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# Naso-Temporal Asymmetry for Signals Invisible to the Retinotectal Pathway

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**Bompas A, Sterling T, Rafal RD, Sumner P.** Naso-temporal asymmetry for signals invisible to the retinotectal pathway. *J Neurophysiol* 100: 412–421, 2008. First published May 14, 2008; doi:10.1152/jn.90312.2008. Monocular viewing conditions show an asymmetry between stimuli presented in the temporal and nasal visual fields in their efficiency for automatically triggering eye saccades and grasping attention. For instance, observers free to make a saccade to one of two stimuli presented together orient preferentially to the temporal stimulus. Such naso-temporal asymmetry (NTA) has been assumed to reflect the asymmetry in the retinotectal pathway to the superior colliculus. We tested this hypothesis using S cone stimuli, which are invisible to the magnocellular and retinotectal pathways. The observed NTA in choice saccades to bilateral stimuli was no less present for S cone stimuli than for luminance stimuli. Additionally, the amplitude of the NTA can be enhanced when S cone signals are added to luminance signals. These results suggest that behavioral NTA in humans is not diagnostic of retinotectal mediation. Furthermore, we found no asymmetries in latency, suggesting that the NTA in saccade choice does not originate simply from a bottom-up asymmetry in any low level visual pathways.

## INTRODUCTION

In mammals, information originating from each half of the visual scene (left or right hemifields) is processed in the contralateral brain hemisphere (right and left hemispheres, respectively) for both left and right eyes. This is allowed by the hemidecussation of retinal ganglion cell axons at the optic chiasm. For each eye, axons from the nasal hemiretina, which receives inputs from the temporal hemifield (left hemifield for the left eye and right hemifield for the right eye), cross at the optic chiasm to project contralaterally. Axons from the temporal hemiretina, which receives inputs from the nasal hemifield (right hemifield for the left eye and left hemifield for the right eye), project ipsilaterally.

Experiments under monocular viewing conditions have shown several behavioral naso-temporal asymmetries (NTAs). For instance, stimuli in the temporal hemifield have been shown to summon automatic and volitional orienting of gaze (Lewis and Maurer 1992; Lewis et al. 1985; Rothbart et al. 1990; Walker et al. 2000) and attention (Berger and Henik 2000; Rafal et al. 1989, 1991) more efficiently than nasal stimuli. In the study by Posner and Cohen (1980), whose paradigm has been used in this paper, participants were asked to perform choice saccades between a left and a right stimulus, viewed through the left or right eye. Results showed a pronounced preference for saccading toward temporal stimuli (left stimulus with the left eye and right stimuli with the right

eye), a bias that occurred only in response to peripheral visual targets—and not to central visual or peripheral auditory stimuli—and could therefore not be accounted for by a simple motor preference. A similar temporal bias has been observed in newborns (Lewis and Maurer 1992; Lewis et al. 1985; Rothbart et al. 1990). Also, the presence of a temporal distractor has been shown to produce a larger cost (distractor effect) on the latency of saccades directed to nasal targets than vice versa (Walker et al. 2000). The same tendency was observed in reflexive orienting of attention, with larger cueing benefits and costs on saccade latencies for cues presented in the temporal hemifield (Rafal et al. 1991), including larger inhibition of return (Berger and Henik 2000; Rafal et al. 1989).

It has often been proposed that these behavioral asymmetries might originate from the retinotectal pathway, the evolutionary ancient visual system that directly connects the retina to the superficial layers of superior colliculus (SC) (Berger and Henik 2000; Lewis and Maurer 1992; Rafal et al. 1989, 1991; Rothbart et al. 1990), although not unanimously (Walker et al. 2000; Williams et al. 1995). Anatomically, superficial layers of SC in cats predominantly receive inputs from the nasal retina, sampling the temporal visual field (Sterling 1973), whereas in monkeys, the asymmetry is less pronounced but still clear (see Williams et al. 1995 for a review). In humans, functional imaging has shown a larger response in SC [in functional MRI (fMRI), superficial and deeper layers cannot be distinguished] for temporal than nasal visual stimuli, a difference that was not found for other visual structures, including lateral geniculate nucleus (LGN) and visual cortex (Sylvester et al. 2007). Moreover, although the geniculostriate pathway takes time to develop in infants, the midbrain seems to be developed anatomically at birth (Johnson 1990), which would explain the observed NTA in babies (Lewis and Maurer 1992; Lewis et al. 1985; Rothbart et al. 1990).

Posner and Cohen (1980) reported a behavioral dissociation between their asymmetrical saccadic responses and the absence of asymmetry in perceptual temporal order judgments. Thus saccadic choice seemed to be influenced by a pathway separate from those supporting perception. The retinotectal route was a natural candidate to play this role because the SC has long been known to be important for saccade generation (Sparks 1986). This basic idea assumed that retinotectal inputs had privileged access to the saccade initiation cells in deeper layers of SC, but in fact they may not: direct connections between superficial and deeper layers seem to be relatively weak (Isa 2002; Moschovakis et al. 1988). However, the retinotectal pathway might play a role instead through fast onward projections to

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structures such as the cortical eye fields that show very rapid visual responses (Schmolesky et al. 1998).

Following the early studies of saccade choice (Posner and Cohen 1980; Rothbart et al. 1990), subsequent studies used the NTA as a diagnostic test for retinotectal mediation in other phenomena, such as attentional orienting and inhibition of return (Rafal et al. 1989, 1991). Furthermore, the presence of NTA in blindsight (in which patients with geniculostriate damage can guess the location of stimuli they claim not to see) has been thought to bring support to the view that blindsight relies on the preserved retinotectal pathway (Dodds et al. 2002; Rafal et al. 1990; but see Walker et al. 2000). Another example is face perception, where evidence of NTA in normal adults but not in prosopagnosic patients is interpreted as diagnostic for the involvement of subcortical mechanisms in normal face perception in adults (de Gelder and Stekelenburg 2005).

However, there are several reasons to doubt that the retinotectal route is the major source of NTA. For instance, Walker et al. (2000) failed to replicate the findings of Rafal et al. (1990), reporting no evidence of NTA in hemianopic patients, while it was present in normal observers. Furthermore, measures of cell density and retrograde labeling showed several other potential sources of NTA. Importantly, although these asymmetries increase dramatically with eccentricity, it should be noted that they are already observed at the visual eccentricities relevant in blindsight and other behavioral NTAs (8–10 deg). These include the retinal level, with larger density of cones and ganglion cells on the nasal hemiretina in monkey (Perry and Cowey 1985) and human (Curcio and Allen 1990), and the projections from the retina to cortex (Tychsen and Burkhalter 1997). According to Williams et al. (1995), monkey brain would in fact exhibit the same level of NTA in the retinogeniculostrate pathway as in retinotectal pathway.

