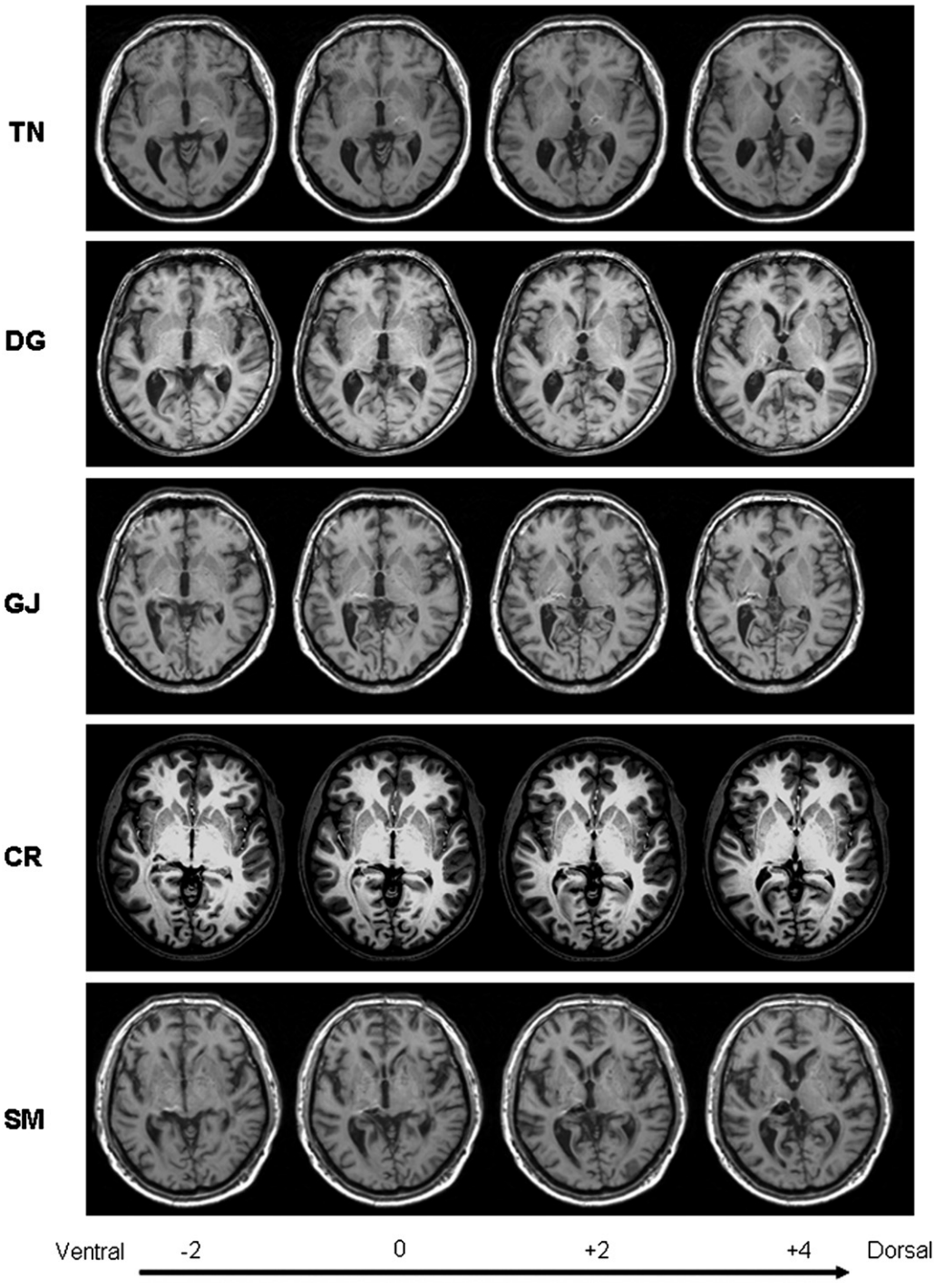

Fig. 2. Reconstructed T1-weighted axial MRI images for each patient. Anatomical convention: slices running from ventral to dorsal and showing millimetres above or below the anterior–posterior commissural (AC–PC) plane.

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Results

Saccadic decision task

For the 17 ms condition, the mean proportion of correct ipsilesional and contralesional saccades responses was computed for each patient for both the ipsilesional target first and contralesional target first conditions. A one-way ANOVA showed a main effect of field, $F(1,4) = 9.40$, $p = 0.037$, confirming a bias to saccade towards ipsilesional targets in preference to contralesional ones (Fig. 3, top.) This was the case for all patients except CR, who showed no difference between fields. For the 0 ms SOA, where ipsilesional and contralesional targets appeared simultaneously, mean proportion of contralesional choices for each patient was computed. All patients, except DG, made more saccades to their ipsilesional than to their contralesional field when both targets were presented simultaneously. Although the proportion of contralesional choices were less than ipsilesional ones (Fig. 3, top), this difference did not reach significance $t(4) = 1.307$, $p = 0.26$.

