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The oculomotor distractor effect in normal and hemianopic vision

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The present study investigated the inhibitory effect of visual distractors on the latency of saccades made by hemianopic and normal human subjects. The latency of saccades made by hemianopic subjects to stimuli in their intact visual field was not affected by visual distractors presented within their hemianopic field. In contrast, the latency of saccades made by normal subjects was increased significantly under distractor conditions. The latency increase was larger for temporal than nasal distractors. The results are inconsistent with previous proposals that the crossed retinotectal pathway from the nasal hemiretina to the superior colliculus may mediate a blindsight inhibitory effect when distractors appear within a hemianopic temporal visual field. Instead, the distractor effect appears to reflect the normal processes involved in saccade target selection which may be mediated by a circuit involving both cortical and subcortical structures.

Keywords: blindsight; saccade; distractor; superior colliculus

1. INTRODUCTION

'Blindsight' is the term used to describe the ability shown by some patients with cortical blindness to process visual stimuli presented within their blind field in the absence of conscious awareness (Sanders *et al.* 1974). One simple technique used to demonstrate residual visual functioning in blindsight involves recording eye movements (saccades) made to stimuli presented within the patients' apparently blind visual field. A number of eye-movement studies have reported a relationship between the amplitude of eye movements and the eccentricity of visual stimuli presented within a hemianopic visual field (Pöppel *et al.* 1973; Weiskrantz *et al.* 1974; Zihl 1980; Zihl & Von Cramon 1980; Barbur *et al.* 1988; Braddick *et al.* 1992). A slightly different approach used by Rafal *et al.* (1990) examined the latency of saccades made by hemianopic patients to stimuli presented in their intact visual field under conditions in which visual distractors appeared in the blind field. Rafal *et al.* (1990) tested three hemianopic patients under monocular viewing conditions and found that distractors in the temporal visual field increased their saccade latency, while distractors in the nasal visual field had no effect. This blindsight interference effect was observed when the distractor appeared simultaneously with the target or at short intervals prior to target onset, but not when the distractor appeared at longer intervals before the target. In contrast, the oculomotor distractor effect was not observed in a group of normal subjects and was not observed in hemianopic subjects when manual response times were recorded instead of eye movements. These findings were taken as showing that the distractor effect was specific to the oculomotor system and may be observed only when the cortical (geniculostriate) visual pathway is inoperative.

The explanation proposed by Rafal *et al.* (1990) to account for the naso-temporal asymmetry 'blindsight' oculomotor distractor effect was based on differences in the strength of the direct retinal projection to the superior colliculus (SC), a midbrain structure which is involved in the control of saccades (Sparks & Hartwich-Young 1989). The SC receives visual inputs from a number of sources including the retina, dorsal lateral geniculate nucleus (dLGN) and cortical regions such as the occipital lobe, posterior parietal lobe and frontal and supplementary eye fields (FEFs and SEFs) (see Schall (1995), for a review). Neuroanatomical studies have shown that the small crossed retinotectal projection from the nasal hemiretina (temporal visual field) has a greater number of ganglion cells projecting to the SC than does the temporal hemiretina (nasal visual field). Rafal *et al.* (1990) argued that, under monocular viewing conditions, visual stimuli presented in the patients' temporal visual field would produce a greater interference effect due to the numerical superiority of the nasal hemiretina projection to the SC. The absence of a distractor effect for the normal subjects was interpreted as showing that the effect may depend on 'an isolated extrageniculate visual system' which may be 'critically dependent on the absence of perceptual awareness of the distractor' (Rafal *et al.* 1990, p. 120).

However, the retinotectal explanation for the naso-temporal asymmetry in the blindsight distractor effect has been questioned on anatomical grounds (Williams *et al.* 1995). Williams *et al.* (1995) noted that much of the evidence for a larger nasal hemiretina projection to the midbrain than to the dLGN was based on indirect evidence from the cat (Sterling 1973). An earlier study by Perry & Cowey (1984) found little evidence of naso-temporal asymmetry, although it was thought possible that the labelling technique used may not have detected all of the retinal ganglion cells. Williams *et al.* (1995) performed a cellular labelling study to examine possible

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Table 1. *Details of patients*

(HH, homonymous hemianopia; upper, upper quadrantanopia; lower, lower quadrantanopia; R, right; L, left. Time post-onset indicates the interval between the lesion and date of testing. MMS represents the score on the mini mental state questionnaire. Neglect indicates the presence of visual neglect assessed using the behavioural inattention test (Wilson *et al.* 1988).)

