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Repulsive bias in egocentric localization*

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The accuracy of localization of a briefly presented visual target is compromised when external references are not available. It is thought that in such conditions, localization depends on egocentric cues, such as gaze direction. In the current study, we examined the pattern and magnitude of mislocalization and its underlying mechanism. Human subjects moved a visual probe to report the remembered location of a visual target in an otherwise dark condition. We found that spatial memory was influenced by the very act of localization if a visual probe was used for response. There was a robust bias in localization depending on the initial probe position. When the probe initially appeared on the same side as fixation with respect to the target, the remembered target location was systematically biased beyond the target eccentricity, whereas when the probe initially appeared on the side opposite to the fixation with respect to the target, localization was relatively accurate (Experiment 1). This asymmetric localization bias depending on the initial probe position was robustly found regardless of gaze direction during response period (Experiment 2) and response device (Experiment 3). The pattern of localization bias was consistent with the hypothesis that the perceived target location was repulsed from both the probe and fixation loci. Thus, depending on spatial arrangement, the repulsions from the fixation and probe accumulated to result in a larger localization error overestimating the target eccentricity, or the two repulsions annihilated each other to result in a relatively accurate localization.

Key words : eye movements, spatial localization, visual short-term memory, foveal repulsion

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Spatial location of a visual target can be registered with respect to concurrent visual references, or with respect to the observer. When a visual reference is not available, e.g. in the dark, spatial localization depends on only egocentric cues, and its accuracy is often compromised. Various factors have been identified in such processes. Egocentric representation of the target location is easily revised by intrinsic events, such as gaze fixations or shifts, or extrinsic factors, such as the visual probe used to report the perceived target location. Studies examining the pattern of interaction among these factors have reported rather complex results, sometimes in seemingly conflicting ways. For example, perception of target location may be biased toward current fixation (Awater & Lappe, 2006; Kerzel, 2002; Musseler, Van der Heijden, Mahmud, Deubel, & Ertsey, 1999; O'Regan, 1984; Osaka, 1977; Rose & Halpern, 1992; Sheth & Shimojo, 2001; Van der Heijden, Van der Geest, De Leeuw, Krikke, & Musseler, 1999) or away from it (Bock, 1993; Eggert, Ditterich, & Straube, 2001; Enright, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998). Also, the perceived target location may be biased toward a concomitant visual stimulus in the scene (Diedrichsen, Werner, Schmidt, & Trommershauser, 2004; Hubbard & Ruppel, 2000; Sheth & Shimojo, 2001; Shim & Cavanagh, 2006), or away from it (Diedrichsen et al, 2004; Fischer & Adam, 2001; Kerzel, 2002; Schmidt, Werner, & Diedrichsen, 2003; Suzuki & Cavanagh, 1997; Van der Heijden et al, 1999; Werner & Diedrichsen, 2002). Experimental conditions varied across these studies in terms of control of gaze direction during target presentation and response, background luminance, and the method of response, and these and other factors may interact in complex ways to result in varying results. The goal of the current study was to understand the observed localization bias based on underlying representational processes as explained below.

Imagine a typical task of egocentric localization along the horizontal dimension (Fig. 1). A visual target (e.g., a laser spot) is briefly presented in the periphery while the subject maintains fixation in an otherwise dark condition (Fig. 1A). The remembered location of the target is reported by adjusting the position of a visual probe (another laser spot). The process underlying this simple task turns out to be not as simple as it may appear. Since the probe itself is visual, the problem arises when it appears to the subject. The probe may first appear on the side opposite to fixation with respect to the target (OS condition, Fig. 1B), and the subject moves the probe inward toward the remembered target location until the probe matches the location where he or she thinks the

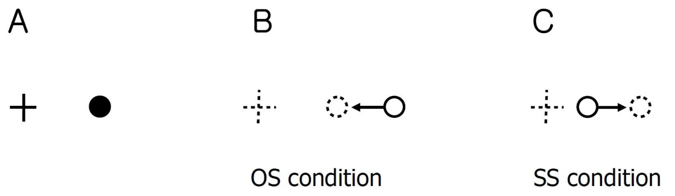

Fig 1. Reporting the perceived target location with a probe. A: The visual target (filled circle) is presented while the subject's gaze is maintained around the location of the fixation target (cross). B: Later, the perceived target location (dotted circle) is reported by moving a visual probe (open circle) onto it. The probe appears on the opposite side (OS) of the fixation with respect to the target. C: Alternatively, the initial probe location is on the same side (SS) as the fixation with respect to the target.

target has appeared. Alternatively, the probe may appear on the same side as the fixation with respect to the target (SS condition, Fig. 1C), and the subject moves the probe outward. We found that the mislocalization patterns in the two conditions were drastically different.

We assume that representational processes responsible for spatial memory of the target interact with fixation and the probe. We further assume that there can be two kinds of interaction in the situation like Fig. 1, attraction or repulsion, between target representation and fixation or the probe. An attractive (or repulsive) interaction between the target and fixation results in a localization bias toward (or away from) fixation. Similarly, an attractive (or repulsive) interaction between the target and probe results in localization bias toward (or away from) the probe. Similar interactions have been assumed for cooperative and competitive interactions for neural representation in a shared spatial map (Szabo, Almeida, Deco, & Stetter, 2004).

