The “Diagonal Effect”: a Systematic Error in Oblique Antisaccades

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Koehn JD, Roy E, Barton JJ. The “diagonal effect”: a systematic error in oblique antisaccades. J Neurophysiol 100: 587–597, 2008. First published May 21, 2008; doi:10.1152/jn.90268.2008. Antisaccades are known to show greater variable error and also a systematic hypometria in their amplitude compared with visually guided prosaccades. In this study, we examined whether their accuracy in direction (as opposed to amplitude) also showed a systematic error. We had human subjects perform prosaccades and antisaccades to goals located at a variety of polar angles. In the first experiment, subjects made prosaccades or antisaccades to one of eight equidistant locations in each block, whereas in the second, they made saccades to one of two equidistant locations per block. In the third, they made antisaccades to one of two locations at different distances but with the same polar angle in each block. Regardless of block design, the results consistently showed a saccadic systematic error, in that oblique antisaccades (but not prosaccades) requiring unequal vertical and horizontal vector components were deviated toward the 45° diagonal meridians. This finding could not be attributed to range effects in either Cartesian or polar coordinates. A perceptual origin of the diagonal effect is suggested by similar systematic errors in other studies of memory-guided manual reaching or perceptual estimation of direction, and may indicate a common spatial bias when there is uncertain information about spatial location.

INTRODUCTION

Antisaccades are the unusual ocular motor task of looking away from a suddenly appearing target rather than at it (Hallett 1978; Hallett and Adams 1980). Examinations of the parameters of these responses in behavioral and neurophysiological studies has provided insights into the process of saccade generation (Munoz and Everling 2004). Many of these studies (Everling and Munoz 2000; Everling et al. 1998) have focused on the factors that contribute to reaction time and reflexive errors, the occasions when a subject looks at the target by mistake, which tends to occur on 10–20% of trials (Everling and Fischer 1998; Hutton and Ettinger 2006).

Less discussed is the spatial accuracy of “correct antisaccades”—that is, eye movements that are directed at least approximately at the goal instead of the stimulus. How close do these responses comply with the standard instruction to shift gaze to a location equidistant but in opposite direction to the stimulus? The spatial accuracy of antisaccades can tell us something about the ability of the saccadic system to estimate goal coordinates in the absence of direct visual stimulation at the goal site.

Spatial accuracy of saccades can be divided into variable and systematic errors (White et al. 1994). Variable error refers to a random inconsistency of saccadic endpoints from trial to trial. Reports have documented greater variable error of the antisaccadic endpoint when compared with prosaccades, and this variability is larger for the amplitude than for the direction of the antisaccade vector (Hallett and Adams 1980; Krappmann 1998). Given estimates that uncertainty in the sensory signals indicating target location is the source of over one half of the variability in prosaccade endpoints (van Beers 2007), this increased variability of antisaccades is not surprising. Increased variable error may reflect reduced signal/noise ratio: of note, studies show that in key saccadic structures like the superior colliculus and frontal eye field, the neural burst (i.e., signal) at the location of an antisaccade goal is far less than that at the location of a prosaccade goal or even the location corresponding to the antisaccade stimulus (Everling and Munoz 2000; Everling et al. 1999). Hence a behavioral corollary of this reduced antisaccade signal may be increased variable error in generating the antisaccade endpoint.

Systematic error, on the other hand, refers to a bias in endpoint that is apparent over many trials: therefore this is often measured as a deviation between mean saccadic endpoint and the goal (Gnadt et al. 1991; White et al. 1994). If mean saccade endpoint is not significantly different from goal location, there is no systematic error. Low systematic error but high variable error implies that the mean location of the signal estimating desired endpoint in the system is accurate, but degraded in individual trials by factors such as low signal/noise ratio, shallow tuning curves, etc. A significant systematic error indicates a more fundamental problem with estimating goal coordinates. For antisaccades, studies have shown that the amplitudes of antisaccades are more hypometric than prosaccades (Lueck et al. 1990; Tatler and Hutton 2007), a systematic error that suggests underestimation of the antisaccade goal. Whether systematic and variable errors in the saccadic system stem from the same processes is unclear. For memory-guided saccades, one study found similar temporal profiles in the accumulation of variable and systematic errors (Gnadt et al. 1991), whereas another reported a dissociation between the temporal profiles of these two types of errors (White et al. 1994).

As with the original reports (Hallett 1978; Hallett and Adams 1980), most antisaccade studies have been conducted with targets along the cardinal meridians, mostly along the horizontal and occasionally along the vertical meridians (Goldring and Fischer 1997). Rarely have subjects been asked to make antisaccades to locations in oblique directions, and those that have done so have used goals located on the 45° diagonal meridians (Bell et al. 2000; Dafoe et al. 2007; Fischer and
APPARATUS AND PROCEDURE. Subjects were seated in standard dim illumination 57 cm away from the screen, with head position maintained by chin and forehead rests. The Eyelink 1000 system (SR Research, Mississauga, Canada) was used to record eye movements. Stimuli and trials were created using SR Research Experiment Builder 1.1.2 and presented on a NEC Multisync FE 2111SB monitor at 85 Hz.