case	age (years)	sex	field defect	time post-onset	MMS	visual neglect?
hemianope 1	30	female	RHH	25 years	30/30	no
hemianope 2	83	male	R upper	6 months	30/30	no
hemianope 3	37	male	R lower	7 years	30/30	no
hemianope 4	49	female	R lower	7 years	30/30	no
hemianope 5	34	female	LHH	6 years	30/30	no
hemianope 6	60	male	LHH	1 year	30/30	no

naso-temporal asymmetries in the primate (*Macaca mulatta*) visual system. Although they found more retinal ganglion cells in the projection from the nasal than temporal hemiretina, this asymmetry was observed for both the small direct projection to the midbrain and for the much larger projection to the dLGN which projects to the visual cortex. Williams *et al.* (1995) argued that their findings invalidated Rafal *et al.*'s (1990) retinotectal hypothesis of the temporal field distractor effect as 'there is nothing numerically anomalous about the projection to the midbrain' (p. 585).

The demonstration of an oculomotor blindsight distractor effect in some hemianopic subjects is in contrast to an earlier eye-movement investigation of the well-known blindsight subject G.Y. (Barbur *et al.* 1988). Barbur *et al.* (1988) found that distractors in G.Y.'s blind field did not influence saccades made towards stimuli in his intact visual field under binocular viewing conditions. However, an unpublished attempt to replicate Rafal *et al.*'s (1990) study did observe a saccadic distractor effect for G.Y. but not for a group of hemianopes similar to those tested by Rafal *et al.* (1990) (Cochrane 1995; see Weiskrantz 1997, p. 67). Importantly, it was thought that G.Y. might have had some 'awareness' of the distractors in his hemianopic field (L. Weiskrantz, personal communication). This would suggest that the distractor effect might not be dependent on the absence of perceptual awareness for stimuli in the blind field.

It should be noted that the absence of a distractor effect in the normal subjects tested by Rafal *et al.* (1990) contrasts with numerous reports of a saccadic distractor effect observed under binocular viewing conditions. Lévy-Schoen (1969) first noted an increase in saccade latency (of some 20–40 ms) in normal human subjects when stimuli appeared bilaterally in both visual fields. Further studies have replicated this effect and shown it to be a highly consistent finding (Findlay 1983) which is influenced by the spatial and temporal relationship of the distractor and target (Walker *et al.* 1995, 1997). A consistent finding is that distractors in the opposite visual field to the target increase latency but have no influence on saccade metrics. These behavioural effects are thought to be consistent with inhibitory processes operating within the deep layers of the SC (Munoz & Wurtz 1993*a*,*b*, 1995*a*,*b*; Olivier *et al.* 1999). Such inhibitory processes may also operate within other structures known to be involved in saccade generation such as the lateral intraparietal lobe (LIP) and the FEFs and SEFs (see Wurtz & Goldberg (1989) for a review). However, as all of the studies of normal subjects have used binocular viewing conditions it is not possible to examine the presence of a naso-temporal asymmetry in the distractor effect and it remains a possibility that a naso-temporal asymmetry is only observed with hemianopic subjects.

The present investigation was designed to examine further the saccadic distractor effect in hemianopic and normal subjects under monocular viewing conditions. One prediction of the 'retinotectal' hypothesis of the distractor effect is that hemianopic subjects may show a greater distractor interference effect than normal subjects because damage to the cortical visual pathways results in a greater reliance on the retinotectal pathway for saccadic orientating. However, if the distractor effect depends on the cortical pathways then the opposite prediction is made and normal subjects should show a stronger distractor effect than hemianopic subjects. The anatomical evidence of the numerical superiority of projections arising from the nasal hemiretina (to the midbrain, dLGN and cortex) also predicts a greater interference effect when distractors appear in the temporal visual field. Finally, flickering distractors may produce a greater interference effect than do static distractors due to enhanced sensitivity of visually responsive neurons (e.g. in the SC) (Schiller & Koerner 1971) to flickering stimuli.

2. METHODS

(a) *Subjects*

All neurological patients and normal controls gave informed consent to participating in the study. Six hemianopic patients (three males and three females) with cortical brain damage following infarct or haemorrhage/haematoma, age range 30–83 years and eight normal people (five females and three males), age range 20–35 years, acted as subjects. Tables 1 and 2 show the clinical details for each patient. The visual field defect of each patient was plotted using a Humphrey automated perimeter and the resulting field plots are displayed in figure 1.

