



Saccadic Eye Movements Smear Spatial Working Memory

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Why do saccades interfere with spatial working memory? One possibility is that attention and saccades are tightly coupled, and performing a saccade momentarily removes attention from spatial working memory, degrading the memory representation. This cannot be the entire explanation, because saccades cause greater interference than do covert attentional shifts (Lawrence, Myerson, & Abrams, 2004). In addition, this saccadic degradation is limited to spatial but not object, configural, or verbal representations. We propose that saccadic remapping is partially responsible for this increased interference. To test this, we used a spatial change detection task, and during the retention interval, participants either performed a central task, a peripheral task without an eye movement, or a peripheral task that required a saccade. Using the method of constant stimuli allowed us to fit psychophysical functions in which we derived measures of spatial memory precision, guessing, and response bias. It is important that we found a directionally specific loss of memory precision, such that memory representations were less precise along the axis of the saccade. This was beyond the general loss of precision we found for covert shifts, suggesting that part of the effect is because of remapping. Saccades also increased guessing, but unlike the loss of precision, the effect was nondirectional.

Public Significance Statement

It has been known for some time that saccadic eye movements can interfere with spatial working memory but have no effect on other types of working memory, such as verbal, object, or configural. What has not been known is the mechanism that leads to this interference. As in previous research, we find that shifting attention can lead to an overall loss in memory precision. However, when an eye movement is made, we also find a loss of spatial memory precision along the path of the eye movement. This can best be explained by saccadic remapping, which is a mechanism that allows for spatial updating when viewing scenes.

Keywords: eye movements, working memory, attention, remapping

Spatial working memory (SWM) is a limited-capacity system for holding and manipulating spatial information over a short period of time. Working memory acts upon internally stored representations, whereas visual attention enhances processing of visual-perceptual information originating in the outside world. Because this enhancement occurs internally through changes in neural processing, visual attention is sometimes known as *covert* attention. In contrast, saccades, a form of *overt* attention, are quick ballistic eye movements that enhance processing by bringing the image to the high-density fovea.

Visual attention and SWM show a great deal of overlap, and may be different manifestations of the same underlying neural mechanism (Chun, 2011). For example, holding a spatial location in working memory can enhance the detection of stimuli presented at the memorized location (Awh & Jonides, 2001). Conversely, shifting covert attention during a retention interval disrupts spatial, but not visual (e.g., object), working memory, suggesting that spatial attention is used for spatial rehearsal (Awh & Jonides, 2001; Lawrence et al., 2004; Pearson, Ball, & Smith, 2014; Smyth, 1996). In support of this, Olsen, Chiew, Buchsbaum, and Ryan (2014) found that retention interval eye movements predicted the likelihood of correctly recalling spatial locations. Specifically, when the eyes visited the encoded locations during the blank retention interval, these locations were more likely to be correctly recalled, implying that these overt shifts of attention were indications of covert spatial rehearsal. However, saccadic eye movements (overt shifts) are more than a shift of covert attention, because task-irrelevant saccades disrupt SWM more than pure covert shifts of attention (Lawrence et al., 2004). Note that this interference seems to be limited to spatial information, as saccades have no effect on visual-object (Carlson-Radvansky, 1999), visual-configural (Carlson-Radvansky, 1999), or verbal (Irwin, 1998; Lawrence et al., 2004) working memory.

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What remains unanswered is why saccadic eye movements lead to greater interference than covert shifts of attention. Specifically, is there an additional mechanism that might be responsible for saccadic interference with SWM? We propose that saccadic *remapping* is the mechanism responsible, and as we will see later, saccadic remapping makes specific predictions about the types as well as the patterns of memory errors.

Saccades are fast ballistic eye movements that bring the eyes from one fixation area to the next. By necessity, saccades induce a change in the retinal image, and to maintain a stable percept of the world, the brain must be able to account for, and predict, shifting retinal images because of eye movements. To do this, the visual system uses an efferent motor copy of the eye movement signal to update (remap) the retinotopic locations of visual objects (Bays & Husain, 2007; Hall & Colby, 2011). Neurons demonstrating spatial remapping have been found in the lateral intraparietal area (LIP), a macaque analog of human intraparietal sulcus (IPS), the frontal eye fields (FEF), and area V4 (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Andersen, Essick, & Siegel, 1985; Duhamel, Colby, & Goldberg, 1992; Neupane, Guitton, & Pack, 2016; Sommer & Wurtz, 2002; Umeno & Goldberg, 1997, 2001; Wang, Fung, Guan, Wu, Goldberg, & Zhang, 2016), as well as human parietal cortex (Medendorp, Goltz, Vilis, & Crawford, 2003). The receptive fields of these eye-movement sensitive neurons are known as *gain fields* and have a planar (directional) layout (Andersen et al., 1985).

Areas that show remapping (e.g., FEF, IPS) are some of the same areas (FEF, IPS) that appear to be involved in SWM (Ikkai & Curtis, 2011). If these same neural circuits that are used to localize objects are also used to hold locations in SWM, then these memory representations should also undergo spatial remapping when eye movements are made. One key difference is that during perception, remapping is used to *predict* the retinotopic locations of objects postsaccade. In contrast, in memory tasks that have demonstrated increased interference from saccades, the saccadic eye movements are made when the to-be-remembered-items are no longer visible, and typically one or more saccades are made to peripheral locations before returning to the initial location where the items were encoded (Lawrence et al., 2004).

Why should remapping lead to an additional degradation in SWM over pure covert shifts? If we assume that remapping is not perfect, then performing multiple saccades should lead to a build-up of spatial errors. For everyday perception, this is not a problem, because small prediction errors can be corrected after

viewing the new retinal image upon landing (Deubel, Schneider, & Bridgeman, 1996). Because not all objects may be stationary during a saccade, it is important for the new retinal image to take precedence over the prediction.

