

Spatial compression: Dissociable effects at the time of saccades and blinks

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Various studies have identified systematic errors, such as spatial compression, when observers report the locations of objects displayed around the time of saccades. Localization errors also occur when holding spatial representations in visual working memory. Such errors, however, have not been examined in the context of eye blinks. In this study, we examined the effects of blinks and saccades when observers reproduced the locations of a set of briefly presented, randomly placed discs. Performance was compared with a fixation-only condition in which observers simply held these representations in working memory for the same duration; this allowed us to elucidate the relationship between the perceptual phenomena related to blinks, saccades, and visual working memory. Our results indicate that the same amount of spatial compression is experienced prior to a blink as is experienced in the control fixation-only condition, suggesting that blinks do not increase compression above that occurring from holding a spatial representation in visual memory. Saccades, however, tend to increase these compression effects and produce translational shifts both toward and away from saccade targets (depending on the time of the saccade onset in relation to the stimulus offset). A higher numerosity recall capacity was also observed when stimuli were presented prior to a blink in comparison with the other conditions. These findings reflect key differences underlying blinks and saccades in terms of spatial compression and translational shifts. Such results suggest that separate mechanisms maintain perceptual stability across these visual events.

Introduction

Our visual system maintains a visually stable percept despite frequent disruptions to the flow of visual input caused by motor events such as eye blinks and high-velocity saccadic eye movements (Burr & Morrone, 2011; Melcher, 2011). Both forms of disruption are accompanied by reductions in contrast sensitivity, called blink suppression and saccadic suppression, that begin before a blink or saccade occurs (Ross, Morrone, Goldberg, & Burr, 2001). This suppression is suggested to promote a stable representation of a scene by preventing the perception of visual information that would produce an unstable experience (e.g., a burst of motion energy during saccades and an absence of external visual information during blinks). The similarity of these perceptual effects makes it plausible that a common mechanism maintains visual stability during both blinks and saccades by modulating perception around the time of these visual disruptions (Ridder & Tomlinson, 1993, 1997; Volkmann, 1986; Watson & Kregelberg, 2009).

As an example of perceptual stability, one does not notice the displacement of a target during a blink or saccade, but one does notice this change when the same magnitude of displacement occurs during a stimulus “blanking” event that lasts for the same duration (Deubel, Bridgeman, & Schneider, 1998, 2004). This suppression of displacement is thought to help maintain visual stability across these disruptions via an active influence on visual processing by the motor

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commands required for saccades (Sylvester, Haynes, & Rees, 2005) and blinks (Bristow, Haynes, Sylvester, Frith, & Rees, 2005). In fact, even intending to blink causes the suppression of target displacement (Higgins, Irwin, Wang, & Thomas, 2009). The similarity of these findings for blinks and saccades suggests that the same processes might be engaged to promote perceptual stability in both cases—indeed, some argue that blink suppression is simply saccadic suppression (Wibbenmeyer, Stern, & Chen, 1983).

A related perisaccadic visual phenomenon is the compression of space (Burr, Ross, Binda, & Morrone, 2010; Lappe, Kuhlmann, Oerke, & Kaiser, 2006; Richard, Churan, Guitton, & Pack, 2009; Ross, Morrone, & Burr, 1997). Studies have shown reductions in the perceived distances between objects presented around the time of a saccade, which are usually observed as a one-dimensional “compression” along the path of the saccade (Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross et al., 1997). For example, when an object is presented 0 to 25 ms before the onset of an approximately 20° saccade, observers mislocalize this object in the direction of the saccade by up to 10° (Ross et al., 1997). While saccadic compression is generally thought of as a compression toward the saccade endpoint, the perceived object locations depend on the timing of the stimulus onset relative to the saccade (Ross et al., 2001) and on the timing and position relative to other objects on the display (Awater & Lappe, 2006). In fact, several studies indicate a perisaccadic compression of visual objects toward each other in two dimensions (Hamker, Zirnsak, Calow, & Lappe, 2008; Kaiser & Lappe, 2004).

This two-dimensional perisaccadic compression is similar to the spatial compression found when reproducing object locations held in visual working memory (Sheth & Shimojo, 2001), which produces other systematic errors that bias memory by increasing the remembered regularity in the spacing between objects (Dent & Smyth, 2006; Huttenlocher, Hedges, & Duncan, 1991; Verbeek & Spetch, 2008). Because scene information is held in visual working memory during saccades (Henderson & Hollingworth, 2003), it is therefore possible that perisaccadic spatial compression is a combination of both compression from holding a spatial representation in working memory and a mislocalization effect caused by the execution of the saccade. Examining this possible relationship, which has not been examined within the context of eye movement studies, was one of the goals of the current study.

Blink and saccadic suppression may be related. Therefore, we wanted to identify whether the pattern of localization errors when participants make downward saccades is similar to that when they blink because visual attention and the eyes tend to move downward when blinking (Irwin, 2011, p. 1374). That is, some

findings indicate that the relationship between blinks and attention is similar to that between eye movements and attention. Although different muscular contractions occur during a saccade than during a blink, which are related to eye contractions rather than high-velocity saccadic movements (Bour, Aramideh, & de Visser, 2000), such eye movements could still produce a similar neural response that triggers the suppression. (If so, this speculation would require further neurophysiological testing.) If blink suppression and saccadic suppression rely on a shared mechanism, then we would expect to find similar spatial compression effects both when blinking and when performing a saccade down and then back up to the starting point because blinks involve a downward eye movement and a return of focus to the initial gaze location. If blinks do not show any compression over and above that caused by simply holding the representation in working memory, however, then we may conclude that suppression and compression are not intrinsically linked and must be caused by at least partially independent processes.

To better understand the visual processes occurring around the time of visual disruptions, the current study examined observers’ spatial representations of randomly positioned objects around the time of blinks and saccades, which were compared with a fixation-only condition in which the representation was held in working memory. This design allowed a within-subject comparison of individuation and localization errors among these conditions using a task developed to test capacity limitations when localizing sets of briefly viewed objects (Haladjian & Pylyshyn, 2011; Haladjian, Singh, Pylyshyn, & Gallistel, 2010). This localization task presents brief, masked stimuli consisting of randomly placed discs and asks observers to remember the locations of these discs and indicate them on a subsequent blank display. This test provides a measure of individuation capacity for the number of objects that can be reported (a numerosity recall measure related to subitizing processes) as well as a measure of spatial memory accuracy. In previous studies, there was little improvement in localization accuracy for presentation durations longer than 200 ms, indicating that spatial information tends to be encoded quickly (Haladjian & Mathy, 2015; Haladjian & Pylyshyn, 2011). There were also systematic errors in reproducing the locations of multiple objects, supporting a nonindependent encoding of object locations, such that observers tend to place objects closer together than they actually were on the stimulus displays (i.e., spatial compression) while also adding more regularity between the spacing of objects (Haladjian et al., 2010).

By using this localization task to test errors around the time of saccades and blinks, we can extend the findings from studies that test this phenomenon on single objects or objects along one spatial dimension (as

has been typically tested) to displays with multiple objects. Because real-world situations often involve attending to multiple objects distributed among multiple dimensions (e.g., when glancing over your shoulder as you prepare to switch lanes when driving), it is important to understand how the visual system treats and possibly misrepresents the locations of multiple objects. Furthermore, this localization paradigm allows us to test the compression that is generally found when reproducing multiple object locations from visual working memory and distinguish these systematic errors from those found around the time of a saccade. More specifically, we can measure localization errors that occur along the trajectory of the eye movement, which can be better described as *translational shifts*, as well as the tendency to place objects closer to each other on two dimensions, which is characteristic of an overall spatial compression.

Material and method

Participants

Five adults (two females, three males) from the University of Western Sydney participated in this study. Three participants were naïve to the study (paid \$20/hr), and two were authors of this article. Each participant completed 10 to 12 sessions until sufficient valid trials (as defined below) were collected. On average, each participant completed 3,300 trials, of which 59.7% were valid (84.8% of fixation-only, 77.0% of blink, 43.6% of saccade-down, and 47.4% of saccade-right trials were valid). Most invalid trials were excluded because of an incomplete gaze event; for example, in the saccade conditions the saccade did not land within the target region (~60% of invalid saccade trials), the return saccade was not made in time (~25%), no saccade was made (~10%), or too many saccades were made to the target region (~5%). In the blink condition, most exclusions were due to the blink not being completed within the required time frame (~40% of invalid blink trials), a saccade being made before the response stage (~31%), too many blinks (~12%), or no blinks made (~10%). A session lasted less than 45 min, and no more than two sessions per day were allowed. Informed consent was obtained from participants under a research protocol approved by the University of Western Sydney Ethics and Human Subjects Committee.

Apparatus

The experiment was programmed using MATLAB version 2011b and Psychophysics Toolbox (Brainard,

1997) on an Apple Mac Pro computer (Apple Inc., Cupertino, CA) with an ATI Radeon HD 5870 graphics card (Advanced Micro Devices, Inc., Sunnyvale, CA). Eye movements were recorded with an EyeLink 1000 desktop eye tracker (SR Research, Ltd., Ontario, Canada) (tracking the left eye at 500 Hz), and data were obtained using the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002). Stimuli were presented on a G520 Trinitron 21-in. cathode ray tube monitor (Sony Corp., Tokyo, Japan) at a resolution of 1280×960 pixels (100 Hz).

Visual stimuli

The initial display was a black background with a gray central fixation cross (0.9° visual angle). Test stimuli consisted of one to five solid gray discs, each 0.9° visual angle and randomly placed within a central $17.6^\circ \times 17.6^\circ$ (600×600 pixels) region of the screen. They were not closer than 4° to the edges of nearby discs (to avoid crowding effects) and never appeared in the location of the central fixation cross. The stimuli were masked with a full-screen random-dot texture created by randomly assigning white or black values to a grid of 4×4 pixel squares.

The saccade target cues were identical to the central fixation cross and appeared either 10° to the right of or 10° below fixation. The target cues indicated the nearest boundary of the acceptable saccade landing areas ($5^\circ \times 5^\circ$ regions), which were beyond the stimulus disc display region. After making the first saccade, participants were required to immediately return their gaze to the center of the screen ($10^\circ \times 10^\circ$ central region).

Procedure

Participants sat 61 cm from the screen in a dimly lit room and used a chin rest to control the viewing distance. The eye tracker was recalibrated before each of the four blocks (one for each eye gaze condition).

Each trial began with a black screen with a gray central fixation cross for at least 2500 ms. Stimulus onset was gaze contingent, requiring the participant to fixate within a $2.6^\circ \times 2.6^\circ$ region around the central fixation for 1000 ms. For the saccade gaze conditions, a second cue would also appear during this fixation period to indicate the target region for the eye movement. Only one type of gaze condition was administered in a test block due to the difficulty of switching between different eye movements on a trial-by-trial basis. Because we did not find practice effects for this localization task in previous studies, we fixed the order of block presentation (as follows).