Assuming that the interactions between fixation and the target representation and between the target representation and the probe remain unchanging in both SS and OS conditions, the perceived target location, and thus localization error, can be deduced from the combined knowledge of the initial probe position in any given trial and the nature of each interaction. Fig. 2 illustrates patterns of mislocalization predicted by different kinds (attraction, repulsion, or absence) of interaction between the target and fixation and between the target and probe. For example, the hypothetical condition under which target location is repulsed from both the fixation and probe predicts different patterns of target localization for SS and OS conditions: in the SS trials of Fig. 1C, the target representation is repulsed from both the fixation and probe in the same outward

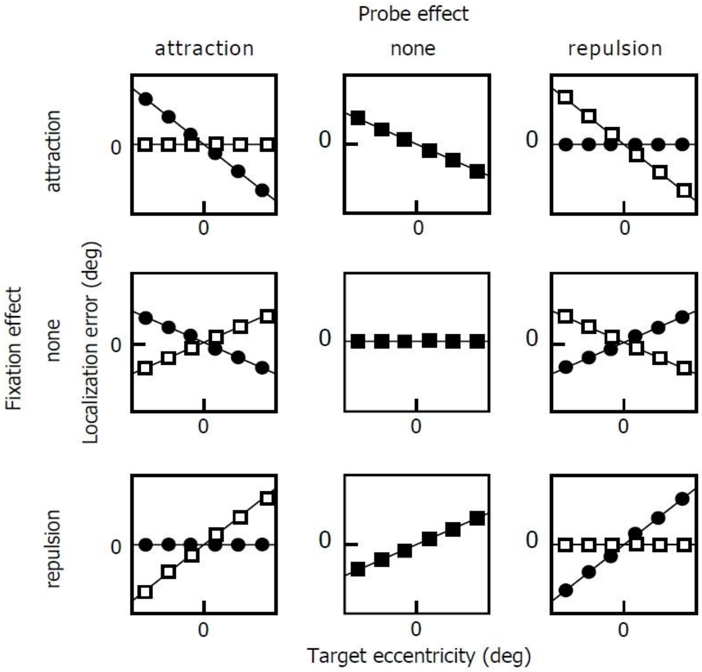

Fig. 2. Pattern of mislocalization under different assumptions. Each panel shows predicted localization error as a function of target eccentricity. Localization error is defined as reported target eccentricity minus actual target eccentricity. Filled circles represent the SS condition, and open squares represent the OS condition. Localization error, measured in terms of visual angle, due to the interaction between the fixation and target representation (fixation effect), is assumed to increase with target eccentricity, and so does the error due to interaction between the probe and target representation (probe effect). Thus, error = $I_{fixation} \times T + I_{probe} \times T$, where $I_{fixation}$ and I_{probe} are the interaction constants (attraction or repulsion) of the fixation and probe, respectively, and T is target eccentricity.

direction to result in an overestimation of target eccentricity, whereas in the OS trials of Fig. 1B, the target representation is repulsed from the fixation and probe in opposite directions, and the repulsions from the two sources annihilate to result in a relatively precise localization (lower right panel of Fig. 2).

Target location is likely to be encoded by the activity of spatially-tuned neurons within a non-linear topographic map, such as striate cortex (Horton & Hoyt, 1991). The neural activation by the late-appearing probe may modify the profile of population activity corresponding to target location, producing a localization error that increases, not necessarily linearly, with target eccentricity (VanRullen, 2004). Accordingly, in Fig. 2, mislocalization errors due to these interactions are assumed to increase with target eccentricity.

In the current study, we determined the roles of fixation and the visual probe on perceived target location, and found that the localization bias was consistent with the hypothesis that the perceived target location is repulsed from both the probe and fixation positions (lower right panel of Fig. 2). For the first two experiments, a hand-held momentary rotary switch was used as a response device: in Experiment 1, gaze was allowed to move during the response period, whereas in Experiment 2, subjects were required to maintain fixation at the display center during the response period. In Experiments 3, subjects were also required to maintain fixation, but a computer mouse was used as a response device.

EXPERIMENT 1

The goal of Experiment 1 was to examine the effects of initial probe position on the perceived location of a visual target, as outlined in Fig. 1.

Method

Subjects. Three students at the Seoul National University participated in the experiment as paid volunteers. All subjects in this and subsequent experiments had normal vision. For each subject, the nature of the experiment was explained and informed consent obtained.

Apparatus and Stimuli. Subjects were seated facing a 2 m × 2 m frontal rear-projection screen at a distance of 115 cm. The head was immobilized in an erect position with a bite bar. Horizontal positions of both eyes were measured with an infra-red eye tracker (IRIS, Skalar Medical, Netherlands). A small spot of light was produced by a red laser diode, collimated with a series of iris diaphragms, moved by a pair of mirrors described below, and projected onto the screen. The laser spot, which was 4 mm in diameter on the screen (0.2 deg), served as the fixation target, target-to-localize, and probe. There was no ambient luminance, so with the exception of the laser spot, the display was completely dark. Subjects became dark adapted over the course of the experiment. The laser beam was deflected by a two-axis galvanometer scan head, under the control of a microprocessor (General Scanning, DE series, USA) interfaced with a host computer (PC586), and its position on the screen was specified in 16-bit resolution (~0.0009 deg). Horizontal eye positions and currents from the galvanometers corresponding to the horizontal and vertical positions of the laser beam were sampled at 500 Hz with a resolution of 12-bits, and stored for off-line analysis.

Procedures. After a tone signaled the start of a trial, the fixation target appeared at the center of the screen for a variable duration between 1.8 and 2.2 s. The subject was instructed to fixate on the target. At the end of the predetermined fixation period, the fixation target went off and a blank period followed. This period was randomly chosen from 50, 75, and 100 ms. Then, the target-to-localize appeared for 50 ms at a spot pseudorandomly chosen from ten locations along the horizontal dimension, spanning from －18 to 18 deg with a step of 4 deg. With a delay of 300 ms after target offset, the probe was presented at one of six pseudorandomly chosen positions, approximately ±4, ±5, or ±6 deg horizontally with respect to the target. In some trials, the target and probe were presented in the opposite hemifield with respect to fixation; for example, when the target eccentricity was 2 deg and the target-probe distance was 4 deg, the probe eccentricity was －2 deg in the SS condition.

