

Expansion of visual space after saccadic eye movements

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Human subjects reported the perceived two-dimensional location of a visual target that was briefly presented after a saccade in the absence of visual references. Consistent with previous studies, immediately after horizontal saccades, there was a salient horizontal component in mislocalization in the direction opposite to the saccade. However, the horizontal component in mislocalization was not constant and was larger for targets presented further into the visual field contraversive to the saccade. For the same horizontal saccades, the vertical component in mislocalization was also obvious, and it was larger for targets located further away from the saccade trajectory. The saccadic effects resulted in an overall pattern of mislocalization that could be best described as a two-dimensional expansion of visual space. The point of expansive origin was not associated with the saccade goal, but was shifted from the saccade goal in the direction of the saccade. These results suggest that spatial information processing at the time of saccades reflects topographic interactions between neural activations from saccade execution and the visual target. The configuration of mislocalized positions of single point stimuli along a line was not comparable to the pattern of non-veridical motion perception described by [Park, Lee & Lee \(2001\)](#), indicating that spatial mislocalization and non-veridical motion perception after saccades are independent phenomena.

Keywords: spatial mislocalization, visual motion, extra-retinal eye position signal, space constancy, spatial perception

Introduction

In normal viewing, our eye movements are characterized by a sequence of fixations separated by saccades. Saccadic eye movements present a challenging problem to our visual system because they generate rapid image smear on the retina, and change the relationship between spatial locations in external space and the corresponding image positions on the retina. Our perception of a continuous and clear view of a stable world despite eye movements suggests a successful solution of the problem, but under certain conditions, one can show that the solution is not perfect. Notably, at the time of a saccade, spatial localization of a briefly presented target is inaccurate ([Matin & Pearce, 1965](#); [Honda, 1989](#); [Dassonville, Schlag, & Schlag-Rey, 1992](#); [Shlag & Schlag-Rey, 1995](#); [Morrone, Ross, & Burr, 1997](#); [Lappe, Awater & Kregelberg, 2000](#)). This spatial mislocalization starts approximately 100 ms before the saccade onset, and lasts until 100 ~ 150 ms after the termination of the saccade. Recently, a novel postsaccadic visual phenomenon was found in our lab. When a moving stimulus was presented after a saccade in the absence of visual references, the perceived direction of the visual motion was tilted in the direction opposite to the saccade ([Park, Lee & Lee, 2001](#)). The effect of

execution of a saccade on subsequent direction judgments of visual motion was largest immediately after the saccade and gradually decayed over a period of about 100 ms, with a median time constant of 23.7 ms. This non-veridical motion perception could not be accounted for by peripheral mechanisms such as postsaccadic eye drift, transient lens motion or torsional eye movements associated with saccades. It was likely to be centrally generated, as is the case for spatial mislocalization ([Ross, Morrone, Goldberg, & Burr, 2001](#)).

Since, in the absence of visual references, the postsaccadic perception of spatial location ([Honda, 1989](#); [Honda, 1993](#)) and direction of motion ([Park, Lee & Lee, 2001](#)) are both shifted in the direction opposite to the executed saccade with a comparable time course, an important issue arises regarding the relationship between these two phenomena. In the current study, we examined whether non-veridical motion perception during a postsaccadic period can be explained by spatial mislocalization of each locus along the motion's trajectory, as predicted by previous results on spatial mislocalization ([Figure 1](#)). Thus, we determined the two dimensional pattern of mislocalization of a point stimulus presented immediately after a saccade in the dark.

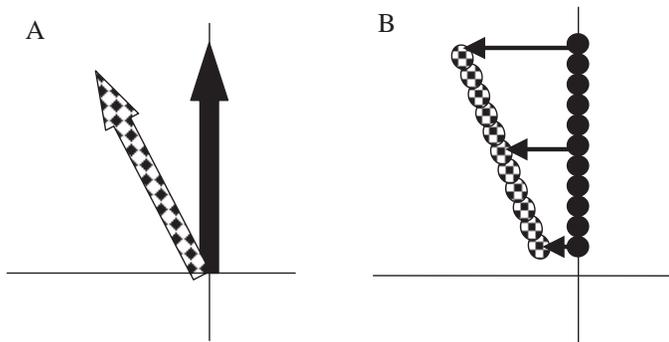


Figure 1. Rationale of a test of relationship between distortions in visual motion and spatial location, after a rightward saccade. A: Perception of the direction of motion of a target presented in the dark (filled arrow) immediately after a rightward saccade is distorted in the direction opposite to the saccade (plaid arrow) (Park, Lee & Lee, 2001). B: Considering visual motion (filled arrow in A) as a successive presentation of single point stimuli (filled circles) along the motion trajectory, we tested whether the configuration made up of the spatially mislocalized positions (plaid circles) of each point stimulus matches the direction in which motion is distorted (plaid arrow in A). Shown in B is a hypothetical case where a variable-magnitude mislocalization would explain the non-veridical motion perception of A.

Methods

Nine human subjects with normal vision (aged 23 to 26 years) participated in the experiment with informed consent. They had no prior history of ocular motility disorders and were not taking any medication. Five subjects participated in both control and experimental conditions, and the other four participated only in the control condition.

Experimental conditions and apparatus were identical to those used in Park et al. (2001). In brief, the subjects were seated with their heads immobilized by a bite board. Horizontal eye positions of both eyes were measured with an infrared reflection method (IRIS, Skalar Medical, Netherlands). Signals related to the horizontal positions of the eyes were sampled at 500 Hz with a resolution of 12-bits, and were stored for off-line analysis. A laser beam was used to present visual targets for fixation (FT), saccade (ST), localization (LT), and probe. The beam was deflected by a two-mirror galvanometer scan head (Z1913, General Scanning, USA), and was projected onto a 2m x 2m tangent rear-projection screen as a red spot of light with a diameter of 0.2°. The galvanometer scan head was moved under the control of a microprocessor (General Scanning, DE series, USA) interfaced with a host computer (PC 586). The distance between screen and subject was 115 cm. The position of the laser target was specified in a 65535 x 65535 grid. The subjects' task was to report the perceived position of a visual stimulus (LT)

briefly presented immediately after the termination of a rapid eye movement as explained below. In Experiment 1, the size of the required saccade was 12 deg, whereas in Experiment 2 it was 6 deg. The experimental procedures are schematically presented in Figure 2 and explained below.