A further reason to question a simple attribution of behavioral NTA, especially in saccade choice, to “bottom up” signals in any visual pathway is that it does not reliably manifest itself in saccade latency. A NTA in latency for saccades directed to single targets has been reported by Kristjansson et al. (2004), but four other studies did not report an asymmetry (Honda 2002; Rafal et al. 1990, 1991; Walker et al. 2000; see DISCUSSION). If asymmetry in choice occurred because of the relative weakness of nasal visual signals, this weakness would be expected to affect latencies, because in simple saccade paradigms, stimuli with lower signal strength (e.g., contrast) generally produce slower responses (Wheless et al. 1967).

In this study, we examine the validity of NTA as a marker for retinotectal mediation. To do so, we exploit the fact that the retinotectal pathway is unable to respond to color contrasts once embedded in luminance noise, because it does not show color opponency (Marrocco and Li 1977; Schiller and Malpeli 1977). Our experiments involve S cone stimuli, a particular type of color contrast, visible to the S cone pathway only, which does not project directly to the superficial layers of the SC. This technique has been successfully applied to probe the role of the retinotectal route in various saccade-related phenomena, including the oculomotor distractor effect, the fixation offset effect, saccadic inhibition of return, and the difference in latency between antisaccades and prosaccades (Anderson and Carpenter 2008; Anderson et al. 2008; Sumner et al. 2002, 2004, 2006; Sumner 2006). Mediation by the retinotectal pathway predicts an absence of temporal preference for S cone

stimuli, whereas evidence for NTA with S cone stimuli would suggest the existence of other sources of functional NTA in humans. Additionally, we further test for the presence of NTA in saccade latencies.

Five experiments were conducted in this study. The first experiment was a replication of Posner and Cohen’s original finding, with relatively high contrast luminance stimuli. The second experiment tested for the presence of the naso-temporal asymmetry for saccades to S cone stimuli. To ensure that our stimuli were truly invisible to the superior colliculus (i.e., were free from achromatic signal), we used low contrast tritan stimuli embedded in spatio-temporal luminance noise. For comparison, *experiment 2* also involved a condition with low-contrast luminance stimuli (in luminance noise), equated in subjective salience with that of the S cone stimuli. In a third experiment, we added tritan signals to the luminance signals used in *experiment 1* to test whether the presence of chromatic signals was able to increase the amplitude of the nasal-temporal asymmetry. Finally, two follow-up experiments were designed to confirm the absence of NTA in temporal order judgments (*experiment 4*) and to test again for the presence of NTA in saccade latencies in the presence of single target trials only (*experiment 5*).

## METHODS

### Observers

In total, 77 naive observers participated in one only of the five experiments, including 12 in *experiment 1*, 24 in *experiment 2* (12 for each of the 2 conditions: S cone and luminance), 9 in *experiment 3*, 24 in *experiment 4* (12 for each of the 2 conditions: S cone and luminance), and 8 in *experiment 5*. Since the task requires free choice between responses, it was important that all participants were naive to the purpose of the study and performed only one condition each. All had normal or corrected to normal vision.

### Material

Stimuli were displayed on a Sony Trinitron 19 inch GDM-F400T9 monitor, driven by a Cambridge Research Systems ViSaGe graphics board at 100 Hz, calibrated with a Cambridge Research Systems ColorCal and associated software. Stimuli were presented monocularly, to the left or right eye alternatively, with 72-cm viewing distance. Eye movements were recorded using the CRS high speed video eye-tracker sampling at 250 Hz (*experiments 1–3*) or an Applied Science Laboratories (ASL) model 504 high-speed remote infrared eye-tracker with an ASL 5000 series controller, sampling at 240 Hz (*experiments 4 and 5*). The subject’s head was stabilized by a chin rest and a head rest. The eye that was not stimulated was covered with an eye patch. The same experimental set-up was kept for all the experiments.

### Stimuli in experiments 1–3

In all experiments, stimuli were small squares (1 deg<sup>2</sup>), presented at 8-deg eccentricity either on the left or on the right of fixation, on a gray background [MacLeod-Boynton coordinates (MLB), 0.643, 0.021]. In *experiment 1*, the background was uniform with 15 cd/m<sup>2</sup>, and the stimuli had a 25 cd/m<sup>2</sup> luminance (Fig. 1).

*Experiment 2* involved lower contrast stimuli appearing on a background with 25 cd/m<sup>2</sup> average luminance. Background and stimuli were modulated with spatio-temporal noise that consisted of an array of squares (7 × 33 squares of 30 × 30 pixels, at a resolution of 1,024 × 768), whose luminance changed randomly every 10 ms

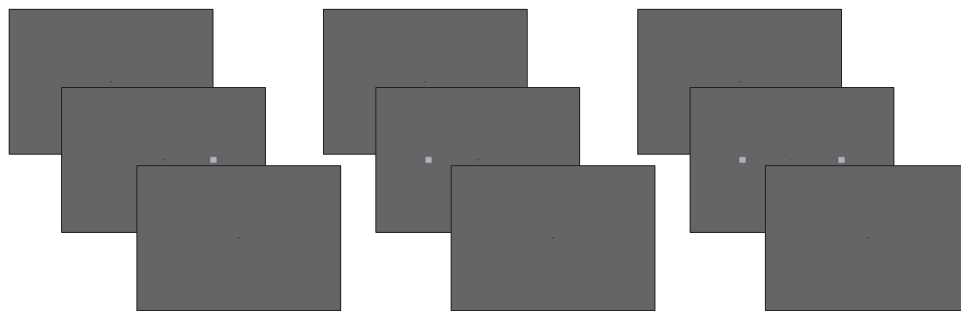


FIG. 1. The 3 main trial types illustrated for *experiment 1*. *Left*: single target trial with a single stimulus on the right. *Middle*: single target trial with a single stimulus on the left. *Right*: choice trial with both left and right stimuli. In single target trials, observers are requested to make a fast eye saccade to the direction of the stimulus. In choice trials, they are asked to move their eyes to one stimulus only, as spontaneously as possible.

within the range 24–26  $\text{cd/m}^2$  (as shown in Fig. 2). S cone stimuli were defined by making a chromatic step along the tritan dimension while keeping luminance signals equal (Fig. 2, *left panel*). Equiluminance between the background and S cone stimuli at 8-deg eccentricity was individually calibrated, using the minimum motion technique (Anstis and Cavanagh 1983; Cavanagh et al. 1987), for each eye separately. The tritan line was obtained by averaging across previous calibrations involving a similar observer population, using the method developed by Smithson et al. (2003; see also Smithson and Mollon 2004). Note that for the purposes of restricting the stimuli to chromatic channels, the equiluminance calibration is the most important, to ensure that the stimuli remain within the range of luminance noise. Luminance stimuli had 30  $\text{cd/m}^2$  on average (they carried on fluctuating with luminance noise around this mean), producing a luminance contrast that, in previous experiments conducted on a similar population, was found to be a good subjective salience match to the S cone contrast we used (Fig. 2, *right panel*). (Note, however, that for the purpose of this study, which tests for effects only within each kind of stimulus, an exact salience match between luminance and S-cone stimuli is not needed).

