

Changes in visual motion perception before saccadic eye movements

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Abstract

Execution of a saccadic eye movement influences subsequent motion perception [Park, J., Lee, J., & Lee, C. (2001). Non-veridical visual motion perception immediately after saccades. *Vision Research*, 41, 3751–3761]. In the current study, we determined the pattern of perceptual changes for visual motion presented before saccades. The accuracy of judging the direction of a moving target was variable depending on the direction of target motion. Based on the pattern of judgment errors, the direction associated with no error, or DNE, could be defined. When a moving target was seen by stationary eyes, the DNE was roughly vertical, and the perceptual judgment for adjacent directions was biased away from the vertical direction. When the same visual motion was seen before horizontal saccades, the DNE shifted in the direction of the impending saccade, and the perceptual judgment of adjacent directions was shifted away from the new DNE, thus, shifting the perceived direction of the vertical in the direction opposite to the saccade. These changes improved the accuracy of direction judgment for visual motion in the visual field ipsiversive to impending saccades. In addition to shift of the DNE, perceptual judgment for oblique directions became near veridical before saccades, which we call the *anti-oblique effect*. These results suggest that motion perception is dynamically and anisotropically modulated at the time of saccades, and the DNE shift may be a part of processes dynamically reallocating computational resources, improving perceptual performance in advance for sensory events to be acquired by impending saccades.

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1. Introduction

Our perception is not isotropic or stationary. The same physical stimulus is perceived and processed differently, depending on the state of our perceptual system. For example, execution of rapid eye movements (saccades) changes the perceptual representation of space, time, and motion: Spatial localization of a visual target presented around the time of saccades is biased, in ways that can be related to the parameters of saccadic eye movements and the experimental condition such as presence of visual references (Cho & Lee, 2003; Honda, 1991; Kaiser & Lappe, 2004; Morrone, Ross, & Burr, 1997). Perceived duration is extended in association with execu-

tion of saccadic eye movements (Park, Schlag-Rey, & Schlag, 2003; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001). Similarly, we found previously that when a linear motion of a point stimulus was visible immediately after a saccadic eye movement, the perceived direction of visual motion was systematically biased in the direction opposite to the saccade (Park, Lee, & Lee, 2001). Interactions between neural signals of saccadic planning or execution and retinal inputs appear to occur in multiple sites, as shown by independent effects of saccadic eye movements on spatial localization and motion perception (Cho & Lee, 2003). These interactions between retinal and oculomotor signals are thought to be related to maintaining visual stability (see for reviews, Burr, 2004; Ross, Morrone, Goldberg, & Burr, 2001).

In the current study, we examined the pattern and time course of perceptual bias for a visual motion seen

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before the saccade. Here, we report that meridional anisotropy in motion perception dynamically changes at the time of saccades, and this change is based on two processes; the shift of DNE and the anti-oblique effect.

2. Methods

Seven normal subjects (aged 22–36) participated in these experiments. For each, the nature of the experiments was explained, and informed consent obtained. The experimental apparatus was identical to that used in a previous report (Park et al., 2001). In brief, subjects were seated facing a $2\text{ m} \times 2\text{ m}$ tangent rear-projection screen at a distance of 115 cm. The head was stabilized in the erect position with a bite bar. Horizontal positions of both eyes were measured with the infra-red reflection method (IRIS, Skalar Medical). Visual stimuli, appearing as red spots of light 0.2 deg in diameter, were provided by a laser beam deflected by a 2-axis galvanometer scan head (model Z1913, General Scanning) onto the tangent screen. Horizontal eye positions and horizontal and vertical positions of the laser beam were sampled at 500 Hz with a resolution of 12-bits, and stored for off-line analysis.

2.1. Experiment 1

The main goal of the current study was to determine the perceived direction of a visual target presented immediately before the onset of a saccade. The following protocol was designed to present motion target immediately before saccades (Fig. 1). After a tone signaled the start of a trial, a spot of light was presented at the center of the screen, on which the subject was instructed to maintain fixation. With a delay of 1200 ms plus an additional random interval after the eye entered an electronic window centered about the fixation point, the spot of light disappeared and briefly reappeared as a saccade target for 50 ms at one of two randomly-determined loci, 10° to the left or right. With a randomly-determined delay of 60, 80, or 100 ms after the saccade target disappeared, a tone of 50 ms duration signaled the subject to make a saccade to the remembered locus of the saccade target as precisely and promptly as possible in an otherwise completely dark and sound-attenuated room. This memory-guided saccade paradigm was designed to alleviate the influence of the saccade target, if any, on perception of subsequent target motion by introducing a temporal gap between the two. With a randomly-varied delay between 50 and 80 ms after tone offset, the laser spot reappeared at the center and made a centrifugal sweep of 10° for a period of 80 ms (thus, the average velocity was 125 deg/s). The temporal delay brought the laser sweep near the time of saccade onset.