How might this degradation differ compared with covert shifts? For one, spatial remapping predicts that errors should build up along the axis of the saccade because of planar gain fields (Andersen et al., 1985). For example, if a participant makes a series of horizontal saccades that are out-and-back (similar to Lawrence et al., 2004 and Golomb & Kanwisher, 2012), then these errors should build up along the horizontal axis. Analogous to a horizontal astigmatism (albeit in memory), this would make detecting displacements along the horizontal axis more difficult compared with the vertical axis (Figure 1). This would predict that there should be a horizontal loss of memory *precision*, with no effect along the vertical axis. **F1**

Another possible explanation as to why saccades lead to increased memory degradation over covert shifts is that the saccade target might automatically be encoded (Tas, Luck, & Hollingworth, 2016). This predicts that if SWM is fully occupied, then the saccade target will boot one item out of working memory (see Bays, Catalao, & Husain, 2009, for an alternative explanation). Rather than affecting precision, this would instead increase the rate of *guessing* (Zhang & Luck, 2008). This idea is supported by studies demonstrating that as the number of items held in SWM increases, guessing also increases (Irwin & Robinson, 2015; Thiele, Pratte, & Rouder, 2011).

Keep in mind that a saccadic shift also entails a covert shift of attention (Deubel & Schneider, 1996; Peterson, Kramer, & Irwin, 2004). How might covert shifts of attention interfere with SWM? One possibility is that shifts of covert attention lead to an overall loss of precision. That is, the removal of attention leads to a noisy representation in working memory, and unlike the saccadic prediction, the effect is nondirectional. Evidence for this possibility comes from Klyszejko, Rahmati, and Curtis (2014). In their task, color was used to code the likelihood that a spatial location would be probed at the end of a memory task, and presumably high-likelihood items received more attention during encoding and maintenance. Memory precision was highest for those items with the highest likelihoods of being probed. Bays (2014) found a similar effect using a nonspatial line-orientation task, with precued items showing greater memory precision. Taken together, this would predict that covert shifts should lead to an overall loss of

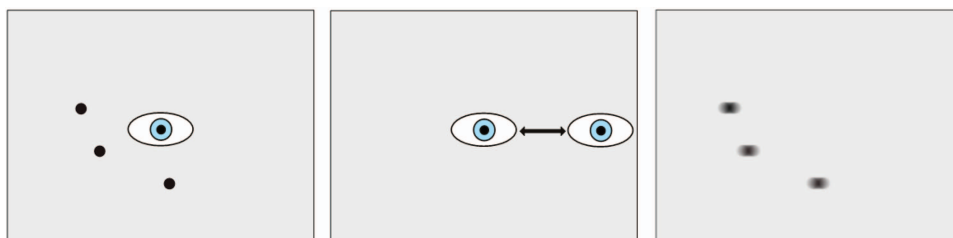


Figure 1. If spatial remapping affects spatial working memory, then making a series of horizontal saccades (center panel) should lead to a buildup of errors along the horizontal axis, effectively “smearing” the memory representation (right panel), which should make detecting horizontal displacements more difficult than vertical displacements. See the online article for the color version of this figure.

memory precision, and if a saccade is also made, then there will be an additional loss that is directionally specific.

The following study is designed to test these three hypotheses by separately measuring guessing, response bias, and the spatial precision of working memory. Participants performed a spatial change detection task in which one of the memory items could be displaced by varying degrees in either the vertical or horizontal direction. By using the method of constant stimuli, this allowed us to map out participant's sensitivity to spatial changes along the vertical and horizontal axes. We fit Gaussian probability density curves (probability of "yes, there was a change") with three free parameters to each participant's data, and this allowed us to derive measures of spatial precision (width of the Gaussian PDF in SDs), guessing, as well as response bias. Separate curves were fit for the horizontal and vertical changes. Although previous studies, such as Golomb and Kanwisher (2012) used mouse clicks to derive spatial precision, we opted against this, because we were afraid that the direction of covert or overt shifts might lead to a bias in manual planning that could affect the results.

To isolate the effects of covert attention and saccadic eye movements on SWM, participants performed one of three go/no-go tasks (detect an X, ignore an O) during the memory retention interval. The go/no-go task was either centrally located (control condition), peripherally located and required a covert shift of attention, or peripherally located and required an eye movement. The direction of the required shifts (horizontal or vertical) was counterbalanced across subjects, and the three tasks were performed during separate sessions so as to minimize carry-over effects.

Method

Participants

Participants were 12 individuals from George Mason University (eight men and four women) with a mean age of 28 years. Sample size was based on Klyszejko et al. (2014, nine participants) and Zhang and Luck (2008, eight participants). Originally 16 were recruited, but two were dropped from the data analyses because they failed to complete all sessions. Two others were dropped because of low accuracy in the easy control condition, and post hoc interviews suggested that there might have been some confusion about the experimental instructions. All participants had normal or corrected-to-normal vision. The direction of covert and overt shifts were counterbalanced across subjects, with half of the participants performing horizontal shifts, and the remainder performing vertical shifts.

Equipment

The experiment was run on an Apple Mac Pro Dual-Core Intel Xeon computer and with a 19" ViewSonic monitor. Participants were positioned 665 mm away from the monitor and their head position was secured via a chinrest. Eye movements were monitored by an Eye Link 1000+ remote eye-tracker. The EyeLink 1000+ has an accuracy of 0.25°–0.50°, with a sampling rate of 2,000 Hz. Incorrect eye movements (e.g., moving the eyes during the two no eye movement conditions or failing to make the appropriate saccade in the overt condition) elicited an error mes-

sage. Error trials were recycled at a randomly designated time later in the experiment.

Design

This experiment used a 3×2 design, with task (central, peripheral covert, or peripheral saccade) and change direction as the within-subjects factor. Each participant participated in two sessions of all three task conditions, for a total of six sessions.

Each experimental session consisted of 180 trials, 160 of which contained changes, and 20 that did not. When there was a change, half of the changes were vertical and half were horizontal, and all four possible directions of change occurred equally often. Memory items (disks) could move ± 60 , ± 40 , ± 20 , or ± 10 pixels (0.28° to 1.67°) in either the horizontal or vertical direction (Figure 2), and each occurred 10 times.