The subject was instructed to move the probe onto the remembered location of the target by manipulating a momentary rotary switch, a spring-loaded jog wheel, on a hand-held response box. When the wheel was rotated in clockwise (or counter-clockwise) direction, a series of clock pulses were allowed to enter the host computer and used for rightward (or leftward) probe motion until the wheel was released. The jog wheel enabled the subject to move the probe at a constant speed (approximately 6 deg/s) from its initial position to the perceived target location in a horizontal direction. The subject reported the remembered target location by pressing a button on the response box, or skipped trials for which location was uncertain by pressing another button. The next trial started 1.5 s after this button press.

The visual stimuli were viewed binocularly, and no feedback regarding the response was provided. Localization error was defined as reported target location minus actual target location.

Invalid trials were discarded during off-line analysis. These included trials that subjects skipped and trials in which the subject either did not maintain fixation for the last 1 s of the fixation and target presentation period, the criteria being that fixation remained within a 2-deg window centered on the fixation target and that mean eye velocity did not exceeded 5 deg/s during target presentation. Subjects were allowed to move their eyes after the probe onset.

We used Matlab (The MathWorks Inc.) to analyze the eye position signal, and SPSS (SPSS Inc., Chicago, IL) to test the statistical significance of effects of the fixation and probe on mislocalization.

Results and Discussion

From a total of 6060 trials collected from three subjects, 4809 (79.36%) valid trials were obtained (YB: 1397 trials, 77.61%; HJ: 1726 trials, 70.16%; HN: 1686 trials, 93.67%).

The magnitude and direction of mislocalization were different between SS and OS trials. In the OS trials, the subject moved the probe inward toward the remembered target location until the probe fairly accurately matched the target location (open squares in Fig. 3). However, in the SS trials, there was a systematic mismatch between target and final probe locations (filled circles in Fig. 3), with positive errors for targets in the right visual field and negative errors for targets in the left field. Thus, subjects moved and positioned the probe beyond the target location, exaggerating target eccentricity. The difference between SS and OS trials indicates that the initial probe location influenced target localization.

The mismatch between target and final probe locations in the SS condition increased with target eccentricity up to 10 ~ 15 deg (Fig. 3). The eccentricity effect on the mislocalization

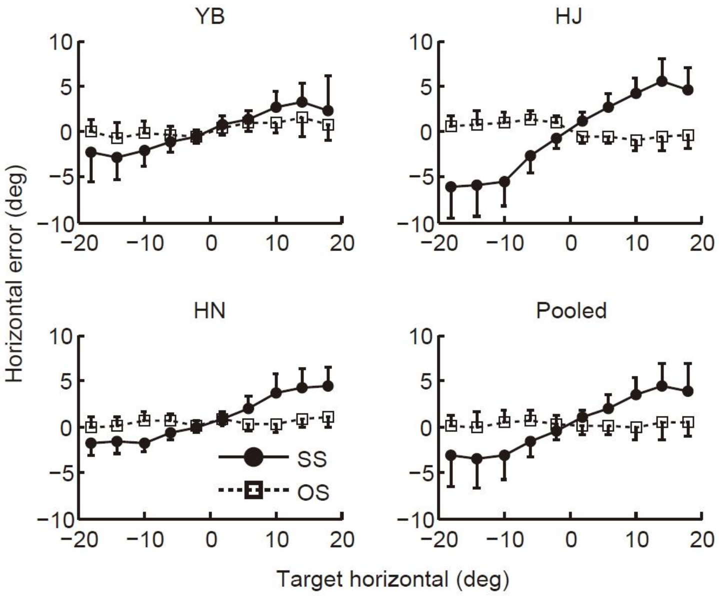

Fig. 3. Localization error as a function of target eccentricity for each of the three subjects and for the pooled data. Filled circles represent the mean errors of localization from SS trials, and open squares represent those from OS trials. Vertical bars represent one-standard deviation. Note that the slopes of the SS trials are more positive than those of the OS trials, which are near zero, consistent with repulsions from both the fixation and probe locations (see Fig. 2).

within the central 10 deg could be described by regression lines for the pooled data: for the SS, error = 0.33 × eccentricity + 0.21, showing a strong correlation between mislocalization and eccentricity ($R^2 = .65$); for the OS, error = -0.03 × eccentricity + 0.28, showing little correlation ($R^2 = .04$). The two regressions were significantly different, with $X^2(1) = 1135.40$, ($p < .001$, Jöreskog & Sörbom, 1994). Analysis of the variance of mislocalization showed significant interaction between target eccentricity (ten conditions) and the initial probe position effect (SS vs OS) within all three subjects (YB: $F(9, 1377) = 23.75$, $p < .001$; HJ: $F(9, 1706) = 337.19$, $p < .001$; HN: $F(9, 1666) = 147.04$, $p < .001$).

The pattern of localization bias in the SS and OS trials within the central 10 deg matched the predicted pattern based on eccentricity-dependent repulsion of the perceived target location from both fixation and probe locations (lower right panel of Fig. 2). In this scheme, in the OS trials, the spatial representation of the target is repulsed from fixation and probe positions in opposite directions, and thus the two repulsions annihilate to result in relatively accurate localization. On the other hand, in the SS trials, the target representation is repulsed from the fixation and probe in the same direction, and the repulsions accumulate to result in large localization errors overemphasizing the target eccentricity.

When the localization error is assumed to be determined by summing the two repulsive effects, as in error = $R_{fixation}$ × eccentricity + R_{probe} × eccentricity, where $R_{fixation}$ is repulsion from the fixation and R_{probe} is repulsion from the probe, the two slopes of the regression lines in Fig. 3 (Pooled) are the sum of $R_{fixation}$ and R_{probe}. The solution of these two equations yields $R_{fixation} = 0.15$ and $R_{probe} = 0.18$, suggesting that localization errors due to repulsions from the fixation and probe are 0.15 and 0.18 deg, respectively, for each degree of target eccentricity. As can be seen by the different slopes for the SS condition, there was inter-subject variability in the difference in localization error between the OS and the SS conditions, suggesting an idiosyncratic strength of repulsion.