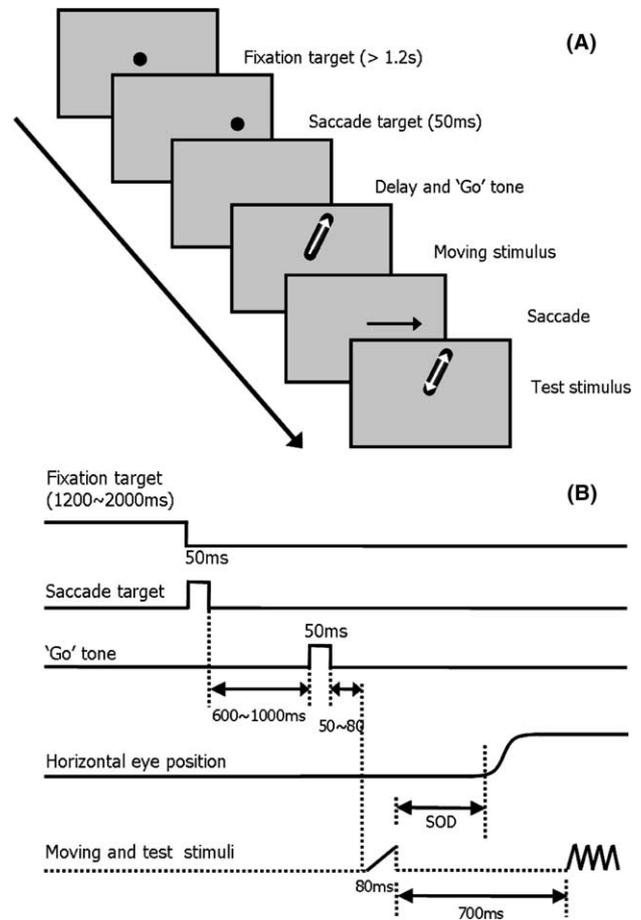


Fig. 1. Paradigm of Experiment 1 in spatial (A) and temporal (B) sequences. A spot of light first appeared at the center of the screen as a fixation target, disappeared, and reappeared as a saccade target to the left or right. With a variable delay after the saccade target disappeared, a tone signaled the subject to make a saccade to the remembered target location. With a variable delay after tone offset, the spot of light reappeared at the center and made a centrifugal sweep of 10° in a variable direction for 80 ms. This paradigm was designed to bring the visual motion near the time of saccade onset. The subject subsequently matched its perceived direction with the orientation of a test stimulus consisting of a radial line segment produced by the same laser rapidly moving back and forth.

Under the conditions of this experiment, the detection threshold for motion of the laser sweep is somewhere between 200 and 250 deg/s , and beyond this, the sweep appears as a line segment instead of a moving spot (Park et al., 2001). The direction of target motion was pseudo-randomly-varied in steps of 5° between 45° and 135° , with 0° to the right and 90° straight up, for each block of 38 trials (19 directions \times 2 saccade directions, right and leftward). Six to seven blocks of data were collected for each subject per day.

After completion of the centrifugal laser sweep, the subject was asked to match its direction of motion with a test stimulus consisting of a radial line segment produced by the same laser rapidly moving back and forth between the center and a point at 10° eccentricity,

presented initially at a randomly-determined inclination between 60° and 120° . By manipulating a momentary dial switch on a hand-held response box ($15\text{ cm} \times 10\text{ cm} \times 3\text{ cm}$), the subject was able to change the locus of the eccentric point, and, thus rotate the orientation of the line segment until it matched the perceived direction of the moving stimulus. Pressing a button on the response box entered the final orientation of the test probe, and started the next trial.

Invalid trials were discarded during off-line analysis. These included trials with unsteady fixation, multiple saccades toward the saccade target, or intervals between offset of moving stimulus and saccade onset larger than 200 ms or smaller than 0 (i.e., saccades starting later than offset of the moving target). Fig. 2 shows an example of a valid trial.

2.2. Experiment 2

As described below, Experiment 1 revealed a novel phenomenon of *presaccadic* motion perception—the anti-oblique effect. In Experiment 2, we determined whether visual motion seen *after* a saccade would show the same phenomenon. Since, in a previous study on *postsaccadic* perception using a different saccade paradigm (Park et al., 2001), no such phenomenon was found, we wondered whether the memory-guided saccade paradigm of Experiment 1 had contributed to this phenomenon. Thus, the same memory-guided saccade paradigm of Experiment 1 was used for *postsaccadic* motion perception.

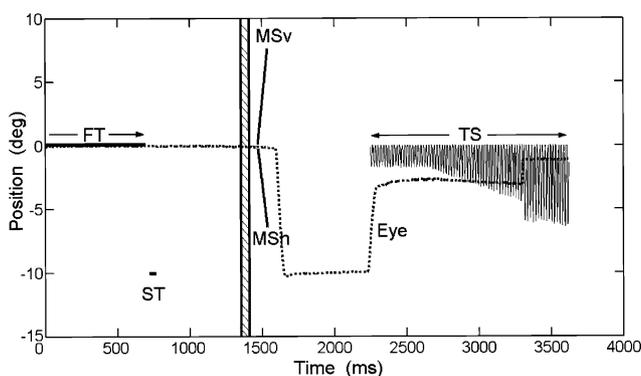


Fig. 2. Example of a valid trial from a representative subject (SH), plotting horizontal positions of the right eye (Eye), central fixation target (FT), saccade target (ST), moving stimulus (MSh), and test stimulus (TS) against time. The vertical position of the moving stimulus (MSv) is also shown, whereas vertical positions of other targets are not shown for clarity. The hatched vertical bar indicates the duration of the tone (50 ms) signaling the subject to make a saccade toward ST. The moving stimulus was presented during fixation and there was no visible target during the saccade. Note that the horizontal position of TS (a radial line segment) eventually approximates MSh as the subject manipulates a dial switch on the response box.

Procedures of Experiment 2 were the same as Experiment 1 except that the motion target was presented after the onset of the centripetal saccade. The subject first fixated the laser target at 10° right or left to the center of the screen for at least 1200 ms, and then the fixation target disappeared and briefly reappeared for 50 ms at the center of the screen. With a delay of 60, 80, or 100 ms after this central saccade target disappeared, a tone signaled the subject to make a centripetal saccade to its remembered location. With a delay of 40 ms after the eye crossed a $4^\circ \times 4^\circ$ window centered on the central target, the laser spot reappeared at the center and then immediately made a centrifugal sweep of 10° at the velocity of 125 deg/s. In a pilot study, it was found that it took approximately 25 ms for the eye to reach the central target after crossing the $4^\circ \times 4^\circ$ window, and so the onset delay of the motion stimulus from the saccade offset was 15 ms. This delay was chosen because it was short enough to reveal saccadic effects given that the median decay time constant of perceptual error for postsaccadic motion was 23.7 ms (Park et al., 2001), while the effects of significant postsaccadic eye drift are reduced. The direction of centrifugal sweep of the laser spot randomly varied from 40° to 140° , in steps of 10° , with 90° straight up. The subject was then asked to match its perceived direction with the test probe, the initial direction of which was randomly chosen between $\pm 30^\circ$ from the direction of the laser sweep.