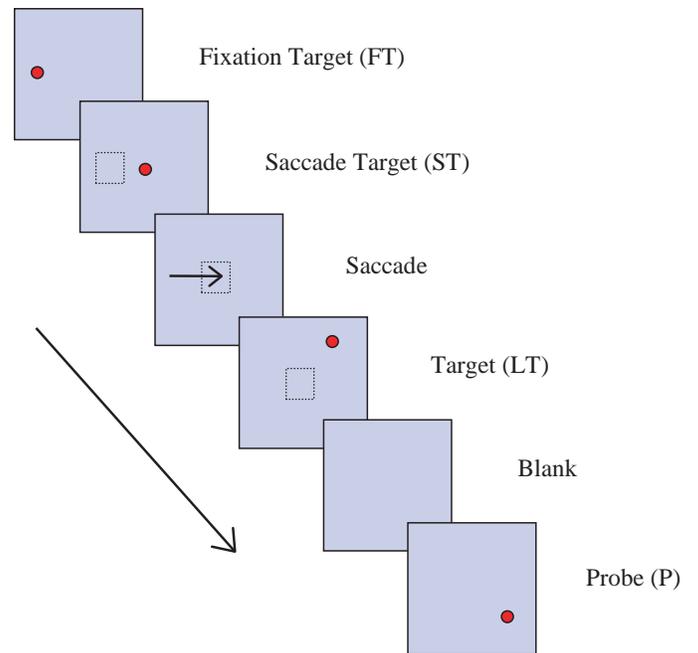


Figure 2. The sequence of stimulus presentation during a single trial. First, the subject fixated the FT. After a variable duration between 1.8 and 2.2s, the ST was briefly presented for 500ms. After a delay period of 300ms, a tone signaled the time to make a saccade. The subject was instructed to maintain fixation until the tone sounded, and then to make a saccade to the remembered position of the ST. If the eye prematurely left an electronic window set about the FT, the trial was aborted and a new one began. A memory-guided saccade paradigm was used to prevent the perception of apparent motion between the ST and the LT. Briefly after the eye entered an imaginary window centered about the ST, the LT was presented for 50 ms. After a blank period of 300ms, the probe appeared at a position chosen randomly within 5 deg from the LT in horizontal and/or vertical directions. The subject adjusted the probe onto the remembered position of the LT with a computer mouse placed before him/her on a flat surface. The large diagonal arrow represents the time sequence.

Experiment 1

In each trial, the subject was instructed to first fixate on the FT, which was presented either 12° left or right to the center of the screen for a variable duration between 1.8 and 2.2 seconds. After the FT was turned off, the saccade target (ST) appeared at the center for 500 ms. Three hundred milliseconds after the ST disappeared, a tone signaled when to make a rapid eye movement to the remembered locus of the ST. A memory-guided saccade

paradigm was used in order to exclude the influence of the ST, and to prevent the perception of apparent motion between the ST and the LT. With a delay of 25 ms after the right eye entered the eye-checking window centered on the ST (this delay was the approximate time taken for the eye to reach the center of the screen as determined empirically in pilot studies), the to-be-localized-target (LT) was presented briefly (50 ms) at one of 25 positions on a 5 × 5 square grid centered on the ST. These positions were spaced 4 deg apart, spanning -8 to 8 deg both horizontally and vertically. The electronic eye-checking window spanned 4° × 4°, and was not visible to the subject.

Subjects reported the perceived position of the LT by adjusting the position of the probe with a computer mouse. The probe was presented 300 ms after the offset of the LT, and was continuously visible until the subject clicked on the left mouse button after they were satisfied that the probe was placed at the perceived position of the LT. The time interval between the offset of the LT and the presentation of the probe was determined through a pilot study. A period of 300 ms was found to be optimal since it was short enough to preserve visuospatial memory (Sheth & Shimojo, 2001), but long enough to prevent the perception of apparent motion between the LT and the probe. The next trial began 1.5 seconds after the mouse click. Subjects were asked to click on the right mouse button if they were not able to see or properly attend to the LT for any reason, and these trials were discarded during off-line analysis. No visual references were provided during the localization procedure. Viewing was binocular in all conditions, and no feedback regarding the correctness of the response was given. Instantaneous eye position, horizontal and vertical position of the LT, and the instantaneous position of the probe were displayed on the experimenter's monitor in the next room.

Experiment 2

In order to find out whether the pattern of postsaccadic mislocalization is affected by the metrics of the saccade, we ran a similar experiment using a 6-deg saccade paradigm. The structure of the experimental trial in experiment 2 was identical to experiment 1 except for the following details. First, the FT which subjects were instructed to fixate was presented 6° left of the center of the screen for a variable duration between 1.8 and 2.2 seconds. After the FT was turned off, the ST appeared at the center of the screen for 500 ms. Three hundred ms after the ST disappeared, a tone signaled when to make a saccade to the remembered locus of the ST. With a delay of 10 ms (determined empirically in pilot studies) after the right eye entered the eye-checking window centered on the ST, the to-be-localized-target (LT) was presented briefly (50 ms for subject HH and 25 ms for subject JH) at one of 18 positions on a 3×6 rectangular grid. In

experiment 2, a smaller size electronic eye-checking window was used (2° × 2°) because the required saccade was smaller in experiment 2. The 18 potential positions of the ST were spaced 4 deg apart spanning -8 to 12 deg horizontally and -4 to 4 deg vertically.

Control Experiment

In order to measure the effects of saccades on errors in localizing the target, we determined the intrinsic errors for each subject through a control experiment in which the subjects localized the LT immediately after a variable fixation period of between 1.8 and 2.2 seconds. There was a considerable individual variability in the pattern and amount of localization errors, and in order to estimate the degree of individual variability in these errors, we compared the pattern of localizing the LT during fixation among eight subjects.

The task in these experiments was not easy, so the subjects were given a few practice trials before the experimental sessions.

Data Analysis

Invalid trials were discarded during off-line data analysis. These include trials with unsteady fixation of the FT, multiple saccades toward the ST, postsaccadic drift velocity exceeding 10 deg/s during the presentation of the LT, and incorrect mouse button responses. Figure 3 shows an example of a valid trial.

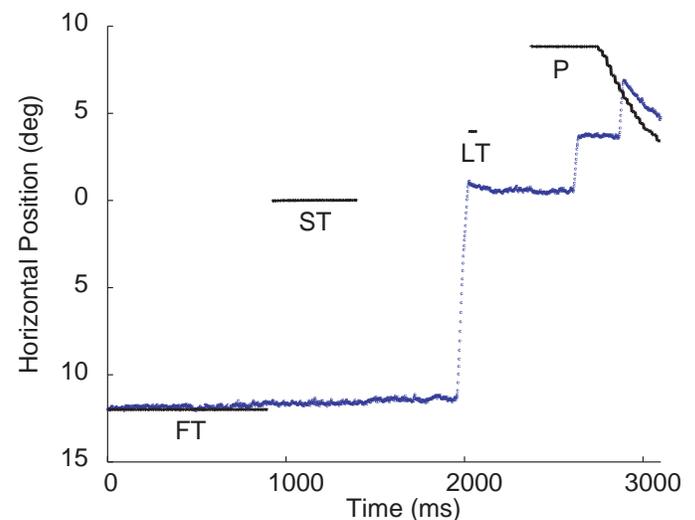


Figure 3. An example of a valid trial from a representative subject (JS). The dotted blue trace represents the horizontal position of the right eye, and the solid black lines represent the horizontal positions of the laser for fixation target (FT), saccade target (ST), localization target (LT), the probe, and response (staircase pattern).

Localization in control trials contained idiosyncratic errors, and these will be referred to as 'intrinsic error'. The saccadic effect, which will be interchangeably used

Table 1. Summary statistics of experiment 1.

