

The influence of stimulus direction and eccentricity on pro- and anti-saccades in humans

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Abstract We examined the sensory and motor influences of stimulus eccentricity and direction on saccadic reaction times (SRTs), direction-of-movement errors, and saccade amplitude for stimulus-driven (prosaccade) and volitional (antisaccade) oculomotor responses in humans. Stimuli were presented at five eccentricities, ranging from 0.5° to 8°, and in eight radial directions around a central fixation point. At 0.5° eccentricity, participants showed delayed SRT and increased direction-of-movement errors consistent with misidentification of the target and fixation points. For the remaining eccentricities, horizontal saccades had shorter mean SRT than vertical saccades. Stimuli in the upper visual field trigger overt shifts in gaze more easily and faster than in the lower visual field: prosaccades to the upper hemifield had shorter SRT than to the lower hemifield, and more anti-saccade direction-of-movement errors were made into the upper hemifield. With the exception of the 0.5° stimuli, SRT was independent of eccentricity. Saccade amplitude was dependent on target eccentricity for prosaccades, but not for antisaccades within the range we tested. Performance matched behavioral measures described previously for monkeys performing the same tasks, confirming that the monkey is a good model for the human oculomotor function. We conclude that an upper hemifield bias lead to a decrease in SRT and an increase in direction errors.

Keywords Antisaccades · Prosaccades · Saccade · Eye movement · Direction · Eccentricity

Introduction

The eye movement system provides an excellent model for the study of flexible control over behavior. The pro- and anti-saccade tasks permit examination of flexible control because the same stimuli are used to elicit different behaviors. Studies comparing stimulus-driven responses to volitional responses include many that use prosaccades and antisaccades to understand the oculomotor system and its neural control (e.g., Munoz and Everling 2004; Pierrot-Deseilligny et al. 1995), and to examine oculomotor performance differences in clinical populations (see Everling and Fischer 1998; Munoz et al. 2005 for reviews). Prosaccades are visually triggered saccadic eye movements from a fixation spot to an eccentric stimulus that appears suddenly. Antisaccades (Hallet 1978) are eye movements from a fixation spot to the direction opposite to the eccentric stimulus and require voluntary suppression of the automatic response.

For both tasks, important sensory information, the sudden appearance of the stimulus, activates the saccade. For prosaccades, the task may include but does not rely on volitional planning; there is a direct sensory-to-motor correspondence between stimulus location and goal of the saccade. Pro-saccade reaction times are usually brief, often including express saccades (reaction times between 90 and 130 ms; Fischer and Ramsperger 1984; Fischer and Weber 1993), times that would deny or minimize a decision process. As such, prosaccades are driven more by sensory stimulation. In

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contrast, to perform an antisaccade correctly, a participant must first suppress the automatic saccade toward the stimulus and then generate a volitional response toward a stimulus-free location (Guitton et al. 1985; Hallett 1978; Munoz and Everling 2004). Thus, stimulus location and the saccade goal are always different. In fact, because of the vector inversion required in this task, the side of the brain processing the stimulus is opposite to the side of the brain processing the saccade. Thus, the antisaccade allows for the dissociation of sensory and motor effects of direction.

Although there are many pro- and anti-saccade studies, few have examined the influence of both direction and eccentricity of the peripheral stimulus in a systematic manner. Studies have examined pro- or antisaccades on the horizontal (Kristjansson et al. 2004; Cornelissen et al. 2002; Reingold and Stampe 2002; Fischer and Weber 1992; Kalesnykas and Hallett 1994; Weber and Fischer 1995; Fischer and Weber 1997; Fischer et al. 1997; Munoz et al. 1998) or vertical (Kalesnykas and Hallett 1994; Goldring and Fischer 1997) meridians. In some cases, researchers have presented various stimulus directions without altering stimulus eccentricity (Krappmann et al. 1998; van Opstal and van Gisbergen 1989) or presented various eccentricities without altering stimulus directions (van Opstal and van Gisbergen 1989). The interaction of the full factorial combination of stimulus directions and eccentricities on SRT has yet to be investigated in human subjects although such research has been conducted on non-human primates (Bell et al. 2000).