Stimuli and Procedure

The stimuli and timing of events are shown in Figure 2 (not to scale). The memory stimuli consisted of a three-disk array, with each disk 0.5° of visual angle. The disks were randomly presented within an area $5.7^\circ \times 5.7^\circ$ of visual angle area centered around fixation, and the stimuli did not overlap. In addition, the stimuli could change spatial locations anywhere from 0.28° to 1.67° of visual angle.

Prior to each trial, a drift correction was performed which required the participant to stare at a centrally presented fixation circle (0.5 degrees) and press the spacebar. Immediately following the drift correction, the trial began and a fixation dot (0.2 degrees) appeared centrally for 250 ms. Participants were instructed to maintain gaze on the fixation dot unless otherwise instructed. The memory array then appeared for 500 ms, and participants were instructed to continue to stare at the fixation dot while encoding

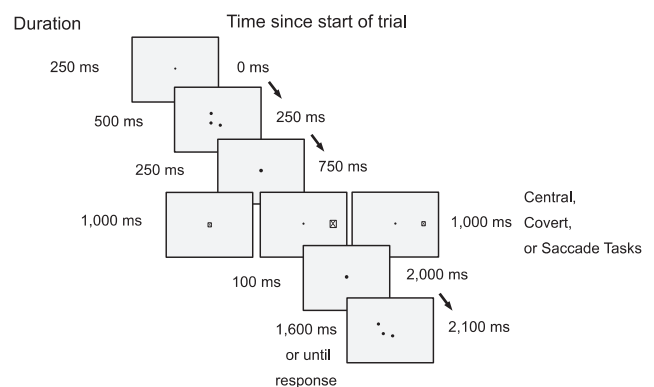


Figure 2. Each trial began with a fixation cross (250 ms) followed by the memory array (500 ms). After a 250 ms, a probe letter appeared during the retention interval either at fixation (Central condition) or peripherally (Covert and Saccade conditions). Participants responded if the probe was a letter X and withheld a response if it was an O. The probe was larger in the covert condition to allow identification without requiring an eye movement. The saccade condition required an eye movement to the probe followed by an eye movement back to fixation. After the retention interval, the test array appear, and participants had to respond whether it was the same or different. In the previous example, the top dot moved leftward in the test array.

the locations of the three stimuli. The stimuli disappeared leaving the fixation dot (250 ms).

Next, a white box containing an X or an O appeared for 1,000 ms. In the central task, the box was located at fixation, whereas in the covert and saccade conditions, the box was located in the periphery, 8.46° to the left or right (horizontal shift) or above or below (vertical shift) the fixation dot. In the central and saccade conditions, the letter box was $0.59^\circ \times 0.59^\circ$, whereas in the covert attention task, the letter box was made larger to aide peripheral identification and discourage eye movements ($1.17^\circ \times 1.17^\circ$). Participants were to press the space bar as quickly as possible if an X appeared and to withhold a response when an O appeared.

In the saccade condition, the letters were small enough that they could not be identified while fixating the center dot, and participants were required to make a saccade to the letter box location and then return their gaze to the fixation dot. If this did not occur within the 1,000 ms allocated for the task, a warning appeared on screen and the trial was recycled later in the experiment.

In both the central and covert conditions, participants were required to maintain their gaze on central fixation during the 1,000-ms retention interval. If the eyes moved outside of a $2^\circ \times 2^\circ$ zone centered around the fixation point, a warning appeared and the trial was recycled later in the experiment.

After a 100-ms delay, the test array appeared for 1,600 ms. Participants responded by pressing either the “z” or “/” keys (counterbalanced across subjects) key to indicate whether the stimuli were located in the same spatial locations in both the memory and test arrays or whether one item had moved to a different spatial location. Participants were instructed to respond as quickly and accurately as they could upon seeing the test array, and

if responses were not made within 1,600 ms, an error message appeared and the trial was recycled to the end of the experiment.

The beginning of each experimental session was preceded by 10 practice trials. Auditory feedback for incorrect responses was provided during practice, but not during the experimental trials.

Psychophysical Fits

For each subject, the data from all sessions of a task condition were combined. Similar to [Zhang and Luck \(2008\)](#), we fit Gaussian probability density functions (PDFs) to each subject’s observed data ([Figure 3](#)), which was the probability of responding “same” as a function of change distance. We allowed three parameters to vary: the *SD* of the distribution, a scaling parameter, and an intercept parameter, which shifted the distribution up and down along the y-axis, and is related to, but not identical to, response bias. The mean of each distribution was set to 0 (allowing the mean to vary had no effect on the fits), and the Gaussian fits were constrained between the range of 0.0001 and 0.9999. In addition, we constrained the standard deviations so that they would be greater than zero. We used Microsoft Excel’s Solver function to minimize the root mean-squared error for each fit.

For each subject, this allowed us to estimate three parameters of interest for each condition: *precision*, *guess rate*, and *bias* ([Figure 3](#)). *Precision* is the *SD* of the Gaussian PDF ([Figure 3C](#)), with larger *SDs* representing less spatial precision. The *guess rate* (see [Equation 1](#)) was calculated by estimating the range of the fit ([Figure 3B](#)). Range was calculated by subtracting an estimated minimum value (estimated at the tenth *SD* of the Gaussian PDF) from the maximum value at change 0 (mean). Because guessing