Subject	JS			EH			HH		AI		MK	MJ	YJ	SH
Saccade	R	L	C	R	L	C	R	C	R	C	C	C	C	C
No. of Sessions (No. of Blocks)	7 (19)	3 (21)	6 (9)	4 (9)	3 (12)	3 (6)	4 (16)	5 (10)	13 (39)	5 (8)	3 (6)	2 (7)	3 (11)	4 (11)
No. of Valid Trials	518	191	404	123	308	296	165	497	396	394	299	333	541	406

'R' represents the rightward saccade conditions where saccades were made from -12 deg to the center, 'L' represents the leftward saccade conditions where saccades were made from +12 deg to the center and 'C' represents the control conditions where eyes were fixated at the center of the screen.

with 'saccade-induced error', was defined as the difference in the reported position between the control and the saccade trials. Therefore, for each LT location, horizontal and vertical saccadic effects were calculated by subtracting the mean horizontal and vertical discrepancies from the probe during fixation trials (i.e., intrinsic errors in control trials) from those of the saccade trials.

Results

Experiment 1

The summary statistics of Experiment 1 are shown in Table 1.

Intrinsic Error - Mislocalization during Control Trials

Mislocalization errors were observed during control conditions. The patterns of these 'intrinsic errors' varied considerably across subjects. There were two cases of compression towards the position of gaze fixation (Figure 4A, 4B) two cases of downward-biased localization (Figure 4C, 4D), one case of expansion in the lower visual field (Figure 4E), and three cases of relatively accurate localization (Figure 4F, 4G, 4H). There was no apparent day-to-day variation in the subjects' reports. An example of a day-by-day analysis for a representative subject is shown in Figure 5.

Saccade-Induced Error – Mislocalization due to Saccade Execution

Four subjects participated in the saccade trials (JS, EH, HH, AI). After the data collection from subject JS and EH was completed, subject HH and AI were additionally recruited in order to confirm the generality of the initially observed results. Since the saccadic effects of the rightward and leftward conditions were found to be symmetric for subjects JS and EH, subjects HH and AI participated only in the rightward saccade condition. The patterns of intrinsic errors obtained from these subjects included two cases of compression (JS, HH), one case of accurate localization (AI) and one case of a downward

bias (EH). The results from the control, rightward and leftward saccade trials from each subject are shown in Figure 6.

The mislocalization during the saccade condition presumably contain both intrinsic error and effects due to the saccade per se. Thus, the effects of saccades on localization (saccade-induced error) were calculated by subtracting the intrinsic error from the mislocalization during the saccade condition (which is the discrepancy between the physical and the reported loci). The saccadic effects from four subjects were pooled, rendering an overall pattern of mean saccadic effects (Table 2, Figure 7). Since the leftward and rightward saccadic effects were found to be symmetric, the two leftward saccadic effects

Table 2. Mean Saccadic Effects from Pooled Data.

Target H, V	Intrinsic H,V (SD)	Saccade-induced H,V (SD)
-8, -8	-7.86, -8.40 (1.72, 2.02)	-9.44, -8.70 (1.70, 2.00)
-8, -4	-7.53, -4.21 (1.84, 1.42)	-9.58, -4.38 (2.00, 1.58)
-8, 0	-7.35, -0.28 (1.64, 0.76)	-9.70, -0.12 (1.82, 1.15)
-8, 4	-7.44, 3.54 (2.01, 1.04)	-9.96, 3.99 (2.10, 1.47)
-8, 8	-7.37, 7.15 (1.96, 1.59)	-9.41, 8.51 (1.85, 1.60)
-4, -8	-3.85, -7.90 (1.44, 2.18)	-5.17, -8.79 (1.79, 2.02)
-4, -4	-3.70, -3.94 (1.06, 1.21)	-5.53, -4.50 (1.58, 1.56)
-4, 0	-3.45, -0.11 (1.34, 1.10)	-5.86, -0.39 (1.68, 1.17)
-4, 4	-3.57, 3.21 (1.41, 0.96)	-5.55, 4.27 (1.53, 1.35)
-4, 8	-3.65, 6.81 (1.51, 1.54)	-5.09, 8.58 (1.57, 1.76)
0, -8	0.11, -7.76 (0.78, 1.67)	-0.97, -8.48 (1.82, 1.82)
0, -4	0.10, -3.77 (0.81, 1.21)	-0.70, -4.31 (1.44, 1.47)
0, 0	-0.01, -0.42 (1.10, 1.08)	-1.02, -0.31 (1.29, 1.39)
0, 4	0.09, 2.97 (0.63, 0.70)	-0.80, 4.09 (1.33, 1.27)
0, 8	0.11, 6.79 (1.01, 1.50)	-0.97, 8.49 (2.03, 1.82)
4, -8	4.04, -8.04 (1.43, 2.23)	3.13, -8.49 (1.61, 1.71)
4, -4	3.58, -3.89 (0.96, 1.17)	3.71, -4.05 (1.84, 1.31)
4, 0	3.54, -0.09 (1.31, 1.07)	3.14, 0.06 (1.26, 1.05)
4, 4	3.56, 3.13 (0.99, 0.78)	3.46, 3.73 (1.78, 1.40)
4, 8	3.83, 6.73 (1.38, 1.45)	3.86, 8.40 (1.67, 1.73)
8, -8	7.93, -8.49 (1.65, 2.08)	7.53, -8.83 (1.91, 2.11)
8, -4	7.62, -4.13 (1.73, 1.38)	7.36, -4.77 (1.92, 1.61)
8, 0	7.30, -0.21 (1.50, 0.69)	6.79, -0.12 (1.89, 1.26)
8, 4	7.45, 3.57 (1.86, 1.00)	7.43, 3.99 (1.96, 1.53)
8, 8	7.66, 7.06 (1.96, 1.60)	7.98, 8.62 (2.39, 1.45)