We expected that by varying direction and eccentricity systematically, we will show that reaction time and direction errors are dependent on stimulus location. Previc (1990) proposed that primates are predisposed to make saccades at shorter latencies to the upper hemifield because this field represents extra-personal space that may include food or predators, whereas, the lower hemifield represents peri-personal space. This lower visual field represents the area most requiring skilled movements and consequently more visual processing (Danckert and Goodale 2001). Attentional resolution is greater in the lower visual field (He et al. 1996) yielding a richer visual environment to the lower hemifield. Thus, reaction times should be shorter toward upper hemifield stimuli and longer to lower hemifield stimuli. If there is a bias, is it predominately due to sensory or motor processing? The antisaccade task allows for the dissociation of sensory and motor processes and can therefore test this question. Previously in this lab, Bell et al. (2000) found that reaction time and errors were dependent on target location in monkeys. Introducing many target locations increased

uncertainty and altered the relative importance of the sensory/motor processes. One can easily imagine that a single stimulus location creates a predictable task and results in shorter reaction times for both pro- and anti-saccades because neither the sensory information nor the motor requirements change from trial to trial. In contrast, increasing the number of possible locations of the eccentric stimulus decreases predictability and enhances the amount of inhibition needed to meet the volitional demands of the pro- and anti-saccade tasks.

We expected pro- and anti-saccade performance to depend on the combination of eight radial directions and five eccentricities. In this study we measured SRT, direction-of-movement errors, and accuracy of saccadic amplitude (gain). To encourage errors, all trials were presented with a temporal gap between the disappearance of the start position and the appearance of the eccentric target (Munoz et al. 1998; Munoz and Corneil 1995; Kalesnykas and Hallett 1987; Saslow 1967).

Methods

Participants

All experimental procedures were reviewed and approved by Queen's University Human Research Ethics Board. Five men and three women ranging in age from 18 to 25 years participated in the study. Five participants were right-hand dominant. All subjects reported no known neurological, psychiatric, or visual disorders. Participants gave written consent and they received \$10 for each of four 1-h sessions.

Materials and procedure

Participants sat upright 66 cm from a 17" monitor with a resolution of 640 × 480 pixels at a frame rate of 120 Hz. A chin rest stabilized head position, and infra-red cameras (Eyelink, SR Research Ltd) tracked subjects' vertical and horizontal eye position (see Cabel et al. 2000 for details) with a sampling rate of 250 Hz. The system monitored head position and automatically compensated for small head movements. The Eyelink system provided real time button press data transfer, saccade position and gaze position.

The start of each trial was marked with a colored, centrally located octagonal fixation point that subtended a visual angle of 0.5°. When ready to begin, the participant pressed a button and the fixation point extinguished after one of four randomly selected delays (400, 600, 800, 1,000 ms). This was followed by a

gap period of 200 ms during which the screen remained blank. Then a white octagonal target subtending a visual angle of 0.5° appeared for 1,000 ms randomly at one of 40 locations on the computer monitor. Targets were located at one of five eccentricities (0.5° , 1° , 2° , 4° , and 8° of visual angle) from the central fixation point and in one of eight radial directions (0° : right, 45° : up/right, 90° : up, 135° : up/left, 180° : left, 225° : down/left, 270° : down, and 315° : down/right). Trial types were differentiated only by the instruction given to the participant: (a) generate a saccade to the target (pro-saccade trials); and (b) generate a saccade to a position that was opposite the target in both direction and eccentricity (anti-saccade trials). Participants received no feedback. The trial ended when the target disappeared.

Participants completed eight blocks of prosaccades interleaved with eight blocks of antisaccades. Each block consisted of 160 trials (4 fixation delays \times 5 eccentricities \times 8 directions) presented in random order for each participant. Task order was counterbalanced across participants. For half the participants, a red fixation point indicated the pro-saccade task and a green fixation point indicated the anti-saccade task. For the remaining participants, color cues were reversed.