(b) *Apparatus and stimuli*

Stimuli were generated by a Macintosh IICi using Superlab^{TM} software and were presented on a 16 in (1 in = 0.0254 m). colour monitor operating at 60 Hz. Eye movements were recorded at a rate of 250 Hz using an infrared video-based eye tracker (SensoMotoric Instruments^{TM}, GmbH). A chin rest was

Table 2. *Details of patients*

(CI, cerebral infarct and CH, cerebral haemorrhage/haematoma. LH, left hemisphere and RH, right hemisphere.)

case	aetiology	lesion volume (cm^3)	lesion location
hemianope 1	CI	262.90	whole LH including striate cortex
hemianope 2	CI	42.30	LH temporoparietal region
hemianope 3	CH	10.90	LH white matter and cortex of primary visual cortex
hemianope 4	CH	10.40	LH white matter and cortex of primary visual cortex
hemianope 5	CH	9.45	RH white matter and cortex of primary visual cortex
hemianope 6	CI	11.56	RH white matter and cortex of primary visual cortex

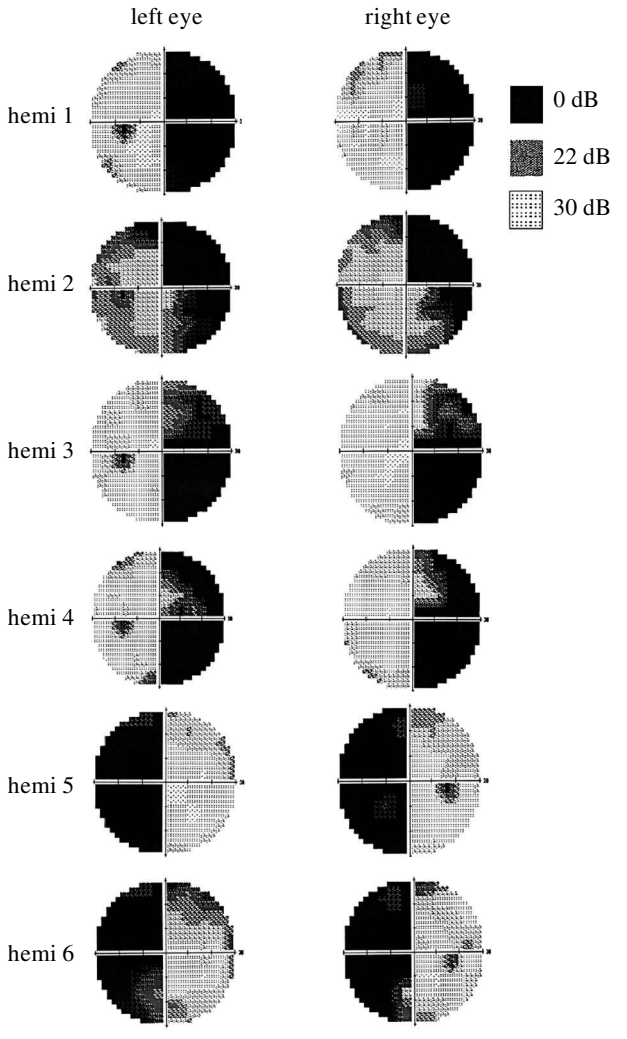

Figure 1. Visual fields for each patient measured with a Humphrey automated perimeter. The central 30° of the visual field was examined using the standard fastpack 30–2 program. The greyscale image denotes the threshold levels (where 0 db = 300 cd m^{-2}, 22 db = 3 cd m^{-2} and 30 db = 0.3 cd m^{-2}).

also used to restrict head movements and the viewing distance was 57 cm. The eye position signal was digitized and written to disk for later off-line analysis. An automated calibration routine was performed at the start of each block of trials. Subjects tracked a small calibration stimulus which moved from the centre of the screen to positions along the horizontal axis to the left and right of centre. A second calibration was then performed as a 'validation' routine which provides an average measure of the spatial accuracy of the calibration ($<0.5°$).

The eye-movement records for each subject were analysed and viewed off-line on a trial by trial basis. Any records contaminated by blinks, incorrect fixation or head movements were excluded from further analysis. Saccades were detected using an automatic velocity threshold criteria which defined the start of a saccade as a change in eye position over two consecutive samples which exceeded a velocity of 25° s^{-1}. A cursor indicating the start of each saccade enabled a visual confirmation that the detection algorithm had detected the first primary saccade in each record correctly.

