



Non-veridical visual motion perception immediately after saccades

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Received 1 June 2000; received in revised form 1 April 2001

Abstract

It is widely assumed that combining the eye movement vector with the motion vector of the retinal image is both sufficient and necessary for recovering the direction and speed of visual motion. Here, we report that execution of a saccadic (rapid) eye movement in the dark systematically biased subsequent perceptual judgment of the direction of visual motion in the direction opposite to the saccade. This non-veridical motion perception reached a maximum immediately after saccade offset and then decayed in ≈ 100 ms. These results suggest that the oculomotor signal interacts with central mechanisms related to motion and possibly form perception, as well as spatial vision, as documented with mislocalization of visual objects at the time of saccades. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Saccadic eye movement; Oblique effect; Human; Orientation; Line-motion illusion

1. Introduction

Rapid motion of the retinal image may be caused by a rapidly moving visual target seen by a stationary eye or by a stationary target seen by a rapidly moving eye. When human subjects intend to move paralyzed or immobilized eyes, a stationary object and thus its stationary retinal image, is interpreted as moving. Successful interpretation of visual motion thus requires information regarding ocular motion as well as information from retinal image motion. While these and other results (Stark & Bridgeman, 1983; Carpenter, 1988; Roll, Velay, & Roll, 1991) demonstrated that motion perception is more than the result of retinal image motion and pointed out the importance of oculomotor information, direct investigations of how and when the oculomotor information is integrated for motion perception have seldom been done. In this report, we present results obtained from experiments where the influence of saccadic eye movements on perceived direction of a visual motion was directly measured. Execu-

tion of a saccade systematically biased the subsequent perceptual judgment of the direction of visual motion and this perceptual bias was dependent on the direction of the saccade and the timing of target presentation with respect to the saccade offset, indicating that motion perception after a saccade is non-veridical.

2. Methods

Eight normal subjects (aged 24–33) participated. For each, the nature and possible consequences of the experiments were explained, and informed consent to participate was obtained. The subjects had no prior history of ocular motility disorders and were taking no medication. They were seated facing a 2×2 m tangent rear-projection screen at a distance of 115 cm. The head was held still with a bite bar and dental impression material. Horizontal positions of both eyes were measured with the infra-red reflection method (IRIS, Skalar Medical). The output signal obtained by this method was checked against the scleral search coil method and no discernable delay was found.

A laser beam with a wavelength of 670 nm was produced by a fast-acting laser diode (LDM135, Imatronic Limited, UK) and was used as a visual stimulus. The beam was deflected by a two-mirror and two-axis

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galvanometer scan head (Z1913, General Scanning) and projected onto the tangent screen. The projected red spot of light (0.2°) was used to guide saccades and to produce a moving stimulus and a test line segment (see below). The scan head was moved by a scanner controller (General Scanning, DE series) that was interfaced with a host computer (PC586) via a parallel port. The position of the laser beam on the screen was specified in a 63535×63535 grid.

The experimental procedures are schematically presented in Fig. 1. After a tone signaled the start of a trial, the projected spot of light was first presented 15°

to the left or right to guide initial fixation. (In Fig. 1(A) the fixation point is shown to the left.) With a delay of at least 1000 ms after the eye entered an electronic window centered about the fixation point, the laser disappeared and briefly reappeared for 50 ms at the center, which is subsequently referred to as saccade target. Subjects were instructed to follow the laser spot as precisely and promptly as possible in an otherwise completely dark and sound-attenuated room. With a variable delay (from 10 to 100 ms, stimulus onset delay (SOD)) after the eye entered another electronic window centered on the saccade target, the laser target reappeared at the center and immediately made a centrifugal sweep (Fig. 1(B) and Fig. 2). This laser sweep is referred to as the moving stimulus. When examined off-line, the time taken for the eye to arrive at the final fixation position from the moment of window crossing was determined to be 10 ms on average. Thus, SODs of 10–100 ms indicate initiating target motion at 0–90 ms after saccade offset.

The specification of the movement dynamic of the scanner head was sent by the host computer at the time of target presentation and was executed by a microprocessor internal to the scanner controller. When the scanner rotated to a new position with the laser light on, a sweep motion of the laser beam was visible on the rear-projection screen. The rotation of the mirror consisted of fast travel and slow settling for a fast and accurate positioning (Fig. 2). Nominally, the slow settling phase accounted for 1% of the rotation. For the highest velocity of target sweep used in this study, a 10° rotation of the mirror was made in 12 ms, with a peak velocity of ≈ 2430 deg/s, determined from sampled positions of mirrors. Ignoring small movement during the settling period (~ 2 ms), the average velocity of the projected target was ≈ 1000 deg/s. We use this average velocity to refer to the speed of target. The spot of light always centrifugally swept from the center of the screen. The direction of target motion varied from 45° to 135° , with 0° to the straight right and 90° straight up.