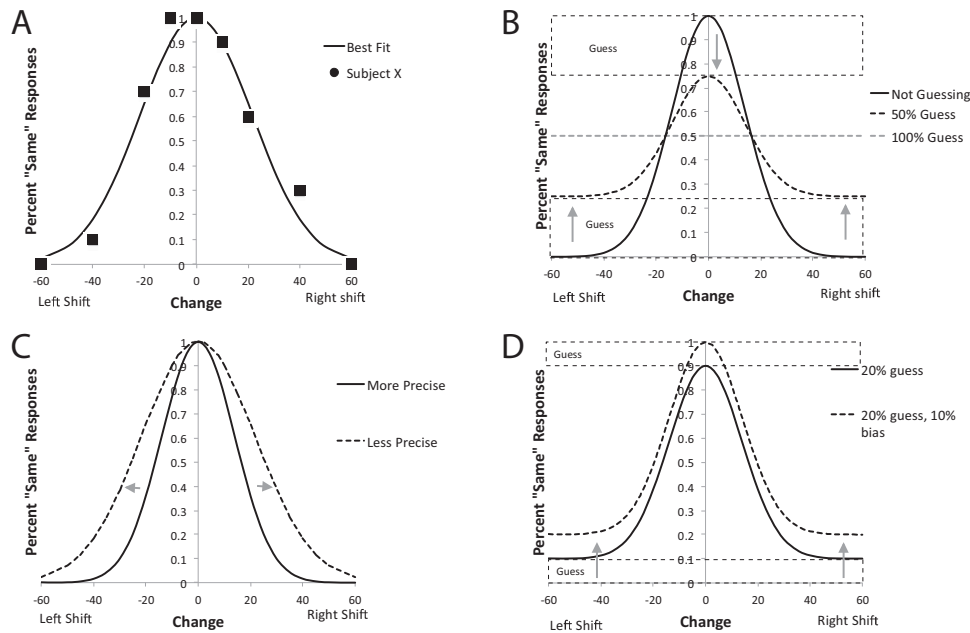


Figure 3. (A) Gaussian curve fit to a hypothetical subject’s data (horizontal change condition). (B) Effect of guessing on response distributions (dashed distribution). (C) How a loss of precision affects the width of response distributions. We used the *SD* of the curve fits as our measure of precision. (D) The effect of bias on responses (example shows a bias to respond “same”).

should produce symmetric effects along the *y*-axis, *bias* accounted for any remaining asymmetries (Figure 3D). *Bias* was calculated by subtracting half the guess rate from the intercept parameter (see Equation 2).

$$\text{Guess Rate} = 1 - \text{Range} \tag{1}$$

$$\text{Bias} = \text{Intercept} - \frac{\text{Guess Rate}}{2} \tag{2}$$

In simulations, we found that extreme bias could lead to ceiling or floor effects. For example, if a participant, when in doubt, had a tendency to respond “same,” this could potentially lead to a ceiling effect, which would clip the data at 1, and could potentially change the standard deviation parameter (precision) of the fit model. Because of this possibility, we ran a second set of fits in which the model was allowed to produce values <0 and >1. This unconstrained model did not yield statistical results that were qualitatively different from the results reported in results section.

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Although it is customary to use maximum likelihood estimates for optimization in psychophysics, simulations showed that this produced erroneous results. Specifically, simple shifts in bias up or down also produced changes in the standard deviation (precision) when model fitting, and these two parameters should be independent. This occurs because MLE does not weigh errors (difference between observed and fit) equally. That is, for a given error difference (e.g., 0.10), it returns different likelihoods depending on the value of the observed data (e.g., the difference between 0.05 and 0.15 is given a higher likelihood than the difference between 0.45 and 0.55, despite both differing by 0.10). Because of this nonindependence when using the maximum likelihood estimate, we used the root mean squared error, because it is agnostic to the location on the scale, and also allowed us to fit unconstrained models with values <0 and >1.

Results

In the following analyses, *same-axis* and *orthogonal-axis* refer to the direction of change (when a memory item moved) relative to the movement of attention or the eyes. For example, for subjects that made horizontal shifts, a vertical change in a memory item was coded as an orthogonal change, and a horizontal change was coded as a same-axis change. Likewise, for subjects that made vertical shifts, a horizontal change was coded as an orthogonal change, and a vertical change was coded as occurring along the same axis.

For the central task, in which the eyes remained at fixation and no covert or overt shifts were made, *same-axis* and *orthogonal-axis* are coded relative to the direction of the shifts required of a participant while performing in the covert and saccade tasks. For example, for participants that made horizontal shifts (in the shift conditions), horizontal changes in the central task were coded as a same-axis change, whereas for the vertical shift group, these would have been coded as an orthogonal change. This was done to control for any visual field differences along the vertical or horizontal axes (see the Normalized Precision analysis below).

Secondary Detection Task

A one-way repeated-measures analysis of variance (ANOVA) was performed to determine if the type of retention interval task

affected accuracy on the secondary go/no-go task. The effect of task failed to reach significance, $F(2, 22) = 1.07, p = .36, \eta^2_{\text{partial}} = 0.09$, 90% confidence interval (CI) [.25, .0], and overall accuracy was 97.5%.

Memory Accuracy

To test whether the type of task had an effect on memory response accuracy, we performed a two-way repeated-measures ANOVA, with task and change axis (same-axis or orthogonal) as factors (see Figure 4). As expected, there was a main effect of task $F(2, 22) = 12.65, p < .001, \eta^2_{\text{partial}} = 0.53$, 90% CI [.66, .24], and as in Lawrence et al. (2004), we found that accuracy in the central condition was higher than in the two shift conditions, $F(1, 22) = 25.45, p < .001, \eta^2_{\text{partial}} = 0.54$, 90% CI [.68, .26], and accuracy in the covert task was higher than in the saccade task, $F(1, 22) = 9.47, p < .001, \eta^2_{\text{partial}} = 0.30$, 90% CI [.50, .06]. The main effect of change axis did not reach significance, $F(1, 22) = 2.86, p > .1$, 90% CI [.32, 0].

Crucially, task and change axis interacted, $F(2, 22) = 3.89, p < .05, \eta^2_{\text{partial}} = 0.26$, 90% CI [.44, .01]. To determine the nature of the interaction, we performed two sets of Helmert contrasts for the orthogonal and same-axis conditions separately with Bonferroni corrections for multiple tests. For the same-axis condition, accuracy in the central condition was significantly better than the two shift conditions, $F(1, 22) = 65.6, p < .001, \eta^2_{\text{partial}} = 0.75$, 90% CI [.82, .55], and accuracy in the saccade condition was significantly worse than in the covert condition, $F(1, 22) = 8.45, p = .033, \eta^2_{\text{partial}} = 0.28$, 90% CI [.45, .05]. For changes that occurred along the orthogonal axis, accuracy was significantly higher in the central condition compared with the two shift conditions, $F(1, 22) = 19.67, p = .001, \eta^2_{\text{partial}} = 0.47$, 90% CI [.63, .20], but the two shift conditions did not differ significantly from each other, $F(1, 22) = 2.09, p > .20$, 90% CI [.29, 0], indicating that saccades uniquely affect the detection of changes that occur along the same-axis.