Each trial began with a fixation display, which showed a white fixation cross at the center of a black screen. After 750 ms, the cross disappeared and a target appeared, a white disk with a diameter of 25 pixels. The target was replaced after 850 ms by the fixation display, and the next trial began when the subject successfully fixated the fixation cross.

There were eight possible target locations in each block, all in the same right hemifield. All targets were located at a directional eccentricity of 250 pixels (9.5° of visual angle). Target directions were located above and below the horizontal meridian at 5°, 15°, 45°, and 75° (Fig. 1). In all blocks, the order of targets was randomized.

Prosaccades and antisaccades were tested in separate blocks. Blocks consisted of 40 trials, and eight blocks were given, four for antisaccades and four for prosaccades, resulting in 160 antisaccade trials (20 in each location), and 160 prosaccade trials. Before each block, subjects were told with both written and verbal instructions which target locations were possible in that block.

The hemifield location of prosaccades and antisaccades was counterbalanced across the group. Two subjects performed both prosaccades and antisaccades to the right; two performed both prosaccades and antisaccades to the left. Two made prosaccades to the right and antisaccades to the left, and the last two did the opposite. One half the subjects performed antisaccade blocks first and one half performed prosaccade blocks first. Data for both experiments 1 and 2 were obtained in the same session. Within each block of prosaccades and antisaccades, one half of the subjects started with the blocks for experiment 1 and one half with the blocks for experiment 2. Experiments 1 and 2 were separated by a short rest break.

METHODS

Experiment 1

SUBJECTS. Twelve right-handed subjects of mean age of 24.3 yr (range, 17–31 yr) participated: seven females and five males. All subjects tested had normal or corrected-to-normal vision. The protocol was approved by the institutional review boards of Vancouver Hospital and the University of British Columbia, and all subjects gave informed consent in accordance with the Declaration of Helsinki.

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ANALYSIS. Data were obtained using SR Research Data Viewer 1.7.5, at a sampling rate of 500 samples/s. Saccades were detected when eye velocity was >31°/s, acceleration exceeded 9100°/s², and position change by >0.15°. The first saccade after target onset was considered the saccadic response. Reaction time was calculated as the time from target onset to saccadic onset. Those saccades with reaction time <80 ms (considered as anticipatory eye movements) and >800 ms (considered delayed movements) were excluded from further analysis. If the first saccade (>1.5°) in a given trial started from a point >50 pixels from the fixation cross, it was also discarded. These eye movements constituted 3.1% of prosaccade trials and 1.4% of antisaccade trials.

Because healthy subjects make a saccade toward the stimulus rather than the goal on ~10% of antisaccade trials, it was also important to exclude large directional errors. We erred on the conservative side by excluding trials on which the angular error in saccade direction was >30°, as in prior reports.

We first collapsed the data across both vertical and horizontal hemifields, by inverting the sign of the vertical positional data for saccades to lower hemifield targets and inverting the sign of the horizontal positional data for saccades to left hemifield targets (data in the result figures are thus displayed as though all trials were directed into the right top quadrant).

For each trial, we defined the vectors for the goal and the saccade, where the goal vector was the vector from screen center to the goal location, and the saccade vector was that from screen center to the saccade endpoint. Angular error was calculated as the difference

FIG. 1. Examples of the goal locations used in blocks in the 3 experiments. Each graph depicts the goal locations used in a block of trials. Experiment 1: a block contained 8 different goal locations in 1 horizontal hemifield. In one half of the blocks, subjects performed prosaccades to these locations, whereas in the other half, subjects performed antisaccades. Experiment 2: the same stimuli and goals as in experiment 1 were used, but now in 4 separate smaller blocks containing only 2 locations each, using mirror-symmetric locations across the horizontal meridian. Again, these goal locations were used for both prosaccades and antisaccades in separate blocks. Experiment 3: 1 set of goal locations for 7 blocks is shown for targets in the right top quadrant. Goals in each block have the same direction but different eccentricity. A similar set of goal locations was designed for the other 3 quadrants, and each subject performed antisaccades to all 28 blocks (whereas in experiments 1 and 2, each subject was tested in only 1 horizontal hemifield; 250 pixels = 9.5° visual angle).
between the angles of the goal and saccade vectors. By convention, we defined a positive angular error as one where the saccade vector was closer to the horizontal meridian than the goal vector. Amplitude error was calculated as the difference between the magnitude of the saccade and goal vectors, so that a positive value indicated that the saccade vector was larger than the goal vector.