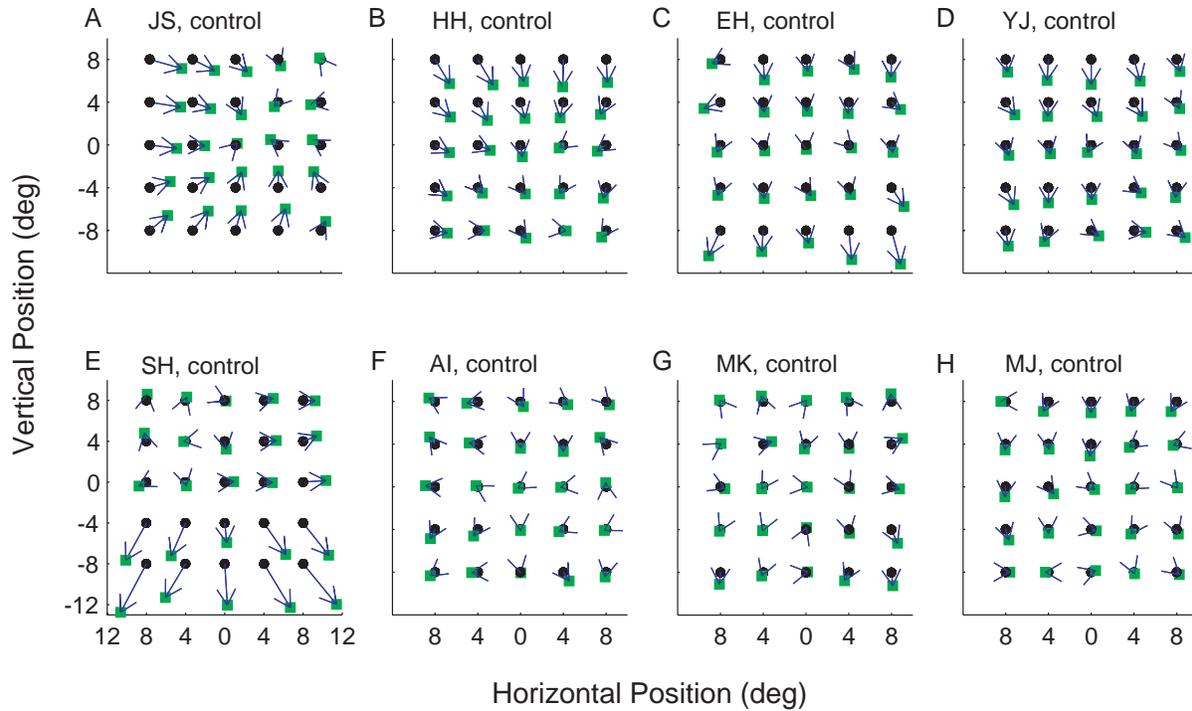


Figure 4. Intrinsic errors. The subject's initial is shown above each figure. Each black dot represents the physical location of the LT. Each green square represents the reported position of the LT. Each arrow indicates the direction and magnitude of mislocalization, i.e. intrinsic error.

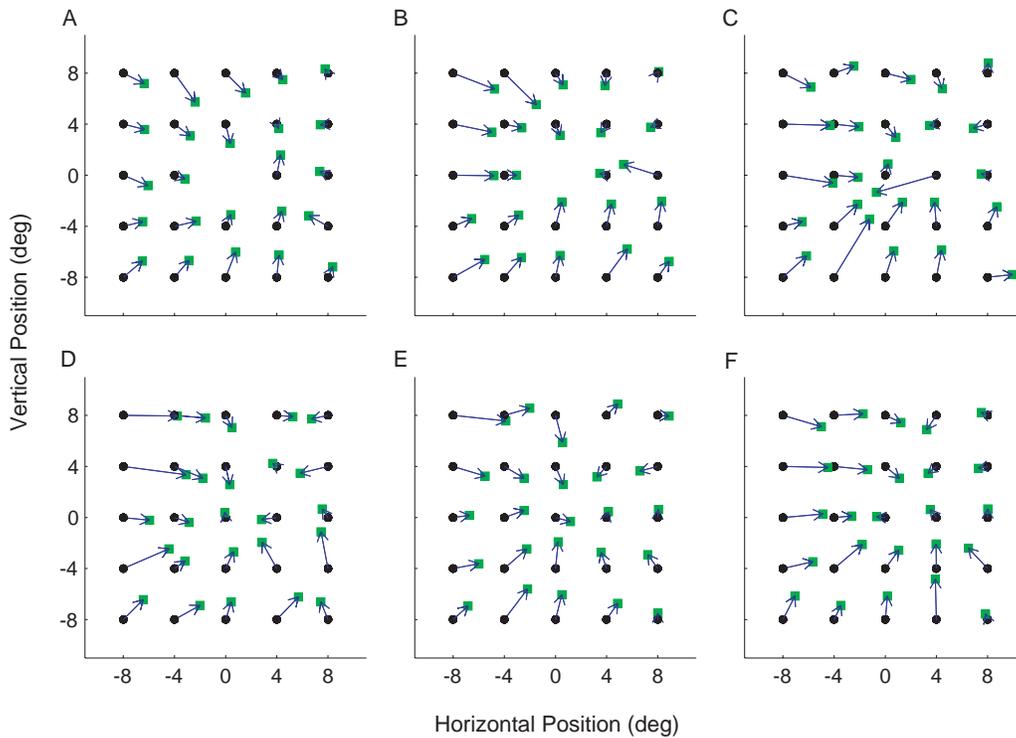


Figure 5. Day-by-day analysis of intrinsic errors in localization (subject JS). A : The first day (03/13/2002), B : The second day (03/15/2002), C : The third day (03/19/2002), D : The fourth day (03/20/2002), E : The fifth day (03/22/2002), F : The sixth day (03/25/2002). Same convention as Figure 4.

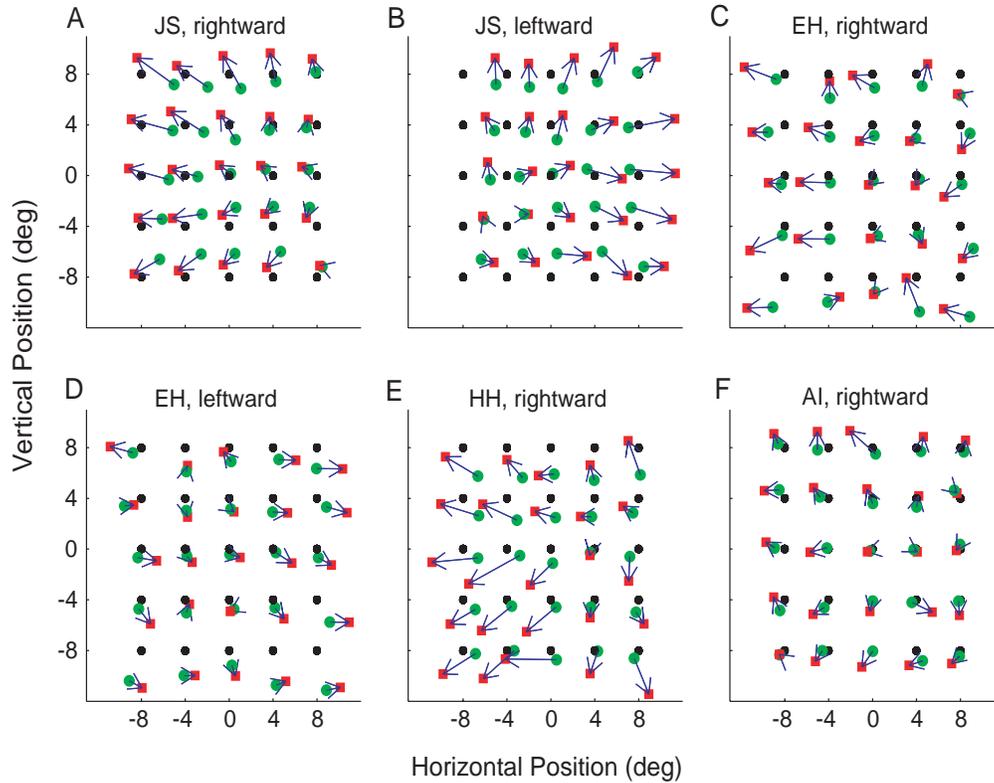


Figure 6. Effects of saccadic eye movements on spatial mislocalization for subject JS, EH, HH, AI. The subject's initial and experimental condition is shown above each figure. Each black dot represents the actual position of the LT, each filled green circle represents the reported position of the LT during fixation, and each red square represents the reported position of the LT after a saccade. Each arrow represents the saccade-induced error for each target.