(c) *Stimuli*

A black fixation cross (1°) was presented in the centre of the VDU screen. The saccade targets were small black open circles (0.5°) and the distractors were filled black circles (0.5°). Stimuli were presented against a white background (120 cd m^{-2}) and the target and distractor luminances were 0.8 cd m^{-2}. Stimuli were presented at eccentricities of 5 and 10° along a horizontal axis level with fixation. The distractors were static (they appeared and stayed on) or were flickered (square wave) on and off at 12.5 Hz.

(d) *Procedure*

Before each block of trials, the subjects were informed whether the targets would appear to the right or left of fixation. At the start of each trial the fixation cross appeared in the centre of the screen. After a random foreperiod (600–1000 ms in steps of 100 ms), the fixation cross was removed (zero gap) and the target simultaneously appeared randomly at one of two eccentricities for 480 ms. The random duration of the foreperiod and location of the target were designed to prevent the participants from preparing a saccade in advance of the presentation of the target. At the end of each trial the screen was cleared and an intertrial delay of 1 s occurred.

In some trials a single target appeared, whereas in others a distractor appeared simultaneously at an equal eccentricity in the opposite visual field. Saccades were made to targets which appeared in either the nasal or temporal visual field under three different distractor conditions (no distractor, static distractor or flickering distractor) producing a total of six different conditions. Static distractors appeared with the target and stayed on for the duration of the trial and flickering distractors also appeared with the target but were flashed at a rate of 12.5 Hz. This flicker rate was chosen as it enables some two to three distractor onsets to occur during the expected saccade latency period of some 200 ms (Carpenter 1988).

Testing took place under monocular viewing conditions, with one eye being covered with an eye patch. Subjects completed ten to 20 practice trials prior to the main testing session. For hemianopic subjects, the targets were always presented in their

Table 3. *Mean saccade latency (ms) and s.e.m. (in parentheses) for six hemianopic subjects*

(Nasal and temporal refer to the visual field in which the saccade target appeared (the latency is collapsed for two target eccentricities). The latency difference is the mean latency from the distractor trials minus the mean latency from the no-distractor trials (ms).)

	no distractor		static distractor		flickering distractor	
	nasal target	temporal target	nasal target	temporal target	nasal target	temporal target
hemianope 1	242.0 (6)	224.1 (6)	247.5 (6)	223.8 (5)	233.0 (7)	225.3 (7)
latency difference	—	—	+5.5	−0.3	−9.0	+1.2
hemianope 2	240.0 (6)	252.0 (7)	243.2 (6)	246.8 (6)	250.6 (5)	243.0 (8)
latency difference	—	—	+3.2	−5.2	+10.6	−9.0
hemianope 3	264.7 (3)	258.6 (4)	257.2 (4)	260.1 (4)	265.1 (4)	263.2 (7)
latency difference	—	—	−7.5	+1.5	+0.4	+4.6
hemianope 4	246.0 (10)	223.6 (6)	254.0 (9)	226.9 (6)	239.0 (8)	216.6 (6)
latency difference	—	—	+8.0	+3.3	−7.0	−7.0
hemianope 5	220.4 (3)	213.0 (3)	217.7 (5)	208.7 (4)	210.4 (5)	213.7 (3)
latency difference	—	—	−2.7	−4.3	−10.0	+0.7
hemianope 6	297.5 (10)	276.4 (11)	275.4 (9)	265.1 (8)	298.7 (11)	246.8 (9)
latency difference	—	—	−22.1	−11.3	+1.2	−29.6
overall mean	251.8 (11)	241.3 (10)	249.2 (8)	238.6 (9)	249.5 (12)	234.8 (8)

sighted hemifield and the distractors always appeared in their blind field. Each block contained 20 single, 20 static distractor and 20 flickering distractor trials and each subject completed four blocks of 60 trials producing a total of 240 trials per subject. Hemianopic subjects completed two blocks of nasal target trials and two blocks of temporal target trials and the order of testing was randomized across subjects (nasal–temporal or temporal–nasal). Normal subjects completed four blocks of trials (left eye nasal targets, left eye temporal targets, right eye nasal targets and right eye temporal targets) and the order of testing was counterbalanced across subjects.

All subjects were given the same instructions, which emphasized the required saccade direction for that block. The instructions were as follows: 'Please look at the small cross when it appears in the centre of the computer screen. Small circles will then appear to the left (right) side of the cross and you should move your eyes as quickly as possible to that circle. On some trials a second circle may also appear to the right (left) of the cross which you should ignore. So, you should move your eyes to the left (right) and never move your eyes to the right (left). Try to move your eyes as quickly as possible but do not anticipate the onset of the circle.'