Data analysis

Saccades were recorded automatically by Eyelink when peak velocity was greater than $30^\circ/\text{s}$, acceleration was greater than $9,500^\circ/\text{s}^2$, and a minimum position change of 0.15° occurred after saccade onset. Saccadic reaction time (SRT) was calculated from the appearance of the eccentric stimulus to the initiation of the saccade. Saccades with latencies shorter than 90 ms, were classified as anticipatory (Wenban-Smith and Findlay 1991) and excluded from the analysis. Saccades with latencies longer than 500 ms (>3 SD above longest mean anti-saccade SRT), trials with blinks, and trials with no eye movement were also removed automatically from the analysis. Many of the non-movement trials (40%) were specific to target presentations at 0.5° eccentricity; hence, all trials related to 0.5° target eccentricity were analyzed separately.

Saccades directed within $\pm 45^\circ$ of their expected goal were classified as correct. For prosaccades, the expected goal was the target. For antisaccades, the expected goal was the stimulus-free position opposite the target; saccades made towards the target ($\pm 45^\circ$) in this case were classified as direction-of-movement errors, and those made to all other positions were classified as misdirected saccades ($<1\%$ of trials). Finally,

we calculated gain, a measure of the accuracy of a saccade defined as the ratio of the magnitude of the first saccade (distance from fixation upon the central fixation marker to saccade endpoint) to the eccentricity of the stimulus.

With the exception of 0.5° -target trials, dependent measures were analyzed with a $2 \times 4 \times 8$ repeated-measures Analysis of Variance (task [pro- vs. anti-saccade] \times eccentricity [1° , 2° , 4° , 8°] \times direction [0° , 45° , 90° , 135° , 180° , 225° , 270° , 315°]). The results were collapsed across all participants, and none of the measures was analyzed on an individual basis. A standard correction for heterogeneity of variance in repeated-measures analyses, the Huynh-Feldt epsilon, was applied as needed.

Planned statistical comparisons contrasted the upper (45° , 90° , 135°) versus lower (225° , 270° , 315°) hemifields, the left (135° , 180° , 225°) versus right (45° , 0° , 315°) hemifields and horizontal (0° , 180°) versus vertical (90° , 270°) points. Post hoc comparisons were performed making Tukey's corrections.

Results

Across all participants, 13% of the trials had either no eye movement, blinks or technical problems and were rejected. Forty percent of these trials occurred for stimuli presented at 0.5° eccentricity. Enough differences existed in the pattern of performance in the 0.5° -eccentricity trials to suggest that performance on these trials was uniquely confounded by technical constraints (see below). Figure 1 shows the proportion of rejected trials. By far, the fewest trials with eye movements were to stimuli at 0.5° eccentricity, especially in the pro-saccade task; consequently, these trials were removed from the main analysis, analyzed separately and reported at the end of the Results section.

Saccadic reaction time

Figure 2 shows mean SRT (\pm SE) as a function of direction; individual functions represent eccentricity (excluding 0.5°) for pro- (Fig. 2a) and antisaccades (Fig. 2b). Mean SRT ranged between 170 and 220 ms for prosaccades and between 290 and 350 ms for anti-saccades, $F(1, 7) = 149.49$, $P < 0.001$. SRT was independent of eccentricity across the range tested (1° – 8°), $F(1, 10) = 3.60$, $P > 0.05$ but was dependent on stimulus direction, $F(7, 49) = 6.77$, $P < 0.001$; and interacted with task, $F(3, 21) = 4.49$, $P < 0.05$. Pro-saccade latency was shortest for horizontal saccades, $t(248) = 8.73$, $P < 0.001$ and shorter for saccades into the upper