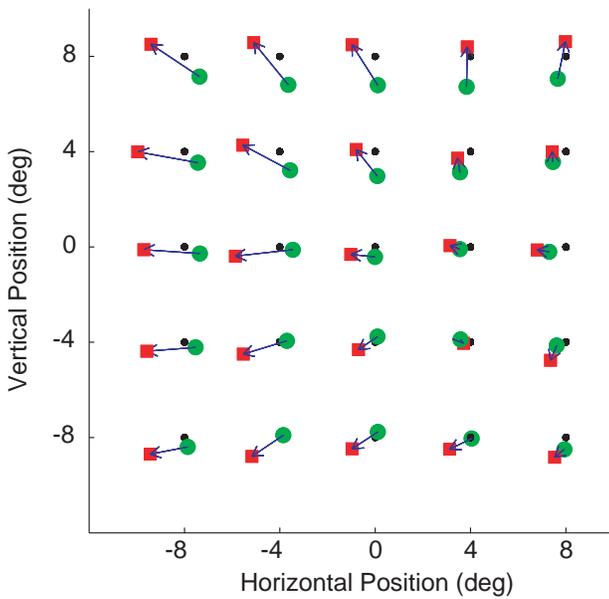


Figure 7. Pattern of spatial mislocalization after a rightward saccade from -12 deg to 0 . Data are pooled from all 6 saccade conditions of 4 subjects and normalized to leftward saccade. Same convention as Figure 6.

from subject JS and EH were mirror reversed to normalize all data to rightward saccade effects in this Figure.

As shown in Figure 8, the magnitudes of horizontal and vertical components of saccade-induced errors were different for each target location. The horizontal components of saccadic effects were larger for targets presented further into the visual field contraversive to the saccade. That is, after a rightward saccade, the targets located more to the left side of the visual field (within the tested range) were horizontally displaced with an increasing amount in the direction opposite to the saccade. However, the magnitudes of the horizontal displacement of the perceived location of the targets were similar for targets that shared the same horizontal location.

The vertical components of the saccade-induced error were larger for targets presented further away from the saccade pathway. That is, the more targets were located above the saccade pathway, the more they were mislocalized in the upward direction, whereas the more targets were located below the saccade pathway, the more they were mislocalized in the downward direction. The magnitudes of vertical displacement of the perceived location of targets were similar for targets that shared the same vertical location. There was a monotonic trend

between the horizontal and vertical components of saccade-induced errors and the horizontal and vertical coordinates of the targets (Figure 8).

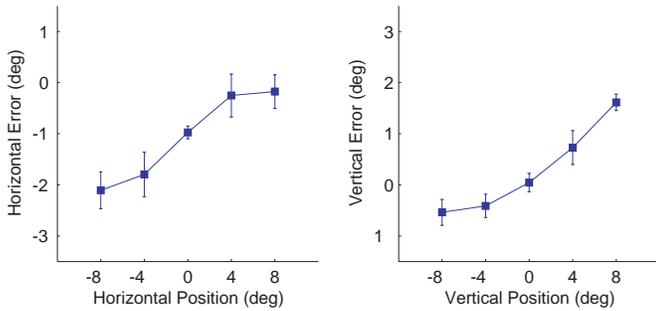


Figure 8. The relationship between target location and saccade-induced error (pooled from 4 subjects). A: Horizontal component of the saccade-induced error as a function of the horizontal coordinates of the targets, B: Vertical component of the saccade-induced error as a function of the vertical coordinates of the targets. Each filled square represents the mean saccade-induced error, and each vertical bar represents one standard deviation.

In order to derive the pattern and magnitude of changes in the overall layout of spatial loci caused by a saccadic eye movement, the reported positions of LTs were connected into a grid representing the spatial extent of perceptual space. The perceived visual extents during fixation and immediately after a saccade are compared for each subject (Figure 9) and for the pooled data (Figure 10). The spatial extent expanded after saccades for all subjects. In order to estimate the magnitude of expansion, the area of each polygon as indicated on the tangent screen was calculated and combined. The amount of expansion in the perceptual space due to an execution of a saccade was 50.11, 55.17, 9.27, 7.51, 44.96, 16.92% for JS rightward, JS leftward, EH rightward, EH leftward, HH rightward, and AI rightward, respectively. The amount of expansion calculated from the pooled data was 30.20% (perceived area during the control condition: 223.70, perceived area after a saccade: 291.25, with the physical area being 256.00 deg²). Note also that during the control condition the perceived area was compressed relative to the physical area by 14.44%.

Experiment 2

The main objective of experiment 2 was to determine whether the pattern of saccade-induced error was affected by the metrics of the saccade. Specifically, since the horizontal component of the saccade-induced error decreased as the LT was located further in the direction of saccade (see Figure 8), we wanted to find out if the horizontal component of saccade-induced error would be zero or even reversed in the opposite direction for some targets further in the direction of the saccade. In a pilot study, the LTs presented briefly at peripheral loci were

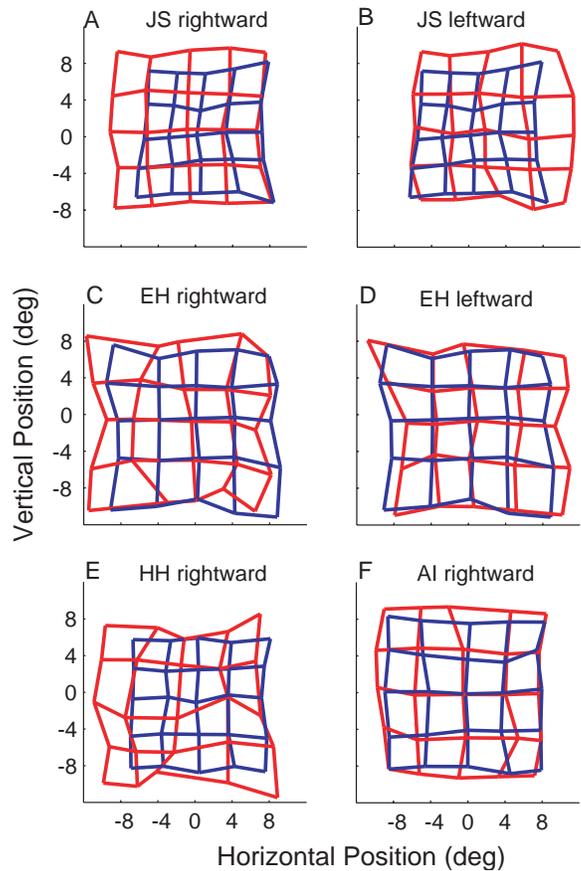


Figure 9. Comparison of the extents of the visual space during and immediately after a saccade. The reported locations of the LTs are connected with each other. The grid outlined by blue lines depicts the extent of the perceived visual space during fixation, and the grid connected by red lines depicts the perceived visual space after a saccade. Rightward (A) and leftward (B) saccade conditions of subject JS, rightward (C) and leftward (D) conditions of subject EH, rightward conditions of subjects HH (E) and AI (F), respectively.

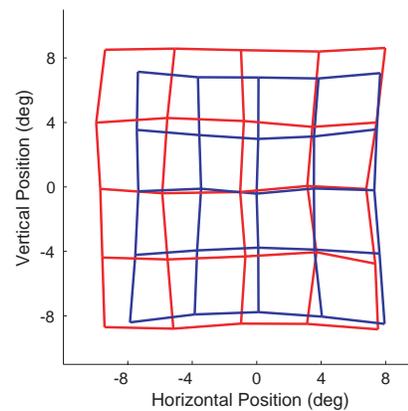


Figure 10. A comparison between the extents of perceived visual space during fixation (blue grid) and immediately after a saccade (red grid) pooled from 6 saccade conditions of 4 subjects. The extent of visual space expanded by 30.20% after a saccade compared to that during the control condition.

difficult to detect, and thus, in order to cover a wider spatial range of the LT with respect to the saccade, we used smaller saccades (6 deg) than the 12-deg saccades of Experiment 1.