For both angular error and amplitude error, we used a general linear model with main factors of goal location (5, 15, 45, and 75°) and saccade type (prosaccade, antisaccade) and subject as a random effect. We used Tukey’s honestly significant difference (HSD) test at an α level of 0.05 to examine for significant contrasts. Finally, we used a t-test with Bonferroni correction for multiple comparisons to determine whether mean subject angular error for prosaccades or antisaccades to specific goal locations was significantly different from zero across the group.

**Experiment 2**

To determine whether within-block Cartesian or polar range effects were generating the diagonal effect, we performed a second experiment in the same subjects, using the same goal locations. This time, however, only two goal locations were used in each block. These were mirror-image pairs across the horizontal meridian (Fig. 1). This block design eliminates potential quadratic directional range effects in polar coordinates, since there is only one target per quadrant. For Cartesian range effects, the key fact is that the horizontal component of the two goal vectors in each block are identical: hence there is no basis for a range effect in the horizontal direction. Therefore any variability in the horizontal component of antisaccade vectors would have to be attributed to other factors than Cartesian range effects.

**SUBJECTS.** The same 12 subjects who performed experiment 1 also performed experiment 2 in the same session.

**APPARATUS AND PROCEDURE.** The same target locations were used in both experiments 1 and 2, the only difference being in the construction of the experimental blocks. In experiment 2, the eight target locations in one hemifield were divided into four pairs of locations mirror-symmetric across the horizontal meridian. This resulted in four blocks of targets: one pairing the targets located 5° above and below the horizontal meridian, one pairing the targets 15° above and below, one pairing the targets 45° above and below, and one pairing the targets 75° above and below.

A block consisted of 40 trials, 20 for each of the two locations, in random order. Prosaccades and antisaccades were tested in separate blocks. Each block was given once, resulting in eight different blocks, given in random order, with a total 160 prosaccades and 160 antisaccades across the entire experiment. Hemifield location was counter-balanced across subjects as in experiment 1, with the same hemifields used in a given subject for both experiments.

**ANALYSIS.** The analysis used in experiment 1 was repeated for the data of experiment 2. Angular error and amplitude error were calculated for each trial and subjected to a general linear model with main factors of goal location (5, 15, 45, and 75°) and saccade type (prosaccade, antisaccade), and subject as a random effect, and Tukey’s HSD test at an α level of 0.05 to examine for significant contrasts. Again, we used a t-test with Bonferroni correction for multiple comparisons to determine whether mean subject angular error for prosaccades or antisaccades to specific goal locations was significantly different from zero across the group.

In addition, we ran a second analysis of the horizontal-component error for antisaccades. If the diagonal effect is generated by a Cartesian range effect operating within blocks, there should be no systematic variation in horizontal component error with target location, because within each block, there is no variability in the horizontal component of the goal locations. We calculated horizontal component error as the difference between the horizontal position of the saccade endpoint and the horizontal position of the goal, with negative values indicating hypometria. We performed a general linear model with goal location (5, 15, 45, and 75°) as the main factor and subject as a random effect. We also performed a t-test with Bonferroni correction to determine whether mean horizontal component error was significant across the group at any of the four goal locations.

**Experiment 3**

To exclude both across-block range effects and within-block spatial interactions, we performed a third experiment. To eliminate within-experiment/across-block range effects, we had all subjects perform antisaccades to locations at regular 15° intervals placed in all four quadrants over the course of a single experiment. Since the stimulus and goal locations are spaced equally across the entire spectrum of directions in the frontal plane, there is no range effect over the whole experiment in either Cartesian or polar terms. To eliminate within-block spatial interactions between goals with different angular values in polar coordinates, subjects performed blocks of antisaccades to two goals that had identical values of angular direction but different eccentricities. This provides a useful contrast to the goals in experiments 1 and 2, which differed in angular value but had the same eccentricity.

**SUBJECTS.** Eight healthy subjects between the ages of 20 and 43 yr (mean = 26 yr) participated (4 males, 4 females). All had corrected-to-normal vision and were right-handed.

**APPARATUS AND PROCEDURE.** The apparatus was similar to that in experiments 1 and 2, except that the recording system was upgraded to an Eyelink 1000 binocular system (SR Research) and protocols were created using SR Research Experiment Builder 1.4.202 RC. Also, a circular mask of black paper was attached to the monitor to make the display screen appear round instead of rectangular in the dark room, eliminating a possible artifactual explanation of similar diagonal effects that has been entertained in studies of reaching arm movements (Smyrnis et al. 2000).

Each trial began with a white fixation cross at the center of a black screen. Subjects pressed the spacebar once they had fixated the fixation cross to indicate their readiness to begin the trial. Following a short variable delay (750, 1,000, 1,250, or 1,500 ms), the cross disappeared and the target appeared, a white disk with a diameter of 25 pixels, at an eccentricity of either 200 (7.6°) or 300 pixels (11.4°). Subjects were instructed to make a saccade of equal size in the direction opposite to the target. (To obtain sufficient data for a larger range of different antisaccades, we did not assess prosaccades in this experiment, because experiments 1 and 2 had already established the directional accuracy of prosaccades.) Once a saccade was made, the target disappeared and the fixation cross reappeared for the start of the next trial.