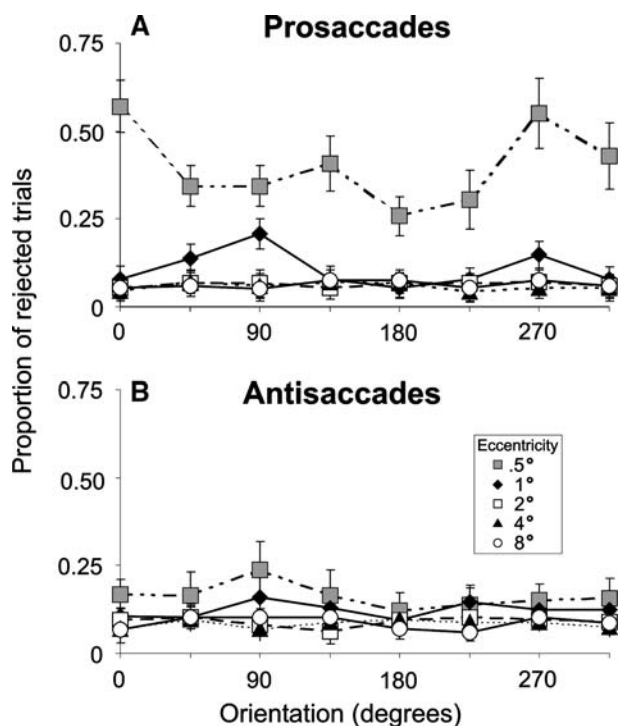


Fig. 1 Proportion of trials with no eye movements or blinks as a function of stimulus direction for prosaccades (a) and antisaccades (b) for stimuli presented at 0.5°, 1°, 2°, 4°, and 8° of eccentricity

hemifield than into the lower hemifield, $t(248) = 7.83$, $P < 0.001$. Anti-saccade latency was shortest along the horizontal, $t(248) = 2.17$, $P < 0.05$, and at 1° eccentricity, was longer in response to upper hemifield stimuli (saccades into the lower hemifield) but otherwise, direction/eccentricity effects on anti-saccade SRT were inconsistent.

Post hoc tests yielded the following homogeneous subsets (i.e., mean SRTs were not different from each other, but, as a group, different from the remaining mean SRTs): shortest prosaccade mean SRT was along the upper hemifield and the horizontal meridian, except at 90° (i.e., 0°, 45°, 135°, 180°); and longest mean SRT was down and diagonally to the left (i.e., 225° and 270°); antisaccades had no homogeneous subsets.

Direction-of-movement errors

Errors in the direction of the first saccade are shown in Fig. 3 and they were almost non-existent for prosaccades, although there were many errors for antisaccades, Wilcoxon $Z = 13.6$, $P < 0.001$. The number of saccades away from the target in the pro-saccade task was so small (Fig. 3a) that many cells in the analysis had zero values and none exceeded 2% of trials.

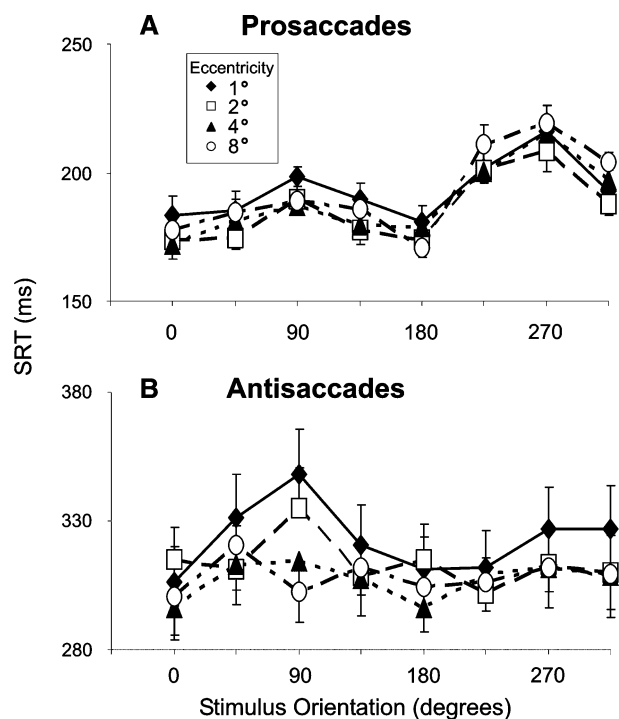


Fig. 2 Mean SRT as a function of direction for stimuli presented at 1°, 2°, 4°, and 8° of eccentricity for prosaccades (a) and antisaccades (b)

Therefore, although the values were not the same (Friedman's $\chi^2(31) = 50.36$, $P < 0.02$), we did not analyze pro-saccade direction-of-movement errors further.