EXPERIMENT 2

In Experiment 1, the subjects freely moved their eyes during the response period. Since previous studies on spatial localization have reported effects of gaze direction during the response period (Enright, 1995; Henriques et al., 1998; Mapp & Ono, 1987), we wondered if the difference in localization between the SS and OS trials was due to the difference in gaze direction during the response period. If so, the differential

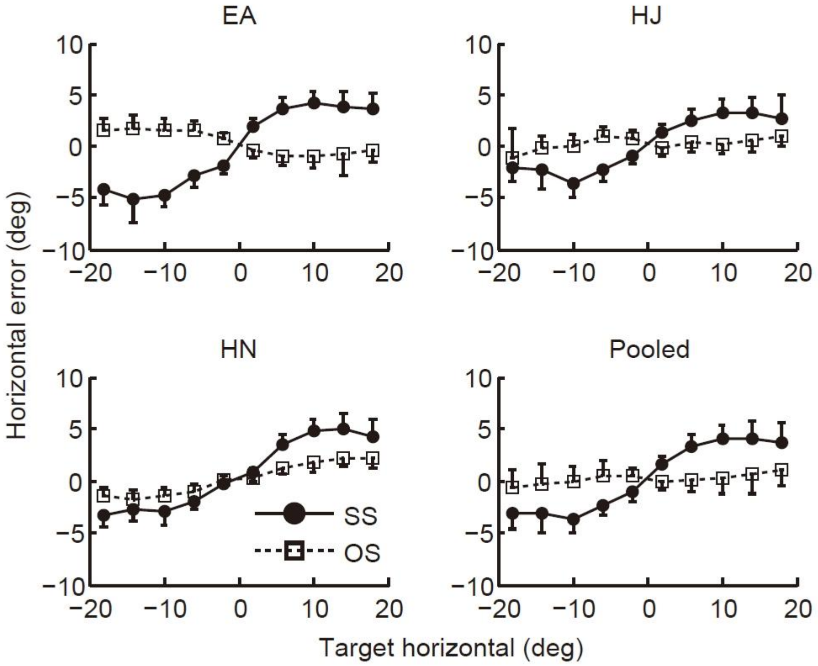

Fig. 4. Localization error as a function of target position in Experiment 2. Same convention as Fig. 3. Gaze was controlled and maintained around the central fixation during response.

effect of the initial probe location would disappear if the gaze direction was maintained on the fixation point through the response period. Experiment 2 was designed to test this possibility.

Method

Subjects. Three students at the Seoul National University participated in the experiment as paid volunteers. Two of these subjects had also served in Experiment 1.

Apparatus and Stimuli. The same apparatus and stimuli as Experiment 1 were used.

Procedures. The same procedures as Experiment 1 were used except that in Experiment 2, the subjects were asked to maintain central fixation after the fixation target went off until the perceived target location was reported. The trials in which the gaze did not remain within a 2-deg window around the fixation-target location until the response was completed were discarded as invalid during off-line analysis.

Results and Discussion

From a total of 6660 trials collected from three subjects, 3637 (54.61%) valid trials were obtained (EA: 1171 trials, 55.76%; HJ: 1159 trials, 41.99%; HN: 1307 trials, 72.61%). The lower percentage of the valid trials compared to Experiment 1 (54.61% vs 79.36%) probably indicates that maintaining central fixation through response period was more difficult.

The obtained pattern of localization error in Experiment 2 (Fig. 4) was similar to that of Experiment 1 in terms of the difference between the OS and SS conditions, the slopes of the two

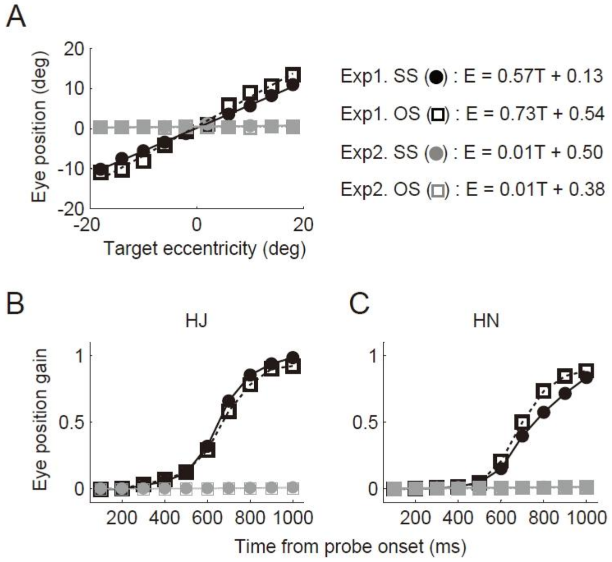

Fig. 5. Eye position during trials. A. Horizontal eye position as a function of target eccentricity in subject HN. Black circles and squares represent the mean horizontal eye position 800 ms after the probe onset in the SS and OS conditions, respectively, in Experiment 1. Similarly, gray symbols represent those for Experiment 2. Linear regression equations relating eye positions (E) to target eccentricity (T) are shown for each condition. The slope of each line is eye position gain. B, C. Eye position gain as a function of elapsed time from probe onset for subjects HJ (B) and HN (C). Each symbol represents the slope of the regression line relating horizontal eye position to target eccentricity as in A, determined every 100 ms after probe onset. In Experiment 1, gaze direction started at the central fixation for all targets (slope = 0) and shifted later toward the perceived target location (or the instantaneous location of the moving probe) as the subject manipulated the probe (slope 〉 0), whereas in Experiment 2, gaze direction remained at the center throughout the trial as instructed. The instantaneous gaze direction for subject HJ was farther out in the SS than in OS conditions, whereas the opposite was the case for subject HN. Note that there were no consistent difference in gaze direction between the SS and OS conditions in both Experiments 1 and 2.

regression lines, and the statistical significance of the difference in the two regression lines. The eccentricity effect of Experiment 2 on the mislocalization within central 10 deg could be described by regression lines, error = 0.41 × eccentricity + 0.28 (R^2 = .85) for the SS, and error = 0.00 × eccentricity + 0.19 (R^2 = .00) for the OS. The two regressions were significantly different, with $X^2(1) = 1119.08$ ($p < .001$). Analysis of the variance of mislocalization showed a significant interaction between target eccentricity and the initial probe position effect within all three subjects (EA: $F(9, 1151) = 408.37$, $p < .001$; HJ: $F(9, 1139) = 163.92$, $p < .001$; HN: $F(9, 1287) = 131.98$, $p < .001$). Thus, in the SS trials, there was a systematic error exaggerating the target eccentricity, and the mismatch increased with the target eccentricity up to about 10 deg, whereas in the OS trials, localization was relatively accurate, as in Experiment 1.