Memory Precision

Memory precision is shown in Figure 5. We initially performed a two-way repeated-measures ANOVA with task and change axis as independent variables, followed by Bonferroni-corrected con-

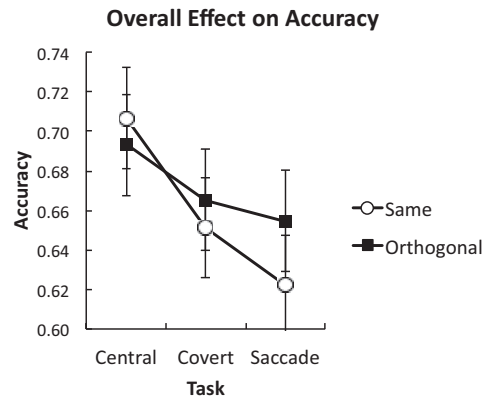


Figure 4. Effect of task and displacement axis on accuracy. Error bars are uncorrected 95% confidence interval. Chance is 50%.

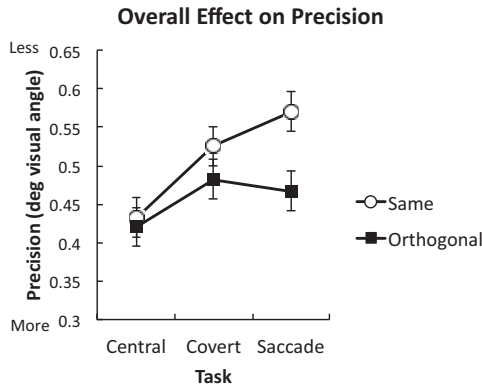


Figure 5. Effect of task and displacement axis on memory precision.

trasts to determine the nature of the effects of saccades on precision. There were significant main effects of task, $F(2, 22) = 6.83, p = .005, \eta^2_{\text{partial}} = 0.38, 90\% \text{ CI } [.54, .09]$, and direction, $F(1, 22) = 18.52, p = .001, \eta^2_{\text{partial}} = 0.63, 90\% \text{ CI } [.76, .24]$, and the two interacted, $F(2, 22) = 15.69, p < .001, \eta^2_{\text{partial}} = 0.59, 90\% \text{ CI } [.70, .30]$.

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We followed up with two sets of contrasts. The first set of contrasts asked whether the task had an effect on precision for the same-axis and orthogonal-axis conditions. The second set of contrasts tested whether the axis effects differed for the covert and saccade conditions.

As with the accuracy data, we performed two sets of Helmert contrasts for the same-axis and orthogonal-axis conditions. For the same-axis, precision in the central condition was significantly better than the two shift conditions, $F(1, 22) = 124.60, p < .001, \eta^2_{\text{partial}} = 0.85, 90\% \text{ CI } [.90, .74]$, and the covert condition showed significantly better precision than the saccade condition, $F(1, 22) = 15.64, p = .004, \eta^2_{\text{partial}} = 0.42, 90\% \text{ CI } [.59, .14]$. Like the accuracy data, the central condition showed significantly better precision than the two shift conditions for changes that occurred along the orthogonal axis, $F(1, 22) = 27.91, p < .001, \eta^2_{\text{partial}} = 0.56, 90\% \text{ CI } [.71, .32]$; however, the two shift conditions did not differ significantly from each other, $F(1, 20) = 1.67, p > .1$.

A second set of contrasts was performed to determine whether the effect of axis differed between the covert or saccade conditions. The same-axis condition demonstrated significantly less precision for both the covert, $F(1, 22) = 11.86, p = .014, \eta^2_{\text{partial}} = 0.35, 90\% \text{ CI } [.54, .09]$, and saccade tasks, $F(1, 22) = 76.61, p < .001, \eta^2_{\text{partial}} = 0.78, 90\% \text{ CI } [.84, .60]$. More important, the two effects are significantly different from each other, $F(1, 22) = 14.09, p = .007, \eta^2_{\text{partial}} = 0.39, 90\% \text{ CI } [.57, .12]$, with the saccade task showing a larger effect (i.e., larger loss of precision).

Normalized Precision

As can be seen in Figure 5, in the central task, there appears to be overall less precision along the same axis compared with the orthogonal axis. However, since no attentional shifts take place during this task, this could be because of individual visual field differences, that in this case, just happen to affect the same axis more than the orthogonal axis. To control for the possibility that these effects were because of inherent differences in directional

sensitivity that varied from subject-to-subject, rather than the addition of the shifting tasks, we calculated a differential sensitivity score for each subject by dividing vertical precision by the horizontal precision based on the data from the central task. Vertical precision for the covert and saccade data was then Scaled \times Dividing \times This score. Because this would cause the central task to have identical scores for the same-axis and orthogonal conditions, the central task was excluded from the analyses. We checked for outliers by checking for residuals that were greater than 3 standard deviations using the median-absolute-deviation method. A two-way repeated-measures ANOVA was performed with task (covert or saccade) and change axis as factors (Figure 6). The main effect of axis, $F(1, 11) = 8.41, p = .014, \eta^2_{\text{partial}} = 0.43, 90\% \text{ CI } [.64, .06]$, reached significance, however, the main effect of task did not, $F(1, 11) = 0.72, p > .1, \eta^2_{\text{partial}} 90\% \text{ CI } [.32, 0]$. It is important that the interaction between task and axis reached significance, $F(1, 11) = 20.29, p = .001, \eta^2_{\text{partial}} = 0.65, 90\% \text{ CI } [.78, .27]$, indicating that the axis effect for the saccade condition was significantly greater than that for the covert condition.