First, in the fixation-only (control) condition, only the central fixation would appear. Participants were instructed to fix their gaze (within an $\sim 1.5^\circ$ radius region) upon the central fixation throughout the trial (even after its disappearance) until the response stage began after the 800-ms mask. Valid trials required that no saccades occurred before or during the stimulus and mask presentations. Microsaccades (liberally defined at $< 2^\circ$) within this region were allowed.

In the blink condition, participants were required to perform a single blink as soon as the central fixation disappeared. Stimulus onset was timed such that it would appear immediately before the blink actually started (due to the lag between the initiation of the blink and its motor execution). A trial was considered valid if a single blink was performed after the stimulus presentation and if no saccades were made around the stimulus and mask presentations (microsaccades were allowed). After completing a blink, participants were required to return their gaze to a $10^\circ \times 10^\circ$ central region.

Next, in the saccade-down and then saccade-right conditions, another cross was presented 10° below or 10° to the right of the central fixation cross during the initial screen. Participants were instructed to saccade to this cue location as soon as the two fixation crosses disappeared. After making a saccade to the target region, participants had to return their gaze to the central region. A saccade trial was valid if a single saccade was made to the target region and if the participant's gaze returned to the central region before the response stage; the number of saccades made for the return to the central region was not restricted. Microsaccades were allowed after the initial saccade to the target region. We required the eyes to return to the center of the display before the response stage in the saccade conditions because we did not want the final fixation location to bias stimulus localization responses—that is, we did not want localization differences between the saccade conditions and the fixation-only or blink conditions to be caused by the eye fixating at the different saccade target region versus the center of the screen. Thus, all responses that were included in the analyses begin with the eye around the center of the display.

After the gaze cue and before participants executed the blink or saccade, the stimulus with one to five discs was displayed for 30 ms. The stimulus appeared approximately 100 to 150 ms after cue offset in the saccade and blink conditions in order to allow time for the preparation of the saccade or blink. After the stimulus offset, the gaze events started after motor delays of approximately 55 ms for blinks, 49 ms for downward saccades, and 46 ms for rightward saccades. The exact delay duration used was optimized for each participant so that stimulus offset was more likely to

occur within 50 ms before gaze event onset. In the fixation-only condition, this delay was set to 150 ms to approximate the maximum delay of the other conditions. The stimulus was followed by a 10-ms black screen and then an 800-ms full-screen mask. This mask was included to reduce possible interference from afterimages and to control how long the stimulus appeared on the test display. The long duration of the mask ensured that it was visible for some time after the saccade or blink was made, particularly because the saccade conditions required two eye movements: from central fixation to saccade target and then back to the central region, which took more time to complete. On average, the gaze events were completed in approximately 230 ms for blinks, 550 ms for downward saccades (which included an 88-ms saccade to the target region, 389 ms of dwell time, and a 73-ms saccade back to central fixation), and 541 ms for rightward saccades (which included a 72-ms saccade to the target region, 408 ms of dwell time, and a 61-ms saccade back to central fixation). The participants were required to return their gaze back to the central region of the screen in order for a trial to be considered valid. In the blink and saccade conditions, participants viewed the mask for 363 ms on average—longer for blinks (589 ms on average) and shorter for saccade-down (245 ms) and saccade-right (237 ms) trials. The mask was visible for 800 ms in the fixation-only condition.

After the mask, a gray “X” cursor appeared in the center of a black screen. Participants used the mouse to place markers (identical to the stimulus discs) at the recalled location of each disc; a placed marker could be removed by clicking on it (e.g., if the participant made a mistake). There were no restrictions on eye movements during the response stage. After the participants finished marking the disc locations, they right-clicked the mouse to initiate the next trial (which began after a 500-ms blank screen). No feedback on performance was given. See Figure 1 for a schematic of a trial in this experiment.

In a single testing session, participants completed 300 trials with 15 repeats of each of the 20 unique test conditions ($5 \text{ numerosities} \times 4 \text{ gaze conditions}$). These stimuli were generated and checked prior to data collection by one of the authors. Each participant completed a practice session (to determine individual saccade and blink latencies) and 10 to 12 test sessions in order to collect approximately 40 valid trials per condition. Also, a baseline block was completed to provide a measure of the magnitude of errors that each participant typically made within the five numerosity conditions for six mask contrast levels—ranging from no mask (0%) to the full contrast mask (100%) used in the main blocks—with 20 repetitions per condition (600 trials total). This allowed us to compare the test blocks with a baseline fixation-only condition with different levels of masking and helped confirm that any

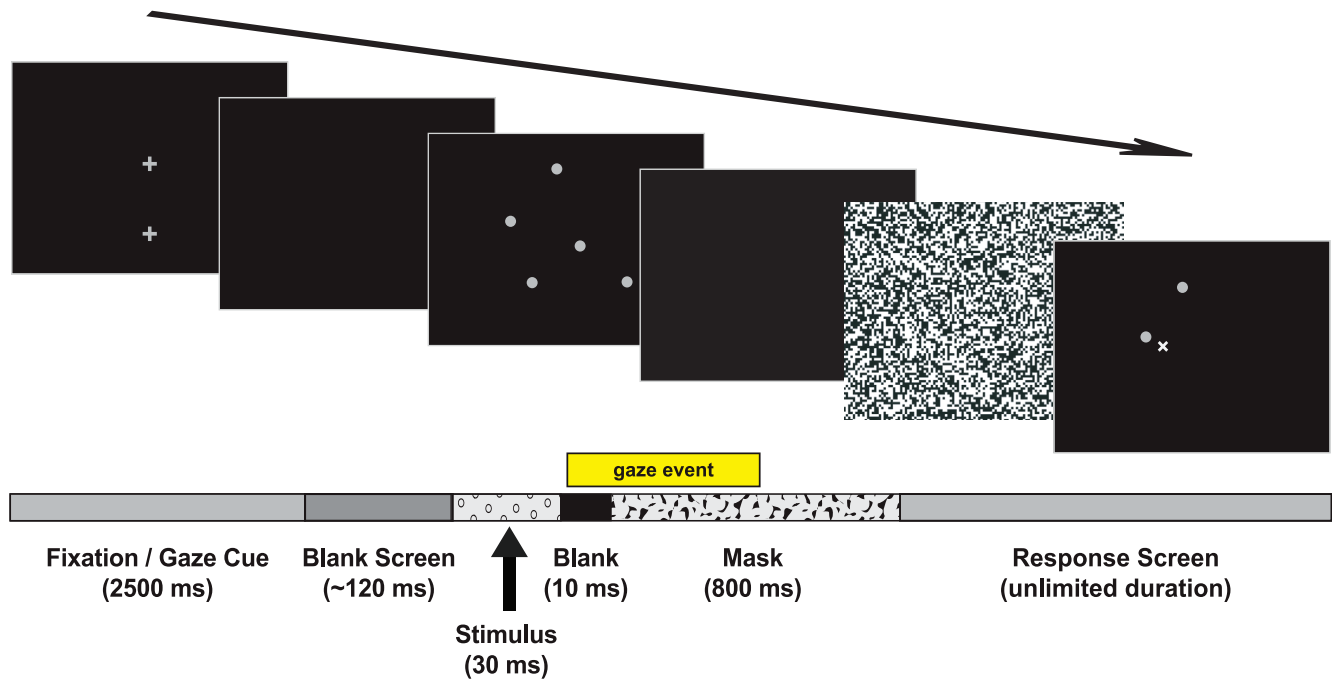


Figure 1. Schematic of the experimental design. The cue to make a saccade or blink was the visual disappearance of the fixation cross(es) shown on the first panel; the disappearance was gaze contingent, occurring after the participant fixated at the central fixation for longer than 1000 ms. This gaze cue was followed by a blank screen (120 ms on average) and then the stimulus (30 ms). The duration of this blank screen was optimized for each participant such that the stimulus would appear and disappear immediately before the saccade or blink began (to compensate for eye-related motor command lags). After the stimulus, a black screen appeared for 10 ms, followed by the random-dot mask for 800 ms. Finally, an empty response screen appeared with an “X” cursor at the center of the screen, and the participant used the mouse to place markers indicating the perceived locations of the stimulus discs.

differences in performance between fixation-only and saccade or blink conditions were due to the gaze events and did not occur simply because the mask was being suppressed during blinks and saccades. Furthermore, this baseline demonstrates the effectiveness of the mask at different levels of contrast strength, which is not affected by the duration that the participant is exposed to the mask—an important clarification because mask visibility is longer in the fixation-only condition than in the blink or saccade conditions. Overall, the results from trials using any level of masking contrast greater than 0% were similar to those of our previous studies that presented a shorter mask of 85 ms (e.g., Haladjian & Pylyshyn, 2011).

Analyses

We report both the numerosity recall accuracy and the localization accuracy. To determine numerosity recall accuracy, we compared the number of responses with the number of stimulus discs in a trial and computed the proportion of trials with the correct number of responses.

The overall localization error was determined by matching each response to a unique stimulus disc in

each trial, and the distance between these matched pairs was analyzed (procedure described in Haladjian & Pylyshyn, 2011; Haladjian et al., 2010). To improve this pairing process, first the response data were fit to the stimulus data using Procrustes transformation methods in MATLAB. This applies uniform scaling, translation, and rotation to the response coordinates to best fit the shape of the stimulus coordinates for each trial. Then, response–stimulus pairs were determined using nearest-neighbor methods (with Delaunay triangulation). Any nonunique pairings were corrected such that only one response was paired with one stimulus disc. This procedure resulted in matches for 96.2% of stimulus discs, with 84.4% of trials having all stimulus discs matched to a response. (This latter percentage is smaller because some trials did not have the correct number of responses.) To avoid reporting results from any possible incorrect pairings, only these correct trials were used in the localization analyses, although the pattern of results does not change when all trials are analyzed. Note that the original distances between the stimulus–response pairs, not the transformed distances that were computed for the matching procedure, were used for the analyses. See Appendix Figure A1 for examples of localization data from single trials.