The mislocalization pattern in Experiment 2 varied across subjects. Subject HJ showed a smaller difference in localization error between the OS and SS conditions compared to Experiment 1, and subject HN showed a positive slope in the OS condition. These results suggest a potential role of gaze direction during the response period. In order to examine whether different patterns of gaze maintenance caused difference in mislocalization pattern between the SS and OS conditions, we examined the horizontal eye position after probe onset in the two subjects (HJ and HN) who participated in both Experiments 1 and 2. In Experiment 1 where the subjects were free to move their eyes after probe onset, gaze direction approached the target as the subjects manipulated the probe toward the perceived location of the target (Fig. 5). Although in Experiment 1 the pattern of gaze control in the two subjects was slightly different (Fig. 5B & C), the same pattern of asymmetric localization bias between the SS and OS conditions was observed (Fig. 3). Similarly, in Experiment 2, gaze direction remained at the center throughout the trial as instructed, with no discernible difference between the SS and OS conditions, and a consistent difference in localization bias between the two conditions was observed (Fig. 4). These results, combined with the similar results between Experiments 1 and 2, indicate that the difference in localization bias between the SS and OS conditions was not due to a difference in gaze direction during the response period.

EXPERIMENT 3

In Experiments 1 and 2, the response device was a momentary rotary switch that the subject used to move the probe at a constant speed (~6 deg/s) from its initial position to the perceived target location in a horizontal direction. Since earlier studies reporting a bias of target memory toward the fixation (e.g., Sheth & Shimojo, 2001) had used a computer mouse as a response device, we wondered whether target memory was differentially affected during the response period by the slow and constant movement of the probe afforded by the rotary switch. Experiment 3 was designed to test this possibility.

Method

Subjects. Three undergraduate students at the Seoul National University participated in the experiment as paid volunteers.

Apparatus and Stimuli. The same apparatus and stimuli as Experiment 1 were used except that in Experiment 3, the subjects used a computer mouse to report the perceived target location. The horizontal position of the mouse was read into the computer, and used to move the mirror galvanometers. Thus, the subjects moved the probe at a variable speed under their control.

Procedures. The same procedures as Experiment 2 were used. The subjects were instructed to maintain central fixation until they report the remembered target location using a computer mouse.

Results and Discussion

From a total of 4620 trials collected from three subjects, 3473 (75.17%) valid trials were obtained (EA: 1343 trials, 74.61%; JHJ: 1371 trials, 87.88%; YM: 759 trials, 60.23%).

The mean duration of the response period (the time from the onset of the probe movement to the probe's arrival at its final position) in Experiment 2 was 970.14 (±402.11) ms, whereas that in Experiment 3 was 957.66 (±560.51) ms. The difference was not significant (independent t-test, $p = .28$).

As in Experiments 1 and 2, in the SS trials, there was a systematic error exaggerating the target eccentricity, and in the OS trials, the localization was fairly accurate (Fig. 6). The eccentricity effect of Experiment 3 on the mislocalization within the central 10 deg could be described by regression lines: error = 0.40 × eccentricity - 0.09 ($R^2 = .78$) for the SS trials, and error = -0.01 × eccentricity − 0.03 ($R^2 = .00$) for the OS trials. The two regressions were significantly different, with $X^2(1) = 899.28$ ($p < .001$). Analysis of the variance of mislocalization showed significant interaction between target eccentricity and initial probe position for all three subjects (EA: $F(9, 1323) = 847.11$, $p < .001$; JHJ: $F(9, 1351) = 159.09$,

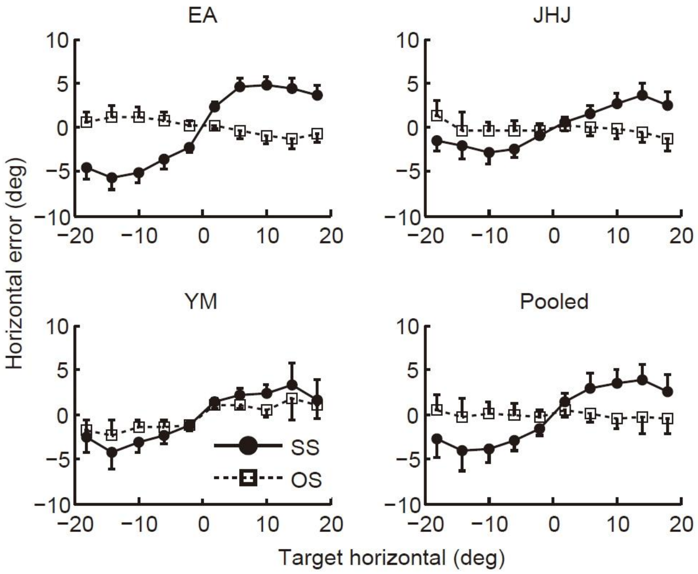

Fig. 6. Localization error as a function of target position in Experiment 3. Same convention as Fig. 3. In this condition, a computer mouse was used as a response device.

p < .001; YM: $F(9, 739) = 17.76$, p < .001).