2.3. Control trials

During Experiments 1 and 2, control trials were also collected. In these, the laser target first appeared at the center, and after the eye maintained fixation for at least 1200 ms within a $4^\circ \times 4^\circ$ window centered on the central target, the target made a centrifugal sweep of 10° at 125 deg/s in a variable direction between 45° and 135° , in steps of 5° in Experiment 1 and between 40° and 140° , in step of 10° in Experiment 2. The subject then matched perceived direction with a test stimulus.

In Experiment 1, the direction of target motion varied between 45° and 135° , with 0° to the right and 90° straight up. In order to examine the effect of this range on direction judgment, the direction of target motion varied between 0° and 90° for four subjects, and between 15° and 165° for two other subjects. In these experiments, procedures were the same as control trials described above, except for the range of target direction.

In all conditions of Experiments 1 and 2 including control trials, the target motion was foveally and binocularly viewed, and no feedback regarding the response was provided. All subjects were right-handed and used the right hand to manipulate the dial switch. Perceptual error was defined as perceived direction minus target direction.

3. Results

3.1. Meridional anisotropy in motion perception during steady fixation

In control experiments where visual motion was presented while the eyes maintained fixation, errors in judging motion direction systematically depended on absolute motion direction (Fig. 3). Perceptual error was negative (clockwise bias) for stimulus directions between 45° and 90° , and positive (counter-clockwise bias) for those between 90° and 135° , indicating that perceived direction was biased away from a direction of no error, or DNE (see Fig. 3 Legend for its definition). The perceptual bias corresponded to approximately 27% of the angular distance from the DNE, as estimated from the slope of linear regression.

In order to determine the error pattern beyond the range of the target direction of Fig. 3, the direction of target motion was varied between 15° and 165° for two subjects (HW, SH) in control experiments. The error was maximal for oblique directions (45° and 135°), and decreased as the direction became smaller than 45° or larger than 135° (not shown). The effects of the range of the tested direction on the pattern of perceptual error have been dealt with in a previous study (Park et al., 2001).

3.2. Changes in motion perception before saccades

In Experiment 1, we determined the perceived direction of a visual target presented immediately before the onset of a saccade. The summary statistics of Experiment 1 are shown in Table 1, and the perceptual errors in direction judgment for presaccadic motion found in Experiment 1 are illustrated in Fig. 4. A systematic bias in direction judgment was found depending on the direction of impending saccades. Most significantly, before saccades the DNE shifted in the direction of impending saccades. The DNE, which was 87.55° in the control trials (Fig. 3), changed to 85.97° (2.07° shift in clockwise direction) before rightward saccades, whereas it changed to 102.33° (14.29° shift in counter-clockwise direction) before leftward saccades (Fig. 4A, Table 2). The shift of DNE was pronounced before leftward saccades in all subjects. Direction judgment was biased away from the new DNE (Fig. 4A). Since the DNE changed in the direction of saccades in all subjects (Table 2), overall direction judgment was biased in the direction opposite to saccades; rightward saccades, compared to leftward saccades, biased direction judgments positively, i.e., counter-clockwise, whereas leftward saccades, compared to rightward saccades, biased negatively, clockwise (Fig. 4A and B). This bias in motion perception in the direction opposite to the impending saccade is the same as

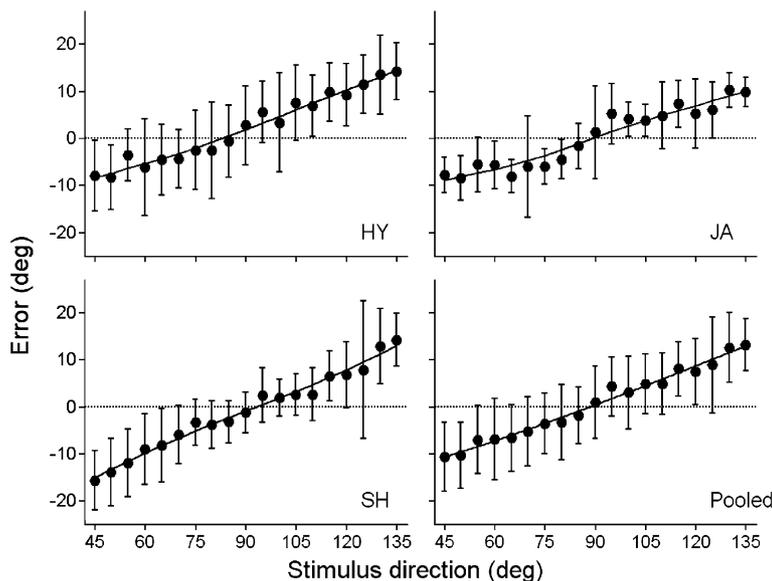


Fig. 3. Perceptual bias in direction judgment. Shown are perceptual errors for target motion presented during fixation for each subject, along with pooled data. Upward motion was assigned a direction of 90° . Symbols represent mean errors and their standard deviations, derived from 597, 304, and 494 total valid trials for HY, JA, and SH, respectively. Positive (negative) errors are counter-clockwise (clockwise). The solid curves are fits derived by spline approximation. The horizontal dotted line in each panel represents zero error. The direction of no error (DNE) was defined as zero-crossing of the curve, and it was 82.74 , 89.65 , 93.11 , and 88.04 for HY, JA, SH, and Pooled, respectively. When the errors were fit with linear regression, the slopes of the regression line were 0.26 , 0.22 , 0.30 , and 0.27 for HY, JA, SH, and Pooled, respectively, suggesting that a fairly constant fraction of the angular distance from the DNE constitutes the error.