Two subjects participated in experiment 2. One, HH, had participated in the previous experiment, and the other (JH) was naïve. The number of experimental sessions and valid trials from the control and saccade conditions for each subject are shown in Table 3 along with average values of saccade duration, saccade amplitude and peak saccade velocity from valid trials.

Table 3. Summary Statistics of Experiment 2.

Subject	Number of Sessions (Number of Blocks)		Number of valid trials		Mean Saccade Duration (ms)	Mean Saccade Amplitude (deg)	Mean Saccade Velocity (deg/s)
	R	C	R	C			
HH	7(15)	4(5)	396	274	61.22	6.37	213.87
JH	7(13)	5(12)	140	600	73.71	6.08	203.24

Intrinsic Error

As in Experiment 1, subject HH showed an error pattern of compression towards the gaze position. Subject JH showed a relatively smaller error (not shown).

Saccade-Induced Error

The patterns of saccadic effects observed for each subject are shown in Figure 11. Replicating the results of Experiment 1, there was a salient horizontal shift in the direction opposite to the saccade, and also some vertical shifts. Both horizontal and vertical saccadic effects varied with target location. The horizontal component of saccade-induced error increased as targets were presented further into the visual field contraversive to the saccade, and the vertical component of errors increased as targets were presented further away from the saccade pathway. Again, the two-dimensional saccadic effects resulted in an expansion of the extent of perceived visual space.

In addition, the horizontal component of saccade-induced error reached zero or reversed in the opposite direction for some targets further in the direction of saccade. In order to find the spatial locus associated with the zero horizontal error, a regression analysis was performed on the horizontal component of saccade-induced error (combined from two subjects) for targets along the saccade meridian (i.e. 0 vertical) as a function of horizontal position of the LT (Figure 12). Horizontal error was estimated to be zero at the position in the visual field 6.38 deg from the saccade goal in the direction of saccade. The sign of the saccade-induced error reversed at this locus.

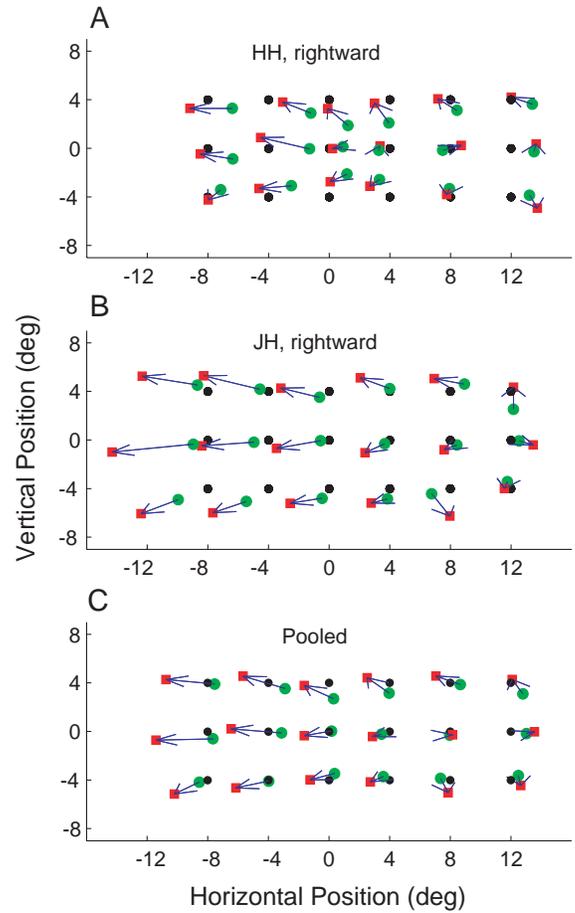


Figure 11. Two-dimensional pattern of saccade-induced errors for subjects HH (A), JH (B), and pooled data (C). Same convention as Figure 6.

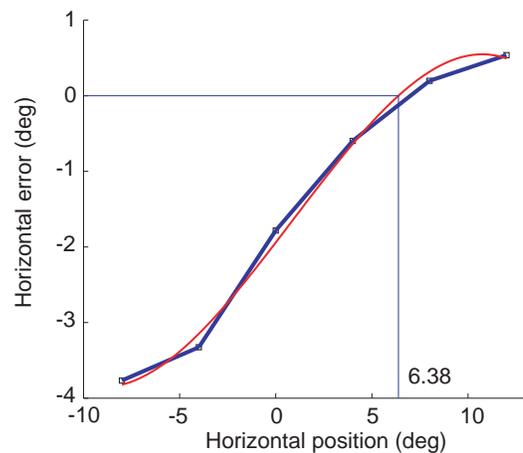


Fig 12. The reversal point of the saccade-induced error. Plotted are mean horizontal errors of the saccade-induced localization error for the targets along the horizontal meridian (saccade path). The red line is the 3rd order polynomial fitting for these points. The fitted equation is, $y = -0.0011x^3 + 0.0029x^2 + 0.3318x - 1.9406$, and the x-intercept is 6.38.

Discussion

Inter-Subject Variability in Intrinsic Errors

Spatial mislocalization at the time of a saccade reflects both intrinsic and saccade-induced errors. Subjects showed an idiosyncratic pattern of intrinsic error in spatial localization during fixation. In addition to three cases of accurate localization, two cases of compression towards the fixation point and two of downward bias were observed.

Several factors may contribute to this intrinsic error. Since the optical paths used for receiving and reporting the LT are different, (i.e., central retina during LT localization, versus eccentric retina during LT presentation), the subject's refractive error may contribute to intrinsic error. The intrinsic error may also be related to perceptual representation, sensory-motor transformation, or motor bias. The downward bias in the lower visual field of the subject SH (Figure 4E) probably reflects refractive error, and the downward intrinsic errors (Figure 4C, 4D) probably reflect a systematic response bias. The two cases of compression towards the fixation position (Figure 4A, 4B) resemble the results of Sheth & Shimojo (2001). In their experiment, subjects showed a compression of visual space toward the center of gaze, irrespective of the visibility of the fixation target. Regardless of the origin of this idiosyncratic intrinsic error, we believe the effects of a saccade on spatial mislocalization should be interpreted with reference to the intrinsic errors, not to the physical location of the LTs, because the discrepancy between the reported location at the time of a saccade and the physical location of the LT includes the intrinsic error in addition to the saccadic effect. Thus, in the current study, the two-dimensional magnitude and direction of spatial mislocalization due to a saccadic eye movement per se (saccade-induced error) was calculated for each target by subtracting the reported positions of LTs during fixation (intrinsic error) from those after a saccade.