Each block contained 10 trials, 5 with targets at 200-pixel eccentricity, and 5 at 300-pixel eccentricity, in random order. Within each block, all targets had the same angular direction (Fig. 1). Before each block, subjects were presented with a written instruction screen that depicted the two possible target locations in that block. Angular directions (with the horizontal meridian in the right hemifield being 0°) started at 0° and were spaced every 15°, for a total of 24 different angular directions. Because our analysis collapses across quadrants, the four blocks with goals on the vertical and horizontal meridians were repeated, for a total of 28 blocks in the entire experiment (280 trials in total): this ensured that all points in the quadrant analysis had...
an equal number of trials. Block order was randomized without replacement.

**ANALYSIS.** Angular error and amplitude error were analyzed using a general linear model, with goal eccentricity (200 and 300 pixels) and goal (angular) location (0, 15, 30, 45, 60, 75, and 90°) as main factors and subjects as a random effect. Tukey’s HSD test at an α level of 0.05 was used to determine whether contrasts between different goal locations were significant. *t*-tests with Bonferroni correction were used to determine whether mean angular error across the group was significantly different from zero for each goal location.

**RESULTS**

**Experiment 1**

**ANGULAR ERROR.** There was no significant effect of saccade type; however, there was a significant main effect of goal location $F(3,2839) = 12.294, P < 0.0001$ and a significant interaction between saccade type and goal location $F(3,2839) = 7.361, P < 0.0001$. For prosaccades, angular error was minimal (Fig. 2A), and Tukey’s HSD test showed no difference between goal locations. For antisaccades, Tukey’s HSD tests showed that all contrasts were significant except those between the 5 and 15° goal location and between the 5 and 45° goal location (Fig. 2C). The pattern of angular error showed that antisaccades to goals close to the vertical or horizontal meridians tended to deviate away from these meridians—that is, toward the 45° diagonal meridian (Fig. 2B). A *t*-test with Bonferroni correction showed that the mean angular error of antisaccades was significantly different from zero for the 75° goal location.

**AMPLITUDE ERROR.** There was a significant effect of saccade type $[F(1,2839) = 19.2, P < 0.0001]$, with antisaccades more hypometric than prosaccades (Fig. 2D). There was a significant effect of goal location $[F(3,2839) = 4.8, P < 0.003]$ and a significant interaction of saccade type and goal location.
DIAGONAL EFFECT IN ANTISACCADES

[\(F(3,2839) = 2.74, P < 0.042\)]. Although Tukey’s HSD test showed no difference between goal locations for prosaccades, antisaccades to the \(45^\circ\) goal location were significantly larger than those to the 5 and 75\(^\circ\) goal locations. Thus antisaccades to goal locations close to the horizontal and vertical meridians tended to be more hypometric than antisaccades to a goal on the 45\(^\circ\) diagonal meridians.

**COMMENT.** These results show that, whereas prosaccades are highly accurate regardless of goal location, antisaccades show a systematic distortion of angular accuracy, with a tendency of oblique antisaccades to deviate toward the 45\(^\circ\) diagonal meridians. In addition, unequal oblique antisaccades are smaller than those to goals located on the 45\(^\circ\) diagonal meridians. In terms of Cartesian \((x,y)\) coordinates, these effects reflect a combination of hypometria of the long component of the antisaccade vector, with normometria or hypermetria of the short component. Thus for an antisaccade to the 75\(^\circ\) location, near the vertical meridian, with a short horizontal \((x)\) vector component and long vertical \((y)\) vector component, amplitude is hypometric in the \(y\)-direction but not in the \(x\)-direction, whereas the reverse is true for antisaccades to the 5 and 15\(^\circ\) locations, near the horizontal meridian. The result is a tendency of oblique antisaccades with unequal horizontal and vertical vector components to deviate toward the 45\(^\circ\) diagonal meridians, which we will call the diagonal effect.

One important question is whether our experimental design was responsible for this pattern of results. In the blocks of this experiment, subjects performed antisaccades to one of eight goals, all located in the same horizontal hemifield. When subjects make saccades to locations that are unevenly distributed across the visual field, range effects may emerge, in which responses deviate toward the center of the spatial range of goals used (Kapoula 1985). This has also been shown for antisaccades but usually for targets of varying amplitude rather than varying direction (Dafoe et al. 2007; Evdokimidis et al. 2006). In polar coordinates, our targets vary in direction but not amplitude. However, even if one postulates that range effects may also occur for direction, the predicted range effect would be a convergence to the horizontal rather than the diagonal meridian, since all experimental blocks contained equal numbers of goals above and below the horizontal meridian. To obtain the diagonal effect, one would have to postulate separate range effects within each quadrant. Whether within-quadrant range effects exist is not known, but given the noncontiguous quadrantic organization of some early visual areas (Allman and Kaas 1974; Engel et al. 1997) and the quadrantic constraints on some attentional phenomena (Carlson et al. 2007; Rizzolatti et al. 1987), this possibility cannot be dismissed without further examination.