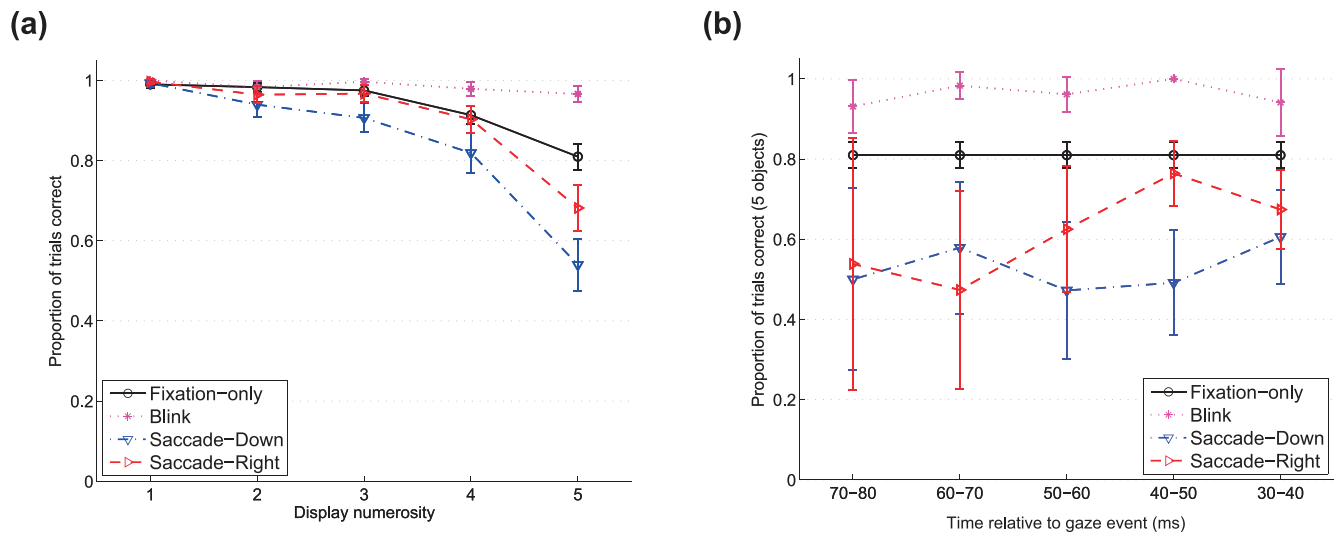


Figure 2. Numerosity recall accuracy. The proportion of valid gaze trials with the correct number of responses by gaze condition as (a) a function of display numerosity and (b) a function of the time course between the onset of the stimulus and the beginning of the saccade or blink for five-disc displays only. Note that there were insufficient data points for plotting results within the 10- to 30-ms time course. Because the fixation-only condition had no time course, the average performance is plotted only to provide a general comparison. Error bars represent 95% confidence intervals in all figures.

These measures were analyzed using within-subject analysis of variance (ANOVA; 5 numerosity conditions \times 4 gaze conditions), with subject identification included as a random variable to account for between-subjects variability. Any comparisons between conditions were adjusted for multiple comparisons using the Scheffé method. All error bars on figures represent 95% confidence intervals.

Results

Numerosity recall accuracy

Here we report the proportion of trials in which participants made the correct number of responses. Figure 2a shows the numerosity recall accuracy for all trials with valid gaze behavior and in which the saccade or blink began within 30 to 80 ms after the onset of the stimulus (i.e., 0–50 ms after the offset of the stimulus) because this was the target period for executing the gaze event based on the results from previous studies. The ANOVA results revealed a main effect for gaze condition, $F(3, 6770) = 4.42$, $p = 0.03$, MS (mean squared error) = 5.1, and for numerosity, $F(4, 6770) = 12.61$, $p < 0.001$, MS = 12.8, with an interaction, $F(12, 6770) = 26.43$, $p < 0.001$, MS = 1.4. Separate ANOVA were run for each numerosity condition to identify which gaze conditions were significantly different from each other. The most important finding from this analysis is that the blink condition was significantly

better than the fixation-only and both saccade conditions for displays with four and five discs ($ps < 0.05$).

Figure 2b shows the recall accuracy for the five-disc displays as a function of the time separation between the offset of the stimulus and the start of the saccade or blink. We present results only from the five-disc displays because this numerosity exhibits the strongest effect of gaze condition (i.e., all gaze conditions were significantly different from each other for five-disc displays). Nevertheless, there is no effect of time course on enumeration accuracy in this analysis. (See Figure A2 for additional breakdowns of time course effects on numerosity recall accuracy and Table A1 for the number of trials per bin that were in the time-course analysis for this and all subsequent figures broken down by time course.)

Localization accuracy

These analyses characterize the magnitude and direction of localization errors and identify differences in the type of errors among the gaze conditions. We believed that there might be two ways in which the stimuli could be mislocalized: as a compression among the objects toward each other (spatial compression) and as a mislocalization along the trajectory of the saccade (translational shifts; horizontal for saccade-right or vertical for both saccade-down and blink conditions).

Prior to looking at compressions and translation separately, the average distance between a stimulus disc and its paired response and the global patterns of localization errors were examined. Figure 3 shows that, on average, overall localization errors for blinks and

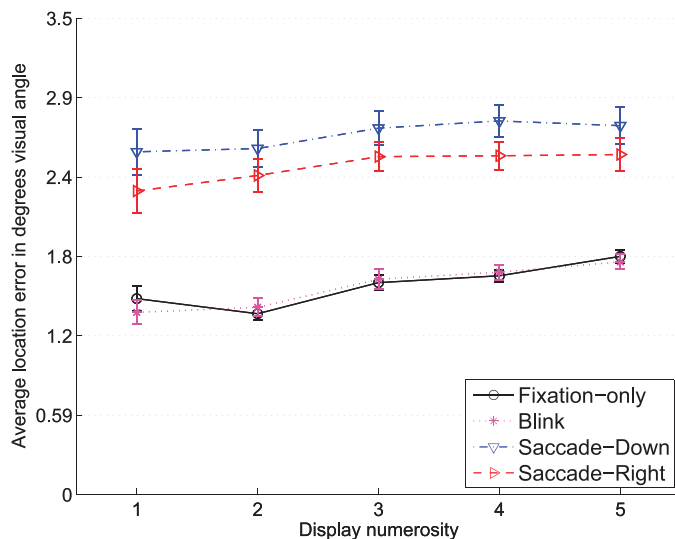


Figure 3. Overall localization errors. The average distance between a stimulus disc and its paired response as a function of numerosity by gaze condition (for valid trials with blink or saccade occurring within 50 ms of stimulus offset). Pixels are indicated on the left y-axis, and degrees of visual angle are indicated on the right y-axis.

fixation-only conditions were nearly identical, with worse performance in saccade conditions, particularly saccade down. Localization errors also tended to increase with display numerosity, but only significantly in the blink and fixation-only conditions. For the average magnitude of localization error in valid trials, the ANOVA indicated a main effect for gaze condition, $F(3, 6033) = 34.59$, $p < 0.001$, $MS = 529300.5$, and for numerosity, $F(4, 6033) = 18.27$, $p < 0.001$, $MS = 25854.4$, but no interaction, $F(12, 6033) = 0.89$, $p = 0.56$, $MS = 752.2$.

Figure 4 provides an overview of the direction of localization errors by region (broken down by time course). This illustrates how localization was affected by the original location of the stimulus disc in relation to the fixation and saccade endpoint. In this figure, the overall compression, or bias, toward the central region of the screen is evident. Also, a translational shift along the trajectory of the saccade path is evident. This translation effect was especially sensitive to the time when the saccade began in relation to the offset of the stimulus. These effects are discussed in more detail in the following sections. For our subsequent analyses it is important to note that spatial localization in the blink condition does not show a pattern that would be consistent with the participant having made a small downward saccade. The rows closest to the center of the screen (i.e., the fixation cross depicted on the figures) do not show a stronger mislocalization than the outermost rows or than the same row in the fixation condition, as would be expected if the blink condition

were equivalent to the participant making a small downward saccade. We are therefore encouraged that the averaging procedure used in the subsequent analyses did not act to reduce any translation or compression effect found in the blink condition.

Spatial compression effects

To compute our measure of spatial compression, we compared (for each trial separately) the distances of stimulus discs to the stimulus centroid and the distances of responses to the response centroid. To do this, we calculated for each trial the centroid (center of mass) on the stimulus displays and the centroid of the responses. Then we calculated the average distance of each stimulus disc from the stimulus centroid on a display (stimulus-to-centroid distance) as well as the average distance of each response from the response centroid for that display (response-to-centroid distance). The difference between these two distances was our compression measure (Figure 5a). Smaller response-to-centroid distances in comparison with stimulus-to-centroid distances indicate compression toward the centroid in the participant's responses for that trial. All trials with the correct number of responses were used in this analysis. (Note that this measure cannot be computed for one-disc displays.)

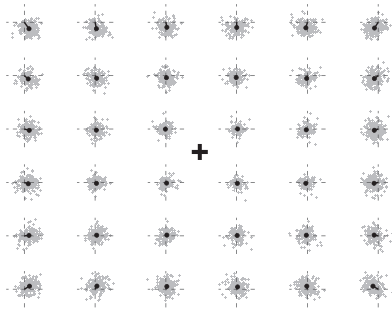
An ANOVA on this compression measure indicated a main effect for gaze condition, $F(3, 11608) = 4.89$, $p = 0.05$, $MS = 211796.5$, but not for numerosity, $F(3, 11608) = 1.47$, $p = 0.34$, $MS = 66387.3$, and no interaction, $F(9, 11608) = 0.21$, $p = 0.98$, $MS = 752.2$. We see greater overall compression for saccade trials compared with blink and fixation-only trials and slightly less compression for blink trials relative to fixation-only trials.

Separate ANOVA (Scheffé adjusted) were run for each numerosity condition to identify which gaze conditions were significant from each other. The fixation-only and blink conditions showed a similar amount of lower compression compared with the saccade conditions for all numerosities except five-disc displays, where the blink condition had less compression than all the other conditions ($ps < 0.05$).

Figure 5b plots the time course of the compression measure for displays with two to five discs. (The data were combined because there was no effect of number of discs or an interaction.) As the figure suggests, the analysis indicated no reliable effect of temporal delay between the stimulus presentation and the onset of the gaze event.