In the anti-saccade task (Fig. 3b), eccentricity alone did not influence direction-of-movement errors, $F(1, 10) = 3.29$, $P > 0.10$; however direction-of-movement errors were dependent on stimulus direction, $F(5, 32) = 3.57$, $P < 0.05$. Planned comparisons showed more errors when stimuli were presented in the upper hemifield than in the lower, $t(248) = 2.98$, $P < 0.01$; and more errors for stimuli presented in the right hemifield than in the left, $t(248) = 3.01$, $P < 0.01$. Post hoc tests showed that direction-of-movement errors were most common when stimuli were presented at 0° and 45° and the least common in response to stimuli presented at 225°. Note in the pro-saccade task the homogeneous subset with the shortest SRT included 0° and 45° and the longest included 225°. So, the stimulus locations that are most likely to evoke short pro-saccade SRT are also the stimulus locations that evoke anti-saccade direction-of-movement errors, and the location with the smallest number of anti-saccade direction-of-movement errors is also a location that elicits the longest pro-saccade SRT (see scatterplot in Fig. 4), suggesting that sensory rather than motor processing, is responsible for the upper versus lower field effects.

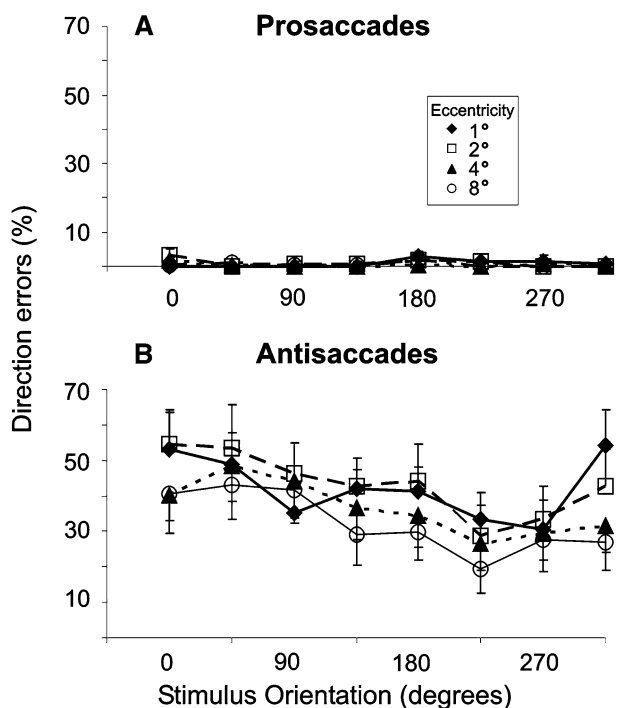


Fig. 3 Percentage of direction-of-movement errors as a function of stimulus direction for stimuli presented at 1°, 2°, 4°, and 8° of eccentricity for prosaccades (a) and antisaccades (b)

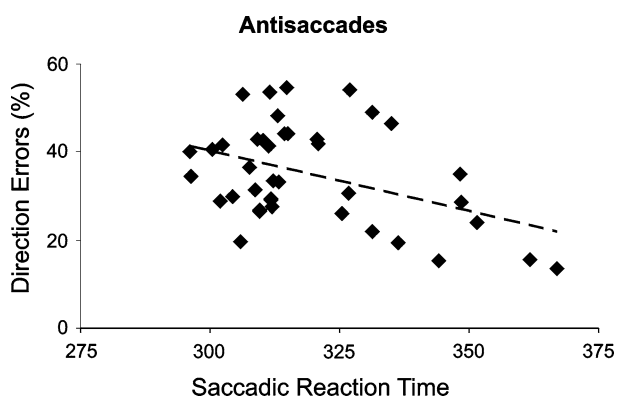


Fig. 4 Saccadic reaction time as a function of anti-saccade direction errors. Each point represents summary data from a different stimulus location. The best-fit regression line is: predicted direction errors = 122.35–0.27(SRT), coefficient of determination, $r^2 = 0.18$