In *experiment 3*, we superimposed an S cone contrast onto the high contrast luminance signals from *experiment 1* on a background with 15  $\text{cd/m}^2$ . Again, the tritan angle was fixed, but equiluminance was measured individually for each eye for the S cone signal, to ensure that luminance signals of the combined stimuli were equal to those involved in *experiment 1* and only chromatic signals were added.

### Procedure in experiments 1–3

Our main factor is the stimulated eye: left and right eyes were tested in two successive blocks in counterbalanced order across participants.

*Experiments 1–3* involved three main categories of trials (shown in Fig. 1), equally probable and randomly spread across each block. Two types consisted of single target trials, in which the target was presented either on the left or on the right, and the participant was asked to make a fast saccade to that location. The third type were the critical “choice trials,” involving the presentation of a left and a right target.

In these choice trials, the observers were requested to saccade toward one stimulus only, the left or the right one, “as spontaneously as possible.” As in the original paradigm of Posner and Cohen, various delays were introduced between the left and right targets. In this experiment, seven possible delays stimulus onset asynchronies (SOA) were introduced in random order:  $-60$ ,  $-30$ ,  $-10$ ,  $0$ ,  $10$ ,  $30$ , and  $60$  ms, with positive delays meaning the right target appeared after the left target (Fig. 2). The stimuli appeared for 100 ms. A variable delay from 1 to 2 s was introduced between the disappearance of the last stimulus in one trial and the appearance of the first stimuli in the next trial. A fixation point was present throughout the trial. Observers were asked to keep their eyes on the fixation point until a stimulus appeared and then to move their eyes as fast as they could in the direction of the stimulus—or one of the stimuli in choice trials—and bring their eyes back to the fixation point for the next trial. Responses for each of the three main trial categories with each of the seven delays were measured 8 times in *experiments 1* and *3* and 10 times in *experiment 2* in random order. Unlimited breaks were offered every 2 min and between the blocks for each eye.

### Follow-up experiments

The purpose of *experiment 4* was to test the dissociation between perception and saccade choice reported by Posner and Cohen (1980). The first part of *experiment 4* consisted of a replication of *experiment 2* with a slightly different experimental design (that we thought was more compatible with the temporal order judgment task). The second part tested for the presence of an asymmetry in temporal order judgments (TOJ). Both parts were performed on the same participants, but S cone and luminance stimuli were tested on different groups. Luminance and S cone stimuli were similar to those in *experiment 2*, although the luminance noise was changing at 20 Hz instead of 100 Hz and the contrast of S cone stimuli was lower than that in *experiment 2*. Five SOAs were introduced,  $-100$ ,  $-50$ ,  $0$ ,  $50$ , and  $100$  ms, with the same conventions as above. The stimuli appeared after a variable time from the start of the trial (between 400 and 800 ms for the first stimulus) and remained visible on the screen until the end of

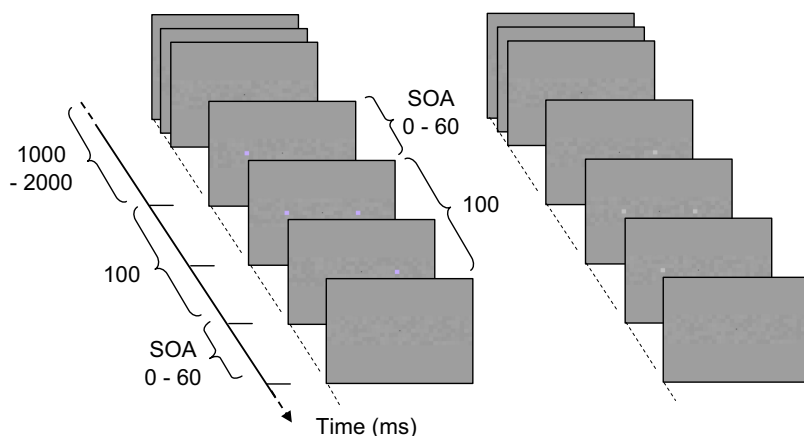


FIG. 2. Temporal sequence for choice trials in *experiment 2*. *Left*: S cone stimuli with 60-ms SOA. *Right*: luminance stimuli with  $-60$ -ms SOA. Positive and negative SOAs correspond to trials where the stimuli appear, respectively, in the left-right and right-left order.

the trial, so that a TOJ could be made for onsets only. For the TOJ, only trials with bilateral stimuli were presented, and the participants were asked to indicate which, of the left or right stimuli, appeared first. Observers were instructed to keep their eyes fixed on the fixation point, which remained present during the whole trial. Participants were not given feedback. Responses in each condition were measured 20 times. Unlimited breaks were offered every 40 trials and between each eye.

Although the single target conditions in the preceding experiments can provide a measure of any asymmetry in saccade latency to nasal and temporal targets, it is possible that the presence of choice trials might interfere with the normal process of making fast reflexive saccades. Therefore in *experiment 5*, saccade latencies were measured again when only single target trials were presented and participants had no other task but to move their eyes as fast as they could in the direction of the single stimulus. The screen background was homogeneous at a luminance of 15 cd/m<sup>2</sup>, and the left and right stimuli could appear at the positions marked by two solid guide boxes, which were continuously displayed. Luminance noise at 20 Hz was added to the boxes and stimuli, whose luminance varied from 24 to 26 cd/m<sup>2</sup>. Saccade latencies to left and right targets were measured 30 times for each stimulus type, S cone or luminance, in a random order, and for each eye in successive blocks.