Since similar results were obtained in Experiments 2 and 3 (Fig. 4 and 6), the use of different response devices does not explain the effect of initial probe position on localization error.

TARGET-PROBE DISTANCE EFFECT

In Experiments 1, 2, and 3, the difference in localization error between the SS and OS trials became smaller as the distance between the target and probe increased (Fig. 7). The direction of the repulsion from the probe is thought to be opposite between the SS and OS trials, and thus, a stronger repulsion from the probe can boost the difference in localization error between the SS and OS trials. Therefore, the inverse relationship between the difference in localization error between the SS and OS trials and the target-probe distance suggests that a closer probe more strongly repulses the spatial memory.

DISSOCIATION OF FIXATION AND PROBE EFFECTS

In order to try to dissociate influences of fixation and the probe on target localization across experimental conditions, we assumed that mislocalization error is contributed by the errors due to the fixation and the probe effects in our

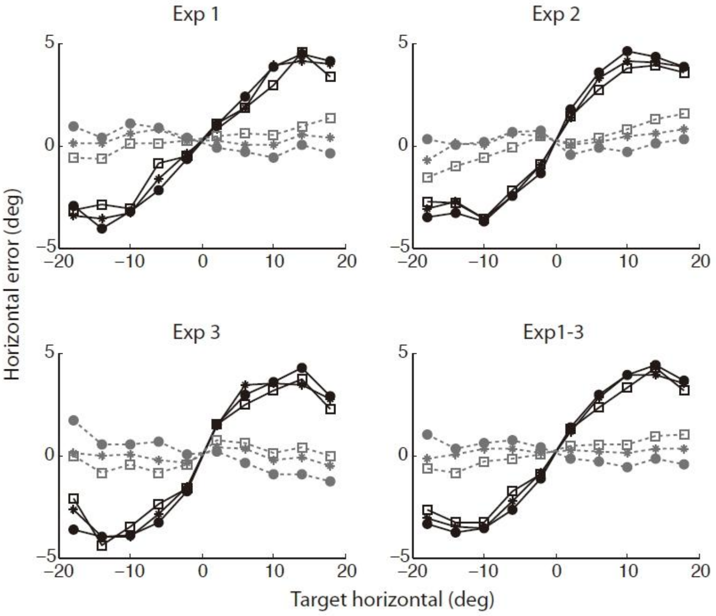

Fig. 7. Effects of target-probe distance. Localization error as a function of target position from Experiment 1 through 3 and combined 1-3, grouped by the target-probe distance. Symbols ●, ＊, and □ are target-probe distances of 4, 5, and 6 deg, respectively.

experimental conditions, and that these errors are consistent across the SS and OS conditions. Then one can obtain the two errors by solving the following equations: $E_{total\text{-}in\text{-}SS} = E_{fixation} + E_{probe}$, and $E_{total\text{-}in\text{-}OS} = E_{fixation} - E_{probe}$, where $E_{total\text{-}in\text{-}SS}$ and $E_{total\text{-}in\text{-}OS}$ are total errors in the SS and OS conditions, respectively, and $E_{fixation}$ and E_{probe} are errors due to the fixation and probe. In the SS condition, repulsions from fixation and the probe are in the same direction, and $E_{total\text{-}in\text{-}SS}$ consists of sum of two errors, whereas in the OS condition, they are in the opposite direction, and $E_{total\text{-}in\text{-}OS}$ consists of the difference of the two errors. Fig. 8 illustrates these dissociated errors; Fig. 8A, B, and C show errors due to fixation, and Fig. 8D, E, and F show errors due to the probe in three experimental conditions. Note that the errors were dissociated under the assumption of linear summation, but there are no empirical evidences to support it. The estimated localization error contributed by the interaction between target representation and fixation showed a dependency on target eccentricity, but not on target-probe distance (Fig. 8A, B, and C), whereas the error contributed by the probe also systematically depended on target-probe distance (Fig. 8D, E, and F). The error due to the probe was larger

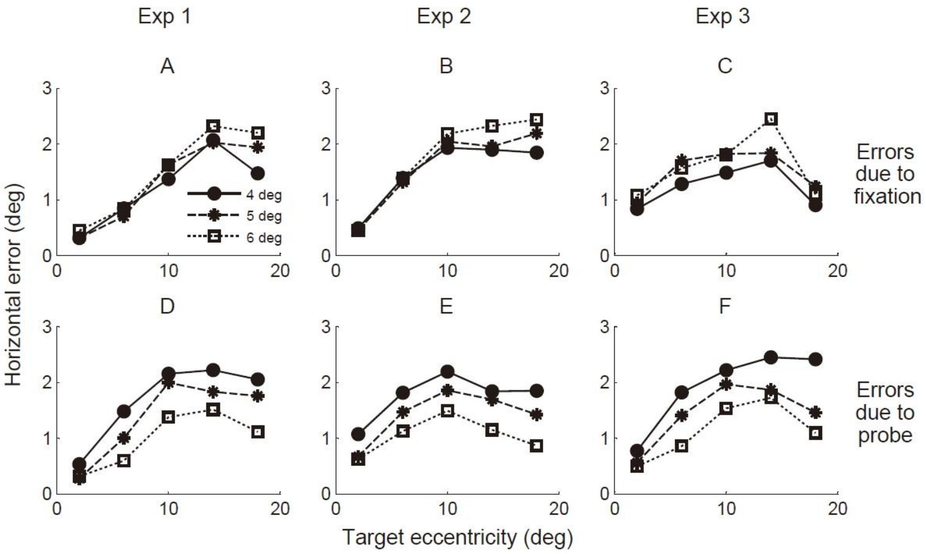

Fig. 8. Estimated localization errors due to the influence of fixation (A, B, C) and the probe (D, E, F) in Experiment 1 (A, D), 2 (B, E), and 3 (C, F). See text for derivation of these errors. Symbols ●, ∗, and □ are target-probe distances of 4, 5, and 6 deg.

with the smaller target-probe distance, consistent with Fig. 7. These results are consistent with the assumptions of summation and consistent interaction across the SS and OS conditions. The influences of both the fixation and probe on the target localization were repulsive (positive error).