For the hemianopic subjects, a measure of their awareness of the distractors presented in their blind field was obtained immediately following the eye-movement recording session. Each hemianope again viewed the stimulus display under monocular viewing conditions and was asked to report the number of stimuli seen (one or two) in each of the trials. None of the hemianopes reported the presence of static or flickering distractors in any trials.

3. RESULTS

Saccades with a latency of less than 100 ms were excluded as being anticipations and those with a latency greater than 2.5 s above the mean were excluded as they were probably not stimulus driven. Records contaminated by blinks and head movements were also excluded. A total of 17% of the trials from the hemianopic subjects and 13% from the normal subjects were excluded from the final analysis. The data from the normal subjects were collapsed across eyes. As the target eccentricity was not found to influence latency for either the hemianopic or normal subjects the data were also collapsed across the target eccentricity to increase the amount of data points in each condition.

The mean saccade latencies (and s.e.m.s) for the hemianopes are displayed in table 3 and those for the normal subjects in table 4. The overall latency difference (distractor mean—no distractor mean) observed in the distractor trials is shown to indicate the magnitude of the distractor effect. The latency differences for the hemianopes varied across the subjects and distractor conditions. For example, in the static temporal distractor condition (nasal targets) three hemianopes (1, 2 and 4) showed a small latency increase, while three others (3, 5 and 6) showed an overall facilitation effect. Similarly, the latency differences observed in the static and flickering temporal distractor conditions also varied across subjects. For example, hemianope 1 showed a small inhibitory effect with static temporal distractors and a small facilitation effect with flickering temporal distractors. However, none of these individual inhibitory or facilitatory effects were found to be significant when examined (using *t*-tests) on a single-case basis. In contrast, an examination of the latency differences observed for the normal subjects (table 4) shows that a latency increase was observed consistently with distractors in the temporal visual field. A latency increase was also observed for six out of the eight normal subjects with distractors in the nasal field.

The mean latency of saccades, collapsed across subjects, with targets in the nasal visual field (temporal distractors) is displayed in figure 2*a*. The important result shown in figure 2*a* is the increase in latency for normal subjects when distractors appeared in their temporal visual field. In contrast, the latency of saccades made by the hemianopic subjects was not increased when distractors appeared in their blind temporal visual field and a small facilitation

Table 4. *Mean saccade latency (ms) and s.e.m. (in parentheses) for eight normal subjects*

(Nasal and temporal refer to the visual field in which the saccade target appeared (the latency for the two target eccentricities is collapsed). The latency difference is the mean latency from the distractor trials minus the mean latency from the no-distractor trials (ms).)

	no distractor		static distractor		flickering distractor	
	nasal target	temporal target	nasal target	temporal target	nasal target	temporal target
subject 1	210.7 (7)	211.1 (6)	232.0 (5)	231.9 (7)	239.8 (8)	235.1 (8)
latency difference	—	—	+21.3	+20.8	+29.1	+24.0
subject 2	248.9 (9)	226.1 (10)	254.7 (10)	232.8 (10)	258.4 (11)	235.9 (9)
latency difference	—	—	+5.8	+6.7	+9.5	+9.8
subject 3	225.1 (9)	234.0 (7)	235.8 (7)	222.3 (10)	242.6 (9)	233.8 (7)
latency difference	—	—	+10.7	−11.7	+17.5	−0.2
subject 4	212.0 (8)	222.1 (8)	224.8 (13)	230.7 (10)	225.8 (12)	232.6 (15)
latency difference	—	—	+12.8	+8.6	+13.8	+10.5
subject 5	197.7 (5)	204.6 (6)	208.8 (5)	206.3 (6)	207.3 (5)	209.9 (7)
latency difference	—	—	+11.1	+1.7	+9.6	+5.3
subject 6	205.1 (9)	201.5 (8)	213.6 (6)	197.1 (7)	216.7 (9)	198.0 (8)
latency difference	—	—	+8.5	−4.4	+11.6	−3.5
subject 7	197.8 (4)	188.0 (4)	213.1 (5)	208.5 (5)	213.6 (4)	206.8 (5)
latency difference	—	—	+15.3	+20.5	+15.8	+18.8
subject 8	237.1 (10)	252.6 (12)	275.4 (13)	267.1 (13)	278.2 (13)	262.4 (12)
latency difference	—	—	+38.3	+14.5	+41.0	+9.8
overall mean	216.8	217.5	232.3	224.6	235.3	226.8

effect was observed. Although latency can be seen to be greater overall for the hemianopes than normal subjects this is still well within the normal human range (Carpenter 1988). The mean latency observed with targets in the temporal visual field (nasal distractors) is shown in figure 2*b*. Normal subjects again showed an increase in latency under distractor conditions while distractors in a blind field had little influence on latency for the hemianopes.