### Analyses

Saccades were detected automatically off-line, all traces were checked visually, and the saccade detection was corrected if necessary. The main measure was saccade direction. Additionally, we analyzed saccadic latencies, defined as the delay between the onset of

the eye saccade and the appearance of the stimuli targeted by the eye saccade. In choice trials, latencies were measured from the appearance of the stimulus that the observer chose to saccade to. We kept all latencies  $\leq 1$  s and removed those  $< 75$  ms, which were considered to be anticipations. In choice trials, when it happened that the participants looked at both stimuli successively, the first direction was kept.

## RESULTS

### Experiment 1

Figure 3A shows the percentage of leftward saccades in choice trials for left and right eyes and for each SOA. A significant difference between left and right eyes can be observed [mean effect of eye = 19%; paired-samples 2-tailed *t*-test:  $t(11) = 2.45$ ,  $P = 0.03$ ]. On average across SOAs, leftward saccades were produced in 55% of trials with the left eye versus only 37% when the stimuli are viewed through the right eye. This confirms a relative preference for saccades directed toward stimuli viewed through the temporal hemifield compared with the nasal hemifield, as observed by Posner and Cohen.

Also, like in Posner and Cohen's original results, participants tended to look more at the first stimuli, producing a large effect of SOA on direction preferences in choice trials, best represented as a linear function. This allowed us to describe the NTA not only in terms of saccade direction preference but also in terms of time delay. To do so, we plotted the percentage of

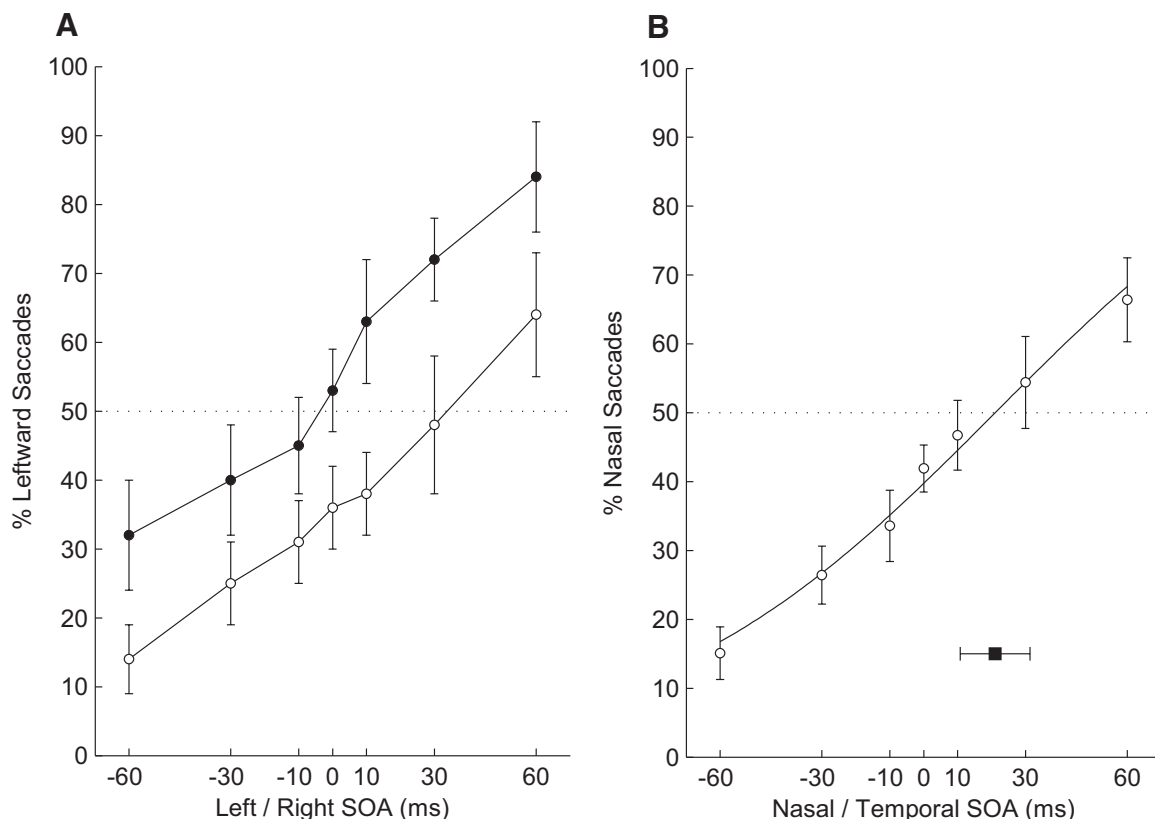


FIG. 3. Results of *experiment 1*, involving luminance stimuli on a homogenous background. *A*: percentage of leftward saccades in choice trials. Data points are averaged responses across 12 observers for left (●) and right (○) eyes and for the different SOAs (−60 to 60 ms), with error bars representing SE. Saccades are more often directed toward the stimulus presented in the temporal hemifield compared with the nasal hemifield. *B*: percentage of saccades oriented to the nasal stimuli, averaged for both eyes, as a function of the SOA between nasal and temporal stimuli (○). Data points are fitted with a sigmoid function (line). The black square is the average point of equal preference (PEP), representing the SOA that cancels the preference for temporal stimuli.

nasal-directed saccades as a function of the SOA between the nasal and temporal stimuli, which we fitted with a sigmoid (Fig. 3B). The center of the fitted curve gave us the SOA that would produce equal preference for nasal and temporal stimuli (50% nasal saccades). This value, referred to in this article as the point of equal preference (PEP) is another measure of the amplitude of the NTA. In *experiment 1*, the PEP was at 21 ms on average and could be interpreted as the additional delay that should be imposed to temporal stimuli to cancel the NTA for saccade direction preference.

Analyses of saccade latency in *experiment 1* showed no significant difference between saccades made to the nasal and temporal direction, either in choice trials (nasal saccades shorter by 8 ms on average) or in single target trials [nasal saccades longer by 5 ms on average, which is not different from 0, paired-samples 2-tailed  $t$ -test:  $t(11) = 1.02$ ,  $P = 0.33$ , and is smaller than the PEPs, paired-samples 1-tailed  $t$ -test:  $t(11) = 2.06$ ,  $P = 0.03$ ]. No correlation was observed between individual PEPs and individual latency differences between nasal and temporal targets.

### Experiment 2

*Experiment 2* tested whether the NTA pattern found in *experiment 1* would also be found for S cone and luminance signals, both low contrast and embedded in luminance noise. Figure 4 shows this to be the case [paired-samples 1-tailed  $t$ -test, S cone:  $t(11) = 2.04$ ,  $P = 0.03$ ; luminance:  $t(11) = 3.14$ ,

$P = 0.005$ ]. The amplitude of the naso-temporal effect does not differ significantly between the two types of stimuli [S cone: mean effect of eye = 20%; luminance: mean effect of eye = 26%; 2-sample 2-tailed  $t$ -test:  $t(11) = 0.52$ ,  $P = 0.6$ ]. PEPs for *experiment 2* were at 21 and 24 ms for S cone and luminance stimuli, respectively (graph not shown).