After the moving stimulus was swept, the subject was asked to match its direction with a test stimulus. The test stimulus was a radial line segment produced by the same laser rapidly moving back and forth between the center point and a randomly chosen point at 10° eccentricity with an inclination between 60° and 120° (Fig. 1B). The subject manipulated a momentary dial switch (a jog/shuttle) to change the locus of the eccentric point and thus, to rotate the orientation of the radial line segment. Subjects reported the perceived direction of target motion by pushing a button when the orientation of the line segment matched the perceived direction of target motion, which then terminated the presentation of the test stimulus and started the next trial. Viewing was binocular in all conditions and no feedback regard-

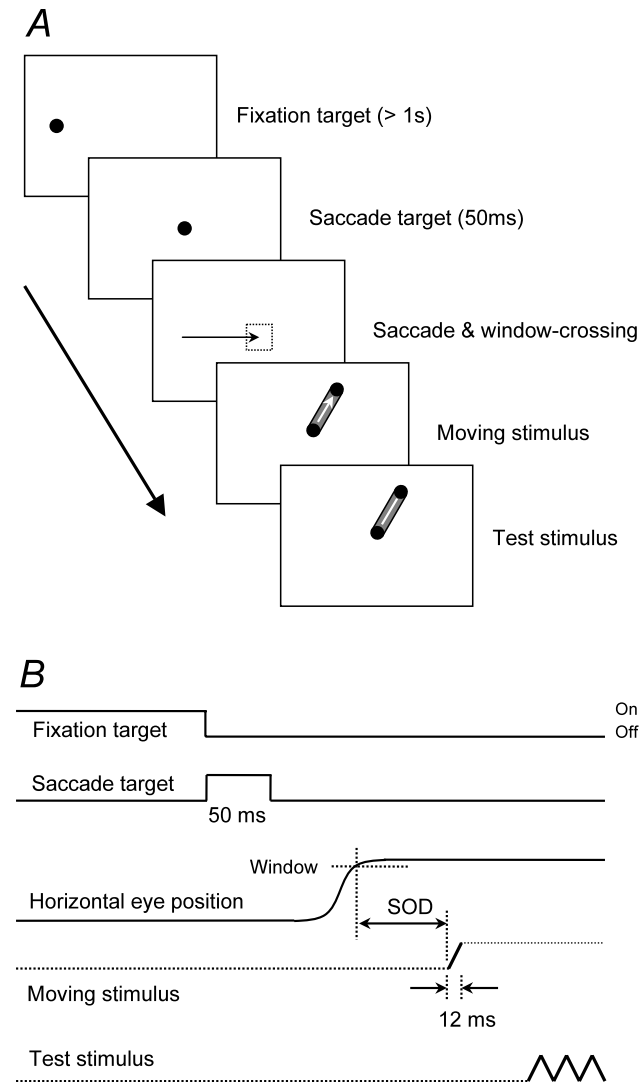


Fig. 1. Trial structure. (A) Stimulus sequence. Fixation point, saccade target, moving stimulus and test stimulus are identical laser spots. A fixation point was first presented 15° to the left (or right) of the center of the screen. When the fixation point was acquired, it disappeared and the saccade target appeared at the center for 50 ms. After the eye shifted to the location of the extinguished target, the target reappeared at the center and moved in a centrifugal sweep for 12 ms with a variable inclination. (B) Temporal structure of a trial. See Section 2 for details.

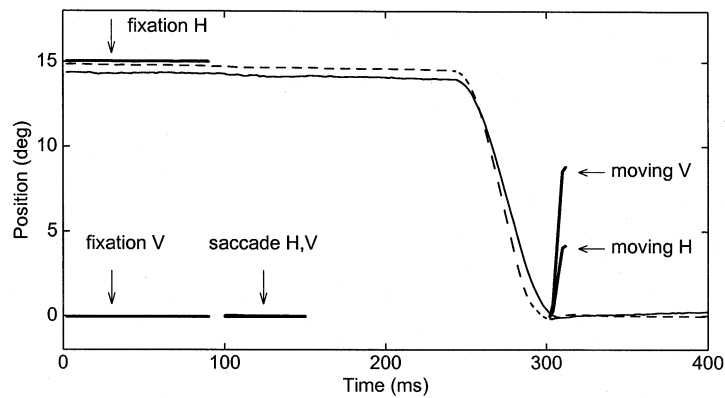


Fig. 2. Example of raw data from a representative trial from a naïve subject, BK, showing horizontal positions of the right (solid) and left (dashed) eyes. Thick traces are sampled positions of two mirrors corresponding to horizontal and vertical positions of the visual stimulus. After more than 1000 ms of fixation on the laser target presented 15° to the right (only the last part of this fixation is shown as 'fixation H' and 'fixation V'), it disappeared and then reappeared at the center for 50 ms as a saccade target ('saccade H, V'). The eyes then made a leftward saccadic movement to the last position of the central laser target. As soon as the eye arrived at the center (≈ 10 ms after crossing a window centered about the central target), the laser moved rapidly in a randomly-chosen direction (in this case, up and to the right, or 65°). For this trial, the stimulus onset delay (SOD, the interval between window-crossing and the start of the stimulus motion) was 10 ms, which corresponds to 0 ms with respect to saccade offset. The SOD varied between 10 and 100 ms. Note that there was no visible target immediately before and during the saccade. Also note that the mirrors do not start and stop abruptly. Their motion is damped somewhat to avoid overshoot while still allowing rapid and accurate positioning.

ing the correctness of the response was provided. Horizontal positions of both eyes and the currents to the galvanometers were sampled at 500 Hz with a 12-bit resolution and stored for off-line analysis.

To obtain a rough idea of the detection threshold for motion, six new subjects were asked to report the direction of target motion. The subject first maintained fixation on a laser target presented at the center of screen and then the laser target momentarily disappeared and reappeared 5° above or below the fixation locus and swept 10° downward or upward, crossing the fixation locus at an average velocity of 1000, 250, 200, 150 deg/s. For a laser sweep with an average velocity of 1000 deg/s, 59% (JY), 48% (CL) and 51% (JJ) correct responses were obtained (chance level corresponding to 50%). Similarly, for 250 deg/s, 63% (JJ), 57% (HK), 71% (JY), 54% (SH) correct responses and for 200 deg/s, 90% (JY), 79% (CL), 70% (SH), 71% (JO) correct responses were obtained. For 150 deg/s, a perfect response was obtained for the single subject so tested (JY). Thus, the detection threshold for motion for these stimuli was approximately between 200 and 250 deg/s. In contrast, in the experimental paradigm of the current study, the sweep of the laser target always began at a point (in the center of the screen) being fixated and this made a clear difference in perception of motion. The stimuli, which moved at 1000 deg/s (for only 10 ms) produced a strong sense of motion from the center toward the periphery, although the laser sweep at this speed is beyond the motion threshold and is practically the same as a flash of a line segment. This phenomenon is in essence the 'line-motion effect', first described by Hikosaka, Miyauchi, and Shimojo (1993) and repeat-