This compression measure was also computed using the central fixation instead of the centroid, and the results indicate similar trends in performance, with a slightly higher magnitude of compression in all conditions. We present results from only the compres-

(a) Fixation-only

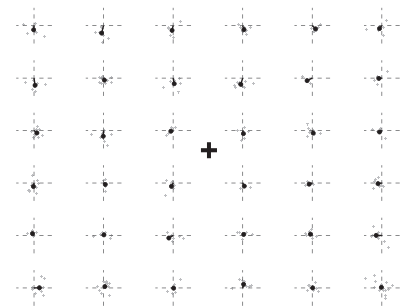
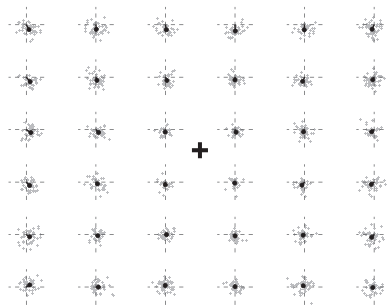
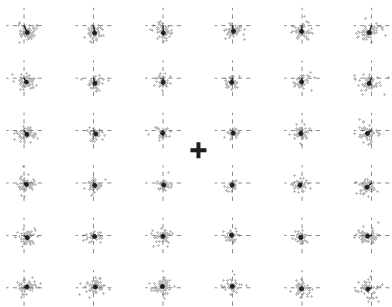


(b) Blink

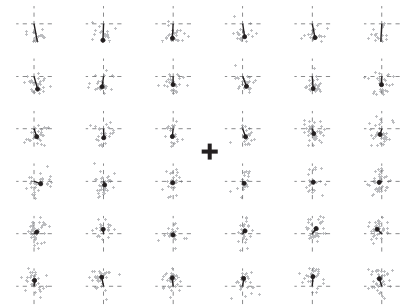
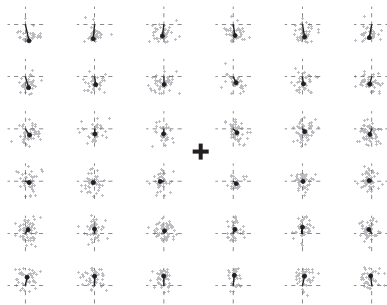
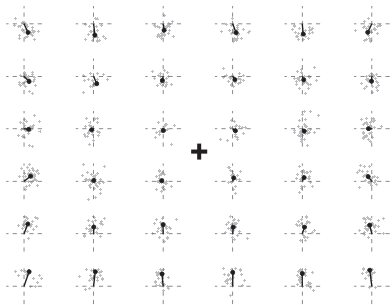
50–70 ms

30–50 ms

10–30 ms



(c) Saccade-down



(d) Saccade-right

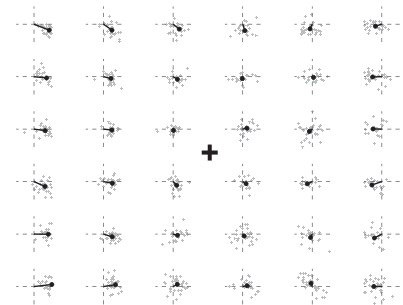
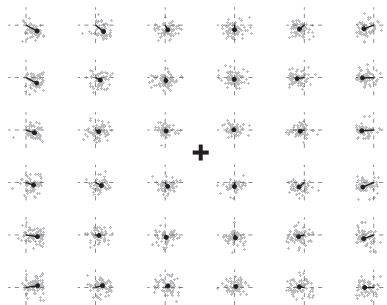
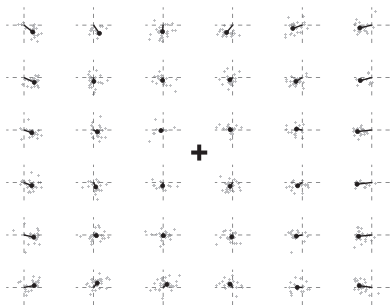


Figure 4. Average localization error by region. This represents the average localization error direction of targets placed within different regions on the screen by time course. For each gaze condition, the stimulus display was divided into a 6×6 grid (600×600 pixels, or $17.6^\circ \times 17.6^\circ$). Each subplot represents the average localization for stimulus discs appearing in each section of this grid; these were further divided into time course. The small gray “+” signs represent a response in relation to the paired stimulus disc location, and

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the average localization error is marked with a circle. The line connecting the circle to the center of each subplot illustrates the direction and magnitude of localization errors. The bold cross at the center of each subplot represents the central fixation cross on the stimulus displays.

sion measure based on the centroids because this measure is a better reflection of the relationship among the disc locations; because the stimuli discs were not necessarily centered around the fixation cross, using the screen center as the reference point tends to exaggerate the compression effect.

Translational shift effects

Because previous studies have shown that compression-like localization errors occur along the trajectory of a saccade, Figure 6 separately plots the average horizontal (Figure 6a) and vertical (Figure 6b) localization errors as a function of the time course of the saccade or blink (in relation to the onset of the stimulus). Negative values on the y-axis in Figure 6a indicate that there is a stronger overall rightward shift in localization errors, which represents a shift toward the first saccade target in the saccade-right condition. Negative values on the y-axis in Figure 6b indicate a stronger overall downward shift in localization errors, representing a shift toward the first saccade target in the saccade-down condition. As these figures show, when the saccade is made during stimulus presentation

(indicated by the shaded region on the graphs), there is a shift toward the first saccade target; this effect could be related to a “smearing” of the stimulus because it is present during part of the saccade. When the saccade is made >10 ms after the offset of the stimulus, the shift reverses in the direction of the second saccade that returns gaze to the center of the screen. Both blink and fixation conditions show no horizontal bias in localization, but they do show a small downward bias reflecting a general tendency to place the discs lower than they appeared in the stimulus. These errors are also evident in Figure 4, where the average localization error is separated by different regions of the display. See Figures A3 and A4 for overall response distributions. (Note that when examining these results for one-disc displays only, we get the same trend in performance. We report all numerosity conditions together because this shift appears to be uniform.)

Follow-up experiment

We conducted a follow-up experiment to determine whether the differences between the saccade-down and

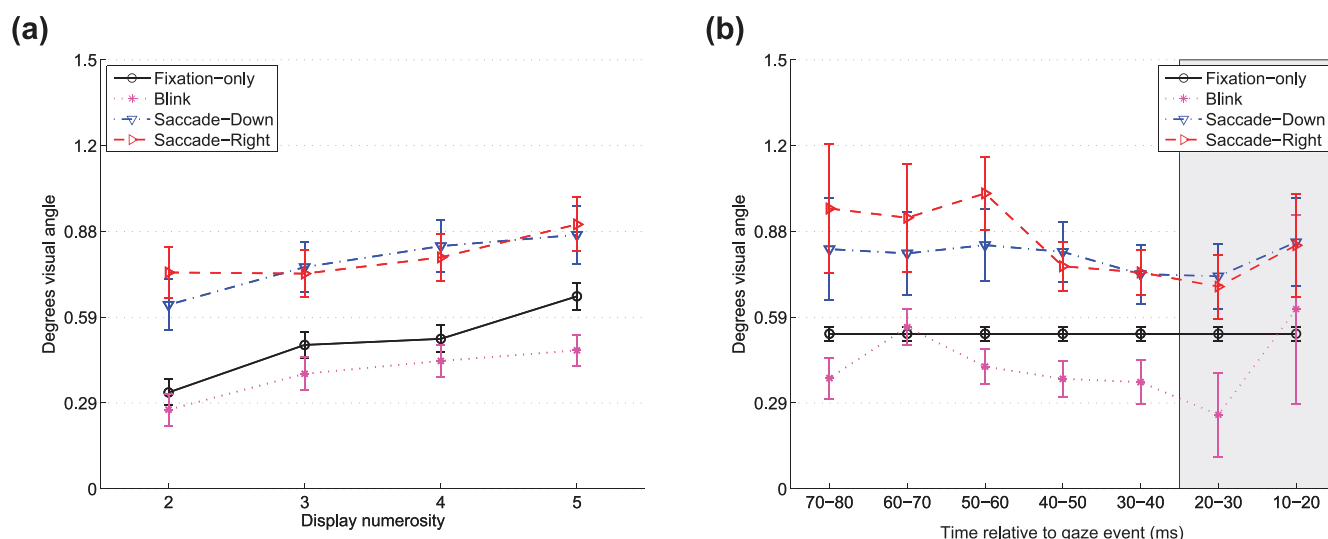


Figure 5. Compression effects. (a) The overall magnitude of compression based on the average stimulus-to-centroid distance minus the response-to-centroid distance for each valid trial (includes 10- to 80-ms time course), and (b) this compression measure as a function of the time course by gaze condition (numerosities two to five combined, with overall average performance in the fixation-only condition plotted for reference because there is no time course in that condition). Higher values on the y-axis indicate greater compression around the centroid in participant responses. These plots show higher compression in saccade conditions, with no reliable effect of time course.

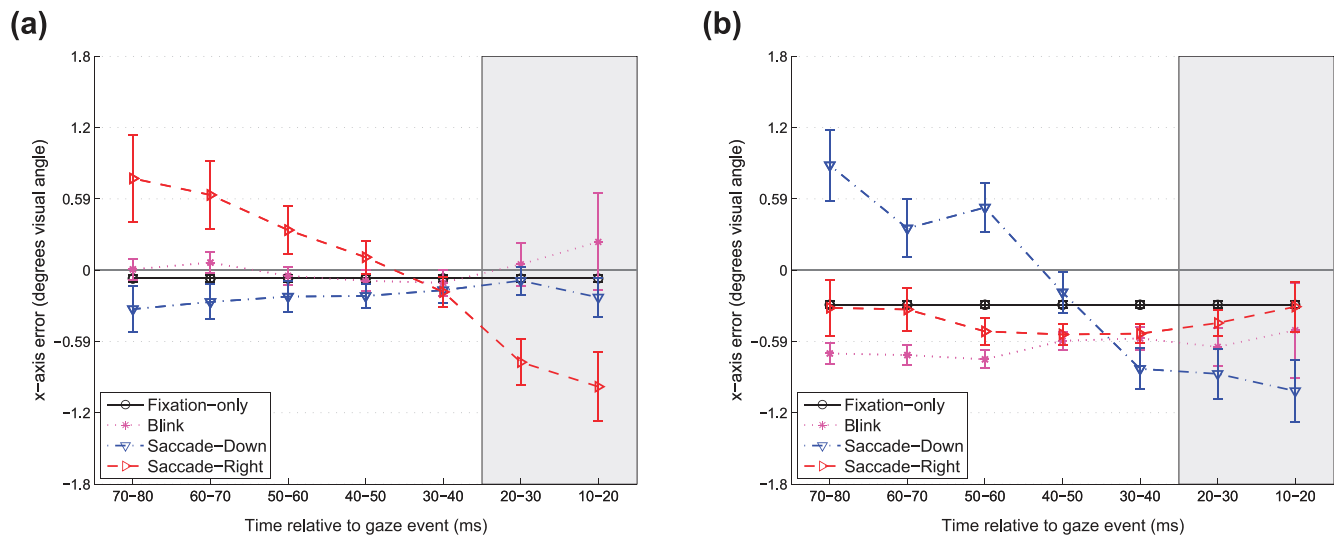


Figure 6. Time course of translational shifts. These panels plot the time course of directional errors along a saccade's trajectory on the (a) horizontal and (b) vertical dimensions by gaze condition (valid trials, all numerosities combined). The stimulus appeared from 0 to 30 ms, followed by the mask at 40 ms (stimulus presence indicated by the shaded region; 0–10 ms data omitted due to few instances within this range). Negative values on the y-axis in panel a indicate a rightward shift in localization errors, which represents a shift toward the first saccade target in the saccade-right condition. Negative values on the y-axis in panel b indicate a downward shift in localization errors, representing a shift toward the first saccade target in the saccade-down condition.

blink conditions were due to the different nature of the cues on the fixation displays. On the fixation screens for the saccade-down condition reported above, a fixation cross was presented on the bottom region of the display during the initial fixation screen to cue participants where to make an eye movement in that condition. The blink condition had no such cues. The presence of such targets has been shown to increase the spatial compression and the translation effects (Cicchini, Binda, Burr, & Morrone, 2013; Lappe et al., 2000), which we did not find in the blink condition. Furthermore, because studies show that constantly visible landmarks indicating the location of the saccade endpoint tend to play an important role in creating a translational compression effect even without making a saccade (e.g., Atsma, Maij, Corneil, & Medendorp, 2014; Zimmermann, Born, Fink, & Cavanagh, 2014; Zimmermann, Fink, & Cavanagh, 2013), we wanted to confirm that the difference in performance between our blink and saccade conditions was not due to the absence of saccade target landmarks in the design of the first experiment.