The difference in localization bias between the SS and OS conditions (Fig. 3, 4, & 6) and dissociated errors (Fig. 8) increased up to around 10-15 deg of target eccentricity. The increase may be explained by representing target location within a non-linear topographic map, as stated in Introduction. The falloff of increase beyond 15 deg of target eccentricity may be explained by the spatial extent of repulsive interactions between the target and fixation and between the target and probe within the map.

The errors due to probe appear to saturate earlier with an increase in target eccentricity, compared to the errors due to fixation (Fig. 8). This suggests that the repulsion from fixation extends farther than repulsion from the probe.

GENERAL DISCUSSION

When a visual probe was used for target localization, the initial position of the visual probe robustly influenced the target localization. When the probe appeared on the same side as the fixation with respect to the target (SS condition), the remembered target location was systematically biased beyond the target eccentricity. On the other hand, in the OS conditions where the probe appeared on the side opposite to fixation with respect to the target, localization was relatively accurate. The difference in localization bias between the SS and OS conditions persisted regardless of whether gaze was free to move (Experiment 1) or central fixation was maintained through the response (Experiment 2). This difference persisted regardless of response device tested (Experiment 3). The spatial location of the visual target is thought to be stored as a spatial representation and retrieved for comparison with the probe location. The difference in localization bias between the SS and OS conditions indicates that target representation is robustly influenced by the very act of localization if a visual probe is used for response. These results are consistent with previous studies on spatial mislocalization in that spatial representation is susceptible to modification (e.g., Diedrichsen et al., 2004; Kerzel, 2002; Musseler et al., 1999; Van der Heijden et al., 1999).

Based on the pattern of localization bias, we attempted to infer the nature of interactions underlying localization bias. The asymmetric pattern of mislocalization between the SS and OS conditions was the closest to the prediction that follows from the hypothesis that the spatial memory was repulsed from both fixation and the probe (lower right panel of Fig. 2). Thus, repulsion from fixation and the probe either annihilated to result in near veridical localization in the OS condition, or accumulated to result in a larger localization error in the SS condition. The relatively accurate localization in the OS trials suggested that repulsions from the fixation and probe were comparable in magnitude. Under our experimental conditions, fixation and the probe repulsed the target memory by approximately 0.15 and 0.18 deg, respectively, for each degree of target eccentricity (Experiment 1, Fig. 3).

Note that we used 'bias' for observed mislocalization, whereas we used 'attraction' or 'repulsion' for underlying interactions that were not directly observed. The results obtained in the current study indicate that localization is sensitive to experimental conditions, and that the direction and magnitude of apparent biases in localization do not necessarily match the underlying interactions. The apparent lack of localization bias in the OS condition does not mean absence of interaction between the target representation and fixation. Extending this, we contend that a localization bias toward the direction of fixation does not necessarily mean that the underlying interaction between the target representation and fixation is attractive, because under some circumstances, an apparent bias toward the direction of fixation (e.g., data from the OS condition of subject EA in Fig. 4 & 6) may result from a stronger repulsion of the target representation from the visual probe toward fixation to overcome foveal repulsion.

The distinction between apparent bias and underlying interaction may help explain some of the discrepancies in the localization literature (see Introduction). The previous experiment closest to the current study is Experiment 3 of Van der Heijden et al. (1999), both in terms of stimulus arrangement and method of response. In that study, a short vertical target line appeared for 30 ms at one of seven horizontal positions while the subject maintained fixation at the center of display, and the subjects were instructed to bring a movable cursor dot as close as possible to the perceived position of the target. Notably, in that study, the initial position of the movable cursor was controlled, and its effect was found significant. They concluded that target position was underestimated when the initial cursor position was more peripheral than the target, and overestimated when the cursor initially appeared at middle. Furthermore, one can note in their Fig. 3 that when the cursor was initially positioned on the side opposite to the fixation with respect to the target (for example, target at the position -3 and the cursor at the position -6), corresponding to our OS condition, target position was underestimated, and when the cursor was at the same left side as fixation with respect to the target (for example, target at the position 3, with the cursor at the position -6) corresponding to our SS condition, target position was overestimated. Thus, underestimation of target position in their peripheral cursor conditions and overestimation of target position in their middle cursor condition can be explained with the same underlying repulsive interaction. Musseler et al. (1999) also reported a localization bias toward fixation when a movable cursor was used to report target location. In that study, the bias toward the fixation was stronger in the condition in which the cursor was initially positioned more eccentric than the target compared to the condition in which the cursor was central than the target. This is also compatible with the idea that the apparent bias toward fixation does not necessarily indicate attraction toward fixati on.

In the current study, we investigated the interaction of the target representation with fixation by assuming that interactions with the fixation and probe will remain unchanging in both SS and OS conditions. If the interactions of the target memory with the fixation and that with the probe are indeed independent and linearly summated, then interaction with the fixation should be independent of the target-probe distance. Our results are consistent with this prediction. The estimated localization error due to repulsion from the fixation, compared with that from the probe, showed less dependency on the target-probe distance (Fig. 8).

It is possible that there is an interaction between fixation and the probe, because, for a given target eccentricity, the distance between the fixation and the probe in the OS condition is always larger than that in the SS condition. However, for the same fixation-probe distance, the difference in localization error between the OS and SS conditions was consistently observed. For example, consider an OS condition in which the target appears at 6 deg and the probe at 10 deg. And consider a SS condition in which the target appears at 14 deg and the probe at 10 deg. In both conditions, the probe appears at an identical eccentricity (10 deg), and the target-probe distance (4 deg) is identical. When the localization error in Experiment 1 was analyzed for such trials, the error was -0.35 (±0.88) in the OS, and 4.50 (±2.30) in the SS conditions, with a significant difference between these ($t(101) = 17.66$, $p < .001$). This suggests that the interaction between fixation and the probe is negligible.