F6

To investigate the nature of the interaction, we performed four sets of contrasts Bonferroni corrected for multiple comparisons. For the orthogonal condition, performing a saccade had no effect on precision compared with the covert condition, $F(1, 11) = 1.71, p > .1, \eta^2_{\text{partial}} = .13, 90\% \text{ CI } [.41, 0]$, but saccades did decrease precision in the same-axis condition, $F(1, 11) = 25.61, p = .001, \eta^2_{\text{partial}} = .70, 90\% \text{ CI } [.81, .34]$. For the covert condition, there was no difference in precision between the same-axis and orthogonal-axis changes, $F(1, 11) = 6.73, p = .10, \eta^2_{\text{partial}} = .38, 90\% \text{ CI } [.60, .03]$; however, same-axis changes led to a loss of precision for the saccade condition, $F(1, 11) = 80.36, p < .001, \eta^2_{\text{partial}} = .88, 90\% \text{ CI } [.92, .69]$, indicating that performing a saccade led to a loss of memory precision along the axis of the saccade. Like the uncorrected precision data, the axis effect for the saccade condition was significantly greater than that for the covert condition, as shown by the significant interaction. For these last three analyses, we followed up with Bayesian *t* tests (JASP). For the covert condition, there was not convincing evidence for the axis effect when eval-

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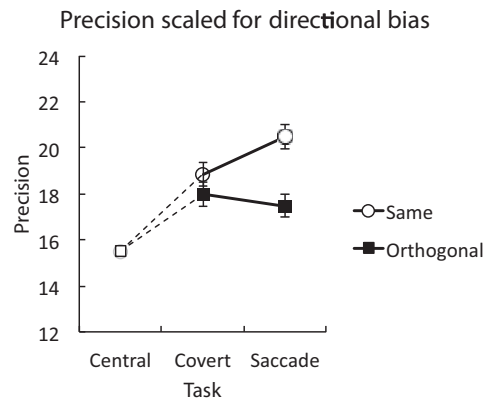


Figure 6. Normalized precision. To correct for any inherent differences in directional sensitivity, the ratio of the vertical:horizontal precision in the central task was used to scale the vertical precision in the two shift tasks. Because applying this to the central condition scores removes any directional differences, the central task was excluded from the analysis. Error bars are uncorrected 95% confidence interval.

uated with Bayesian statistics ($BF_{10} = 0.58$), but there was for the saccade condition ($BF_{10} = 15.46$). In addition, there was strong support for a larger axis effect for the saccade condition compared with the covert condition ($BF_{10} = 33.67$).

Memory Response Bias and Guess Rates

Two-way ANOVAs with task and change-axis as within-subject variables were performed for both the bias and guess rates. For the bias measurement, none of the main effects or interactions reached significance (smallest $p = .102$ for change axis).

F7

For the guess rates (Figure 7), there was a main effect of task, $F(2, 22) = 6.08$, $p = .008$, $\eta^2_{\text{partial}} = .36$, 90% CI [.52, .07]. Helmert contrasts revealed that saccades led to significantly more guessing than the other two tasks, $F(1, 22) = 12.07$, $p = .002$, $\eta^2_{\text{partial}} = .35$, 90% CI [.59, .09], but there was no significant difference in precision between the central and covert tasks, $F(1, 22) = 0.09$, $p > .10$, supporting the hypothesis that saccades led to some items being dropped from memory. None of the other main effects or interactions reached significance (lowest $p = .334$ for change axis).

Discussion

The present study evaluated three potential sources of saccade-driven SWM interference, and evidence was found supporting all three. As predicted by the saccade-target encoding hypothesis, we found that the rate of guessing increased when a saccade was made to a response target during the retention interval, which is expected if the saccade-target is also encoded into working memory. In addition, we found evidence that covert shifts of attention, with or without eye movements, led to an overall loss of spatial memory precision. Finally, and of primary interest, we found that saccades led to a directionally specific loss of precision, as predicted by spatial remapping.

Spatial Remapping

It has been known for some time that performing a saccade leads to the updating of spatial locations, and this in turn allows for stable trans-saccadic perception (Andersen et al., 1985; Bays &

Husain, 2007; Duhamel et al., 1992; Irwin, 1991). Anatomical structures where this updating has been observed include the parietal cortex (LIP/IPS), the FEF, and area V4, and the first two of these structures have been implicated in maintaining SWM representations. We hypothesized that if saccade generation, perception, and SWM share a common representation system, then SWM should be susceptible to spatial remapping.

In support of the remapping hypothesis, we found that performing a saccade lead to an additional loss of memory precision for items displaced along the axis of the saccade compared with those displaced orthogonally. In addition, when comparing the saccade task to the covert shift task, the loss of precision associated with same-axis changes was significantly larger when a saccade had been performed compared with when the task required a covert shift, which is in line with the predictions of the spatial remapping hypothesis. Of note, there is some evidence suggesting that downward and rightward saccades might impair SWM more than upward or leftward saccades (Vasquez & Danckert, 2008); however, because our participants had to make a series of out-and-back saccades, we were unable to examine this in our data.

It is interesting that saccade *target* displacements are more difficult to detect when the displacement occurs along the axis of the saccade (*saccadic suppression of displacement*) compared with when they are displaced orthogonally (Wexler & Collins, 2014). At first glance, this may sound very similar to our findings—orthogonal changes are easier to detect than same axis changes—but there are some fundamental differences that suggests that they are different phenomena. First, saccadic suppression of displacement disappears when there is a blank period between a saccade landing and the target reappearing (Deubel et al., 1996). Because our retention interval acted as a long blank period, one that was much longer than the 250-ms blank periods used in previous research, this would seem to rule out saccadic suppression of displacement. Second, none of our memory items were saccade targets, and saccadic suppression of displacement only occurs for items that are close to the saccade target location.