In this follow-up experiment, we presented the saccade cues for all saccade regions during the initial and poststimulus displays in all four gaze conditions. These stimuli were not masked so that the saccade cues remained visible throughout the fixation and stimulus presentation durations and disappeared only during the response stage (i.e., after the gaze event was completed). This design helped us determine whether the presence of constant saccade cues affected the system-

atic localization errors we observed in the first experiment. Otherwise, the procedure was identical in the two experiments. Three participants from the first experiment (two females, one male) completed this experiment; one was paid \$20/hr. On average, the participants each completed 3,215 trials, of which 68.2% were valid (91.5% of fixation-only, 79.2% of blink, 53.4% of saccade-down, and 64.6% of saccade-right trials were valid).

Not surprisingly, numerosity recall was near perfect in this experiment, with the only substantial decrease in the proportion of correct trials occurring for both saccade conditions on four-disc displays (~93% accuracy) and five-disc displays (~80% accuracy). Overall, localization performance in this experiment did not differ from that in the original experiment. As found in previous studies using a constant appearance of landmarks (i.e., saccade targets), we found an effect of the translation toward and away from the saccade target. This was similar in trend as in the first experiment but at a slightly greater magnitude for trials in which the onset of the saccade occurred during the stimulus presentation (i.e., the 10- to 30-ms time course), which may be related to the smearing effect mentioned earlier. This stronger magnitude of compression is closer to the usual range of perisaccadic mislocalization identified in previous studies (e.g., Burr et al., 2010; Lappe et al., 2000). The two-dimensional spatial compression effects, however, were not enhanced in this version and were slightly lower. (See Appendix Figure A6 for the figures representing the

localization, compression, and translational shifts in this follow-up experiment.) These results further suggest that spatial compression effects are distinct from translational shift effects and highlight the mislocalization pattern differences between the blink and saccade conditions, even when the stimuli were not masked and constant landmarks were present on the screen in all four test conditions.

Discussion

In this study, we found several effects related to the differences between the visual processes around the time of saccades and blinks as well as those related to working memory. First, when asked to recall the locations of five discs presented just before an eye gaze event, participants were significantly worse at placing the correct number of discs on the screen when the gaze event was a saccade and significantly better when the event was a blink (compared with the fixation-only control condition). This result contrasts with previous studies that found localization and iconic memory interference when a blink was made immediately after stimulus presentation (Irwin, 2014; Thomas & Irwin, 2006). This effect was not observed for smaller numerosity displays, which suggests that blinks may aid the individuation process when the capacity of the individuation mechanism is exceeded. This capacity limit has been reported in previous studies (e.g., Trick & Pylyshyn, 1994) to be approximately four objects, similar to the performance observed in our current study.

Second, overall localization errors (in any direction) were greater when the stimulus was presented prior to a saccade, whereas localization errors around a blink were the same as those found in the fixation-only control condition. This was true even in the follow-up experiment that presented constant landmarks on the screen without masking the stimuli. These localization errors can be broken down into compression effects and translational shift effects. For both types of effects, blinks were comparable to the fixation-only condition and showed no relationship to the time delay between the onsets of the stimulus and the blink, suggesting that no additional forms of localization errors occurred as a result of executing a blink. Both effects, however, did occur around the time of a saccade. Here, two-dimensional spatial compression showed little dependency on the timing of the stimulus appearance relative to a saccade and was consistently greater than in the blink and fixation-only conditions. The translation effects, however, showed a clear dependency on the relative time between the stimulus and the first saccade onset such that saccades that started during the

stimulus produced a translation toward the first saccade endpoint, whereas saccades after the stimulus offset produced a translation toward the second saccade endpoint. We discuss the implications of each effect in turn.

Greater numerosity recall accuracy around a blink

The observed greater numerosity recall accuracy around a blink could have two causes. The first possibility is that the mask was less efficacious because its onset was occluded by the eyelid for the duration of the blink. The second is that this information was held with higher fidelity across a blink. To rule out the first explanation, we examined the time course of this effect. The mask appeared 10 ms after stimulus offset; therefore, accuracy data during the 30- to 40-ms time window depicted in Figure 2b (i.e., 30–40 ms after the onset of the stimulus) reflects cases in which the onset of the mask occurs during the blink. At the 70- to 80-ms data point in Figure 2b, the mask was visible before the blink for approximately the same duration as the stimulus itself. In this time window, it could be the case that the mask was also reduced in effectiveness by blink suppression. Separate baseline results, however, show that even a low 44% contrast mask presented in fixation-only trials achieved a masking equivalent to that of a 100% contrast mask (see Figure A5). This indicates that the strength or visibility of the mask did not contribute to the difference in performance found between the blink and saccade conditions. Furthermore, even when the stimuli were not masked, we get the same trend in differences between the blink and saccade conditions. Therefore, the accuracy achieved by participants when the stimulus was presented prior to a blink is not an artifact created by a reduction in the strength of the mask but rather is a feature of the blink itself. Furthermore, the relatively poor performance prior to a saccade beginning in the same time window, where the mask should be suppressed by saccadic suppression, highlights the surprisingly good performance found in the blink condition (particularly because participants viewed the mask for an average of 589 ms after a blink was completed in our main experiment).

These results suggest that despite blink contrast suppression, certain kinds of visual information (i.e., the number of items in our stimuli) were retained with higher fidelity across blinks than across saccades and, more importantly, than in fixation-only (control) trials. Given that other aspects of a visual scene are identified less accurately after a blink—for example, a displacement is not perceived if it happens during a blink (Higgins et al., 2009), and the color and orientation of

specific elements are poorly remembered (Irwin, 2014)—our findings suggest that the existence of individuated landmarks is actively well preserved through visual disruptions but that their exact location and other identifying details are not. Blinks seem to uniquely aid perceptual stability by allowing the approximate matching of pre- and post-blink scenery, which minimizes the disturbance caused by errors in returning the eye to the same location after blinks or by minor changes in object locations during blinks. This speculation is in line with the idea that blinks may serve to disengage attention from external objects and act as an attentional reset at points of transition in the external input (Fogarty & Stern, 1989; Nakano, Kato, Morito, Itoi, & Kitazawa, 2013). If this were the case, the visual scene may be maintained in an “unbound” state during a blink. That is, the individual features of each object in the scene (e.g., location, color, orientation) are not linked together such that they represent a complete object; rather, they remain separate aspects of neural responses to each location in retinotopic space (Crick & Koch, 1990). The presence of individual objects seems to be available within the visual system across a blink, but reporting fidelity may be compromised in the face of specific external interference (e.g., an object changes color during the blink). This ability appears to be related to the visual indexing mechanism (Pylyshyn, 1989, 2001), which is thought to guide attention by individuating and “pointing to” a limited number of visual objects.

Spatial compression before a blink

The above hypothesis is also supported by the finding that localization errors around the time of a blink were indistinguishable from those found in the fixation-only condition (see Figures 3 and A6i), whereas saccades promoted larger compression and translation effects. This effect was also observed in our follow-up experiment using unmasked stimuli, where landmarks indicating the saccade targets were visible during and after the period where the gaze event occurred in all conditions. This finding, however, implies that blink suppression—which has been proposed to recruit the same mechanism as saccadic suppression—is unaccompanied by blink-related spatial compression despite blinks causing a downward movement of the eyes and attention (Irwin, 2011). This difference is likely due to the different muscular contractions that occur during blinks in contrast to those made during saccades (Bour et al., 2000). Therefore, the possibility that blink suppression and saccadic suppression are triggered by the same neural signals from downward eye movements is not evident in our experiment.

This in turn suggests two further possibilities. First, the perceptual effects experienced around blinks may be separate from the effects experienced around the time of saccades, with each caused by distinct neural mechanisms despite similarities in perceptual effects. Alternatively, if saccadic and blink suppression are indeed caused by a common mechanism (see Wibbenmeyer et al., 1983), then the lack of greater spatial compression around the time of a blink compared with the working memory (control) condition implies that saccadic suppression and saccadic compression are caused by dissociable and independent mechanisms.

Our results appear to refute the idea that both saccadic suppression and saccadic compression are byproducts of the mechanism responsible for reallocating attention to the location of the saccade target prior to executing the saccade, as could be the case in the saccadic compression model proposed by Hamker et al. (2008). This is because blink suppression (which has been likened to saccadic suppression) should have been accompanied by appreciable spatial compression if these two effects were generated by one neural mechanism. Instead, it appears that suppression and compression are driven by separable mechanisms and that blink and saccadic suppression are likely important contributors to perceptual stability in their own right. Although our current data do not directly differentiate the suppression and compression effects prior to a saccade, the nonexistence of blink compression beyond that usually occurring in visual working memory (as found in our fixation-only condition) warrants further research to differentiate the two effects in order to better understand perisaccadic visual processing.

Perisaccadic spatial compression versus spatial translation

We found both compression and translation components to the localization errors around both horizontal and vertical saccades, as did Kaiser and Lappe (2004). These components also showed relative differences in their time courses. Spatial compression is less determined by the relative timing of saccade and stimulus onset than are translational shifts. Because the observed saccadic compression was only slightly greater than the visual memory compression (fixation-only condition), the lack of temporal modulation of the two-dimensional compression effect could be due to the involvement of visual memory. Scene information is held in visual memory during a saccade (Henderson & Hollingworth, 2003), which is susceptible to spatial compression (Sheth & Shimojo, 2001). Any time-sensitive compressive effect around a saccade could be combined with (and possibly overshadowed by) the

working memory effect to create a flatter temporal profile—a possibility that warrants further testing. Furthermore, the constant presence of visible saccade target landmarks during this stimulus presentation and gaze event tended to reduce the two-dimensional spatial compression effect in this localization task.

The translation effect, however, was clearly modulated by the relationship between stimulus offset and the first saccade onset. A spatial translation in the direction of the first saccade endpoint was observed when the saccade began during the stimulus. When the first saccade onset began after the stimulus offset, but prior to the mask appearing, there was a smaller effect of translational error. When the first saccade began after the stimulus and during the mask, that translation shifted in the direction of the second saccade (similar to Lavergne, Dore-Mazars, Lappe, Lemoine, & Vergilino-Perez, 2012). We replicated these results in a follow-up experiment in which no mask was used and saccade target landmarks were visible during the gaze event period, which is thought to enhance the compression effect (Cicchini et al., 2013; Lappe et al., 2000). In this follow-up experiment, the visibility of the saccade target cues did in fact increase the translational shift effect when the saccade began while the stimuli were still present on the screen (possibly due to an increased “smearing” effect when no mask was present) but did not increase the spatial compression effect. This suggests that translation effects are more sensitive to such landmarks than overall compression that tends to occur in spatial memory.