In addition to the additive model (Fig. 2), many other schemes can also explain the obtained results, but with more assumptions. For example, repulsive interactions between the target representation and fixation and between the target representation and probe may be postulated to become zero in the OS condition to produce little error in localization, whereas they accumulate in the SS condition. Or, a different tendency of overshooting between the OS and SS conditions may be postulated. We believe that given the obtained results, repulsive interactions between the target representation and fixation and between the target representation and probe are the most parsimonious.

Previous localization studies using open-loop arm-pointing in the dark (Bock, 1993; Enright, 1995; Henriques et al, 1998) consistently reported that target eccentricity was overestimated. For example, in the peri-foveal magnification effect of Bock (1993), a visual target presented in the periphery during fixation was localized more peripherally when subjects pointed with their unseen hand, and this suggested that target eccentricity is overestimated. Since arm pointing required no visual stimuli for response, the observed bias is more likely to reflect the underlying interaction between the target representation and fixation. The repulsive interaction between the target representation and fixation in the current study was similar in many aspects to the peri-foveal magnification effect found with arm pointing. First, these effects monotonically increased with target eccentricity up to around 10-15 deg and saturated at that point (Fig. 8A-C of the current study; Bock, 1993; Fig. 6 & 8B of Henriques et al, 1998). Additionally, in the current study, a similar decay of repulsion from the probe beyond a target eccentricity of around 10 deg is thought to accompany the saturation of repulsion from the fixation (Fig. 8) to result in a relatively constant localization error beyond 10 deg of the target eccentricity in the OS condition (Fig. 3). Second, the repulsion coefficient for the fixation, $R_{fixation}$, was 0.15 in the current study, similar to 13.4 - 17% overestimations of the target from fixation (Henriques et al, 1998). The overestimation of target eccentricity is directly explained by the repulsive interaction of the fixation. Repulsion from fixation is also consistent with the attentional repulsion effect in which briefly-presented stimuli appear displaced from the focus of attention, originally described by Suzuki and Cavanagh (1997) and subsequently studied by others (e.g., DiGiacomo & Pratt, 2012; Pratt & Arnott, 2008).

In the study of Eggert et al. (2001), subjects compared the locations of two sequentially presented laser spots on an otherwise dark screen in a two-alternative, forced-choice procedure. Although a quantitative comparison is impossible due to the high dependency of localization bias on a number of parameters, they found overestimation of target eccentricity in egocentric localization conditions (their Experiments 6-8), which can be explained by repulsion from fixation, and a variable pattern of localization with changes in experimental sequences, which is not incompatible with the current study.

The brain 's typical strategy for representing a spatial location is achieved by a spatially-tuned population of neurons within a topographic map, in which adjacent spatial locations are encoded in adjacent anatomical locations. One possible neural mechanism for the repulsive effect of the fixation and probe on spatial representation is the roles of neural activation due to fixation and probe for modification of the profile of population activity representing the target. For example, the late-appearing probe may result in neural activation that overlaps in time with the on-going neural activation from the target, and modifies the latter, resulting in localization bias. The competition for neural representation among multiple objects mediated by suppression of the competing neural activations has been reported (Desimone, 1998), and a similar competition between neural activations representing two sequentially-presented visual targets has been proposed to explain forward and backward visual masking (Keysers & Perrett, 2002). The dependency of the magnitude of localization error on target-probe distance (Fig. 8D, E, and F) is consistent with such a competitive interaction because more competition is predicted when the overlap between the target and probe representations in the spatial map is larger (Mounts & Tomaselli, 2005). The repulsion between the target and probe may be a result of competition between the two representations in spatial localization.

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자기중심적 위치 기억에서 반발 편향

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참조할 수 있는 외부 표지가 없는 상태에서, 잠깐 제시되는 시각표적의 위치를 정확히 보고하는 것은 쉽지 않다. 그런 상태에서는 시선의 방향과 같은 자기중심적 표지에 의존하게 된다. 본 연구는 인간 참가자를 대상으로 자기중심적 위치 기억의 오류의 방향과 크기, 그리고 그 기전을 다루었다. 참가자가 암흑 상태에서 잠깐 보았던 시각표적의 위치에, 이후에 나타나는 탐사자극을 이동시키도록 하였다. 탐사자극을 사용하여 기억된 표적의 위치를 보고하는 행위 자체가 표적의 공간적 위치에 대한 기억을 왜곡함을 발견하였다. 탐사자극을 응시점과 같은 편에 처음 보여주면(SS 조건), 참가자는 탐사자극을 표적이 실제 있던 위치보다 응시점에서 체계적으로 더 멀리 이동시켰고, 탐사자극을 응시점을 기준으로 시각자극이 있던 위치의 반대편에 처음 보여주면(OS 조건), 비교적 정확하게 탐사자극을 표적의 실제 위치로 이동시켰다(실험 1). 탐사자극의 초기 위치에 따라 관찰되는 이러한 비대칭적인 왜곡은, 기억된 위치를 보고하는 동안 시선이 어디를 향하는가에 따라 달라지지 않았으며(실험 2), 위치를 보고하는데 사용한 장치에 따라서도 달라지지 않았다(실험 3). 관찰된 왜곡 패턴은, 지각된 표적의 위치가 탐사자극과 응시점 모두로부터 반발된다는 가정 하에서 예측되는 결과와 일치하였다. 공간적 배열에 따라서, 응시점과 탐사자극으로부터의 반발이 동일한 방향으로 누적되어 표적의 이심도를 실제보다 더 크게 보고하기도 하고(SS 조건), 반대 방향으로 작용하여 서로 상쇄되어 상대적으로 정확한 보고를 하기도 하였다(OS 조건).

주제어 : 안구운동, 공간위치지각, 시각단기기억, 와반발