To examine the influence of distractors on latency in more detail the overall latency difference between the distractor and no-distractor conditions was calculated. Figure 3*a* shows the resulting latency difference produced by the temporal distractors and figure 3*b* that for the nasal distractors. With distractors in the temporal visual field the normal subjects showed a latency increase of 15–18 ms with the static and flickering distractors, respectively. In contrast, the hemianopic subjects showed a small latency facilitation effect of some 3 ms with distractors in the blind temporal field. A similar result was produced with distractors presented in the nasal visual field (figure 3*b*). Latency was again increased for normal subjects with distractors in the nasal field, although this inhibitory effect was smaller in magnitude (7–9 ms) than was observed with the temporal distractors. The latency difference for the hemianopic subjects again showed a small facilitation effect with distractors in the blind nasal field.

The data for the normal and hemianopic subjects in the different distractor conditions were analysed using two-factor, repeated-measures analysis of variance (ANOVA). The factors included were visual field (nasal and/or temporal) and distractor condition (no distractor, static distractor and flickering distractor). For the normal subjects there was no main effect for their visual field ($p > 0.05$) but there was a significant main effect for the distractor condition ($F_{2,14} = 15$ and $p < 0.001$). A significant two-way interaction effect (field × distractor) was also observed ($F_{2,14} = 4.7$ and $p < 0.05$). The two-way interaction effect arises because, for normal subjects, latency in the no-distractor condition was similar for saccades directed towards the nasal and temporal fields, but an additional latency increase was produced for saccades made to nasal targets when distractors appeared in the temporal visual field. For normal subjects there was a significant naso-temporal asymmetry in the distractor effect with the greatest inhibitory effect produced with temporal distractors. In contrast, the analysis for the hemianopic subjects showed no significant main effects for their visual field ($p > 0.05$) or distractor condition ($p > 0.05$) and no interaction effects ($p > 0.05$). The analysis confirmed that distractors presented in either the temporal or nasal blind field had no effect on latency for the hemianopic subjects but a latency increase is observed, which is greater with distractors in the temporal field, for normal subjects.

The effects of the distractors on saccade amplitude were examined in separate three-factor ANOVAs for the normal and hemianopic subjects. There was no effect of either static or flickering distractors on saccade amplitude for the normal subjects ($p > 0.05$) or hemianopes ($p > 0.05$). There was also no effect of the target visual field on saccade amplitude for the normal ($p > 0.05$) or hemianopic ($p > 0.05$) subjects, showing that the amplitude of saccades to stimuli in the nasal and temporal visual field were comparable.

4. DISCUSSION

The present study found no evidence of an inhibitory distractor effect on the latency of saccades made by a group of hemianopic subjects when distractors were presented in either the blind temporal or blind nasal

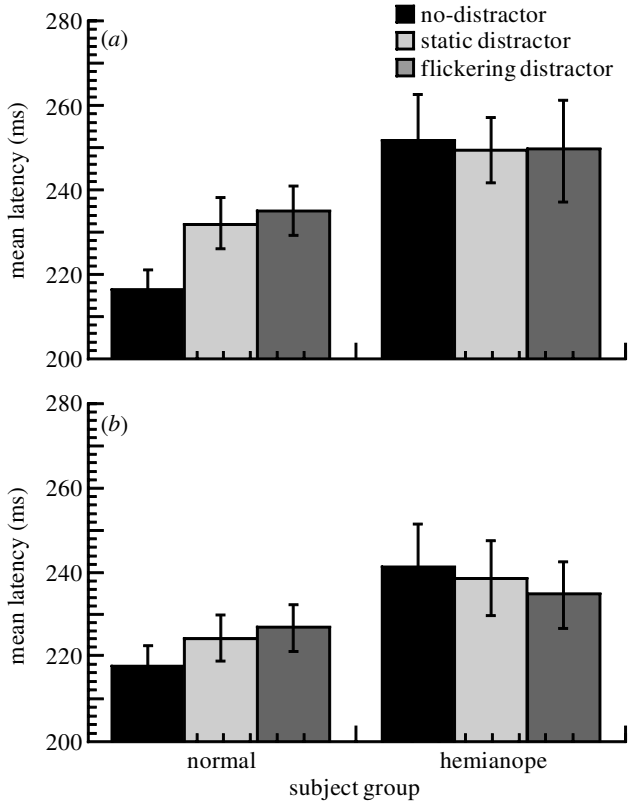

Figure 2. Mean saccade latency obtained for the normal and hemianopic subjects with targets presented in (*a*) the nasal visual field and (*b*) the temporal visual field: static and flickering distractors (12.5 Hz) appeared simultaneously in the temporal and nasal visual fields, respectively. Error bars = 1 s.e.m. (*a*) Nasal target, temporal distractor. (*b*) Temporal target, nasal distractor.