These results can be interpreted in light of a number of models describing different neural mechanisms for characterizing perisaccadic spatial effects (see Hamker, Zirnsak, Ziesche, & Lappe, 2011, for a discussion of saccadic compression models). For example, Lavergne et al. (2012) suggested that the mislocalization of stimuli presented prior to the first of a two-step saccade sequence is caused by the interaction of the processing of the visual stimulus and motor commands related to saccade planning as opposed to saccade execution. They also proposed that both saccades are planned in parallel. This is consistent with our finding that the perceived disc locations are in the direction of the second saccade when the stimulus is presented and masked well before saccade onset, thus avoiding any smearing of the stimulus. Here, the localization effects are likely acting on the stimulus representation now held in visual working memory rather than on an unmasked retinal input. That this effect is biased toward the ultimate saccade endpoint suggests that it is driven by the planning of the complete saccadic sequence (Lavergne et al., 2012). In our experiment, however, despite two saccades having been planned, when the first saccade started while the stimulus was visible, it appears as though the ongoing processing of

the physical stimulus was subject to a stronger effect related to executing the current saccade rather than the planning of the entire saccadic sequence (which drives localization errors toward the second saccade endpoint). This observed reversal of the effect is more consistent with the interaction of a persistent retinal signal and an extraretinal eye position signal that updates through the eye movement—for example, as described by the retinal–extraretinal signal interaction model (Pola, 2004, 2007, 2011).

The smooth transition from a shift toward the first saccade endpoint to a shift toward the second suggests competing mechanisms related to the requirements of localizing stimuli across two saccades. At larger delays between stimulus and saccade, the overall motor plan is predominant in causing spatial shifts. As the onset of the first saccade approaches, however, motor signals relating to the actual execution of the current saccade may increasingly affect the localization judgment. Similarly, recent modeling of spatial updating around two-saccade sequences suggests that various motor signals related to the eye movement motor plan and execution can each contribute to spatial updating within the visual system (Keith, Blohm, & Crawford, 2010). Overall, such results indicate that the translational shifts must occur due to a combination of the presence of visual anchors and the impending motor commands for making a saccade sequence, which is different from the localization errors induced by a blink.

Our spatial compression results are similar to the findings by Zimmermann, Fink, and Cavanagh (2013), who showed that a to-be-localized object flashed near the time of a full-screen mask was mislocalized toward a visual anchor even when no eye movements were made (i.e., there was a strong compression of space around this visual anchor even in the absence of eye movements). This could be due to the modulation of compression by visual anchors (e.g., Cicchini et al., 2013) or the compression that results from just holding object locations in memory (Sheth & Shimojo, 2001), which could be the case because masking the stimulus, as well as blinking, requires more reliance on memory for performing the task beyond what is necessary during the response stage (i.e., while making the sequence of responses on the screen in our study). In another recent study, Zimmermann, Born, Fink, and Cavanagh (2014) found similar mask-induced temporal compression and suppression of displacement effects for both fixation-only and saccade conditions, which they attributed to a more general “correspondence process” that links visual information before and after disruptions—a process that is not necessarily related to the contractions of eye muscles in the oculomotor system. Because our results indicate the presence of this type of compression around the central fixation even

without a mask, we attribute the overall two-dimensional compression to the requirement of holding the object locations in memory and the associated correspondence processes.

As previously mentioned, another way to characterize the compression observed in our study is that it occurs along the trajectory of the saccade, which is what past studies on perisaccadic compression typically have observed (e.g., Lappe et al., 2000; Morrone et al., 1997; Ross et al., 1997). This form of trajectory-related mislocalization may be due to the actual execution of the eye movement and the associated muscular contractions, as this is not found when saccades are planned but not executed (e.g., Atsma et al., 2014) and was not observed in our fixation-only or blink conditions. Therefore, the fact that the compression effects around the time of a blink are more similar to those found in our fixation-only control condition may be due to the absence of the muscular contractions related specifically to saccadic eye movements. (However, such claims require further tests specifically looking at the neural mechanisms.) Again, the reliance on memory still appears to affect how objects are remembered and subsequently mislocalized in a two-dimensional compressed manner.

Another possible explanation for our results is that the different forms of compression (compression vs. translation) are related to either spatial attention or focused attention. We did not find that attention was worse in the case of blinks or that it was more focused toward the lower region (in contrast to the study by Irwin, 2011). Instead, our participants made similar overall localization errors in the blink and the fixation-only control conditions (see Figures 3 and 5a). A possible interpretation for this pattern of results is that they exhibit the presence of two different forms of attention. One is related to spatial attention and is seen through the two-dimensional compression that occurs. The other form of attention is responsible for a more focused, object-based binding of information that may be crucial for matching information across visual disruptions (be it blinks or saccades), which may specifically produce the translation effects.

Conclusions

Our results indicate that despite having similar contrast sensitivity reduction effects (i.e., blink and saccadic suppression), blinks and saccades do not share the same pattern of spatial distortion around their onset. Saccades contribute to an increased spatial compression where objects are remembered as being closer to each other than in the blink or fixation-only control conditions; however, this effect is reduced when

constant saccade target cues are present during an unmasked stimulus presentation and during the gaze event. Additionally, saccades produce translational shifts that were not present around the time of a blink, including in our follow-up experiment that displayed constant landmarks on the screen; this confirms that the differences between the blink and saccade conditions were not due to the target landmarks being visible only in the saccade conditions in the first experiment. This suggests that saccadic suppression and blink suppression are not likely to be a feature or byproduct of the active spatial effects that happen around the time of an eye movement but rather are independent processes. In addition to not enhancing spatial compression (as during saccades), blinks confer greater numerosity recall accuracy across a blink compared with performance after the same duration spent simply fixating. This suggests that blinks may additionally engage a specialist mechanism for maintaining perceptual stability that is not engaged or is ineffective around the time of a saccade. Finally, there was no time-course effect for two-dimensional spatial compression, but there was a time-course effect for the translational shift along the trajectory of the saccade. The time-course effects for saccadic translation suggest that more than one saccade-related motor signal may be concurrently involved in promoting perceptual stability.

Keywords: eye movements, eye blinks, visual working memory, saccadic suppression, blink suppression, spatial compression

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Appendix

Figure	Time relative to gaze event (ms)						
	70–80	60–70	50–60	40–50	30–40	20–30	10–20
Figure 2b							
Fixation only	—	—	—	—	—	—	—
Blink	58	59	78	64	34	—	—
Saccade down	22	38	36	59	71	—	—
Saccade right	13	19	40	106	89	—	—
Figure 5b							
Fixation only	—	—	—	—	—	—	—
Blink	661	838	932	851	519	203	44
Saccade down	212	388	475	726	799	639	414
Saccade right	176	222	499	1080	1200	622	271
Figure 6a, b							
Fixation only	—	—	—	—	—	—	—
Blink	728	920	1044	932	595	246	69
Saccade down	291	519	657	945	1020	796	538
Saccade right	216	304	656	1311	1470	763	348
Figure A6iv							
Fixation only	—	—	—	—	—	—	—
Blink	542	617	626	757	590	231	13
Saccade down	280	524	415	463	283	167	67
Saccade right	396	369	463	709	411	162	63
Figures A6v and A6vi							
Fixation only	—	—	—	—	—	—	—
Blink	627	706	696	820	620	274	49
Saccade down	345	620	506	586	389	198	84
Saccade right	475	483	581	856	499	192	81

Table A1. Number of trials included in the time-course analyses (valid trials per condition). Dashes indicate that analyses were not possible for this time course. Note that the fixation-only control condition does not have a time course and is included in the figures for reference only.

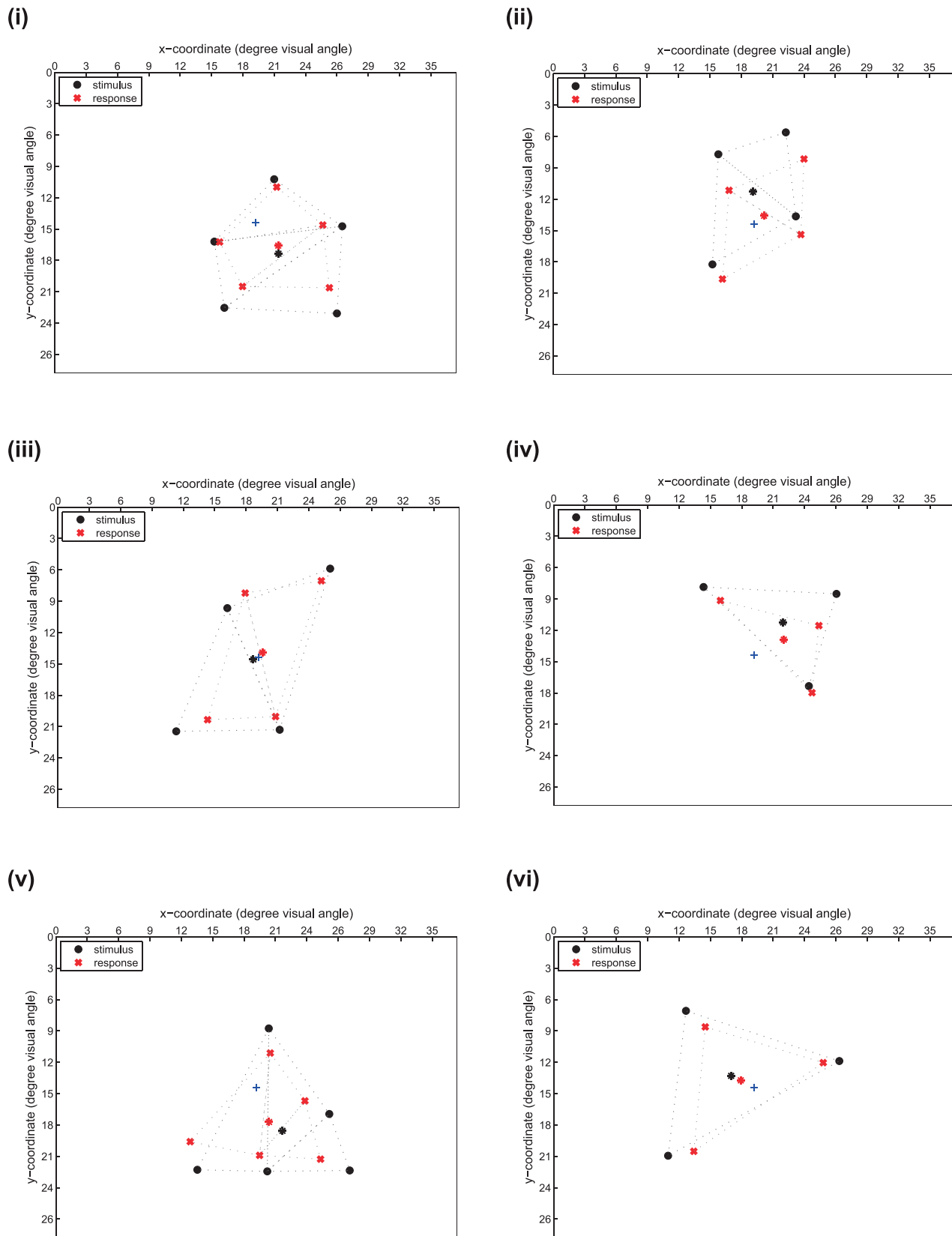


Figure A1. Examples of the localization data and the spatial compression that occurs. Each chart represents data from a single trial; the solid dots indicate the stimulus object locations as they appeared on a stimulus display, and the crosses indicate the response marker locations. The relevant centroids are indicated by the asterisk; the Delaunay triangles from the triangulation methods are indicated with the faint dotted lines (to better illustrate the distances between objects and the compression effect).