In Cartesian coordinates, because goals were located in one horizontal hemifield only, range effects operating in the horizontal direction would increase small vector components and decrease large vector components, a prediction that bears some resemblance to our findings. In the vertical direction, however, because blocks contained goals both above and below the horizontal meridian, a range effect would lead to hypometria of all vector components, although this might be proportionally greater for saccades to goals farther from the horizontal, such as the 75\(^\circ\) locations.

This also might resemble our results to some degree. To address these issues we performed experiment 2.

**Experiment 2**

**ANGULAR ERROR.** There was a significant main effect of saccade type \([F(1,2879) = 10.2, P < 0.002]\). There was a significant main effect of goal location \([F(3,2879) = 90.6, P < 0.0001]\) and a significant interaction between saccade type and goal location \([F(3,2879) = 41.1, P < 0.0001]\). Tukey’s HSD tests showed that for prosaccades the angular error to the 75\(^\circ\) location was significantly different from that to the 5 and 15\(^\circ\) locations (Fig. 3C). For antisaccades, all contrasts were significant except that between the 5 and 15\(^\circ\) locations. A \(t\)-test showed that antisaccades to the 15 and 75\(^\circ\) locations had significant mean angular errors. Prosaccades to the 75\(^\circ\) location also had a small but significant mean angular error. Again, the pattern for antisaccades was a tendency for oblique antisaccades to deviate toward the 45\(^\circ\) diagonal meridian.

**AMPLITUDE ERROR.** There was no significant effect of saccade type, but a significant effect of goal location \([F(3,2879) = 60.2, P < 0.0001]\) and interaction between saccade type and goal location \([F(3,2879) = 37.8, P < .0001]\). Tukey’s HSD test showed no significant contrasts between goal locations for prosaccades, but all contrasts for goal locations were significant for antisaccades, except the contrast between the 5 and 15\(^\circ\) locations. As in experiment 1, the largest antisaccades occurred for the 45\(^\circ\) location (Fig. 3D).

**HORIZONTAL VECTOR COMPONENT ERROR.** The general linear model showed a significant effect of goal location \([F(2,1291) = 166, P < 0.0001]\). Tukey’s HSD test showed that antisaccades to the 5 and 15\(^\circ\) locations differed significantly from those to the 45 and 75\(^\circ\) locations, but there was no difference in horizontal component error between the 5 and 15\(^\circ\) locations and between the 45 and 75\(^\circ\) locations. A \(t\)-test with Bonferroni correction showed a significant horizontal component hypometria for the 15\(^\circ\) location and a significant horizontal component hypermetria for the 75\(^\circ\) location (Fig. 3B).

**COMMENT.** Experiment 2 showed very similar results to experiment 1, despite the change in block design. Again, a diagonal effect emerged, caused by a combination of either normometry or hypermetria for the short vector component and normometry or hypometria for the long vector component.

These findings indicate that the diagonal effect is not generated by range effects operating within experimental blocks in either polar or Cartesian coordinates. In experiment 1, we considered the possibility that within-quadrant polar range effects could explain a convergence of oblique saccades to the diagonal; however, in experiment 2, no such within-quadrant range effects should be generated, since in each block there is only one goal per quadrant.

We also considered whether Cartesian range effects in experiment 1 could generate a hypermetric small horizontal component for antisaccades to the 75\(^\circ\) location and hypometric large horizontal components for antisaccades to the 5 and 15\(^\circ\) locations. In experiment 2, no range effect for the horizontal component should be generated within each block, since all goals within a single block have the same horizontal vector component. Our analysis clearly showed that small horizontal
components were still hypermetric and large horizontal components were still hypometric. This conclusion is further reinforced if one examines the vertical component, since Cartesian range effects would cause convergence to the horizontal meridian, midway between the two target locations in each block and thus predict hypometric vertical components in all blocks. However, Fig. 3 shows if anything a tendency to hypermetria rather than hypometria for the 5 and 15° target locations, more consistent with a diagonal effect than with a range effect.

Thus experiment 2 excludes within-block range effects as responsible for the diagonal effect. However, one might argue that range effects may still be operating if they can be generated over the course of the entire experiment, not just within blocks. Also, there is the possibility that spatial interactions between adjacent goals within the same block may have generated a pattern of results in experiment 2 that resembled those in experiment 1 for different reasons. For instance, in polar coordinates, there may be a range effect that reduces the angular separation between antisaccade vectors to widely separated goals (e.g., the 75° locations) but a mutual repulsion effect that increased the angular separation between antisaccade vectors to narrowly separated goals (e.g., the 5 and 15° locations). Mutual repulsion effects have been described for other phenomena in the visual system (Marshak and Sekuler 1979), and although such an explanation requires a complex combination of range and repulsion effects, complexity in itself is not grounds for excluding a potential explanation. To address these issues, we performed experiment 3.