edly confirmed by others (e.g. Schmidt, 2000) where an instantaneously presented line following a brief visual cue at one end of the line produce a sensation of motion in the line propagating from the cued end toward the uncued end. In their original description of this effect, Hikosaka et al. (1993) reported that the line-motion effect was maximal for a cue lead time of 100 ms (line presented 100 ms after the cue) and was visible for cue lead times of up to 1000 ms of cue lead times when a cue of short duration was used (their Fig. 6). Consistent with the line-motion effect, all subjects in our experiments in which the delay between the saccade target and moving stimulus was found to be < 400 ms (SOD plus saccade latency of < 300 ms), reported that the laser swept from the center toward the periphery, away from the fixation locus. A sweep speed of 200 deg/s (which is above the simple motion threshold) was used to confirm the major results obtained with the 1000-deg/s targets.

In control trials, the laser target first appeared at the center and the target made a centrifugal movement after the eye maintained fixation for at least 1000 ms. Perceived directions of target motion in the experimental condition where centripetal saccades had been made immediately before target motion were compared to those in the control condition where there were no preceding saccades.

Perceptual error was defined as perceived direction minus veridical direction of the laser target. Perceptual error appeared to exponentially decay with increases in SOD. In order to derive a function describing the pattern of this decay, the means of perceptual error for

each SOD were fitted with an exponential function with a single time constant using an optimization routine provided by MATLAB (The MathWorks, Inc.).

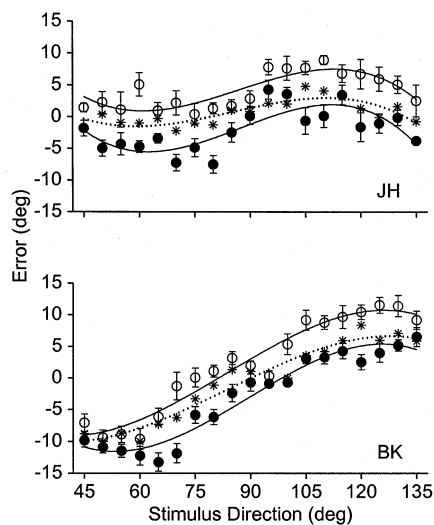


Fig. 3. Perceptual errors in two representative subjects as a function of target direction. Each symbol represents the mean and S.E. of the error in perceived direction of target motion in rightward (open circle) and leftward (filled circle) saccade conditions. Asterisks are means from control trials with no preceding saccade. Curves are least-square equations derived by 3rd-order polynomial fitting; solid curves for two experimental conditions and dotted curve for control condition. Positive errors are in the direction of counter-clockwise. Data from all SOD conditions were combined (for JH, SOD of 10, 25, 50, 90 were used and for BK, 10, 25, 50, 75, 90, 100 were used). Note that errors in the perception of motion direction for control trials (dashed) were systematically related to direction of target motion. For straight up motion (90°), the error was smallest and the error increased as visual motion deviated from vertical. The pattern of this increase was idiosyncratic, as illustrated by these two representative subjects. Note, most importantly, that the perceptual error shifts in positive (counter-clockwise) or negative (clockwise) directions after rightward or leftward saccades, respectively.

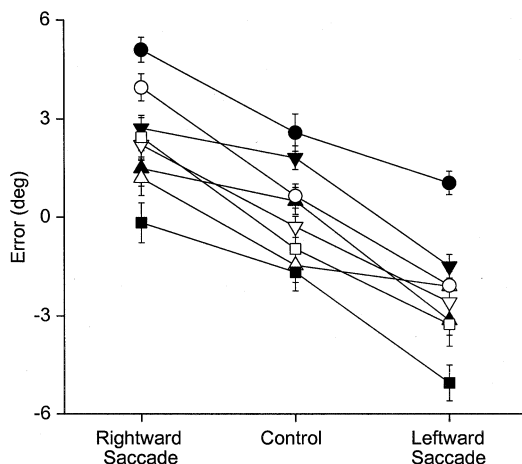


Fig. 4. Perceptual errors for each of the eight subjects in experimental (rightward and leftward saccade) and control conditions. Each symbol represents the mean error with its S.E. across all SODs. Each subject's data are shown in Table 1.

Table 1

Perceptual errors after rightward and leftward saccades

Subject	Rightward	Control	Leftward
BK (▲)	1.49 (0.54) (N = 279)	-0.61 (0.34) (N = 540)	-3.14 (0.46) (N = 316)
BJ (●)	5.10 (0.38) (N = 223)	0.65 (0.37) (N = 235)	1.05 (0.36) (N = 216)
HC (□)	2.44 (0.67) (N = 104)	-0.96 (0.77) (N = 108)	-3.25 (0.68) (N = 108)
JH (○)	3.96 (0.41) (N = 127)	0.65 (0.37) (N = 101)	-2.07 (0.43) (N = 121)
SB (△)	1.20 (0.54) (N = 192)	-1.46 (0.52) (N = 241)	-2.10 (0.52) (N = 199)
SM (▽)	2.21 (0.37) (N = 208)	-0.29 (0.32) (N = 244)	-2.59 (0.42) (N = 204)
SY (▼)	2.71 (0.32) (N = 195)	1.82 (0.36) (N = 213)	-1.49 (0.36) (N = 195)
TY (■)	-0.17 (0.61) (N = 205)	-1.67 (0.55) (N = 204)	-5.10 (0.48) (N = 206)

Numbers are mean errors in degrees and S.E. of mean are given in parentheses. *N*, number of trials.