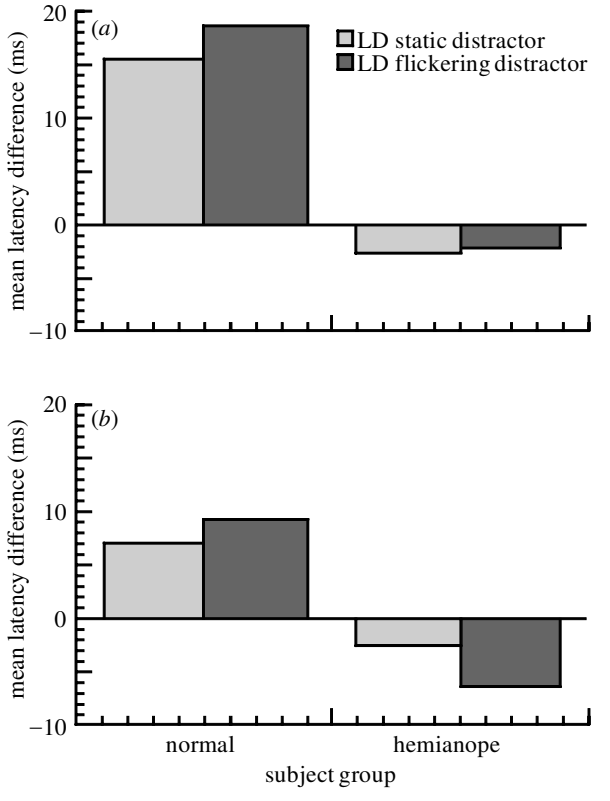

Figure 3. Mean latency difference (distractor mean− no-distractor mean) observed in (*a*) the temporal field distractor trials and (*b*) the nasal field distractor trials for normal and hemianopic subjects.

visual field. The hemianopic subjects were not aware of the distractors in their blind field. In contrast, the distractors increased the latency of saccades made by normal subjects, regardless of whether they were static or flickering and whether the distractors appeared in the nasal or temporal field. The results from the present study are not in accord with those of Rafal *et al.* (1990) who observed an increase in latency when stimuli appeared in a blind temporal visual field. The blindsight distractor effect was attributed to the crossed retinotectal visual pathway which favours the temporal visual field. They suggested that the distractor effect may be dependent on activity within an 'isolated extrageniculate visual system', as would result from unilateral damage to the primary visual cortex. This retinotectal hypothesis of the distractor effect was not supported by the findings of the present study: the distractors had no effect on saccade latency for the hemianopic subjects but a robust latency increase was observed for the normal subjects. Furthermore, the magnitude of the distractor effect shown by the normal subjects in the present study (8–18 ms) is comparable to that found in normal subjects tested under binocular viewing conditions (Lévy-Schoen 1969; Findlay 1983; Walker *et al.* 1995, 1997). Saccade amplitude was not influenced by the distractors, as would be expected from previous studies which revealed an amplitude modulation only when distractors appear in the same hemifield as the target (Findlay 1983; Walker *et al.* 1997).

There are a number of possible explanations which may account for the discrepancy between these findings and those reported by Rafal *et al.* (1990). The first consideration is that blindsight effects may not be observed in all hemianopic subjects, perhaps because of variations in the extrastriate damage which produced the field defect (Milner & Goodale 1995). The prevalance of blindsight in hemianopes is largely unknown although one published group study by Blythe *et al.* (1987) found evidence of residual vision in five out of 25 patients tested. Thus, it is possible that similar variations may occur in the prevalence of the blindsight distractor effect on saccade latency. Similar variations have also been noted in investigations of so-called 'spatial summation' effect in blindsight. Spatial summation refers to the facilitation of manual reaction times when stimuli are presented simultaneously in both visual fields. The spatial summation effect has been observed in a minority of hemianopic subjects when stimuli are presented in both the intact and blind visual fields (Marzi *et al.* 1986; Corbetta *et al.* 1990). However, the proposed explanation of the oculomotor blindsight distractor effect was that it was mediated by the small direct projection from the retina to the colliculus. There is no reason to suspect that the direct retinotectal projection should not have been operational in the hemianopic patients tested in the present study given the nature of their cortical lesions. The absence of a distractor effect in the hemianopes and the presence of a distractor effect in the normal subjects would suggest that the origin of the inhibitory effect is not retinotectal in origin.