Gain

The gain ratio for pro- and anti-saccades depended on both direction and eccentricity, although prosaccades are generally far more accurate than antisaccades, $t(228) = 6.88, P < 0.001$ (compare Fig. 5a and b). Gain ratios of approximately 1 occur when the first saccade toward a target is of the correct magnitude. Gain ratios greater than 1 occur for hypermetric saccades (over-

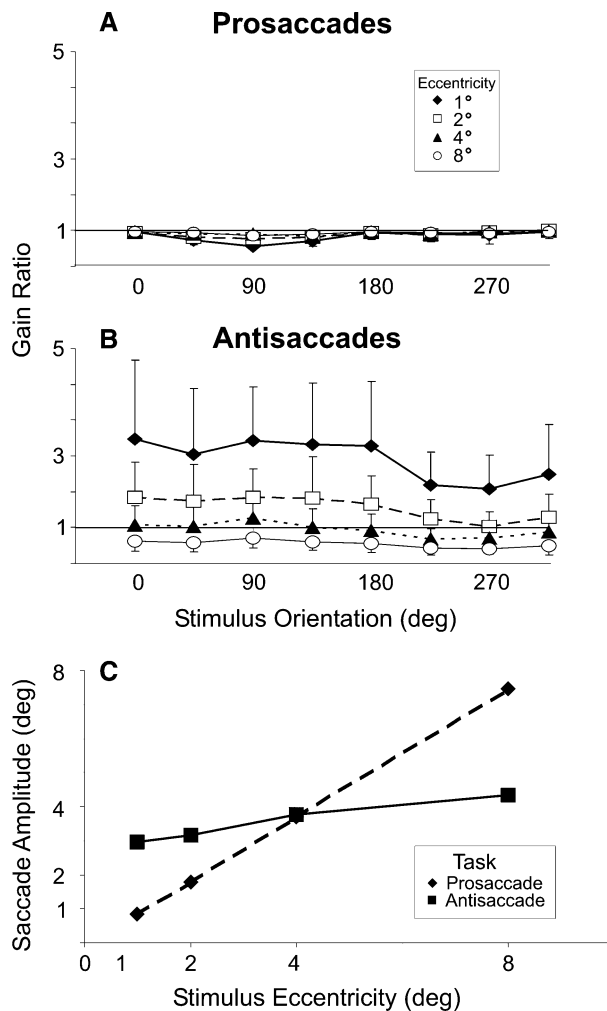


Fig. 5 Gain ratio (gain = 1 for perfect amplitude saccades) as a function of stimulus direction for stimuli presented at 1°, 2°, 4°, and 8° of eccentricity for prosaccades (a) and antisaccades (b). Saccade amplitude as a function of stimulus eccentricity (c)

shoots) and gain ratios less than 1 occur for hypometric saccades (undershoots).

As shown in Fig. 5a, prosaccades were most hypometric towards the 90° direction and at 1° eccentricity and otherwise approximately equal with gain ratios close to 1 for larger eccentricities (2°, 4°, and 8°), $F(3, 252) = 7.05, P < 0.001$. Post hoc homogenous subsets found saccades in the upper hemifield more hypometric than all remaining directions.

Antisaccades (Fig. 5b) to 1° stimuli were about three times as large as needed; to 2° stimuli about 1.5 times as large as needed; and to 8° stimuli about half the required size, $F(3, 220) = 68.95, P < 0.001$, a range effect (Kapoula 1985) not found for prosaccades. Planned comparisons showed more accurate anti-saccade gain ratio for stimuli presented in the lower hemifield, $t(216) = 2.74, P < 0.01$. Fig. 5c shows that pro-saccade

amplitude was almost perfectly aligned with target eccentricity, whereas, anti-saccades amplitude varied only slightly across eccentricity, between 3.5° and 4° from the fixation point. No other comparisons were statistically significant.