Since the velocity of the moving stimulus was in the same range as the velocity of saccades, even small eye movements might shift the orientation of the target sweep on the retina. We examined the extent to which eye drift or corrective saccades in the horizontal direction during target presentation introduced a perceptual error. All trials from two randomly-chosen sessions of two representative subjects where the target velocity was 1000 deg/s were analyzed for this purpose. The magnitude of horizontal displacement of the eye during the 10-ms target presentation was calculated and divided by 10 ms to estimate the velocity of eye drift. The estimated perceptual error produced solely by the eye drift, *e*, is:

$$e = \arctan(1000 \cdot \sin(\theta) / (1000 \cdot \cos(\theta) + d)) - \theta \quad (1)$$

where θ is target direction and *d* is eye drift velocity in degrees. Target motion to the right was assigned a direction of zero, with direction increasing with counter-clockwise rotation from the 3 o'clock position.

3. Results

3.1. Influence of saccades on subsequent motion perception

The perceived direction of moving stimulus was systematically biased in the direction opposite to the preceding saccade. It was biased negative (clockwise) after leftward saccades and positive (counter-clockwise) after rightward saccades (Figs. 3 and 4; Table 1). For example, the perception of a stimulus directed toward 1 o'clock was biased toward 2 o'clock after leftward saccades (from +15° to the center) and toward 12

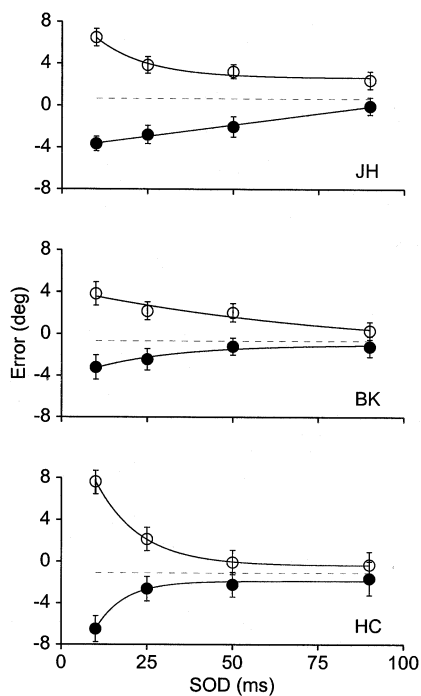


Fig. 5. Perceptual error as a function of SOD for three representative subjects combining all stimulus directions. Open circles are mean errors for rightward and filled circles are for leftward saccade conditions. Bars represent 1 S.E. of the mean. Dashed lines are mean errors of control condition.

o'clock after rightward saccades (from -15° to the center). In control conditions, where the eye maintained fixation for at least 1000 ms, target motion along oblique directions invoked larger errors than for straight-up target motion (Fig. 3). This is consistent with previous reports that discrimination sensitivity for visual motion in oblique directions is lower than that in cardinal directions (Green, 1983; Gros, Blake, & Hiris, 1998). This 'oblique effect' (see below) was more pro-

nounced for certain subjects (e.g. subject BK). The effect of the preceding saccade appears to be an addition of a fixed error to the perceived direction (Figs. 3 and 4). Note that, during the centripetal saccades, no stimulus was present and in all conditions the stimulus started to move while the center position was fixated.

3.2. Time course of perceptual error

The effect of preceding saccades on perceived direction of target motion was largest immediately after the saccade and gradually decayed over a period of ≈ 100 ms (Fig. 5). The pattern of this decay was also idiosyncratic; even within the same subject (e.g. JH) the error for rightward saccades was best fit with an exponential function, whereas the error for leftward saccades linearly decayed. Overall, the median decay time constant was 23.7 ms when each data set for rightward and leftward conditions of all eight subjects was fit with an exponential function with a single time constant. A similar non-stationarity has been documented in oculomotor performance (Nichols & Sparks, 1995; Schlag, Pouget, Sadeghpour, & Schlag-Rey, 1998) for which the amplitude and direction of saccadic eye movements elicited by electrical stimulation of the primate superior colliculus immediately following visually-guided saccades was modified (toward the direction opposite to the direction of preceding saccades). That effect decayed exponentially with a time constant of ≈ 45 ms.

3.3. Effects of stimulus speed

As described in Section 2, the motion threshold in our experimental condition was ≈ 200 – 250 deg/s. In order to confirm the major results obtained with the average velocity of 1000 deg/s, the same experiment was

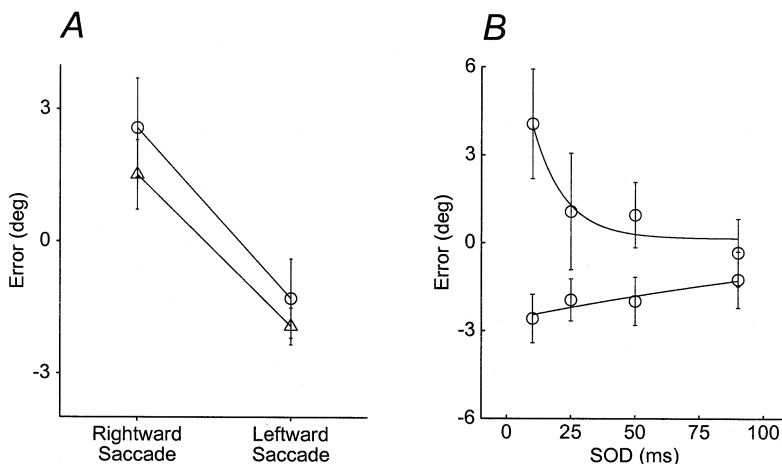


Fig. 6. Perceptual error in direction judgment using stimuli moving at 200 deg/s. (A) Perceptual error as function of saccade direction for two subjects, JO (circles) and SH (triangles). Same convention as in Fig. 4. (B) Perceptual error as function of SOD for subject SH. Same convention as in Fig. 5.