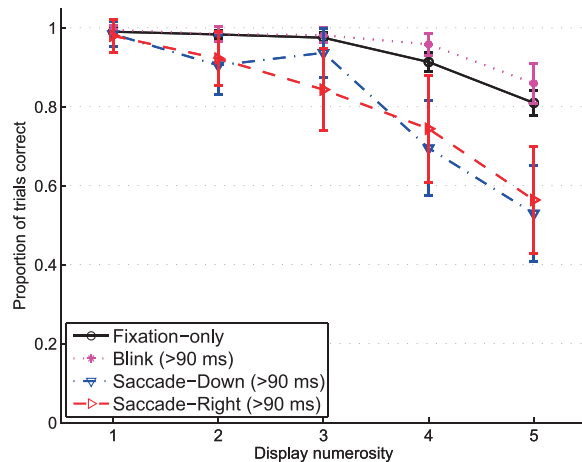
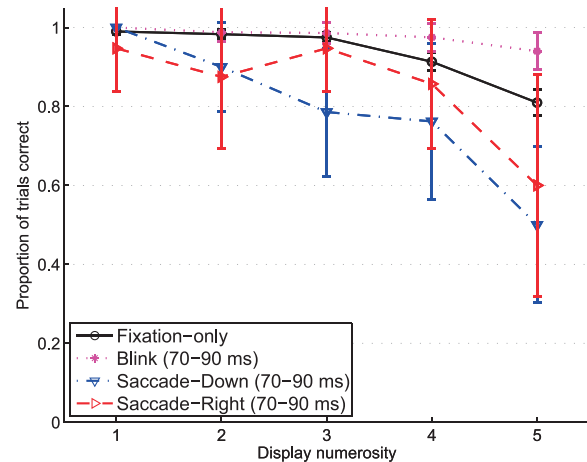
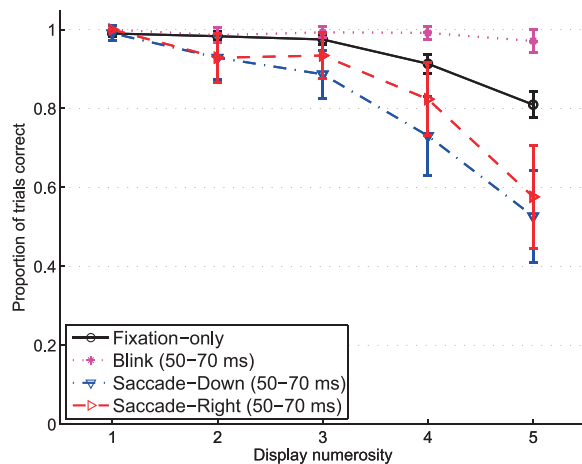
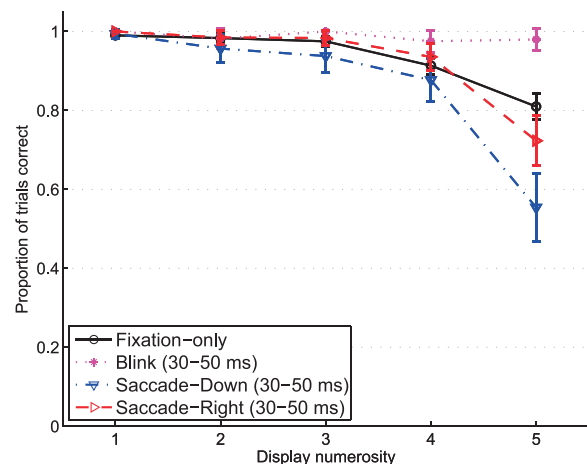
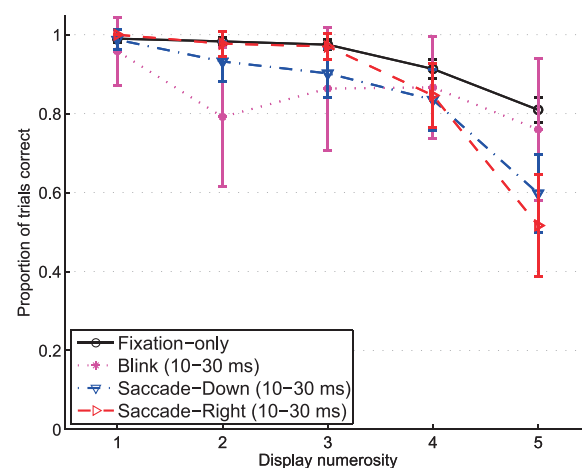
(i) > 90 ms interval**(ii) 70-90 ms interval****(iii) 50-70 ms interval****(iv) 30-50 ms interval****(v) 10-30 ms interval**

Figure A2. Time course of numerosity recall accuracy (proportion of trials with the correct number of responses), with separate panels for the different intervals between the presentation of the stimulus and the onset of the blink or saccade. The fixation-only condition (solid line) is the same on all charts and is presented as a reference for the performance observed in this condition (i.e., there is no time-course equivalent in the control condition).

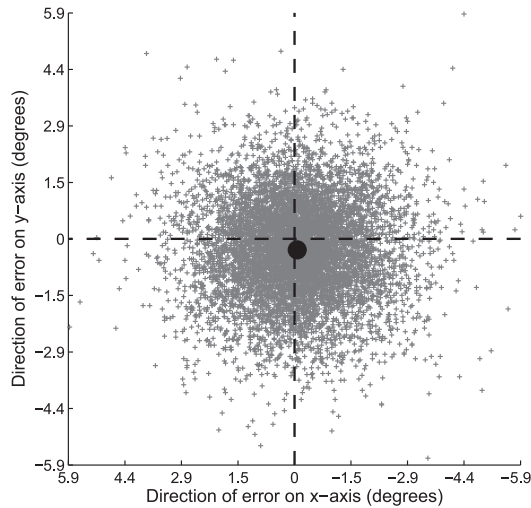
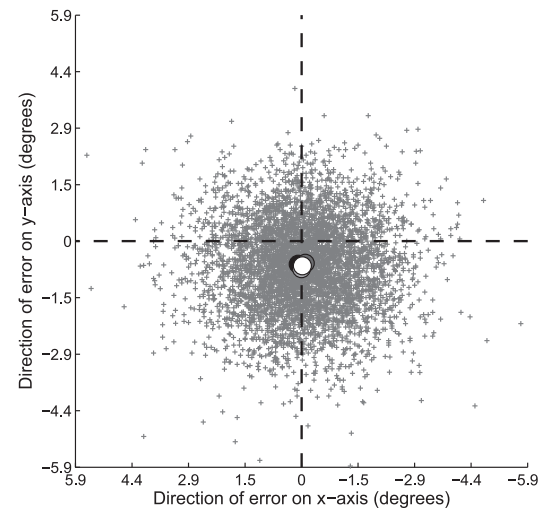
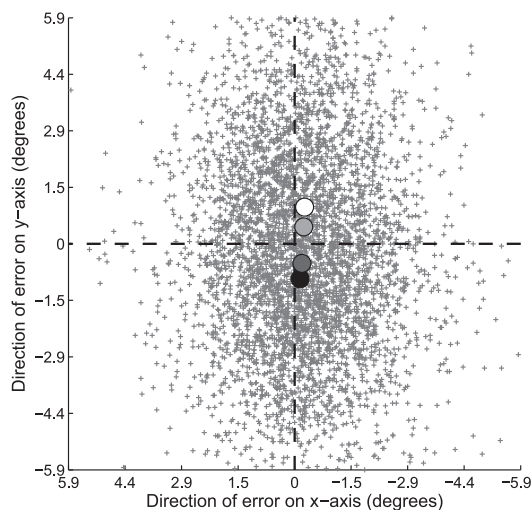
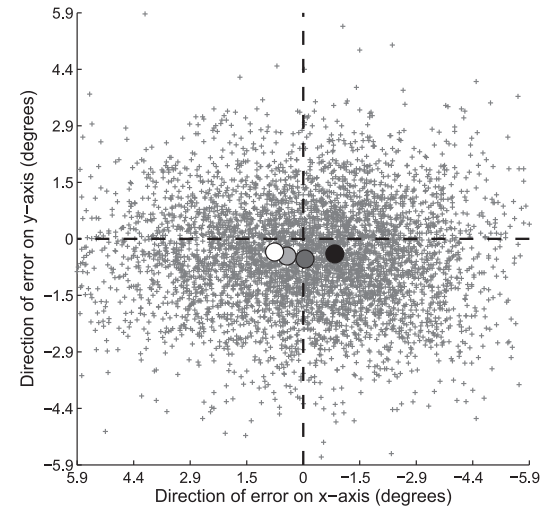
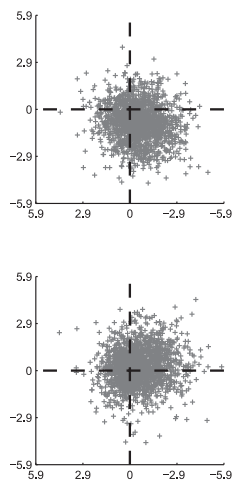
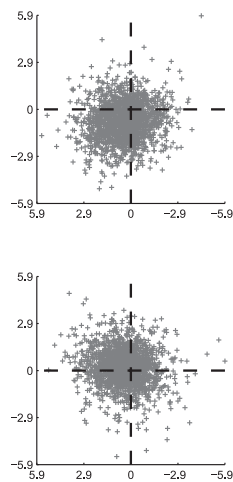
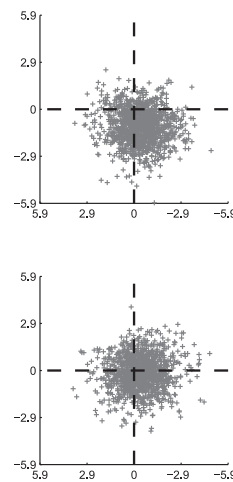
(i) Fixation-only**(ii) Blink****(iii) Saccade-down****(iv) Saccade-right**