**Experiment 3**

**ANGULAR ERROR.** There was a significant main effect of goal eccentricity \( F(1,2000) = 5.94, \ p < 0.02; \) Figs. 4 and 5. There was also a significant main effect of goal location \( F(6,2000) = 146, \ p < 0.0001 \), but no significant interaction between eccentricity and goal location. Tukey’s HSD
test showed that all contrasts were significant except for those between goals at 0 and 45° and goal locations at 0 and 90°. A t-test with Bonferroni correction showed that, for both 200- and 300-pixel locations, mean angular error was significantly different from zero at goal locations of 15 and 75°, with a trend to significance at 60° (Fig. 5C).

AMPLITUDE ERROR. There was a significant main effect of eccentricity \( F(1,2000) = 15.8, P < 0.0001 \), because of slightly larger saccades to goals with larger eccentricity. If we analyzed amplitude error, however, this also showed a significant main effect of eccentricity \( F(1,2000) = 812, P < 0.0001 \) caused by saccades being hypermetric to 200-pixel eccentricity but hypometric to 300-pixel eccentricity goals. In neither analysis was there a significant effect of goal location or interaction between eccentricity and goal location (Fig. 5D).

COMMENT. Despite a very different design, experiment 3 reproduced the diagonal effect seen in experiments 1 and 2, indicating that neither across-block range effects nor within-block interactions between goals with different angular directions are responsible for its generation.

The importance of excluding range effects as a cause of the diagonal effect in angular error is underscored by the range effect for amplitude error in experiment 3, reproducing other reports of range effects that are more prominent for antisaccades than prosaccades (Dafoe et al. 2007; Evdokimidis et al. 1996). Antisaccades to the closer goal locations were significantly hypermetric, whereas those to the farther goal locations were significantly hypometric in polar coordinates. In contrast, within-block range effects for angular direction did not exist because there was only a single angular direction in each block, and across-block range effects were eliminated by ensuring that angular directions were evenly distributed across the entire 360° spectrum.

**DISCUSSION**

The reproduction of the diagonal effect for antisaccades across all three experiments despite significant differences in block design suggests that it represents a consistent systematic error in generating the coordinates for oblique antisaccades. Experiments 1 and 2 indicate that this systematic error does not occur with prosaccades (or very minimally so, see experiment 2). The error seems to partially reduce asymmetries between the horizontal and vertical components of an oblique antisaccade, causing the direction of the antisaccade vector to veer toward the 45° diagonal meridians.

Systematic errors are not unknown in the saccadic system. Large prosaccades tend toward hypometria, or undershoot, falling short of their goal by ~10% (Becker 1989). Antisaccades in turn are more hypometric than prosaccades to targets of a similar distance (Hallett and Adams 1980; Krappmann 1998). However, these systematic errors primarily affect amplitude; similar errors for direction have seldom been reported. Perhaps the most notable finding is that, in well-trained research monkeys, memory-guided saccades are deviated upward in all quadrants (Stanford and Sparks 1994; White et al. 1994), a directional systematic error that differs significantly from the diagonal effect we report here for antisaccades in untrained human volunteers. The diagonal effect has not been reported before because of the simple fact that most if not all antisaccade studies have confined their targets to the horizontal, vertical, and diagonal meridians.

Where does the diagonal effect originate and what does it tell us about the sensorimotor transformations involved in antisaccade but not prosaccade generation? Most importantly, where does this systematic error arise in the process of locating a stimulus, inverting its vector, and generating the eye movement to this opposite location? To consider this, it is useful to ask whether this error arises before or after the level of the superior colliculus.

*Oblique saccades and the brain stem generation of saccades*

Although oblique antisaccades with unequal vertical and horizontal components have not been studied before, similar oblique prosaccades have been investigated frequently because of their significance for models of sensorimotor transformations between various levels of the ocular motor system. Structures that use a topographic map for encoding location (place-coding), for example, striate cortex and superior colliculus (Robinson 1972), are often depicted as coding stimulus location and/or movement vectors in polar coordinates. The ocular motor plant, however, has different muscles for motion in vertical and horizontal directions and hence executes saccadic vectors in Cartesian coordinates. Medium- or short-lead burst neurons in the parapontine reticular formation and rostral interstitial nucleus of the medial longitudinal fasciculus may also use “rate-coding” in Cartesian coordinates rather than polar place-coding (but see Quaia and Optican 1997 for a dissenting opinion), a statement supported by the clinical evidence of selective horizontal and vertical saccadic palsies associated with these structures.