Table 1
Summary of Experiment 1

	Experiment 1 (38 trials/block)		
	HY	JA	SH
Subject	HY	JA	SH
Number of sessions	4	4	4
Number of blocks (total trials)	26 (988)	22 (836)	25 (950)
Valid trials (%)	495 (50.1)	241 (28.8)	488 (51.4)
<i>Total valid trials by saccade direction</i>			
Rightward	241	128	247
Leftward	254	113	241

that for postsaccadic motion perception reported previously (Park et al., 2001).

The DNE shift in the direction of impending saccades resulted in a smaller judgment error for the target motion presented in the visual field ipsiversive to impending saccades compared to that for contraversive saccades (Fig. 5, Table 3).

The effect of saccade direction was maximal for the straight-up direction, and minimal for oblique directions (Fig. 4B). The large perceptual errors of direction judgment for oblique directions (45° and 135°) in the control condition diminished in the saccade condition, and the subjects' perceptual judgments were almost veridical (Fig. 6A). We term this the *anti-oblique effect*. The effects related specifically to the saccade (i.e., errors in the saccade condition minus errors in the control condition) were larger for oblique directions than for vertical directions (Fig. 6B).

The magnitude of perceptual error for oblique directions varied depending on the range of target direction

Table 2
Shift of DNE before saccades

Saccade direction	HY	JA	SH	Total
Rightward	81.36 (-1.38)	87.81 (-1.84)	86.89 (-6.22)	85.97 (-2.07)
Leftward	97.03 (14.29)	107.17 (17.51)	106.71 (13.59)	102.33 (14.29)

Shown are DNE (deg) and its shift size (deg) in parenthesis. The DNE is x -intercept of the fitted curve derived by spline approximation, and shift size is the magnitude of change of DNE from that of control trials. Note that the DNE shift is larger before leftward than rightward saccade conditions.

tested in a given block of trials. When the target direction varied between 45° and 135°, with the vertical axis at the center of the range, the error for oblique direction was maximal. When the range was between 0° and 90°, with the diagonal axis at the center of the range for three subjects, the oblique direction (45°) was still biased away from the vertical, but with a smaller error compared to the condition of range between 45° and 135° (not shown). The horizontal direction was also biased away from the vertical, approximately 3° downward, while the vertical was perceived accurately. This superiority of the vertical to the horizontal is consistent with the conclusions of Pettorossi, Bambagioni, Bronstein, and Gresty (1998).

In Experiment 2, we determined in two subjects whether the anti-oblique effect lasts after saccades. When the same memory-guided saccade task of Experiment 1 was used for visual motion presented after completion

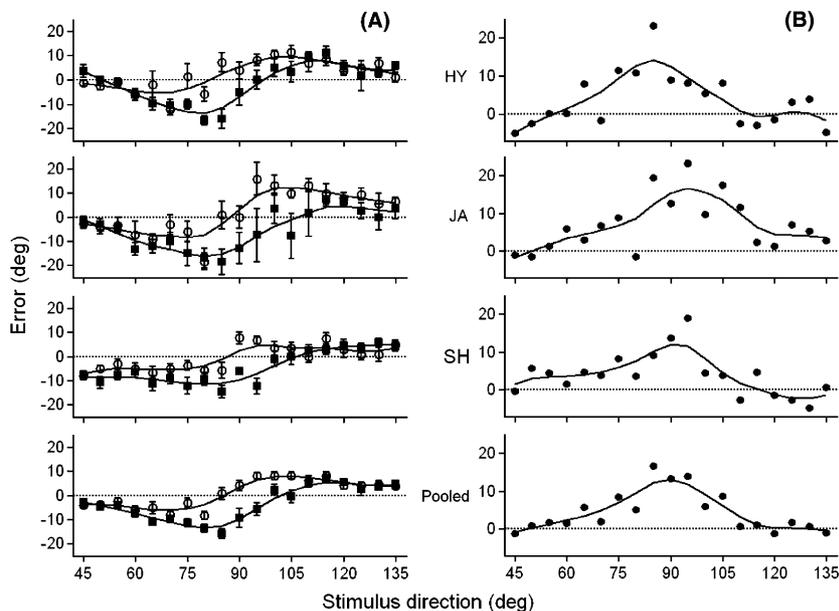


Fig. 4. Perceptual error in saccade condition from Experiment 1. (A) Perceptual error before rightward (open circle) and leftward (filled square) saccades. Perceptual error is perceived direction minus veridical direction of the target motion. Symbols represent mean errors and their standard errors. (B) Difference of error between rightward and leftward saccade conditions in A. Curves in (A) and (B) were derived by spline approximation. Note that the effect of saccade direction is maximal for the vertical direction (90°) and minimal for oblique directions (45° and 135°). The dotted horizontal line in each panel represents zero error.

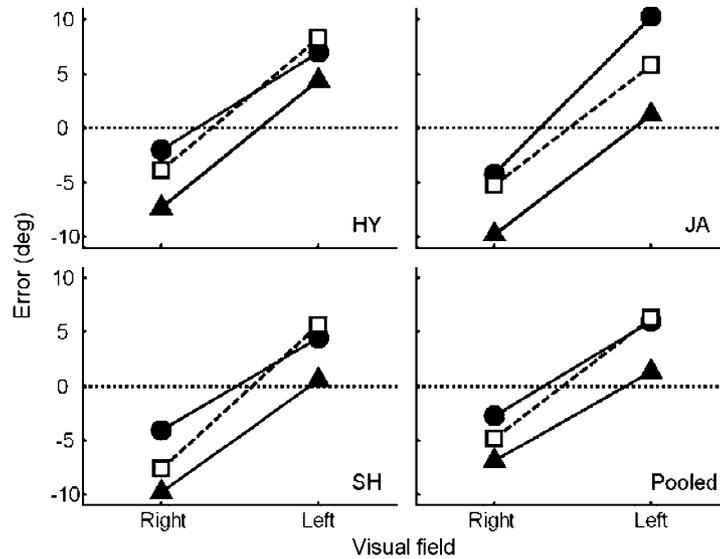


Fig. 5. Effects of saccade on perceptual error by stimulus location. Open squares represent judgment errors for visual motion in the right (45° – 90°) or left (90° – 135°) visual field during steady fixation (control). Filled circles and triangles are those before rightward and leftward saccades, respectively. Leftward saccades, compared to rightward ones, had a relatively larger effect. Note that before leftward saccades, errors for targets in the left visual field were reduced, compared to the control condition, and before rightward saccades, those in right visual field were reduced. Horizontal dotted lines indicate zero error.