Trials at 0.5° eccentricity

As noted earlier, about 40% of the 0.5°-eccentric trials were rejected. On correct trials, SRT was about 20 ms longer compared to other eccentricities ($P < 0.05$, not shown). Direction-of-movement errors at the smallest eccentricity were as likely for a prosaccade (i.e., subjects would incorrectly look away from the target) as for an antisaccade, when subjects would incorrectly look towards the target, and eye movements were more likely into the upper hemifield suggesting that participants were unable to discriminate reliably between the fixation point and the stimulus. Therefore, participants may have moved their eyes arbitrarily to accommodate the experimental instructions.

The large number of 0.5°-stimulus trials were rejected for several possible reasons: first, the eye movement did not satisfy the minimum criteria, or the eyetracker could not discriminate a minimal eye movement from recording noise; second, the stimulus may have been near enough to foveate without an eye movement, or third, participants were already fixated on the stimulus because of its proximity to the fixation point.

Discussion

Stimulus direction affected pro-saccade SRT and anti-saccade direction-of-movement errors in an associated manner. Stimuli that were up and right resulted in shorter pro-saccade SRT and more anti-saccade direction-of-movement errors, and stimuli that were down and left resulted in longer pro-saccade SRT and fewer anti-saccade direction-of-movement errors. Anti-saccade SRT depended on both stimulus direction and eccentricity showing shorter SRT away from stimuli in the lower hemifield but only for close stimuli. Stimulus eccentricity had no effect on pro-saccade SRT except for stimuli closest to fixation, at 0.5° eccentricity. This near eccentricity yielded the longest SRT and resulted in the most rejected trials. Although pro-saccade amplitude was accurate, the anti-saccade amplitude was not scaled appropriately across eccentricity. In what follows, we consider the contribution to the literature of our manipulations of SRT, direction errors and gain before discussing the upper hemifield bias in non-human primates and in this study.

Saccadic reaction time

Prosaccades had shorter mean latency than correct antisaccades when the tasks were blocked (Everling and Fischer 1998; Munoz et al. 1998; Reingold and Stampe 2002). The latency difference in the current study was larger than earlier studies likely due to the uncertainty introduced by a large number of possible stimulus locations.

Consistent with earlier work (Goldring and Fischer 1997), pro- and anti-saccades along the horizontal meridian had the shortest latencies. The horizontal advantage in SRT could reflect the importance of the horizontal meridian in our daily lives (e.g., reading patterns of fluent English readers; Abed 1991). Pro-saccade SRT was shorter into the upper hemifield, except at 90° (i.e., the vertical meridian). No hemifield preference was observed for anti-saccade SRT.

Stimulus eccentricity within our experimental range of 0.5°–8° affected pro-saccade SRT only at 0.5° eccentricity. At 0.5 eccentricity, saccades were either never executed, undetected, or they were about 20 ms longer than other prosaccades, consistent with the findings of Weber et al. (1992). In contrast, eccentricity effects in SRT have been shown for prosaccades in the past (Weber et al. 1992; Kalesnykas and Hallett 1994; Krauzlis and Miles 1996) and antisaccades (Fischer and Weber 1997) across larger eccentricity ranges, but these studies limited stimulus direction to the horizontal or vertical meridians.

Direction-of-movement errors

The large number of anti-saccade direction-of-movement errors (38%) in the current study reflects the uncertainty introduced by many possible stimulus locations. Participants had to suppress prosaccades to one of 40 locations, and not merely attend to two directions as in the past (Goldring and Fischer 1997; Fischer et al. 1997; Munoz et al. 1998; Kristjansson et al. 2001, 2004).