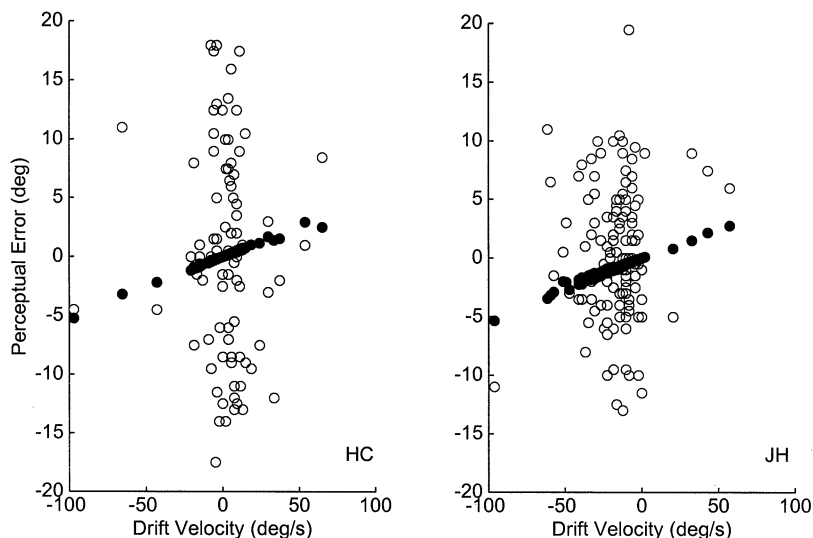


Fig. 7. Effects of the eye drift during target sweep on perceptual error in two representative subjects, HC (left) and JH (right). Each open circle represents a perceptual error obtained in one experimental trial. The velocity of the eye drift during target motion in most trials was < 30 deg/s (mean = 11.98 and S.D. = 15.55 for subject HC and mean = 19.63 and S.D. = 18.81 for subject JH, for absolute velocity disregarding the drift direction). The least square linear regression equation was $y = -0.0202x + 0.2260$ (HC) and $y = 0.1040x + 4.1677$ (JH), where y is error and x is drift velocity. Filled circles plot expected errors for the drift velocity and the associated target direction of each datum, under the assumption that eye drift is combined with the target velocity vector and that the resulting retinal image vector solely determines the perceived direction of the target sweep. Note that one A/D point was $\approx 0.02^\circ$ for this data set and the displacement of one A/D point during 10-ms period was ≈ 2 deg/s.

repeated on two subjects (of the six for experiments determining the motion threshold) using an average velocity of 200 deg/s, which is above the motion threshold. Fig. 6 illustrates the results that perceptual bias was counter-clockwise (positive) after rightward saccades and clockwise (negative) after leftward saccades (Fig. 6A). The error was maximal for targets presented immediately after saccade offset and decayed over 100 ms (Fig. 6B). The pattern and time course of perceptual error was similar to those found with an average velocity of 1000 deg/s (Figs. 3 and 4).

3.4. Effects of eye drift during stimulus presentation

We next examined the contribution of eye drift or corrective saccades during the sweep of moving stimulus. Fig. 7 illustrates the relationship between eye drift velocity during target presentation and perceptual error estimated with Eq. (1) for randomly-chosen single sessions of two representative subjects. From these sessions, all trials are included, except four of 88 for subject HC, with perceptual errors larger than 50° and two of 130 trials for subject JH, with drift velocity $> 100^\circ$. The eye drift velocity in most trials was < 30 deg/s during target presentation. The computed perceptual errors resulting from eye drift (filled circles) increase, of course, with drift velocity. However, there was no such relationship between perceptual error and eye drift velocity (open circles). Most experimentally-obtained perceptual errors were larger than predicted errors based on eye drift alone, especially with drift

velocity below ± 30 deg/s where the bulk of data were obtained, indicating that they were associated with other factors than eye drift. Subject JH showed an asymmetric drift velocity; for most trials the eye drifted leftward (negative velocity) after both rightward and leftward saccades. Yet the same subject showed perceptual errors biased both clockwise (negative error) and counter-clockwise (positive error), again indicating that eye drift did not determine perceptual error.

3.5. Effects of vergence velocity

In order to determine if differences in the velocity profile between the two eyes contributed to the direction and magnitude of the judgment error, we calculated the peak vergence velocity during presentation of the moving stimulus. For two representative subjects, the mean and S.D. of the peak vergence velocity (time differential of the difference in horizontal eye positions between the right and left eyes during target presentation) were 13.33 ± 16.76 deg/s (JH) and 31.33 ± 15.52 deg/s (HC). Considering that a shift of the A/D resolution in each eye (one point in stored eye position data) in opposite direction corresponded to a peak vergence velocity of 20 deg/s and that vergence velocity was smaller than drift velocity, asymmetric velocity profiles between the two eyes were negligible. Furthermore, for rightward saccades subject JH showed both positive and negative vergence velocities, whereas subject HC showed mostly positive vergence velocities and yet both showed perceptual errors in the same direction, again

indicating that asymmetric vergence velocity contributed little to the direction of perceptual errors.