### Experiment 3

Results for combined tritan and luminance signals are shown in Fig. 5. They show the presence of naso-temporal asymmetry [mean effect of eye: 44 ms; paired-samples 2-tailed  $t$ -test:  $t(8) = 6.01$ ,  $P = 0.0001$ ], whose amplitude was significantly larger than that obtained in all three conditions reported above. In particular, the naso-temporal effect was larger than that obtained in *experiment 1*, produced by equivalent luminance signals alone [2-sample 2-tailed  $t$ -test:  $t(21) = 2.64$ ,  $P = 0.03$ ]. The PEP for *experiment 3* was at 51 ms.

Saccade latency analysis in choice trials showed a difference [nasal saccades >19 ms on average, paired-samples 1-tailed  $t$ -test:  $t(8) = 2.24$ ,  $P = 0.03$ ], but no significant difference was observed in single target trials (nasal saccades >5 ms on average). Furthermore, a significant difference was observed between PEPs and the latency difference in single target trials [paired-samples 2-tailed  $t$ -test:  $t(8) = 3.6$ ,  $P = 0.007$ ]. As in *experiment 1*, no correlation was observed between individual PEPs and individual latency differences between nasal and temporal targets, neither for choice nor for single target trials.

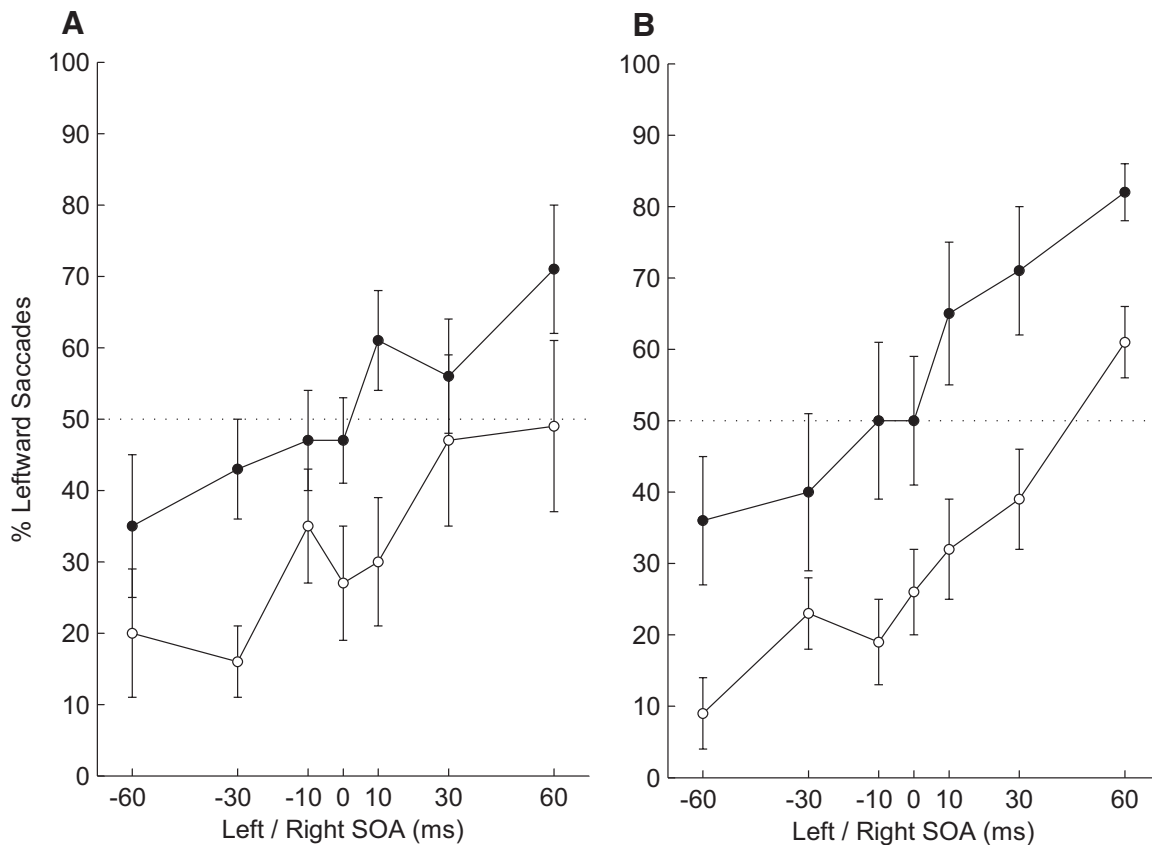


FIG. 4. Percentage of leftward saccades in choice trials for *experiment 2*, involving low contrast S cone stimuli (A) or luminance stimuli (B) embedded in spatio-temporal luminance noise. Data points are averaged responses across 12 observers for left (●) and right (○) eyes and for the different SOAs (−60 to 60 ms), with error bars representing SE. Saccades directed to S cone and luminance stimuli both show evidence for naso-temporal asymmetry.