Table 3
Comparison of perceptual error by stimulus location relative to saccade direction

Saccade direction	Subject							
	HY		JA		SH		Pooled	
	Right	Left	Right	Left	Right	Left	Right	Left
<i>Visual field</i>								
Right field	-1.99 (0.99)	-7.32** (0.88)	-4.22 (1.18)	-9.78** (0.85)	-4.04** (0.71)	-9.76* (0.75)	-2.74** (0.48)	-6.86* (0.41)
Left field	6.99* (0.75)	4.43** (1.15)	10.28** (0.83)	1.23** (1.43)	4.45 (0.73)	0.57** (0.88)	6.02 (0.39)	1.38** (0.52)
<i>Control condition</i>								
Right	-3.88 (0.48)		-5.24 (0.52)		-7.67 (0.48)		-4.82 (0.24)	
Left	8.24 (0.48)		5.76 (0.50)		5.64 (0.52)		6.25 (0.24)	

Shown are mean perceptual errors and their standard errors (parenthesis). Effects of saccade direction on judgment error were tested with paired sample *t*-tests. For this, errors for visual motion in each visual field (e.g., right visual field) from each saccade condition (e.g., rightward saccade) were compared with those in the same visual field (e.g., right visual field) from the control condition within the same subject. The motion directions between 45° and 90° , and between 90° and 135° fall in the right and left visual fields, respectively. Significant differences are marked with * ($p < .05$) or ** ($p < .01$). Note that for targets presented in the visual field ipsiversive to impending saccade (e.g., left visual field before leftward saccades), smaller judgment errors were associated, compared to contraversive saccades (e.g., left visual field before rightward saccade). These data are also shown in Fig. 5.

of saccades, the anti-oblique effect was absent (Fig. 7), and the pattern of perceptual errors was similar to that found in a previous study using a visually-guided saccades (Park et al., 2001), indicating that the anti-oblique effect is specific to the presaccadic period.

3.3. Time course of saccadic effects

The saccadic effect on motion perception consisted of two processes related to the vertical and oblique direc-

tions, and was more pronounced before leftward saccades. We examined the time course of these two processes by plotting perceptual error for two representative target motions along 45° and 90° before leftward saccades, against the interval between the target offset and saccade onset (Fig. 8). The saccadic effect on meridional judgment started at least 150 ms before the onset of saccade and appeared to increase until saccade onset for both the 45° (Fig. 8A) and 90° (Fig. 8B) directions. Since the average latency of these saccades across all subjects, measured from the onset of 'Go' tone to sac-

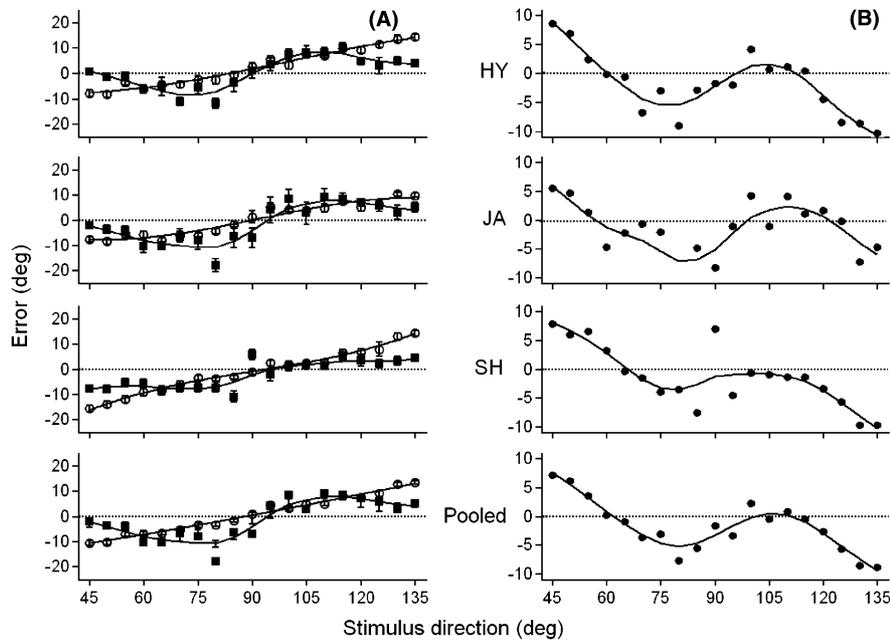


Fig. 6. Anti-oblique effect in motion perception. (A) Comparison of error pattern between control condition (open circle) from Fig. 3, and saccade condition (filled square). Each point for the saccade condition is the average of rightward and leftward saccade conditions of Fig. 4A. Positive errors are in counter-clockwise direction. The dotted horizontal line in each panel represents zero error. Note that errors for oblique directions (45°, 135°) in saccade conditions are considerably smaller than those for control condition in all subjects. (B) Perceptual error in saccade condition minus that in control condition, i.e., difference between the two curves in each panel of A. Curves in (A) and (B) were derived by spline approximation. Effects of saccade are larger for oblique directions (45°, 135°) than for the vertical directions (90°).