Perceptual decision task

In contrast to the bias observed at the 17 ms SOA in the saccade decision task, Fig. 3 (bottom) shows that patients were very accurate in correctly reporting which target appeared first, 97% correct or better in all cases. For the simultaneous (0 ms SOA) condition, mean proportion of contralesional choices for each patient was computed. A one-sample *t*-test showed that patients were more likely to judge the ipsilesional target as appearing first $t(4) = 4.32$, $p = 0.012$ (Fig. 3, bottom). All five patients had an ipsilesional bias in this task.

Antisaccade task

Error rates were very low (mean $< 4\%$). No patient made more than 7% errors in any condition, and errors were not further analysed. After excluding trials with latencies more than four standard deviations from the conditional mean, individual *t*-tests for each patient were conducted, with trial as the unit of analysis. GJ and TN showed longer mean latencies to initiate antisaccades away from contralesional targets than ipsilesional targets: GJ — contra 442.4 ms (SEM = 7.5), ipsi 353.1 ms (SEM = 4.6), $t(339) = 10.1$, $p < 0.0005$; TN — contra 344.0 ms (SEM = 4.9), ipsi 329.5 ms (SEM = 3.5), $t(316) = 2.35$, $p = 0.020$. SM, in whom the lesion extended into dorsomedial thalamus, did not have an asymmetry of antisaccade latencies in this task: contra 427.3 (SEM = 13.5), ipsi 425.8 (SEM = 9.5), $t(263) = 0.03$, $p = 0.925$.

Discussion

Results reported here are in accord with previous research in these patients showing deficits of attention in the field contralateral to the pulvinar lesion (Rafal and Posner, 1987; Ward et al., 2002; Danziger et al., 2004; Michael and Desmedt, 2004; Ward and Arend, 2007; Ward et al., 2007). In a temporal-order judgment task, attention to one of the two simultaneous events results in its 'prior entry' into awareness. (Zackon et al., 1999; Shore et al., 2001; Spence et al., 2001; Vibell et al., 2007). All five patients showed an ipsilesional bias in the perceptual decision task. When the two targets were presented simultaneously, the patients were more likely to perceive the ipsilesional target as appearing first.

A similar bias was observed for simultaneous targets in the saccade decision task (although this difference did not reach statistical significance). This performance does not, by itself, indicate a specific oculomotor function of the pulvinar. The attentional deficit identified in the perceptual decision task would be expected to affect saccade responses no less than it did for manual responses. Importantly, however, the patients also showed a bias against making a saccade towards a contralesional target in the 17 ms SOA condition. In the perceptual judgment task, all patients performed almost flawlessly in this condition. At this temporal interval between the two targets, they had no difficulty in reliably judging which appeared first. Thus, in the saccade task, the patients showed a bias against making a saccade towards the contralesional target

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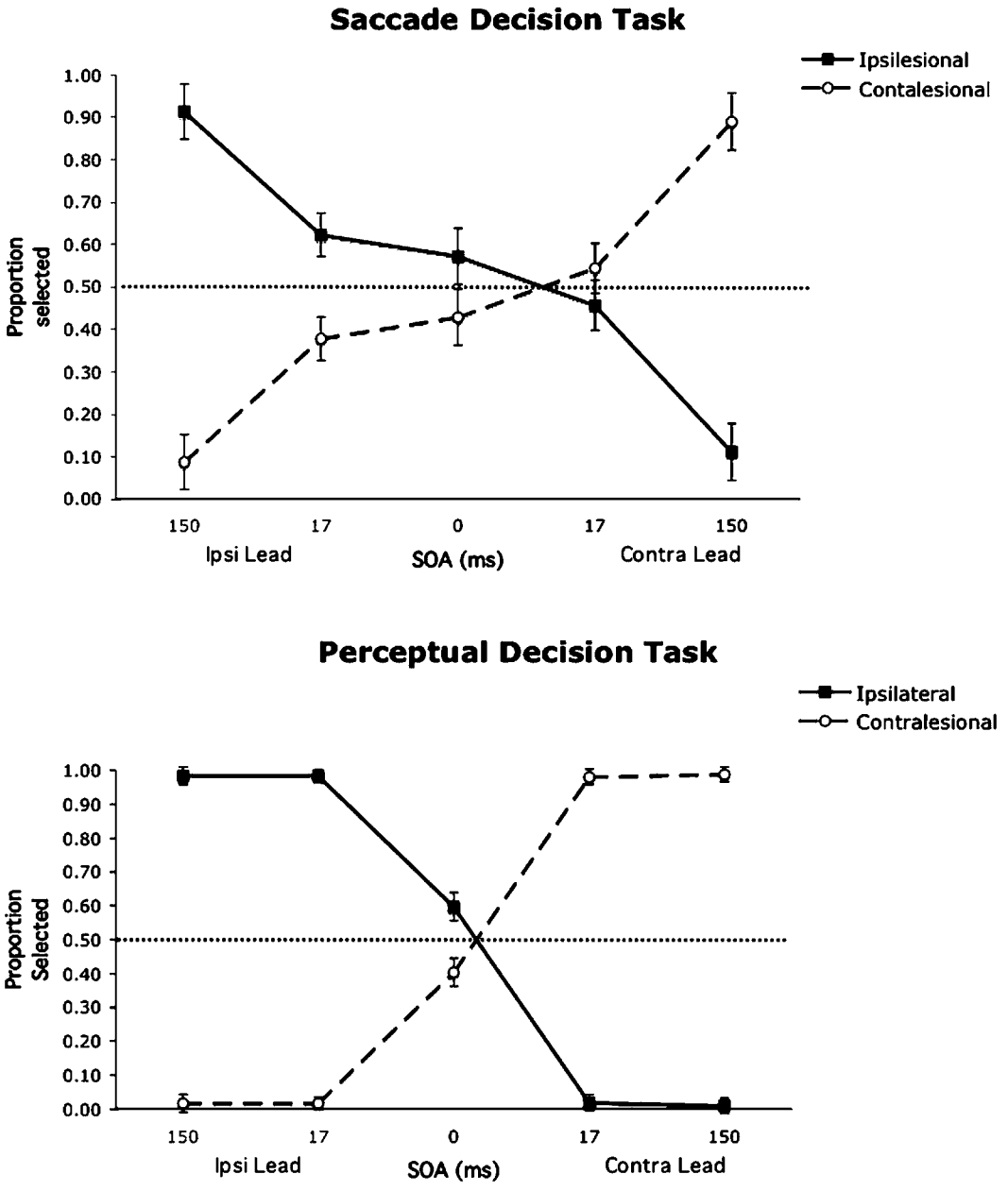