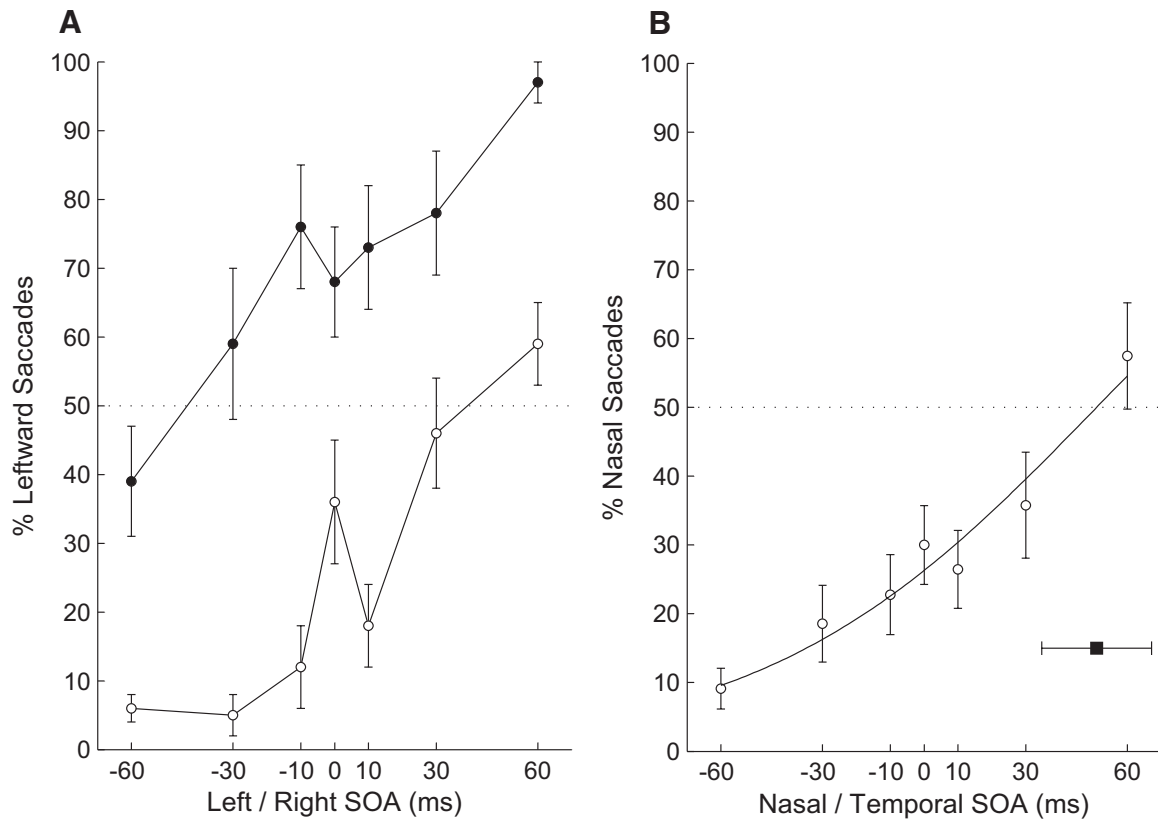


FIG. 5. Results of *experiment 3*, involving S cone stimuli superimposed on luminance signals on a homogenous background. *A*: percentage of leftward saccades in choice trials. Data points are averaged responses across 9 observers for left (●) and right (○) eyes and for the different SOAs (−60 to 60 ms), with error bars representing SE. The asymmetry is larger than in *experiment 1*. *B*: percentage of saccades oriented to the nasal stimuli, averaged for both eyes, as a function of the SOA between nasal and temporal stimuli (○) with the average PEP (black square).

#### Follow-up experiments

For saccade direction preference, the pattern of results in *experiment 4* confirmed those obtained in *experiment 2*, with both S cone and luminance stimuli producing a naso-temporal asymmetry [paired-samples 1-tailed *t*-test, S cone:  $t(11) = 1.78$ ,  $P = 0.05$ ; luminance:  $t(11) = 2.42$ ,  $P = 0.015$ , graphs not shown]. The amplitude of the naso-temporal effect did not differ significantly between the two types of stimuli (S cone: mean effect of eye = 6%; luminance: mean effect of eye = 12%; 2-sample 2-tailed *t*-test:  $P = 0.4$ ). PEPs were at 11 and 17 ms for S cone and luminance stimuli, respectively.

For the temporal order judgments, the percentage of responses in which the nasal stimulus was reported first was calculated for the five delays introduced between the nasal and temporal stimuli. The corresponding curves were fitted individually with a sigmoid to define the point of subjective simultaneity (PSS). NTA in preference predicts positive PSS values, indicating that nasal stimuli were perceived later than the temporal stimuli. In contrast, the mean PSSs were −10 ms for S cone stimuli and −1 ms for luminance stimuli and not significantly different from zero (graphs not shown). No correlation was found between PSSs and PEPs, either for S cone or luminance stimuli. These results provide no evidence for a perceived temporal discrepancy between nasal and temporal signals and replicate Posner and Cohen's finding of a dissociation between saccade choice and TOJ, in this case for both luminance and S cone stimuli.

Saccade latencies in *experiment 5* showed no evidence for NTA (data not shown). In S cone trials, average saccade latencies across the eight participants were 337 and 328 for nasal and temporal stimuli, respectively, showing a 9-ms difference that was not significant [paired-samples 2-tailed *t*-test,  $t(7) = 1.29$ ,  $P > 0.2$ ]. In luminance trials, average saccade latencies were 298 and 301 for nasal and temporal stimuli, respectively, and were not significantly different [paired-samples 2-tailed *t*-test,  $t(7) = 0.64$ ,  $P > 0.5$ ]. The only significant effect was that of signal type, with longer latencies for S cone stimuli [mean effect = 30 ms; paired-samples 2-tailed *t*-test,  $t(7) = 2.73$ ,  $P < 0.03$ ], as expected (Anderson et al. 2008; Bompas and Sumner 2008).

#### DISCUSSION

##### NTA for choice saccades

Our first result is the confirmation of the original finding of Posner and Cohen (1980) for luminance stimuli (*experiment 1*), even in the presence of luminance noise (*experiments 2 and 4*). Given that certain manifestations of behavioral NTA, such as the distractor effect and attentional cueing, have not always been replicated in the past (Sumner et al. 2002), it is worth mentioning that some departures from the paradigm described in this study caused a failure to replicate the NTA for saccade choice in preliminary studies. In particular, variability in SOA between left and right stimuli and participants' inexperience of saccade tasks seemed necessary for obtaining a reliable effect.

This could be because any factor that helps participants keep track of the saccades they have made with respect to any expectation they have formed (such as the expectation to make 50% choices to left and right with simultaneous stimuli) may encourage participants to try to strategically adjust the numbers of saccades they make to each side. In this study, verbal instructions given to the participants encouraged them to think about something else while doing the task and not to strategically interfere with their spontaneous behavior.

Importantly, the fact that the amplitude of the effect depends on the nature of the stimuli (*experiment 1* vs. *experiment 3*) supports Posner and Cohen's conclusion that the asymmetry in saccade choice does not reflect only a motor preference for saccading centrifugally (or away from the eye patch). Their conclusion relied on two control experiments, in which no evidence of NTA occurred for central visual stimuli, and only a small tendency was found for binaural auditory targets (Posner and Cohen 1980) and was subsequently supported by the presence of NTA for attentional shifts as well as for saccades.

Our results also replicated the symmetry for TOJs (*experiment 4*) and confirmed the dissociation observed by Posner and Cohen between saccade preferences and these perceptual judgments.