Other Effects

We found that covert shifts and saccades had two additional effects on memory. First, any shift of attention, whether covert or overt, led to an overall loss of precision. This is unlikely to be because of a central dual-task cost, as endogenously driven shifts do not demonstrate dual-task interference during a Psychological Refractory Period (PRP) task (Pashler, Carrier, & Hoffman, 1993). Instead, this loss of precision suggests that the removal of attention leads to a noisy representation in working memory. Support for this idea comes from Klyszejko et al. (2014). In their task, color was used to code the likelihood that a spatial location would be probed at the end of a memory task. Precision was highest for those items with the highest likelihoods. Bays (2014) found a similar effect using a nonspatial line-orientation task, with precued items showing greater memory precision. However, it is not clear if this effect is because of prioritization during encoding or maintenance. If some of this effect is because of prioritization during maintenance, then shifts of covert attention should lead to a loss of memory precision. It is also possible that in our task, that less attention was paid to the memory item in the shift sessions in anticipation of the peripheral probe, and this led to the overall loss

AQ: 5

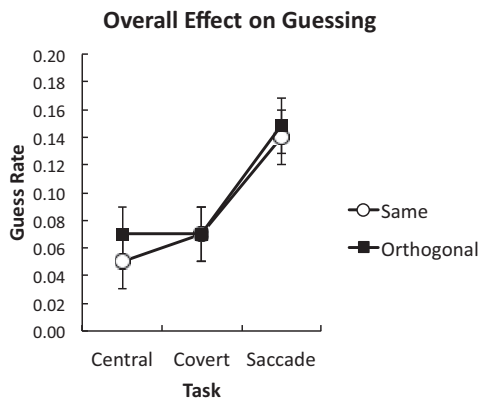


Figure 7. Effect of task and displacement axis on guessing. Error bars are uncorrected 95% confidence interval.

of precision compared with the central no-shift sessions because of poorer encoding.

AQ: 6 It is interesting that some of the same brain areas involved in SWM that show neural evidence of remapping, such as FEF and LIP, also show evidence for covert shifts (Neupane et al., 2016; Rao, Mayo, & Sommer, 2016; Wang et al., 2016; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). Spatial remapping (“forward remapping”) is indicated by receptive fields that shift in the direction of the saccade. For example, if a neuron currently has a receptive field 1° above fixation, its receptive field will move parallel to the saccade, so that it remains 1° above the future fixation target. In contrast, in neurons that show “compression” or “convergent remapping,” a receptive field that is currently 1° above fixation will shift to the saccade target, as would be predicted by a shift of covert attention preceding an eye movement.

Second, saccades lead to a marked increase in guessing. This effect was not directionally specific, which rules out remapping as an explanation (Balan & Ferrera, 2003). One possibility is that the saccade target is automatically encoded into working memory, effectively increasing the memory load (Tas et al., 2016). A number of studies have shown that as the number of items held in SWM increases, guessing also increases (Irwin & Robinson, 2015; Thiele et al., 2011). Although neither article reported precision, Irwin did provide us with their data, which we then analyzed for spatial precision. We found no meaningful changes in precision because of load, but did find an increase in guessing. Taken as a whole, these experiments suggest that if performing a saccade automatically leads to the encoding of the saccade target, then this should increase the number of locations held in SWM and result in increased rates of guessing.

Finally, our task is very similar to that used by Golomb and Kanwisher (2012), except that their task required participants to memorize a single location and to mouse click on that location after the retention interval. Of particular importance are their no-saccade and return-saccade conditions, which are conceptually similar to our central and saccade tasks, respectively. Localization errors were significantly greater in their return-saccade condition (J. Golomb, personal communication, May 30, 2017), and were unaffected by instruction type (encode retinotopically or spatiotopically). However, they did not examine the two-dimensional distribution of spatial error for skewness. Overall, their pattern of results suggests that spatial errors increase when multiple saccades are performed.

Conclusion

We found evidence for three different sources of saccade-related interference. Of the three effects, two of them, increased guessing and the directionally specific loss of memory precision, are uniquely driven by saccades, with only the latter being spatial in nature. Specifically, compared with covert attention shifts, saccadic eye movements lead to an increased loss of memory precision along the axis of the saccade, and this directionally specific effect cannot be explained by shifts of covert attention. This evidence is consistent with imaging studies showing that brain areas that are active during SWM tasks are also active during visually guided saccades (Kastner et al., 2007). In particular, shared parietal areas (intraparietal sulcus—IPS) have a retinotopic organization, suggesting that they might be the source of a common spatial repre-

sentation used by both SWM and eye movements (Bray et al., 2015; Ikkai & Curtis, 2011).