Fig. 3. Mean proportion of contralesional and ipsilesional responses for each target. Target stimulus onset asynchrony (SOA) in the saccade decision task (top) and perceptual decision task (bottom). Error bars display standard errors of the mean.

even under conditions in which they presumably correctly judged that the contralesional target had appeared first. These patients with chronic lesions of the pulvinar show a saccade decision bias similar to patients with chronic lesions of intraparietal cortex (Ro et al., 2001).

Like patients with chronic lesions of intraparietal cortex (Machado and Rafal, 2004), two patients

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tested in the antisaccade task had longer latencies to initiate saccades away from contralesional targets. One patient, SM, in whom the lesion extended into the dorsomedial thalamus did not show this effect. On the basis of physiological observations in antisaccade and memory-antisaccade tasks, Zhang and Barash (2000) have postulated a specific role of intraparietal cortex in computing visuo-motor transformations. Given its extensive and reciprocal connections not only with IPL, but also with frontal areas (Grieve et al., 2000; Shipp, 2003), the pulvinar may also be involved in such transformations.

This function is consistent with previous research suggesting that the pulvinar is involved more generally in visuo-motor transformations. We have previously found that spatial coding within the pulvinar is defined by multiple frames of reference, including retinotopic and object-based codes most likely generated within the cortex (Ward and Arend, 2007). In conjunction with the present results, it appears that the cortex and pulvinar may be jointly involved in a variety of spatial transformations, presumably to facilitate different kinds of action. More generally, however, as we discuss below, our results support a conceptual framework that considers the pulvinar as critical in flexibly linking visual stimuli with context-specific motor responses.

Sherman (2007) has recently invited us to consider the possibility that "all direct corticocortical pathways are modulatory [rather than 'driver'], which would mean that information routes between cortical areas depend on higher order thalamic relays. This would imply that all information reaching a cortical area, whether originating in the periphery (e.g. retina) or another cortical area, must pass through the thalamus. In other words, just as retinal information is relayed by thalamus, so is corticocortical information."

This hypothesis is consistent with the conceptual framework outlined here that the pulvinar is critical in integrating visual information with action systems. Specifically, we suggest that the pulvinar coordinates activities of visual and motor systems by enabling direct stimulus–action linkages that can be rapidly implemented in a specified context.

Using a flanker task with manual responses, we have shown that pulvinar lesions eliminate automatic response channel activation by contralesional visual stimuli (Danziger et al., 2004). A similar effect is seen in patients with chronic lesions of lateral prefrontal cortex (Rafal et al., 1996). In the flanker task, a specific visual stimulus becomes associated with a specific response that is automatically activated whenever the stimulus is presented (e.g., red square — push a button with index finger), resulting in interference by distracters coding for a response incompatible with the target stimulus. Similar to the case of the antisaccade task, pulvinar lesions do not prevent patients from making appropriate key-press responses to targets in their contralesional field but, when the stimuli are presented there as distractors, they do not automatically activate their associated response code and, hence, produce less interference with responses to a target presented at fixation.

Having implicated the pulvinar in attention and visually guided behaviour across a range of studies in our laboratories, we must also note that these patients generally do not complain about their vision, and do not report impairment of visually guided behaviours in their everyday life. That is, attentional impairments in patients with pulvinar lesions, although pervasive and consistent, are nevertheless 'sub-clinical.' Presumably corticocortical connections can mediate successful, if perhaps somewhat less efficient, perceptual processing and visually guided behaviour, even in the absence of the quick and efficient cortico-thalamo-cortical circuits. Even if cortico-cortical pathways do not normally function as 'drivers,' they could be recruited to do so in a reorganized brain during recovery from brain damage.

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