3.6. An oblique effect

In Fig. 3, misjudgment of the direction of target motion along oblique directions was biased toward the horizontal meridian in control trials; negative errors (biased clockwise) for the stimulus direction between 45° and 90° and positive errors (biased counterclockwise) for the stimulus direction between 90° and 135° . In order to understand the origin of this pattern of bias, we did a series of follow-up experiments where subjects reported perceived direction of moving stimulus at 1000 deg/s , starting from fixation locus without preceding saccades. Here, we briefly report results obtained from these experiments on six new subjects with no previous experience of oculomotor tasks. In the experiment of Fig. 3, the initial direction of the moving stimulus was randomly chosen between 45° and 135° and the initial orientation of the test bar was randomly chosen between 60° and 120° . One immediate concern was whether this difference in range influenced perceptual judgment. To investigate this, in an experiment on three of the six subjects, the test target was randomly presented within $\pm 30^\circ$ from the direction of the moving stimulus and a similar pattern of perceptual bias was observed for oblique direction. Thus, the perceptual bias toward horizontal meridian for target motion along oblique direction was not due to the difference in the range of orientations between motion and test targets. In another experiment, three other subjects were presented with stimuli moving at 1000 deg/s beginning at the fixation locus, with directions between -45° and $+45^\circ$ (horizontal series) and with the test bar randomly presented within $\pm 30^\circ$ from the target direction. The perceived direction of the moving stimulus along the oblique direction was biased away from 0° . That is, stimuli moving in the 2 o'clock direction were misperceived with a bias toward 1 o'clock, whereas motion along 4 o'clock was misperceived with a bias toward 5 o'clock. In another experiment on four of the six subjects, a whole range of motion direction (360°) was used for the moving stimulus and the test bar was randomly presented within $\pm 30^\circ$ from the direction of moving stimulus. In this condition, perceptual judgment was relatively accurate in cardinal directions and relatively more errors were associated with moving stimuli along oblique directions, but no consistent pattern of bias either toward horizontal or vertical meridian was found.

Overall, these results indicate that perceptual bias shown in Fig. 3 includes an oblique effect and a set effect, such that in vertical (or horizontal) series where the set of direction of moving stimulus was between $+45^\circ$ and 135° (or between -45° and $+45^\circ$), the perceived direction of a stimulus moving along oblique directions was biased away from the vertical (or horizontal) meridian.

4. Discussion

4.1. Non-veridical motion perception immediately after saccades

A rapid sweep of a laser spot starting from the locus of fixation produced a strong sense of visual motion propagating away from the starting point. When this target sweep was made immediately after saccadic eye movement toward the start locus and the subject was asked to match the direction of this target motion with the orientation of a short line segment, the orientation was systematically inclined toward the direction opposite to the saccade. The amount of inclination was time dependent; it was maximal immediately after saccades and decayed over $\approx 100 \text{ ms}$ after saccade offset. Similar patterns and time courses of this perceptual bias were found for stimulus velocities of 1000 deg/s , which is below threshold for motion perception and for 200 deg/s , which is above threshold.

4.2. Possible contributions of peripheral mechanisms to perceptual error

We cannot make definitive statements regarding the origin of misperception of motion direction immediately following saccades. However, four possible peripheral mechanisms can be excluded. First, Deubel and Bridgeman (1995a,b) reported a transient lens displacement during and immediately after a saccade and its psychophysical consequences; magnitude of relative mislocalization of two small targets, one above the other, (the bottom one presented at the end of the saccade and the top one 30 ms later) in the direction opposite to the saccade was up to 0.03° for each degree of saccade. Presumably, lens displacement would contribute to misperception of motion direction. However, lens displacement is too small to account for perceptual error found in the current study. Assuming the magnitude of relative mislocalization of two targets with an interval of 10 ms (corresponding to the start and end points of the moving stimulus in the current study) after a saccade of 15° is $\approx 0.15^\circ$, the expected perceptual error is 0.86° ($\arctan(0.15/10)$), which is far less than the maximal perceptual error found in the current study (see Figs. 5 and 7). Furthermore, lens displacement is too brief to account for the perceptual error of the current study, which was observed for 100 ms after a saccade. Second, the eye undergoes a transient torsion during and immediately after saccades (Straumann, Zee, Solomon, Lasker, & Roberts, 1995; Lee, Zee, & Straumann, 2000) that would rotate the direction of retinal image motion, but the magnitude of the unwanted torsion is too small ($< 2^\circ$) and its slow recovery over more than 1 s is too long to account for the perceptual errors seen in the current study. Third,

the eyes make corrective saccades and/or slow drifts, called glissades (Weber & Daroff, 1972) often in the direction of saccades following a horizontal saccades to precisely acquire visual targets. Furthermore, based on binocular coordination of horizontal saccades voluntarily made between two continuously visible targets in a dimly illuminated display, Collewijn, Erkelens, and Steinman (1988) showed that abducting saccades were larger than paired adducting saccades, producing transient divergence and that larger postsaccadic drift in the adducting eye compensated for the transient divergence. This raises the possibility that the rapid sweeping of the laser target projected onto the moving retina caused the retinal image of the sweep to be inclined in the direction opposite to postsaccadic drift, especially in trials with short SODs. In our experimental condition, the central target for centripetal saccades was presented for only 50 ms in the dark. This prevented image sweeps on the retina during centripetal saccades and also significantly reduced the occurrence of corrective saccades (but did not suppress them completely). The analysis of the estimated perceptual error based on eye movement during target presentation (Fig. 7) indicates that corrective saccades were seldom underway during target presentation and slow drift was not a determinant of perceptual error. Finally, the saccade target was projected onto a tangent screen that was binocularly viewed. This inevitably introduced vergence eye movements during and immediately after saccades toward the central target. It is known that vergence and saccades interact and vergence eye movements are enhanced when they occur in association with saccades (Erkelens, Steinman, & Collewijn, 1989). Thus, a vergence component in postsaccadic drift compensating for divergence during horizontal saccades (Collewijn et al., 1988) may be enhanced with targets presented on a tangent screen. However, the vergence velocity during target presentation was low and idiosyncratic in our experimental condition and the pattern of vergence had little explanatory power for consistent direction of perceptual error which, on the other hand, was robustly related to the direction of version of the primary saccades. We conclude that the perturbations of perceived direction of moving stimuli observed in the current study are likely to be centrally generated and next turn our attention to potential contributions from perception (visual space, form and motion), attention and memory systems.