#### *Several sources of NTA in human visual pathways*

Our main finding is the ability for S-cone signals alone to induce a NTA for saccade direction preference (*experiments 2* and *4*). Moreover, we found that the presence of S-cone signals added to luminance signals (*experiment 3*) enhanced the effect. This shows that direct projection to the superior colliculus is not necessary for the production of the NTA and suggests the involvement of other sources of NTA. In this case, the presence of behavioral NTA, like that observed in attention studies (Rafal et al. 1989, 1991), blindsight (Dodds et al. 2002; Rafal et al. 1990) or face perception (de Gelder and Stekelenburg 2005), could not be considered as the exclusive signature of the retinotectal pathway, as already suggested for blindsight (Walker et al. 2000). Our results do not support the idea that the retinotectal pathway is the major source of NTA, given that our luminance stimuli did not produce significantly bigger asymmetries than our S cone stimuli (*experiment 2*).

#### *Retinogeniculostriate pathway: NTA in activity?*

Since the NTA for saccade choice does not originate (at least exclusively) from the retinotectal route, what alternative asymmetric mechanism could be responsible for it? At first sight, the retinogeniculostriate pathway seems to be the most straightforward explanation. The evidence for anatomical NTA in the retina (Curcio and Allen 1990; Perry and Cowey 1985), LGN (Connolly and Van Essen 1984) and V1 (Tychsen and Burkhalter 1997) would argue in favor of this conclusion. One plausible line of argument would be that the larger representation of the temporal visual field in the sensory pathway ensures a higher neural response to the temporal stimulus compared with the nasal stimulus. In this scenario, the temporal domination could be equivalent to a higher intensity. Although this scenario cannot be rejected, at least two facts cast doubt on it. First, there is no evidence for NTA in discrimination threshold

at the eccentricities relevant in behavioral studies of NTA (8–10 deg; Anderson et al. 1991). Second, although Sylvester et al. (2007) have observed NTA in BOLD responses in SC (that could be attributable to an asymmetry in the size of the hemiretinae), they reported no asymmetry for LGN and visual cortex.

#### *Retinogeniculostriate pathway: NTA in processing time?*

Another possible scenario would be that the NTA originates from differences in processing times rather than activity levels. The use of variable SOAs confirmed that the NTA can be canceled by delaying the stimuli in the temporal field. Does this mean that the transmission time of nasal signals is longer than that of temporal signals? The absence of NTA for TOJs, as reported by Posner and Cohen and confirmed in *experiment 4*, does not bring any support to this hypothesis. However, the relationship between TOJ and differences in processing times is known to be indirect (see Cardoso et al. 2007 for a review). In particular, it has been observed that differences in processing times between the magnocellular and S cone pathways are reflected in manual and saccadic response times but seem to leave perceived times unaffected (Bompas and Sumner, 2008). Thus contrary to Posner and Cohen's conclusions, the dissociation between asymmetry in responses and symmetry in TOJs is not a sufficient condition to rule out the mediation of response asymmetry by differences in geniculostriate processing times. A better test for this hypothesis is to compare saccade latencies.

A delay in processing time in any sensory pathway that supplies important information about saccade targets ought to produce a delay in saccade initiation to those targets. We found no evidence for an NTA in latency for saccades to single targets. The only asymmetry in latency we found was for choice trials in *experiment 3* (Fig. 6A). However, this comparison is confounded by the frequency difference between nasal and temporal saccades. Moreover, some oculomotor distractor effect is likely to occur between the two targets and the asymmetry could be caused by a larger distractor effect from the temporal stimuli, as reported in Walker et al. (2000). It is possible that the presence of luminance noise may have washed out or masked a potential asymmetry in latency by increasing all latencies (300 ms on average for luminance stimuli), but it is important to note that the NTA in choice occurred both with and without luminance noise.

Thus the symmetry of latencies in single target trials (along with the symmetry in TOJ) in our study does not leave much room for the hypothesis that faster processing time for inputs from the temporal hemifield can account for the larger proportion of saccades to the temporal side. Rather, the fact that PEP shows no correlation with latency or PSS suggests that these different measures rely on different mechanisms. It should be noted as well that symmetrical saccade latency also seems inconsistent with our first scenario, in which temporal domination is equivalent to an intensity asymmetry, since more intense stimuli are also known to produce faster responses (Bell et al. 2006; Doma and Hallett 1988; Wheelless et al. 1967). For these reasons, we conclude that NTA in choice is unlikely to be produced simply by an imbalance in early visual pathways, either in the retinogeniculostriate or in the retinotectal pathways.

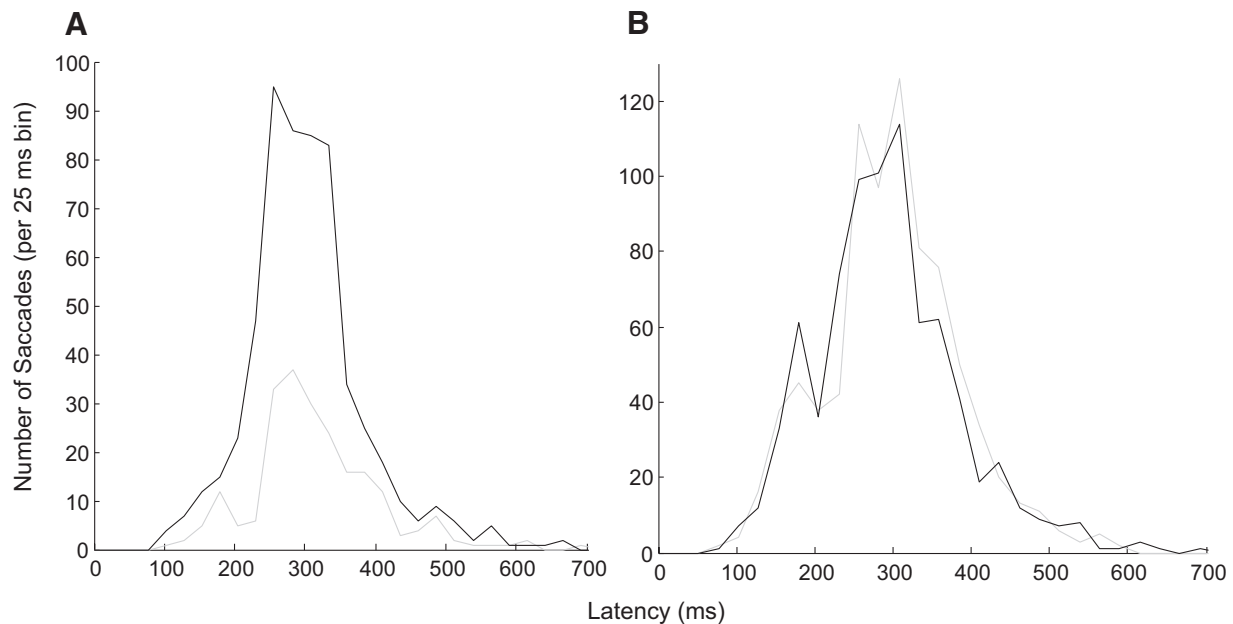


FIG. 6. Latency distributions in choice (A) and single target trials (B) for saccades made in direction of the nasal (gray line) or temporal (black line) stimulus in *experiment 3*. Note the frequency difference between nasal and temporal saccades in choice trials (A), which spreads all over the latency range. Note also the presence of an early mode in all conditions, which although they are not at extremely short latency, may represent express saccades. Similar patterns were obtained in all the other experiments.