Two-Dimensional Postsaccadic Spatial Mislocalization in the Absence of Visual References

Spatial perception in the presence and absence of visual references seem to reflect different mechanisms. A large mislocalization observed in the absence of visual references (dark condition) is substantially decreased when a visual frame pattern is projected against the dark background or when the background is illuminated (Honda, 1999). In the presence of visual references, mislocalization was found only for targets presented before and during a saccade, and no errors were observed for targets presented after the termination of the saccade (Honda, 1993; Lappe, Awater & Krekelberg, 2000; Ross, Morrone & Burr, 1997). Furthermore, in the presence of visual references, mislocalization depends on target

position (Honda, 1999), and the perceived positions of visual targets are biased toward the saccade target, resulting in a compression of presaccadic visual space (Ross, Morrone, & Burr, 1997; Morrone, Ross, & Burr, 1997), whereas removing the visual reference greatly diminished the amount of this compression (Lappe, Awater & Krekelberg, 2000). Also, in the presence of visual references two-dimensional target localization did not reveal a vertical component within the tested target range (Honda, 1993). Several researchers have found evidence suggesting that an extra-retinal eye position signal is not used when sufficient retinal information for localization is available at the time of saccades (Deubel, Schneider & Bridgeman, 1996; Deubel, Bridgeman & Schneider, 1998; Schlag & Schlag-Rey, 1995). The fact that postsaccadic spatial error is minimized when a visual reference is present implies that a postsaccadic visual reference plays a critical role in the recalibration of spatial position after a saccade. Deubel, Schneider & Bridgeman (1998) showed that the visual stimulus which is visible immediately after the termination of a saccade, takes on the role of a stable reference object which mediates the recalibration of space (see also Matsumiya & Uchikawa, 2003).

In the current study, the pattern of two-dimensional spatial localization was examined in the absence of visual references. The perceived spatial locations of visual targets presented after a saccade were shifted in both horizontal and vertical directions compared to those of the control trials. The saccade-induced error systematically varied according to target location. The magnitude of the horizontal component of saccade-induced error was larger for targets presented further into the visual field contraversive to the saccade, and the magnitude of the vertical component increased as targets appeared further away from the saccade pathway, resulting in an expansive pattern of the perceptual space (Figure 7, Figure 11). The dependency of mislocalization on the retinal position of the target has been reported in previous studies on presaccadic mislocalization in the presence of visual references (O'Regan, 1984; Honda, 1993; Morrone, Ross, & Burr, 1997), a similar dependency, but in the opposite direction (compressive vs expansive), was found for postsaccadic localization in the absence of visual references.

The magnitude of mislocalization observed in our experiment was slightly smaller than that of previous studies. The maximum amount of mislocalization was approximately 3 ~ 4 deg in our experiments (which amounts to 1/3 ~ 1/4 of the amplitude of the saccade), whereas in previous experiments it was about half the amplitude of the saccade. These variations, at least partly, seem to be related to differences in target duration. Adam, Ketelaars, Kingma & Hoek (1993) have reported a robust increase in the accuracy of localization with increasing target duration. In their experiment, subjects localized the position of a visual target flashed during

fixation. Considering that the previous studies have used a target duration of 2 ~ 8 ms (Honda, 1989; Honda, 1993; Honda, 1999; Ross, Morrone & Burr, 1997, Lappe, Awater & Krekelberg, 2000; Schlag & Schlag-Rey, 1995), the smaller saccadic effect in the current study probably resulted from the longer target duration (50 ms).

The Origin of Spatial Expansion

The main goal of Experiment 2 was to examine the effects of saccade size on the pattern of saccade-induced error. The results indicated that, for targets sufficiently displaced in the direction of the saccade along the saccade meridian (0 vertical), the horizontal component of saccade-induced error reached zero or even reversed in the opposite direction. A regression analysis indicated that this reversal point was not associated with the saccade goal, but was 6.38 deg from the saccade goal in the direction of saccade, after a saccade of 6 deg (Figure 12). After a rightward saccade, LTs presented to the left of this point were mislocalized in the direction opposite to the saccade, and LTs presented to the right of this point were mislocalized in the direction of the saccade. Since the vertical component of the saccade-induced error also systematically varied according to the vertical position of the LTs, the pattern of the saccade-induced error (error vectors) could be described as expanding from this reversal point, i.e. the origin of expansion.

In experiment 1, where subjects were asked to make a 12 deg saccade before localization, we were unable to accurately locate the reversal point of the saccade-induced error due to a small target range. The horizontal component of the saccade-induced error for all targets along the saccade meridian pointed in the direction opposite to the saccade (Figure 7). The overall pattern of the decreasing horizontal error of the saccade-induced error indicated that the reversal point was beyond 8 deg along the saccade meridian (see Figure 7). However, in experiment 2, where we used a sufficiently large range of targets relative to the saccade amplitude of 6 deg, the reversal point was 6.38 deg, suggesting that the locus of the reversal point might be dependent on saccade amplitude. Our hypothesis that the origin of spatial mislocalization is related to saccade amplitude is currently under further investigation.

Distortions in Space and Motion Perception are Independent Phenomena

One goal of the current study was to determine whether the pattern of spatial mislocalization of two-dimensional loci could account for the distortion of motion perception after saccades observed by Park et al. (2001) (see Figure 1). The filled arrow in Figure 1A represents an example of a visual motion stimulus. This upright linear motion can be decomposed into sequential single point stimuli along the vertical axis (as in Figure 1B). The filled blue arrow in Figure 13 represents an analogous visual motion constructed from sequential

presentations of three point stimuli presented during steady fixation. The red plaid arrow in Figure 13 represents the perceived location of these point stimuli, and the apparent motion that would result from their sequential presentation after a rightward saccade. The plaid arrow in Figure 13 is not tilted in the direction opposite to the saccade as is the plaid arrow in Figure 1A. Rather, it is displaced horizontally in the direction opposite to the saccade without a significant change in orientation. Thus, the configuration constructed from the perceived positions of each point stimuli along the trajectory of a visual motion does not correspond to the pattern of visual motion distortion observed by Park et al. (2001). In that study, visual motion was produced by sweeping a laser from start to end loci in 12 ms. Since the laser target at the start locus was temporally closer to saccade offset than was the end locus, the mislocalization error would be smaller for the latter than the former. Thus, if this temporal gap is taken into account, the predicted perceived motion will deviate further from the experimental finding. The two-dimensional pattern of the saccade-induced error found in the current study indicates that the non-veridical motion perception after a saccade is independent process of spatial mislocalization.

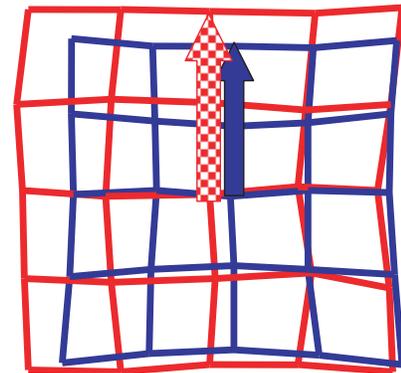


Fig 13. The predicted motion perception based on spatial mislocalization. If each spatial locus along the visual motion is sequentially mislocalized, and if these spatial mislocalization leads to distorted motion perception, the motion vector (filled blue arrow) should be perceived as the red plaid arrow. The predicted motion vector (plaid arrow) does not correspond with the direction in which motion was distorted (fig1A) indicating that spatial mislocalization can not account for the non-veridical motion perception after a saccade.

It has been repeatedly shown that the visual target presented before a saccade is mislocalized in the direction of a saccade, whereas the target presented after a saccade is mislocalized in the direction opposite to saccade (Honda, 1989; Honda, 1999; Schlag & Schlag-Rey, 1995; Cai, Pouget, Schlag & Schlag-Rey, 1997; Lappe, Awater & Krekelberg, 2000). The saccadic effect on motion perception appears to be different. When a visual motion is presented before a saccade, its perceived direction is

shifted in the direction opposite to the saccade (Lee & Lee, in preparation) which is same as visual motion presented after a saccade (Park et al., 2001). This again suggests that distortions in spatial and motion perception are independent processes.