Anti-saccade direction-of-movement errors were generated more often when stimuli were presented in the right hemifield (Fischer and Weber 1997; Fischer et al. 1997; Munoz et al. 1998). Also more anti-saccade direction-of-movement errors were made in response to stimuli presented at all locations in the upper right quadrant of the visual space. This was not shown in earlier studies, because stimuli were presented only along a single meridian.

Gain

Prosaccades were generally accurate across all eccentricities although slightly hypometric into the upper

hemifield. In contrast, Kalesnykas and Hallett (1994) showed that saccades overshoot the stimulus at eccentricities less than 2° . Their study used stimuli presented at eccentricities up to 66° from fixation along the horizontal meridian. Thus, within a block of trials, participants made some very large saccades which may have biased smaller saccades. In the current study, the largest stimulus displacement was only 8° and participants rarely made inaccurate prosaccades.

Anti-saccade amplitude was approximately 4° , the midpoint of stimulus eccentricities used in the current study (Fig. 4b, c), although amplitude varied slightly dependent upon stimulus eccentricity. This range effect (Kapoula 1985), near stimuli are overshoot and far stimuli are undershot, was not found for prosaccades.

Antisaccades were less hypermetric into the upper hemisphere, the same direction that produced a few hypometric prosaccades. Thus saccade amplitude into the upper hemifield was reduced for both prosaccades and antisaccades.

Comparison to monkeys

Clear eccentricity effects in SRT were also shown by Bell et al. (2000) using multiple stimulus locations similar to the current study. However, their display field was twice as large (32° range) as the field used in the current study (16° of visual angle), and their participants, monkeys, were over-trained compared with humans. As a result they have shorter SRT than human participants, they make more express saccades and fewer errors than human participants. Consistent with the human findings, they found an upper hemifield SRT advantage using monkeys. However, monkeys did not produce the same pattern of direction-of-movement errors as in the current study; there was no reduction of errors for stimuli presented at greater eccentricities, presumably because the monkeys were over-trained at the task. The range effect was also observed in monkeys (Bell et al. 2000), who made 8° antisaccades, the midpoint of their stimulus set. Bell et al. (2000) suggested that, in monkeys, the directional bias reflects the influence of cortical structures, such as the lateral intraparietal area and the frontal eye fields that are related to stimulus and goal selection.

The association between pro-saccadic reaction time and direction-of-movement errors

Participants made the most direction-of-movement errors (Fig. 3b) to the same upper hemifield stimuli that yielded the shortest pro-saccade SRTs (Fig. 2a). This association between pro-SRT and anti-saccade

direction errors was analyzed by Klein and Fischer (2005) using principal component analysis. They showed that both factors load the same principal component. The relationship between pro-saccade SRT and anti-saccade direction-of-movement errors suggests a sensory, and not motor, limitation in this oculomotor task. The sensory influence of the stimuli elicits a saccade irrespective of whether the task requires looking toward the target (prosaccade) or looking away (antisaccade). The anti-saccade task allows us to dissociate sensory and motor effects: a motor bias for stimuli in the upper hemifield should have elicited shorter anti-saccade reaction time to stimuli in the lower hemifield but this was not the case in this study. Instead, we found the bias was related to the direction of stimulus and hence this bias appears to be the result of processing in the sensory system.

Conclusions

We have shown that the highest frequency of direction errors in the anti-saccade task occurred in response to stimuli at directions that elicited the shortest pro-saccade SRT. Consequently, we conclude that both sensory information and oculomotor processes limit the saccade direction for both pro-saccade SRT and anti-saccade direction-of-movement errors. We also found an equivalency of performance along the horizontal meridian that is not found along other meridians, hence, studies of saccades using stimuli presented only on the horizontal axis do not necessarily capture oculomotor performance for every direction. Finally, we found that human performance on this task matched monkey behavior; hence, we conclude that monkeys are a good model for the study of oculomotor control. Future studies involving behavioral and neurological assessment of saccade performance, including clinical and neuroimaging studies that make use of pro- and anti-saccade tasks must consider that stimulus eccentricity and direction can influence SRT, direction-of-movement errors and gain.

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