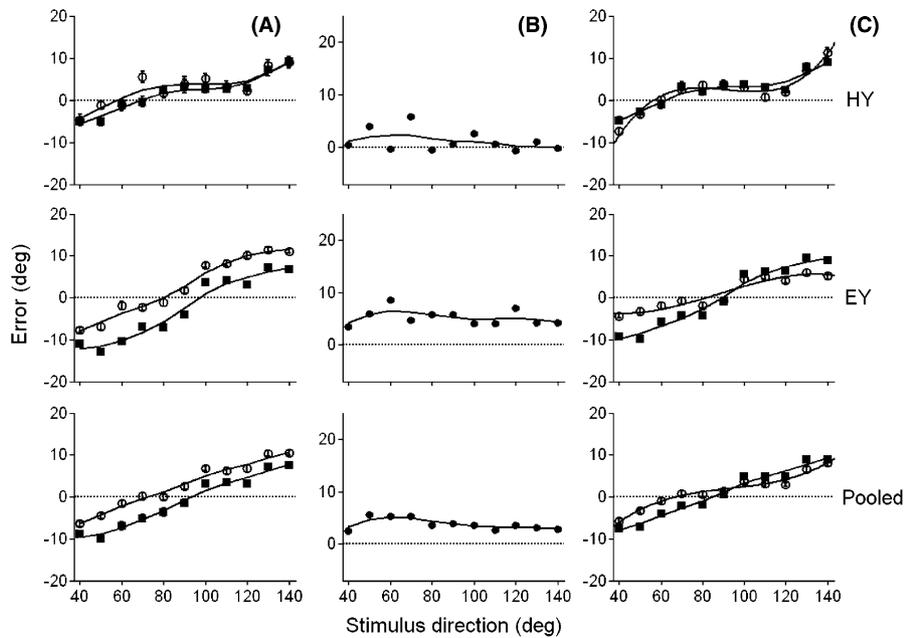


Fig. 7. Absence of anti-oblique effect for postsaccadic target. (A) Perceptual error for visual motion presented immediately after memory-guided saccades. Open circles and filled squares represent rightward and leftward saccade conditions, respectively. Note the systematic perceptual bias away from the DNE. (B) Differences between rightward and leftward saccade error. In contrast to Fig. 4B, the saccadic effect is no larger for oblique than vertical directions. (C) Open circles represent control condition and filled squares represent the mean error of right/left saccade conditions of (A). Unlike Fig. 6A, the anti-oblique effect is absent. Numbers of selected trials are 382, 654 trials for HY and EY relatively. All curves are derived by spline approximation. Symbols in (A) and (C) represent mean errors and their standard errors.

cade onset (Fig. 1B), was 210.75 ms (± 11.01) and 204.24 ms (± 17.29) for 45° and 90°, respectively, these

effects appear to start immediately after the ‘Go’ signal.

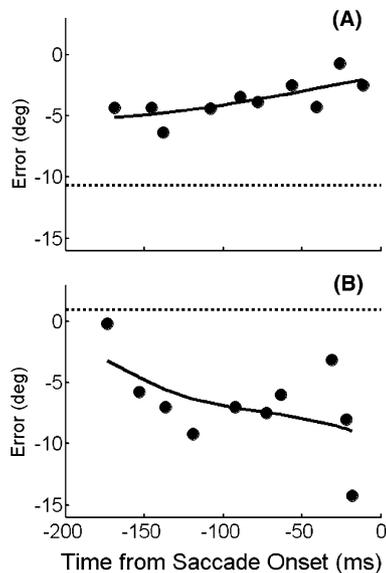


Fig. 8. Time course of saccadic effect on direction judgment of target motion along 45° (A) and 90° (B). Each point represents mean error in perceptual judgment before leftward saccade, averaged with a 50 ms boxcar with a moving step of 20 ms. The curves are derived by spline approximation. Negative time means target offset occurs prior to saccade onset. Dotted horizontal lines indicate mean perceptual error during control trials with no impending saccades.

4. Discussion

Judgment of visual motion direction around the time of saccades revealed two factors related to motion perception: shift of the DNE and the anti-oblique effect. When a visual motion of varying direction was seen, the motion direction associated with no perceptual error, or DNE, could be defined, and immediately before saccades the DNE shifted in the direction of the impending saccade. Perceptual judgment of nearby directions was shifted away from the DNE, and thus before saccades, perceived direction of vertical motion was shifted in the direction opposite to the saccade. In addition to this shift of DNE, perceptual judgments for oblique directions became veridical before saccades.

4.1. Computer simulation based on two processes

We examined whether the pattern of perceptual error could indeed be explained by the two factors, with different time courses, by running a simple computer simulation based on a model of perceptual error (Fig. 9). The model explained much of the perceptual changes in motion perception before and after a saccade (Fig. 10), suggesting that the two processes are important factors related to motion perception at the time of saccades. We now discuss each of these processes and implications for perceptual and neural mechanisms.