One intriguing question has been whether the neural pulse that generates saccadic velocity occurs before the decomposition of oblique movement vectors into separate horizontal and vertical components (common source models) or after (inde-
pendent models) (Leigh et al. 1997; Quaia and Optican 1997; van Gisbergen et al. 1985). Oblique prosaccades have been seen as a test of these models. Although early reports suggested that the vertical and horizontal components of oblique saccades could be temporally independent (Bahill and Stark 1977), subsequent studies suggest a closer link between the durations of the two components (Guitton and Mandl 1980; King et al. 1986). Furthermore, since saccadic duration is a nearly linear function of amplitude (Baloh et al. 1975), separate pulse generators creating vertical and horizontal saccade components independently should lead to completion of the smaller vector component before the larger, leading to curved trajectories. Studies have shown that this is moderated by “component stretching”—that is, the velocity of the smaller component is slowed to at least partially accommodate the time needed to complete the larger component, compared with the execution of a vertical or horizontal saccade of the same size as the small vector component (Guitton and Mandl 1980; King et al. 1986; van Gisbergen et al. 1985). Although these findings have been interpreted as supporting the common source model, they can also be accommodated by separate but linked pulse generators (cross-coupled model) (Becker and Jurgens 1990; Grossman and Robinson 1988).

Regardless of model, component stretching of velocity in prosaccades is either reflected or possibly generated in parts of the ocular motor system organized along Cartesian coordinates. It is possible that the diagonal effect—essentially component stretching of amplitude in antisaccades—represents an analogous phenomenon. Amplitude stretching might occur if the pulse durations in vertical and horizontal directions are linked but the velocity of the smaller vector component is insufficiently reduced, leading to relative hypermetria of the small component and a shift of the antisaccade vector toward the 45° diagonal meridian. This systematic error would be attributable to a combination of inadequate velocity component stretching and a requirement for synchronous vertical and horizontal pulse durations, perhaps under the control of omnipause neurons (Scudder et al. 2002).

If the diagonal effect results from partial failure of velocity stretching, it would raise questions about the statement in FIG. 5. Results of experiment 3. In each experimental block, subjects made antisaccades to 1 of 2 randomly ordered locations that had the same direction but different eccentricities. As an example, the top cartoon shows the 2 target locations for all 7 experimental blocks for the right top quadrant; similar blocks were constructed for the other 3 quadrants. All quadrants were tested in all subjects. Below the cartoon, the results are shown, collapsed for display purposes into a single quadrant (see Fig. 4 for a display of results in all quadrants). A: antisaccades to goals at 200-pixel (7.6° visual angle) eccentricity: the 7 quadran tic goal locations are shown as small black points, and mean saccadic endpoint is the center of the error bars, which indicate SE in both x- and y-directions. B: antisaccades to goals at 300-pixel (11.4° visual angle) eccentricity: similar plotting convention. C: mean angular error for each of the 7 goal locations (goal angle indicating angular distance from the horizontal meridian). A positive angular error indicates a saccadic vector that is farther from the horizontal meridian than the goal vector. (*angular errors significantly different from 0; #trend to significant difference, for both 200- and 300-pixel targets). D: mean amplitudes of the saccadic vector to the 7 different goal locations. Error bars indicate SE in C and D.
common source models that the mappings from collicular or long-lead burst neurons coding polar vectors \((R, \Phi)\) to medium-lead burst neurons generating horizontal and vertical movement have fixed synaptic weights \((\cos \Phi \text{ and } \sin \Phi, \text{ respectively})\) (van Gisbergen et al. 1985). Rather, it would indicate that the accuracy of this geometric transform depends on the strong signals with visually guided saccades and is less reliable with the weaker signals associated with internally generated saccades. In this regard, it is of interest that some have reported that volitional oblique saccades in the dark do not show velocity stretching (Guitton and Mandl 1980), although others suggest that memory-guided saccades do (Smit et al. 1990).

**Potential cortical sources of systematic error in antisaccades**

The estimation of the correct goal location for an antisaccade requires a transformation between the target and movement vectors, a vector inversion that is not required for a prosaccade. Neuroimaging (Moon et al. 2007) and neurophysiological studies of antisaccades suggest that both the lateral intraparietal area (LIP) and the frontal eye field (FEF) may participate in this process. Both areas encode an early visual signal that is appropriate for the location of the stimulus, which is followed after 50 ms in the LIP by a paradoxical response that may represent a remapped visual signal on the side appropriate for the direction of the saccade (Zhang and Barash 2000, 2004). In the FEF, there are neurons which are active when the stimulus is in their reactive field, and other type II neurons with responses when the prosaccade or antisaccade is directed into its field, and which correlate with saccadic latency (Sato and Schall 2003).

Studies have shown a retinotopic organization of responsibility to visual signals in the LIP in monkeys and for activity related to memory-guided saccades in the analogous posterior parietal cortex in humans (Schluppeck et al. 2005; Sereno et al. 2001). Likewise, recordings from the FEF show a vector coding for saccades (Funahashi et al. 1990), although the spatial organization of these neurons may not be as orderly as the polar map of the superior colliculus (Bruce et al. 1985). Critically for our finding, what is not yet known is how the spatial accuracy of visual responses compares with that of paradoxical or type II responses and whether the latter show any systematic mapping errors compared with the former. Compared with the responses to visual stimuli or during prosaccades, the saccade-appropriate responses during antisaccades in LIP, FEF, and the superior colliculus are quite weak, but whereas this reduced signal might account in part for increased variable error, it is not clear if and how it could also generate the systematic error we report.