4.3. Possible contributions of central mechanisms to perceptual error

It has been assumed that the brain may use extraretinal eye position signals to maintain stable perception of visual space at the time of saccades. Support for this assumption comes from the apparent shift in position

of objects briefly flashed around the time of a saccade (Matin & Pearce, 1965; Honda, 1989, 1991; Dassonville, Schlag, & Schlag-Rey, 1992; Schlag & Schlag-Rey, 1995; Cai, Pouget, Schlag-Rey, & Schlag, 1997; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Bockisch & Miller, 1999; Lappe, Awater, & Krekelberg, 2000, also see for review Ross, Morrone, Goldberg, & Burr, 2001). Can the influence of saccades on subsequent motion perception be explained by spatial mislocalization? Honda (1991) described perceptual mislocalization of briefly flashed light in otherwise dark conditions around the time of both horizontal and vertical saccades. The time courses of perceptual mislocalization for horizontal and vertical saccades were similar and mislocalization was in the direction opposite to saccades for targets presented immediately after saccades, whereas it was in the direction of saccades for targets presented before saccades. Thus, the start point of the laser sweep would be mislocalized further in the direction opposite to saccades than the end point if these sites were tested in separate trials using brief spots because the start point is temporally closer to saccade offset than the end point. Assuming a relative gain of maximal mislocalization error (error divided by saccade size) ranging between ≈ 0.5 (Bridgeman, 1995) and 1 (Honda, 1991) and assuming a linear decay of the mislocalization error after saccade offset that is not grossly inconsistent with the time course of the mislocalization error of Honda (1991), the difference in mislocalization error between targets presented with a 10 ms gap (for moving stimulus with a speed of 1000 deg/s) after saccades of 15° would range between 0.325° and 0.75° . The line connecting the mislocalized loci of the start and end points would be inclined *toward* the direction of saccades and the magnitude of inclination would range between 1.86° and 4.29° . This magnitude of inclination, estimated by spatial mislocalization of a point stimulus, is comparable to the size of perceptual error averaged over all SOD conditions (Fig. 4), but the direction of estimated inclination is opposite to our findings. These results indicate that perceptual judgment of motion direction cannot be explained by successive perceptual mislocalization of a series of loci along the path of moving stimulus. This is consistent with the suggestion that separate neural mechanisms are responsible for encoding target motion and absolute target position (Abrams & Landgraf, 1990; Bridgeman, van der Heijden, & Velichkovsky, 1994). However, the above argument assumes that the size of the mislocalization is constant, regardless of the spatial locations of stimuli. If the size of mislocalization depends on two-dimensional spatial location (as opposed to one-dimensional mislocalization of a target presented either horizontal or vertical meridians along saccade trajectory), the inclination of perceived direction of moving stimulus at the time of saccades may still be explained

by spatial mislocalization. A study is underway to examine this possibility.

Ross, Morrone, and Burr (1997) showed that the magnitude and direction of mislocalization of a bar briefly presented around the time of a horizontal saccade strongly depends on the positions of the target along the saccade trajectory, in such a way that targets are mislocalized toward the saccadic target, resulting in 'compression' of the visual space. Can this spatial distortion explain the perceptual errors found in the current study? We think it unlikely for two reasons. Lappe et al. (2000) later showed that mislocalization errors depend on the availability of visual references; in complete darkness, as in our experimental condition, the 'compression' effect subsides. Furthermore, the finding that moving stimuli sweeping in both 1st (moving direction between 45° and 90°) and 2nd (between 90° and 135°) quadrants produced the same direction of perceptual errors depending on saccade direction (Fig. 3), which is inconsistent with the idea of spatial compression toward the saccadic target. Rather, ignoring the issue of experimental condition, the latter predicts that the direction of perceptual error depends on whether the target appeared in the 1st or 2nd quadrant, rather than on whether saccades were made leftward or rightward.

Sheth and Shimojo (2001) reported that a compressed pattern of mislocalization of a briefly presented target on a CRT monitor depended on the time interval between target presentation and judgment and suggested that the visual memory of spatial location is compressed. Since the orientation of the test bar was matched to the remembered direction (or orientation) of the moving stimulus in the current study, the misjudgment of motion direction found may reflect distortion of short-term memory (during the interval between presentation of moving stimulus and pressing a response button) rather than distortion of motion perception. However, although it was not determined whether the effects of short-term memory on motion perception were similar to those for spatial localization, it is not clear how the dependency of judgment error on the direction of preceding saccades would fit with this possibility. Simple compression of space, be it of perception or of memory, is inconsistent with the dependence of non-veridical motion perception on saccade direction.