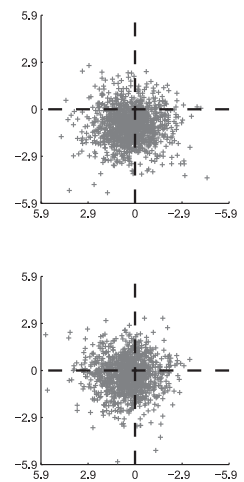
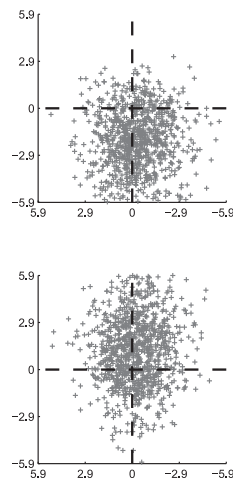
Figure A3. Distribution of errors for each gaze condition (for valid trials in which the gaze event began 10–90 ms after stimulus onset). Each “+” on the plot represents a response in relation to its paired stimulus disc (i.e., stimulus disc centers are at the [0, 0] coordinate of each subplot). The average localization bias is represented by large solid dots, and this average is plotted separately by the time course between the stimulus onset and start of the gaze event in panels ii through iv; white = 70 to 90 ms; light gray = 50 to 70 ms; dark gray = 30 to 50 ms; solid black = 10 to 30 ms. This indicates no difference in the time course for blinks (ii) but a clear effect of time course within the saccade conditions (iii, iv) along the trajectory of the saccade.

(i) Fixation-only

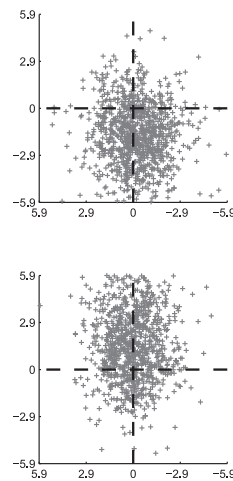
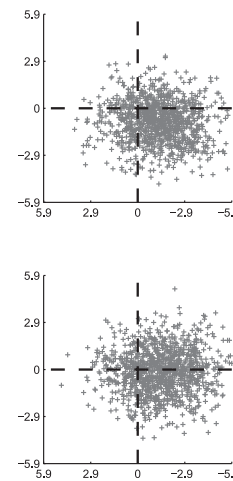
*

**(ii) Blink**

*

**(iii) Saccade-down**

*

**(iv) Saccade-right**

*

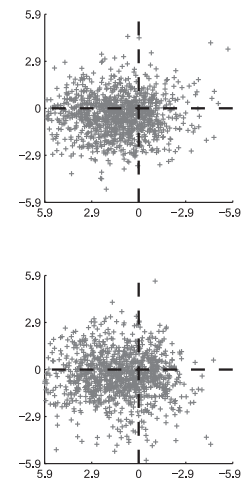


Figure A4. Distribution of localization errors separated by the screen quadrant location of stimulus discs. Each panel (i–iv) plots all the participant responses for the different gaze conditions separately by quadrant where the original stimulus disc was located (valid trials, all numerosities combined for the 10–90 ms offsets in panels ii through iv). Each “+” on the plot represents a response in relation to its paired stimulus disc (i.e., stimulus disc centers are at the [0, 0] coordinate of each subplot). A bias toward the center of the figures, represented by the central asterisks, suggests compression toward the center of a display. For example, in the fixation-only results (i), there is a bias in the distribution of responses on each subplot toward the center of the figure, which indicates a tendency to place responses toward the center of the screen, whereas the saccade-down condition (iii) shows a vertical distribution.

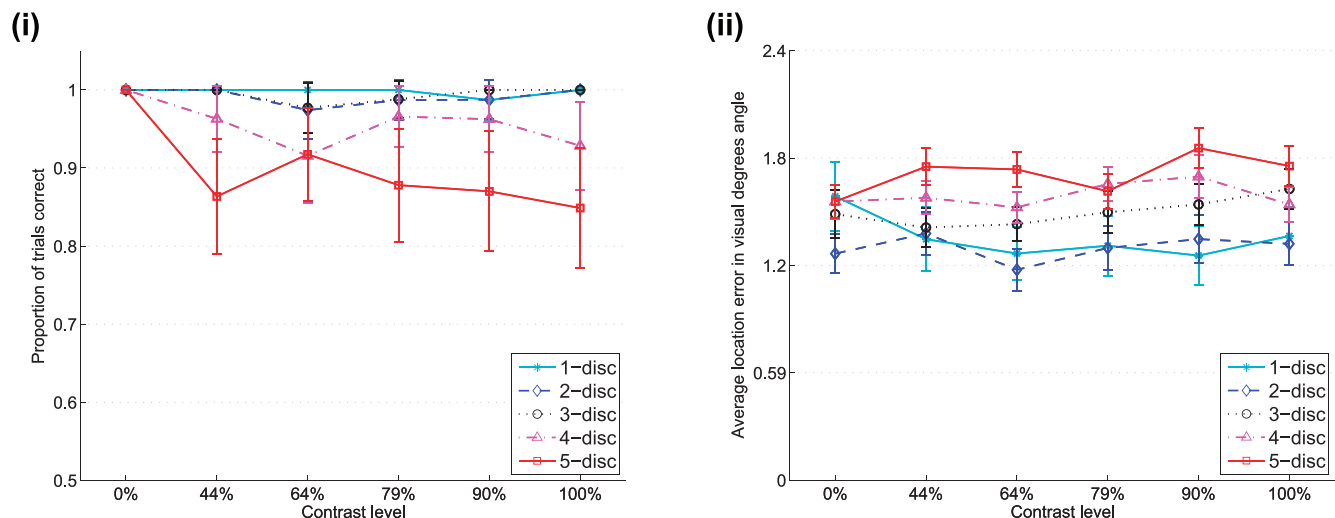


Figure A5. Baseline results (fixation-only trials with six levels of mask contrast) for (i) numerosity reporting accuracy and (ii) localization accuracy. Note that a contrast level of 0% indicates no mask present, whereas a contrast level of 100% indicates the full-strength mask used in the trials reported. ANOVA results did not identify significant differences between the different levels of masking (for levels 44%–100% masking) either for the proportion of trials correct, $F(4, 2021) = 0.3$, $p = 0.88$, $MS = 0.01$, or for localization accuracy, $F(4, 1903) = 2.77$, $p = 0.053$, $MS = 894.9$. Note that when analyzing localization accuracy for each numerosity separately, none of the differences were significant (all $ps > 0.07$).

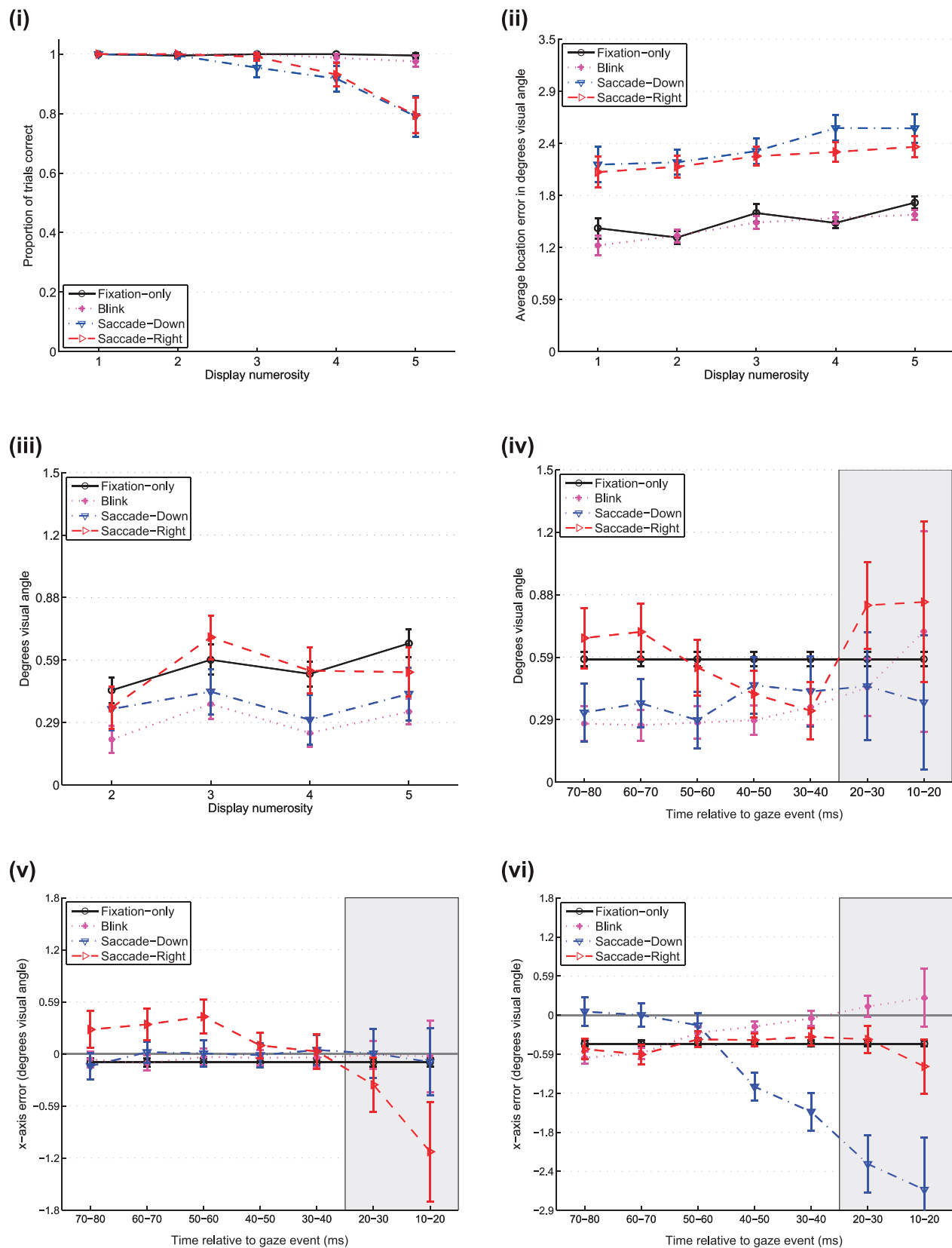


Figure A6. Results from the follow-up experiment using constant landmarks for saccade targets and no masking of the stimuli ($N = 3$). (i) Overall enumeration accuracy; (ii) overall localization errors; (iii) compression effects by numerosity condition; (iv) the time course of the compression effect (numerosities two through five combined); (v) the time course of the translational shift effect along the x-axis; and (vi) the time course of the translational shift effect along the y-axis.