Since these and other cortical regions project to the superior colliculus (Fries 1984; Leichnetz et al. 1981), it would be reasonable to suspect that any systematic error generated at a cortical level would also be evident in the collicular map. Although there are no studies of systematic antisaccade error in the superior colliculus, others have studied tectal responses in relation to the systematic upward bias reported for memory-guided saccades (Stanford and Sparks 1994). This study reported that the directional responses of collicular neurons did not show an equivalent shift with the systematic error, suggesting that that particular systematic error originated at a lower brain stem level rather than in cortex.

**Diagonal effects in perception and other motor responses**

In the absence of definitive neurophysiological evidence on the origins of the diagonal effect, it is worth noting the occurrence of a similar systematic error in other systems. Paradigms testing reaching movements in the horizontal plane with a visual display in a vertical plane (much like using a computer mouse) also show an “oblique effect” (Gourtzelidis et al. 2001; Mantas et al. 2008; Smyrnis et al. 2000; Theleritis et al. 2004) identical to our diagonal effect. Initially, it was speculated that this oblique effect might reflect the existence of “movement primitives” or force fields derived from preferred patterns of muscle activation in the arm (Smyrnis et al. 2000). However, a similar oblique effect occurs when subjects use methods other than reaching to indicate the perceived position of dots on the circumference of a circle, such as reproducing the location with a stylus or pen on a different response sheet (Huttenlocher et al. 1991; Mantas et al. 2008) or using an arrow to indicate the direction of the stimulus from the center of the circle (Mantas et al. 2008; Smyrnis et al. 2007). These findings suggest that the error may originate in perceptual systems and is reflected in a variety of motor responses. The diagonal effect in antisaccades provides more support for this interpretation, since it shows a similar error in an ocular rather than manual response, against a biomechanical explanation based on limb movement.

At least two potential explanations have been offered for a diagonal effect in perceptual localization. Common to both is an emphasis on a special status for the cardinal horizontal and vertical axes. The first explanation relates the effect to a general model regarding how uncertain information is handled using categorical classifications and prototypes (Gourtzelidis et al. 2001; Huttenlocher et al. 1991). In spatial localization, the cardinal axes are boundaries that divide the frontal plane into quadrant categories, in each of which the central or prototypical direction would be the diagonal axis. Estimations of the locations of stimuli within these quadrants would reflect a combination of the veridical stimulus location with the prototype, particularly under conditions of increased uncertainty. The second explanation suggests that the representation of space is nonlinear, with an expansion of representations around the cardinal axes and a contraction of representations around the diagonal axes (Mantas et al. 2008).

These prior studies have also established that the diagonal effect is more pronounced for memory-guided than visually guided reaching and increases as the gap between stimulus offset and movement onset widens to 4–6 s (Mantas et al. 2008; Smyrnis et al. 2000). Thus the requirement to estimate target location in the absence of a stimulus near the time of movement execution may be an important factor allowing this systematic error to emerge. Likewise, antisaccades differ from prosaccades in that they are programmed toward a goal that

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2 We prefer the term diagonal effect because it more specifically indicates the deviation of all oblique movements towards a specific oblique angle, namely the diagonal axes, and because it avoids confusion with another perceptual oblique effect referring to higher thresholds for motion discrimination along the diagonal than the cardinal axes (Ball and Sekuler 1987; Gros et al. 1998; Kruskowski and Stone 2005).
lacks a visual stimulus. The fact that we find the diagonal effect for antisaccades and not for prosaccades is consistent with the suggestion that the bias emerges under conditions of location uncertainty, when the goal of the movement must be estimated without the direct guidance of a stimulus at that location.

Conclusions

The diagonal effect is a novel systematic error that is specific for antisaccades and not prosaccades. It differs from the systemic upward error reported for well-trained monkeys making memory-guided saccades: whether this represents a species difference, a training difference, or a difference between antisaccades and memory-guided saccades is not clear. Without more data on the spatial properties of remapped antisaccade responses in cortical regions or the colliculus, it is also not clear whether this systematic error originates in cortical representations of the antisaccade vector or its later spatiotemporal transformation into Cartesian coordinates during brain stem processing. However, the presence of a similar diagonal effect in manual reaching and perceptual experiments suggests that this may reflect a common systemic error in the perceptual estimation of obliquely located stimuli, particularly in the absence of visual guidance for the response. Clarifying the origins of this systematic antisaccade error can reveal important differences in the generation of visually guided versus internally generated saccades and the role of visual stimuli at the saccadic goal in spatiotemporal transformations.

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