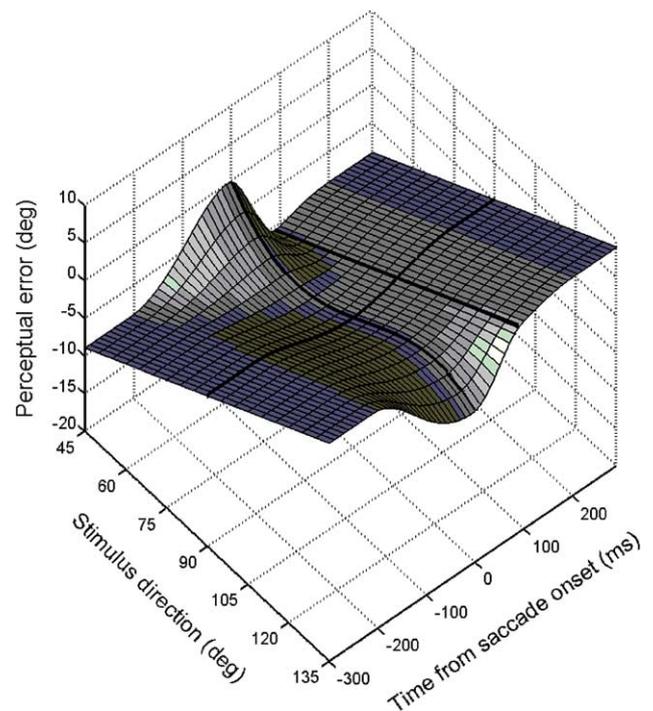


Fig. 9. A model of perceptual bias in direction judgment at the time of leftward saccade. The perceptual error E , for stimulus direction θ , at time t with respect to saccade onset, was modeled as, $E_{(\theta,t)} = 0.27 \cdot (\theta - \text{DNE}_{(t)}) \cdot G_{(\sigma,t)}(\theta - \theta_{\text{oblique}})$, where $\text{DNE}_{(t)}$ starts to change 200 ms before saccade onset and lasts until 100 ms after saccade offset following a contour of a Hanning window, and $G_{(\sigma,t)}$ mimics the anti-oblique effect which decays with deviation from the oblique directions 45° or 135° following a Gaussian-like envelope. Its weight starts to increase 200 ms before saccade onset and peaks at saccade onset and decays during saccade. The constant, 0.27, is from the slope of linear regression in Fig. 3, and reflects the strength of bias away from the DNE. Two thick lines mark saccade onset and offset times. Vertical direction is also marked with a thick line.

4.2. Shift of DNE and meridional anisotropy

We found a systematic meridional anisotropy in the accuracy of direction judgment, based on which we defined the DNE. The DNE without ensuing saccades was 88.04 (Fig. 3), and is most likely related to the gravitational or cranio-centric vertical axis. The perceptual judgment for adjacent directions was biased away from the DNE. The perceptual bias away from the DNE is perhaps related to the ‘reference repulsion’ described by Rauber and Treue (1998). In their study, subjects presented with random dot patterns moving in a variable direction consistently overestimated the angle between the pattern direction and an internal reference direction. In the current experiments the gravitational or cranio-centric vertical axis might have served as such an internal reference direction. When the range of target direction was between 45° and 135°, the DNE was roughly vertical (90°) (Fig. 3), and thus represented an internal reference. In our experimental condition, the head was maintained upright with a bite bar, thus

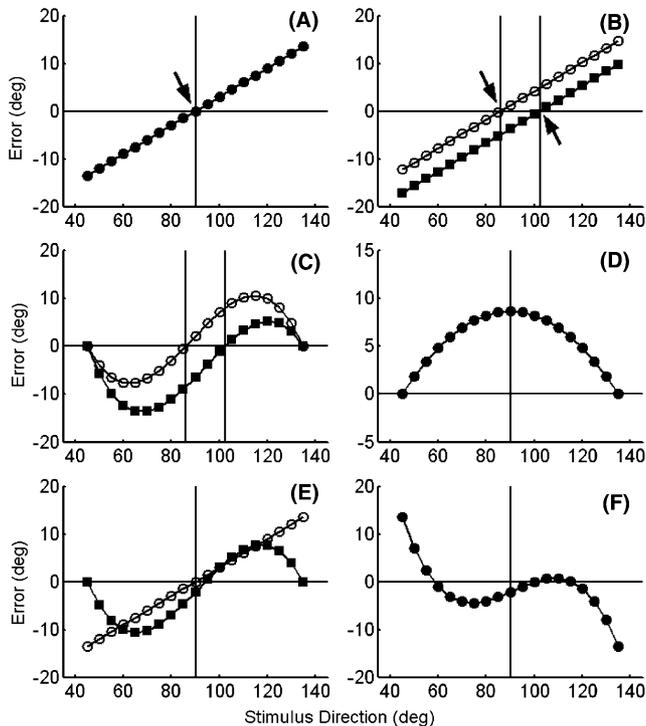


Fig. 10. (A) Perceptual error as a function of stimulus direction, at $t = -200$ ms. Arrow indicates the DNE. (B) Pattern of error at 50 ms after rightward (open circles) and leftward (filled squares) saccades, when the shift of DNE is near maximum. The DNE shift for leftward saccade is larger than that for rightward saccades. The DNE shift, although weakened, lasts until about 100 ms after saccade offset. The pattern of error is similar to Fig. 7A. (C) Pattern of perceptual error around the time of saccade onset, when the anti-oblique effect reaches its maximum. The pattern mimics Fig. 4A. (D) Effect of saccade direction (rightward–leftward) is maximal at the vertical, mimicking Fig. 4B. (E) Anti-oblique effect. Plotted are perceptual error in (A) and mean of perceptual errors in (C), mimicking Fig. 6A (F) Perceptual error in saccade condition minus that in control condition, i.e. difference between two errors in E, mimicking Fig. 6B. The asymmetry in E and F is caused by the larger DNE shift in leftward saccade condition shown in B.

head and gravitational axes were aligned within the variability caused by dental impression on the bite bar. When the range of motion direction was between -45° and 45° , the DNE was the horizontal direction and subjects overestimated the angle between the target direction and the horizontal direction (Park et al., 2001). Thus, during steady fixation, the DNEs correspond roughly to the cardinal reference directions.

Before saccades, the DNE shifted in the direction of saccades, and this shift was pronounced before leftward saccades. Thus, the DNE was not fixed to the earth-fixed reference. Perceptual repulsion away from the DNE was maintained while the DNE was shifted, resulting in an overall perceptual error biased in the direction opposite to impending saccades. Thus, the perceived direction of the earth-fixed vertical (90°) was biased in the direction opposite to saccades (Fig. 4). This is reminiscent of a marked decay of the preference for cardinal directions

during body tilt with respect to gravity (McIntyre, Lipshits, Zaoui, Berthoz, & Gurfinkel, 2001). Since the DNE shifts in the direction of impending saccades, and perceptual repulsion is maintained before saccades, the moving targets in the visual field ipsiversive to impending saccades are perceived more accurately.