The absence of NTA in single target trials contrasts with the 20-ms difference reported by Kristjansson et al. (2004) and a smaller difference reported by Walker et al. (2000) for hemianopic patients for the preserved visual hemifield of each eye [mean effect of eye = 10 ms; paired-samples 1-tailed  $t$ -test:  $t(5) = 1.98$ ,  $P = 0.052$ ]. However, the symmetry we found is consistent with the absence of NTA reported in earlier studies for normal observers (Honda 2002; Rafal et al. 1990, 1991; Walker et al. 2000). Note that these absences can not be caused by lack of power, since Kristjansson et al. (2004) derived their conclusion from 6 participants (60 saccades each for each hemifield), whereas Rafal et al. (1991) obtained no significant difference (actually temporal saccades were 11 ms longer) with 20 participants (80 saccades each for each hemifield), and Honda (2002) tested 12 participants (120 saccades each for each hemifield). More probably, the discrepancies across studies may be attributed to variations in the experimental conditions. In all previously mentioned studies, saccades to single targets were mixed with other trial types, manipulating the task (antisaccades and prosaccades in Kristjansson et al. 2004), the presence of distractor and cues (Rafal et al. 1990, 1991; Walker et al. 2000), and the duration of gap intervals (Honda 2002). If the NTA does indeed depend on task demands, occurring only in more complex situations such as switching between prosaccades and antisaccades (Kristjansson et al. 2004), this is consistent with our conclusion that it does not simply reflect a low level asymmetry in visual pathways. It is also worth noting that the asymmetry reported for hemianopic patients (Walker et al. 2000) could reflect a facilitation for saccading away from their blind field. Unfortunately, since these patients cannot make the saccade choice task, being aware of one visual hemifield only, this latency asymmetry cannot be compared with any asymmetry in choice.

#### NTA in target selection

If the NTA does not reflect imbalance at an early sensory level, it may originate in higher visual or visuo-motor processes associated with target selection. This scenario is compatible with symmetric discrimination thresholds and TOJs, which may rely on perceptual processes that occur independently from, or earlier than, the sensorimotor interface. It is also compatible with asymmetric antisaccade costs (Kristjansson et al. 2004) and even theoretically compatible with asymmetric BOLD responses to visual stimuli in the SC (Sylvester et al. 2007); although these fMRI data are most easily explained by a sensory asymmetry, it is possible that it arose through asymmetric saccade activation responses in deeper SC layers or from the need to suppress such saccades.

However, there is no evidence that signals reaching target selection stages contain information about which eye has supplied these signals, making it difficult to explain how a stimulus-related NTA could arise that is not present in the visual pathways. There is also the question of whether asymmetry in target selection can accommodate symmetric saccade latencies. The activity level of many saccade-related neurons is generally thought to be linked to saccade latency (Bell et al. 2006; Dorris et al. 1997), but there seem to exist other neurons whose activity could be linked to the selection of a saccade but not to its initiation (Basso and Wurtz 1998; Glimcher and Sparks 1992). Thus there is the possibility that asymmetry in this population might produce the temporal preference but no latency asymmetry.

More generally, our results are consistent with the idea that bottom-up luminance signals, in particular those from the retinotectal route, do not have a special status for saccadic target selection. Saccades to many types of stimulus may all share cortical target selection mechanisms and subsequent cortico-collicular projections. However, the issue is not simple.

On the one hand, participants can make normal saccades toward S cone stimuli and S cone stimuli do produce some saccade effects often held to be “bottom-up,” such as the fixation offset effect (Anderson and Carpenter 2008; Sumner et al. 2006) and some antisaccade cost (Anderson et al. 2008). However, on the other hand, S cone stimuli do not behave entirely like luminance stimuli, producing smaller oculomotor distractor effects (Sumner et al. 2002), smaller antisaccade costs (Anderson et al. 2008), and smaller saccadic inhibition of return (Sumner et al. 2004). Thus the way different types of information are used for target selection and saccadic generation remains to be resolved.

#### *NTA in attention orienting*

Another possibility could be that NTA in saccade choice arises from an attention bias that favors the temporal visual hemifield. This hypothesis would be compatible with the observed asymmetric cueing effects (Berger and Henik 2000; Rafal et al. 1989, 1991), because the cue would be expected to be more efficient if attention is already biased to its direction. If a peripheral visual stimulus is needed to show the attentional bias, this hypothesis would also explain why the NTA was not found for saccades to central visual cues or auditory signals (Posner and Cohen 1980). However, it is unclear whether this interpretation can account for the results of *experiment 3*, where the amplitude of NTA was larger for signals containing both color and luminance information than for luminance signals alone.

More importantly, according to the widely held view that attention reduces response latency (Posner and Cohen 1980), an attentional bias toward the temporal hemifield should predict shorter saccadic latency to temporal targets, in both single target trials (this study) and in neutral trials of cueing studies (Rafal et al. 1991). As discussed above, such latency asymmetry has not been found. Indeed, the fact that NTA is found for saccadic target selection, distractor effects, and attentional cueing, but not for saccadic latency, shows a dissociation that could have interesting implications for the view that attention is tightly coupled with saccade selection and generation (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Kowler et al. 1995; Kristjánsson et al. 2001; Kustov and Robinson 1996; Rizzolatti et al. 1994). It is possible that attention may be linked to saccade selection processes but not so closely to saccade generation.

#### *General conclusion*

We showed that signals invisible to the retinotectal pathway induce a NTA for choice saccades to bilateral stimuli. Thus there must be another source of asymmetry either in other visual pathways or in the process of triggering saccades to visual targets. Importantly, this argues against the use of NTA as a diagnostic tool for the involvement of the retinotectal route. Furthermore, the symmetry we find for saccade latency makes it unlikely that the observed NTA in saccade choice originates from any early visual pathway and rather suggests an asymmetry at the target selection level.

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