Although the retinotectal explanation for the oculomotor distractor effect is appealing it is not entirely

consistent with the known functional and connectional segregation of the SC. As noted by Schiller (1986), the retinotectal assumption of orientating effects are 'difficult to reconcile with the observation that the deep colliculus depends for its visual activation on the cortico-tectal pathway' (p. 1376). The colliculus consists of a number of distinct 'layers' which are typically considered as two separate structures on the basis of anatomical and behavioural characteristics, termed the 'superficial' and 'deep' layers (see Sparks & Hartwich-Young (1989), for a review). Cells in the superficial layer have exclusively visual functions and the dominant inputs are from the retina and striate cortex. In contrast, the deep layers receive inputs from cortical regions with visual and motor functions, such as the LIP, FEFs and SEFs, as well as from subcortical structures including the substantia nigra. The deep layers are thought to be critically involved in the translation of sensory signals into motor commands and are known to have direct projections to the brainstem neurons which generate saccades. The smaller crossed projection from the nasal hemiretina to the superficial layers of the SC could influence saccade generation via indirect routes only, such as the projection to the inferior pulvinar (Robinson & McGlurkin 1989) (which in turn projects to the striate and posterior pre-striate cortex) or the small projections from the superficial to deep layers which would involve a mechanism as yet poorly understood (Moschovakis *et al.* 1988*a*,*b*).

The presence of a distractor effect in normal subjects but not in hemianopic subjects with damage to the visual cortex provides evidence that the distractor effect may be a normal characteristic of the oculomotor system. The presence of a small naso-temporal asymmetry in the magnitude of the distractor effect shown by normal subjects may be consistent with anatomical evidence of a naso-temporal asymmetry in the retinal ganglion cell density (Curcio & Allen 1990). This asymmetry is known to be preserved in the projection to the dLGN and the geniculostriate projection (Williams *et al.* 1995). However, it should be noted that such naso-temporal asymmetries in retinal ganglion cells are found in the far periphery beyond the eccentricity of the distractors used in studies of the oculomotor distractor effect. The increase in ganglion cell density in the nasal hemiretina may not provide the whole explanation for the small additional latency increase which is observed with distractors in the temporal field. However, it does appear that the distractor effect may depend on the geniculostriate pathway and not on an isolated retinotectal pathway as was previously thought to be the case.

One of us recently proposed a model of the saccadic distractor effect based on the processes of competitive inhibition operating between separate populations of fixation neurons and neurons involved in representing the distractor, which inhibit saccade triggering (Walker *et al.* 1997). Although this model was heavily influenced by recent neurophysiological discoveries of the properties of neurons in the deep layers of the SC (Munoz & Wurtz 1995*a*,*b*) it was noted that similar effects may be observed in other brain regions. One likely candidate is the LIP of the posterior parietal cortex which is specialized for saccadic eye movements and projects extensively to the deep layers of the SC (see Andersen & Gnadt (1989) and Andersen (1995) for reviews). The LIP area receives inputs from a number of extrastriate visual areas and this input may be diminished in hemianopic subjects following damage to their retinogeniculate pathway or primary visual cortex. Thus, the absence of a distractor effect in some hemianopic subjects may be attributed to a deficient input to the posterior parietal cortex following damage to the primary visual cortex. Some support for the involvement of the posterior parietal cortex in the distractor effect is also provided by studies of patients with unilateral parietal lobe damage (and a concomitant disorder called 'unilateral neglect'). Patients with neglect do not show a distractor effect when distractors appear in their contralesional visual field (Walker & Findlay 1996).

In conclusion, the present study revealed no evidence of blindsight inhibitory effects in hemianopic subjects with cortical lesions. In contrast, distractors presented in the non-target hemifield significantly increased the latency of saccades made by normal subjects. The distractor effect is not observed in humans with unilateral parietal damage and may depend on the cortical visual pathways to areas such as the LIP which are known to project to the deep layers of the SC. The demonstration of an oculomotor distractor effect in some hemianopic subjects may best be characterized as an example of residual visual (visuomotor) functioning. We argue that the distractor effect is a normal characteristic of the saccadic system and may be related to the processes of response competition involved in saccade target selection (Findlay & Walker 1999) which may be mediated by the deep colliculus which depends on the corticotectal pathway for visual input (cf. Schiller 1986).

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