There are at least two possible roles of attention in the current experimental paradigm. The 'line-motion effect' inducing a strong motion sense in our paradigm was possibly due to an attention mechanism (Hikosaka et al., 1993; Schmidt, 2000). In addition, it has been suggested that saccadic eye movements spread attentional span (Hock, Balz, & Smollon, 1998). According to this idea, prior to target motion, the subject's attentional state would be narrowly focused in the control

condition of the current study, i.e. with no preceding saccades, whereas in the experimental condition, the preceding saccade would spread attentional span. If so, the perceptual error would increase in this experimental condition, as is indeed the case, but the dependence on saccade direction of the systematic error contradicts this idea.

Moving stimuli of two speeds above and below the threshold of motion detection (200 deg/s and 1000 deg/s, respectively), resulted in similar perceptual error. In our experimental condition, subjects were literally unable to distinguish between the senses of motion produced with the two speeds. This suggests that illusory and real motion share the same pathway in their interactions with oculomotor signal. However, the dependence of motion perception on the preceding saccade does not necessarily mean that the oculomotor signal interacts with motion pathways of the visual system. Geisler (1999) recently suggested that a spatial 'motion streak' produced by a rapid motion of a point image along its trajectory may constitute a mechanism for estimating motion direction. The streak effect started at a target speed of around 1–5 deg/s, depending on target size and increased with target speed. The spatial 'motion streak' undoubtedly contributed to detecting the direction of the high-velocity moving stimuli used in the current study. Thus, the preceding saccades may have interacted with an orientation mechanism, in addition to motion perception and the orientation of the test stimulus (a line segment of 10° produced by the same laser) may have been compared to the remembered orientation of the motion streak, suggesting that oculomotor signal interacted with a form pathway as well as with spatial and motion pathways of the visual system.

We next consider possible neural mechanisms in motion and form pathways in relation to influence of saccades on subsequent motion perception. The primate middle temporal area is known to be critically involved in motion perception (Salzman, Britten, & Newsome, 1990; Britten, Shadlen, Newsome, & Movshon, 1992) and perceptual decisions on motion direction are determined by a process of population averaging of the motion vectors to which individual neurons are tuned (Groh, Born, & Newsome, 1997). Saccadic eye movements enhance neural activity in the primate middle temporal area when they cause retinal image flow in the cell's preferred direction and suppress activity when the retinal image flow opposes the preferred direction (Bair & O'Keefe, 1998). Such saccade-related activity modulation, which has also been described in human visual cortex (Skrandies & Laschke, 1997), thus may modify the population vector in the direction opposite to saccades. However, it should be pointed out that a simple vector summation or averaging appears to be inconsistent with the data obtained in the current study. If the

perceived direction is a sum or an average of the moving stimulus vector and a retinal image vector caused by a saccade, the magnitude of perceptual error is expected to show an inverted V pattern as function of target direction within the range of 45° to 135°, with the maximum error for the direction 90° (straight up). The predicted perceptual error, e , based on vector summation is calculated by, in the same way as Eq. (1),

$$e = \arctan(\sin(\theta)/(\cos(\theta) + I)) - \theta,$$

where θ and I are target direction and the image motion vector caused by horizontal saccades, respectively. The obtained data did not show such a pattern (Fig. 3).

The non-veridical perception of motion direction found in the current study may be contributed to by the influence of oculomotor signals on the visual form pathway. Lee and Malpeli (1998) reported that cat lateral geniculate nucleus (LGN) cells show postsaccadic facilitation, as well as presaccadic suppression, both in the dark and for visually evoked responses. A similar postsaccadic facilitation has been documented for the visual cortex. The increase in neural activity in the cat visual cortex (areas 17 and 18) associated with saccadic eye movements is coupled to saccade offset and this activity peaks 63 ms after saccade offset (Park & Lee, 2000), which roughly corresponds to a temporal window when the laser sweep at a newly-acquired fixation locus arrives in the visual cortex, suggesting a possible interaction between saccade-related activity and visual response to laser sweep. Furthermore, consistent with the suggestion that estimating the direction of target motion is facilitated by the orientation of motion trajectory (Geisler, 1999), Jancke (2000) reported that the orientation of a moving spot's trajectory could be recovered from the neural population activity in the cat area 17. In addition, the oblique effect of the current study (larger judgment error for target motion along oblique directions than for horizontal and vertical cardinal directions) may be partly explained by an oblique effect in neural orientation-sensitive mechanisms in area 17. This effect is similar to the oblique orientation effects that have been repeatedly reported in psychophysical studies (e.g. Heeley, Buchanan-Smith, Cromwell, & Wright, 1997), and is consistent with electrophysiological findings that more V1 neurons are tuned to cardinal orientations than to oblique orientations (Mansfield, 1974; De Valois, Yund, & Hepler, 1982). Furthermore, optical imaging indicates that a larger area of visual cortex is preferentially activated by cardinal contours than by oblique contours (Coppola, White, Fitzpatrick, & Purves, 1998). Similarly, the relative magnitude of the fMRI response to parafoveal sinusoidal gratings with cardinal orientations is larger than that with oblique orientations and this oblique effect is most distinct in the

primary visual cortex (V1) (Furmanski & Engel, 2000). Thus, saccade-related neural activation in area 17 may modify the population activity profile in response to a moving stimulus in such a way that the recovered target orientation is shifted in the direction opposite to saccade. This possibility leads to testable predictions. For example, orientation tuning of cells in the primary visual cortex may be shifted around the time of saccades.

Acknowledgements

We would like to thank Kyunghan Kim for making the response interface, Jaewon Hwang and Kyunghan Kim for help with computer programming and Soohyun Cho and Jaeok Lee for help with data collection. We also thank Dr John Schlag for helpful discussion and comments on this manuscript and Dr Joseph Malpeli for his thorough reading of the manuscript and making constructive suggestions. This research was supported by the Brain Research Program of the Korea Ministry of Science and Technology.

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