Hypothetical Mechanisms of Spatial Mislocalization

The neural structure responsible for perceptual mislocalization at the time of saccades is not known. However, presumptive visual and oculomotor structures are known to undergo dynamic changes around the time of each saccade, and here, we consider two possible neural mechanisms that might underlie postsaccadic spatial expansion, one based on the visual cortex and the other on the superior colliculus.

First, in the visual cortex, the spatial structure of the receptive fields of neurons in the lateral intraparietal (LIP) area, which is functionally related to saccadic eye movements and spatial information processing, change immediately before a saccade (Duhamel, Colby, & Goldberg, 1992; Ben Hamed, Duhamel, Bremmer & Graf, 2002; Kusunoki & Goldberg, 2003). Receptive fields in other areas of the extrastriate cortex have also been found to be dynamic. Some neurons in these areas have receptive fields that expand at the time of saccades, becoming responsive to stimuli in both the old and new receptive fields (Nakamura & Colby, 2002). On the other hand, some neurons in area V4 have receptive fields that become smaller before saccade onset (Tolias, Moore, Smirnakis, Tehovnik, Siapas & Schiller, 2001). Although it is not clear how these changes in the spatial structure of the receptive fields relate to spatial mislocalization in most cases, there is evidence that the positional information decoded from neural activities of the medial temporal and medial superior temporal areas reflects the spatial mislocalization at the time of saccades (Krekelberg, Kubischik, Hoffmann, & Bremmer, 2003). Considering the dynamic nature of receptive fields in the visual system revealed by previous studies, we can postulate that immediately after the termination of an eye movement, the receptive fields of individual neurons in the cortical areas specialized for visuospatial information processing might change temporarily for recalibration of spatial information. This would be a counterpart mechanism of the presaccadic change in receptive fields.

Next, we consider a hypothetical mechanism involving the superior colliculus that could underlie the two-dimensional spatial mislocalization found in the current study. Execution of a saccade and spatial processing of a visual target both involve neural activations within topographic map. The SC is related to spatial orientation involving the eye, head, pinna, and body movements (Sparks & Hartwich-Young, 1989). Its neurons show both visual responses and saccade-related discharges. Furthermore, the SC undergoes a transient change immediately after execution of a saccade as

described by Nichols & Sparks (1995) and Schlag, Pouget, Sadehghpour, & Schlag-Rey (1998). In their experiments, immediately after a visually-guided saccade a second saccade is evoked with electrical stimulation of the SC. The amplitude and direction of a saccade evoked by an electrical stimulation of the SC depended on the amplitude and direction of the preceding visually-guided saccade, and the direction of the electrically-evoked saccade was in the direction away from the preceding visually-guided saccade.

Suppose the subject first makes a 12 deg saccade to the right. This will result in an activation of a neural population within the topographic map of the SC. A simultaneous electrical stimulation of two separate sites within the SC evokes a vector-averaged saccade (Robinson, 1972). Furthermore, two simultaneously-presented visual targets are localized between the two. In other words, one activation within a topographic map draws the other toward its location, probably because of a population average process. What will happen if one activation within a topographic map precedes the other? We propose that two sequential activation interacts differently within a topographic map due to a presumptive inhibitory phase following the initial excitation. The time course of the inhibitory phase ought to be shorter than the refractory period of saccades, some 200ms. Thus, the initial activation due to execution of a 12 deg saccade undergoes temporary inhibition when another activation develops in other part of the map due to presentation of the LT (Figure 14A). The LT produces neural activation within a circumscribed region in the SC, described as the 'point-image' by Capuano & McIlwain (1981). The inhibitory influence from the preceding saccade on this population activity would modify the population average process as described by Lee, Rohrer & Sparks (1988). In fact, the pattern of the saccade-induced error in localization of the LT is remarkably similar to the

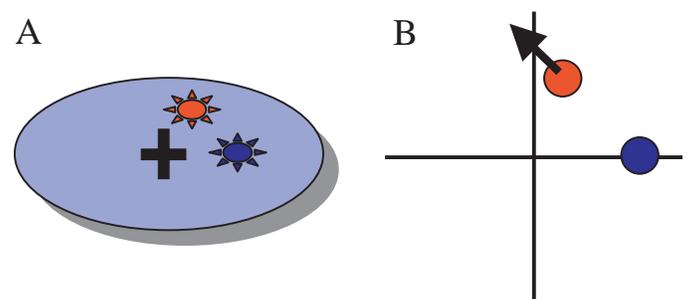


Figure 14. A hypothetical neural interaction within topographic map. A: The oval shape represents a topographic neural representation of visual space, and the cross represents the fovea. A blue starburst represents neural activations caused by execution of a saccade and a red starburst represents activation by the LT (2). B: The perceived locus of the LT is pushed away from the locus corresponding to the ST-guided saccade vector.

expanding pattern of saccadic dysmetria following a focal inactivation of the SC with direct injection of local anesthetic as described by Lee, Rohrer & Sparks (1988). Whereas an excitatory activation will pull other simultaneous excitations toward itself, an inhibitory locus will push away other excitatory activations during localization, as the vector average process predicts (Figure 14B). This interaction will produce mislocalization which is similar to the pattern of the saccade-induced error found in the current study. Some further unknown process might influence this neural interaction to account for the pattern of modulation by target location observed in the current study. Whether the active population of the SC during execution of a saccade undergoes an inhibitory phase immediately after a saccade remains to be seen.

The hypothetical process depicted in Figure 14 need not be in the superior colliculus. Any topographic representation processing spatial information could be the candidate, and the critical element of the process is the interaction between the neural activations due to saccade execution and the appearance of a visual target within a topographic representation.

Morrone, Ross, & Burr (1997) reported a spatial compression towards the saccade goal. In their experiment, the localization targets were briefly presented before a saccade was made toward another target presented earlier. The origin of compression appears to be the saccade goal, and thus their observations can also be interpreted as the result of neural interactions within a topographic map of a saccade target and a visual target presented before saccade start. Compression towards the fixation point observed by Sheth & Shimojo (2001) also suggests an interaction within a topographic map. The neural activation related to fixation may interact with the activation due to the visual target, resulting in a compressing pattern.

Conclusion

We determined the effect of a saccadic eye movement on spatial perception of a subsequently-presently visual target in the dark. There were both horizontal and vertical components in spatial mislocalization. The horizontal component of saccadic effects increased as the targets were located further into the visual field contraversive to the saccade, and the vertical component of saccadic effects increased as the targets' absolute value of the vertical coordinate increased. The overall pattern of postsaccadic spatial mislocalization resulted in a two-dimensional pattern which could be termed as an expansion of perceived visual space. The estimated amount of spatial expansion was approximately 30%.

The two-dimensional pattern of post-saccadic mislocalization suggests that spatial information processing at the time of saccades reflects a dynamic

change in the visual system. Temporary changes in the receptive field properties of individual neurons in the visual system and interactions between neural activations are considered to be the underlying mechanism of postsaccadic spatial mislocalization.

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