Visual stimuli briefly seen during presaccadic period are mislocalized toward the saccade goal and this mislocalization starts approximately 50 ms before saccade onset and peaks when the saccade starts (Kaiser & Lappe, 2004; Morrone et al., 1997). Would this time-dependent spatial mislocalization explain the change in perceived direction of visual motion found in the current study? According to this possibility, since the end point of the target motion was temporally closer to saccade onset than the start point was, the end point would be more mislocalized toward saccade goal, resulting in shift of perceived direction toward the saccade direction. However, this possibility is not supported. For example, the vertical direction was perceived in the direction opposite to the saccade (Fig. 4), and the perceptual error before leftward saccades was more negative (clockwise) than the control condition (Fig. 5). These results are consistent with the conclusion of a previous study (Cho & Lee, 2003) that the stimulus configuration constructed from perceived positions of each point stimuli along the trajectory of a visual motion does not correspond to the pattern of changes in motion perception.

4.3. Anti-oblique effect

Meridional anisotropies in visual performance, known collectively as the oblique effect, have been widely reported for various psychophysical tasks. Notably, observers are better at discriminating horizontal or vertical lines than oblique lines (Appelle, 1972; Heeley & Timney, 1988; Higgins & Stultz, 1950), and direction-discrimination thresholds are significantly higher for motion in oblique directions than that in cardinal directions (Ball & Sekuler, 1980; Gros, Blake, & Hiris, 1998; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997). Anisotropies for motion perception were noted by some but not others (see Gros et al., 1998, for a review). Interestingly, perceptual judgments of oblique directions became near veridical immediately before saccades, while those of vertical directions became biased as discussed above. There have been reports that oblique orientations are better seen for some stimuli. In identifying a line target differing in orientation from a background of lines, the precision of orientation estimates was worst near the cardinal and best around the oblique orientations (Foster & Ward, 1991). Thresholds for detecting translational structure in random dot patterns are lower for oblique than for cardinal orientations (Wilson, Loffler, Wilkinson, & Thistlethwaite, 2001), and visibility is better for oblique than for horizontal structures in

images consisting of broadband spatial content (Essock, DeFord, Hansen, & Sinai, 2003). The reduced error in judging oblique directions before saccades, or *anti-oblique effect*, found in the current study is different from these phenomena, because in the anti-oblique effect, meridional judgments for the *same* stimuli were dynamically changed by saccades.

At the moment, we can only speculate on the origin of the anti-oblique effect and its functional role. Is the anti-oblique effect due to lack of repulsion from the internal reference at the time of saccades? It is not likely so, because before saccades, the DNE shifted, but perceptual bias away from the DNE still existed (Fig. 4). The magnitude of perceptual error for oblique directions varied depending on the range of target direction tested. Since the error for oblique direction was maximal when the range was between 45° and 135°, perceptual error may reflect effects of motion adaptation. Since perception of motion direction appears to be determined by population averaging of responses of direction-tuned neurons (Groh, Born, & Newsome, 1997), moving stimuli presented within the range between 45° and 135° across trials would activate neurons tuned for 90° the most. Would this adaptation effects be related to the anti-oblique effect in such a way that an impending saccade removes this adaptation effects? In order to test this possibility, we analyzed and compared perceptual errors for earlier and later blocks of experiments, and also for earlier and later trials within same blocks, post hoc. We could detect no difference in the magnitude of perceptual error for oblique directions between earlier and later phase of experiments, and we tentatively conclude that adaptive and its reversal processes before saccades, if any, were not responsible for the anti-oblique effect. However, new experiments designed specifically to test the effects of adaptation would be necessary to definitively test this possibility.

4.4. Neural mechanisms of DNE and its shift

We now consider possible neural mechanisms for the shift of DNE at the time of saccades, a major finding of the current study. The oblique effect has often been attributed to anisotropic representation of meridians in the visual cortex; e.g., among numerous reports, smaller number of cells and wider orientation tuning for oblique directions or related intracortical processing (Li, Peterson, & Freeman, 2003; Mansfield, 1974; Rose & Blake-more, 1974) and reduced neural response for oblique stimuli (Arakawa et al., 2000; Furmanski & Engel, 2000). The detection threshold for motion for the moving stimulus used in the current study was approximately between 200 and 250 deg/s, as determined in the previous study (Park et al., 2001). Thus, the moving stimulus in the current study (125 deg/s) is perceived different from a line segment. However, it is likely that the

DNE originates from anisotropic representation of meridians in the visual cortex of such properties as orientation selectivity, since ‘motion streak’ signals coding motion direction (Geisler, 1999) are related to the orientation specificity of neurons (Geisler, Albrecht, Crane, & Stern, 2001). Stimulus orientation appears to be coded by spatially-orderly population of neurons in the visual cortex (Bosking, Crowley, & Fitzpatrick, 2002), and more cells in the active neuronal population may increase orientation discrimination (Samonds, Allison, Brown, & Bonds, 2004). Thus, the DNE appears to be directly related to the abundance of neurons tuned for cardinal directions. Since population activity across a range of preferred orientation determines perceived orientation, the shift of DNE at the time of saccades reflects a shift of tuned orientation among the active population. In accordance with this, we proposed that orientation tuning of cells in the primary visual cortex may be shifted at the time of saccades, producing a perceptual bias in direction judgment (Park et al., 2001). In support of this, recent results from our lab show that the orientation tuning of the cat visual cortex measured immediately after saccades shifts in the direction of saccades (Hwang & Lee, 2004). This may underlie the shift of DNE in the direction of saccades, resulting in a perceptual bias in motion perception in the direction opposite to saccade.

Thus, it appears that motion perception is dynamically and anisotropically modulated at the time of saccades, and because this results in a smaller judgment error for the target motion presented in the visual field ipsiversive to impending saccades (Fig. 5, Table 3), the DNE shift may be a part of processes dynamically real-locating computational resources, improving perceptual performance in advance for sensory events to be acquired by impending saccades.

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