AQ: 7

References

- Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W., & Fogassi, L. (1990). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *10*, 1176–1196. <http://dx.doi.org/10.1523/JNEUROSCI.10-04-01176.1990>
- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, *230*, 456–458. <http://dx.doi.org/10.1126/science.4048942>
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*, 119–126. [http://dx.doi.org/10.1016/S1364-6613\(00\)01593-X](http://dx.doi.org/10.1016/S1364-6613(00)01593-X)
- Balan, P. F., & Ferrera, V. P. (2003). Effects of spontaneous eye movements on spatial memory in macaque periaruate cortex. *The Journal of Neuroscience*, *23*, 11392–11401. <http://dx.doi.org/10.1523/JNEUROSCI.23-36-11392.2003>
- Bays, P. M. (2014). Noise in neural populations accounts for errors in working memory. *The Journal of Neuroscience*, *34*, 3632–3645. <http://dx.doi.org/10.1523/JNEUROSCI.3204-13.2014>
- Bays, P. M., Catalao, R. F., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, *9*, 1–11. <http://dx.doi.org/10.1167/9.10.7>
- AQ: 8 Bays, P. M., & Husain, M. (2007). Spatial remapping of the visual world across saccades. *Neuroreport: For Rapid Communication of Neuroscience Research*, *18*, 1207–1213. <http://dx.doi.org/10.1097/WNR.0b013e328244e6c3>
- Bray, S., Almas, R., Arnold, A. E., Iaria, G., & MacQueen, G. (2015). Intraparietal sulcus activity and functional connectivity supporting spatial working memory manipulation. *Cerebral Cortex*, *25*, 1252–1264. <http://dx.doi.org/10.1093/cercor/bht320>
- Carlson-Radvansky, L. A. (1999). Memory for relational information across eye movements. *Attention, Perception & Psychophysics*, *61*, 919–934. <http://dx.doi.org/10.3758/BF03206906>
- Chun, M. M. (2011). Visual working memory as visual attention sustained internally over time. *Neuropsychologia*, *49*, 1407–1409. <http://dx.doi.org/10.1016/j.neuropsychologia.2011.01.029>
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*, 1827–1837. [http://dx.doi.org/10.1016/0042-6989\(95\)00294-4](http://dx.doi.org/10.1016/0042-6989(95)00294-4)
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*, 985–996. [http://dx.doi.org/10.1016/0042-6989\(95\)00203-0](http://dx.doi.org/10.1016/0042-6989(95)00203-0)
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92. <http://dx.doi.org/10.1126/science.1553535>
- Golomb, J. D., & Kanwisher, N. (2012). Retinotopic memory is more precise than spatiotopic memory. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 1796–1801. <http://dx.doi.org/10.1073/pnas.1113168109>
- Hall, N. J., & Colby, C. L. (2011). Remapping for visual stability. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *366*, 528–539. <http://dx.doi.org/10.1098/rstb.2010.0248>
- Ikkai, A., & Curtis, C. E. (2011). Common neural mechanisms supporting spatial working memory, attention and motor intention. *Neuropsychologia*, *49*, 1428–1434. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.020>
- Irwin, D. E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology*, *23*, 420–456. [http://dx.doi.org/10.1016/0010-0285\(91\)90015-G](http://dx.doi.org/10.1016/0010-0285(91)90015-G)
- AQ: 9

- Irwin, D. E. (1998). Lexical processing during saccadic eye movements. *Cognitive Psychology*, *36*, 1–27. <http://dx.doi.org/10.1006/cogp.1998.0682>
- Irwin, D. E., & Robinson, M. M. (2015). Detection of stimulus displacements across saccades is capacity-limited and biased in favor of the saccade target. *Frontiers in Systems Neuroscience*, *9*, 161. <http://dx.doi.org/10.3389/fnsys.2015.00161>
- Kastner, S., DeSimone, K., Konen, C. S., Szczepanski, S. M., Weiner, K. S., & Schneider, K. A. (2007). Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. *Journal of Neurophysiology*, *97*, 3494–3507. <http://dx.doi.org/10.1152/jn.00010.2007>
- Klyszejko, Z., Rahmati, M., & Curtis, C. E. (2014). Attentional priority determines working memory precision. *Vision Research*, *105*, 70–76. <http://dx.doi.org/10.1016/j.visres.2014.09.002>
- Lawrence, B. M., Myerson, J., & Abrams, R. A. (2004). Interference with spatial working memory: An eye movement is more than a shift of attention. *Psychonomic Bulletin & Review*, *11*, 488–494. <http://dx.doi.org/10.3758/BF03196600>
- Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *The Journal of Neuroscience*, *23*, 6209–6214. <http://dx.doi.org/10.1523/JNEUROSCI.23-15-06209.2003>
- Neupane, S., Guitton, D., & Pack, C. C. (2016). Two distinct types of remapping in primate cortical area V4. *Nature Communications*, *7*, 10402. <http://dx.doi.org/10.1038/ncomms10402>
- Olsen, R. K., Chiew, M., Buchsbaum, B. R., & Ryan, J. D. (2014). The relationship between delay period eye movements and visuospatial memory. *Journal of Vision*, *14*, 1–11. <http://dx.doi.org/10.1167/14.1.8>
- AQ: 10 Pashler, H., Carrier, M., & Hoffman, J. (1993). Saccadic eye movements and dual-task interference. *The Quarterly Journal of Experimental Psychology*, *46*, 51–82. <http://dx.doi.org/10.1080/14640749308401067>
- Pearson, D. G., Ball, K., & Smith, D. T. (2014). Oculomotor preparation as a rehearsal mechanism in spatial working memory. *Cognition*, *132*, 416–428. <http://dx.doi.org/10.1016/j.cognition.2014.05.006>
- Peterson, M. S., Kramer, A. F., & Irwin, D. E. (2004). Covert shifts of attention precede involuntary eye movements. *Perception & Psychophysics*, *66*, 398–405. <http://dx.doi.org/10.3758/BF03194888>
- Rao, H. M., Mayo, J. P., & Sommer, M. A. (2016). Circuits for presaccadic visual remapping. *Journal of Neurophysiology*, *116*, 2624–2636. <http://dx.doi.org/10.1152/jn.00182.2016>
- Smyth, M. M. (1996). Interference with rehearsal in spatial working memory in the absence of eye movements. *Quarterly Journal of Experimental Psychology, A, Human Experimental Psychology*, *49*, 940–949. <http://dx.doi.org/10.1080/713755669>
- Sommer, M. A., & Wurtz, R. H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, *296*, 1480–1482. <http://dx.doi.org/10.1126/science.1069590>
- Tas, A. C., Luck, S. J., & Hollingworth, A. (2016). The relationship between visual attention and visual working memory encoding: A dissociation between covert and overt orienting. *Journal of Experimental Psychology: Human Perception and Performance*, *42*, 1121–1138. <http://dx.doi.org/10.1037/xhp0000212>
- Thiele, J. E., Pratte, M. S., & Rouder, J. N. (2011). On perfect working-memory performance with large numbers of items. *Psychonomic Bulletin & Review*, *18*, 958–963. <http://dx.doi.org/10.3758/s13423-011-0108-7>
- Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, *78*, 1373–1383. <http://dx.doi.org/10.1152/jn.1997.78.3.1373>
- Umeno, M. M., & Goldberg, M. E. (2001). Spatial processing in the monkey frontal eye field. II. Memory responses. *Journal of Neurophysiology*, *86*, 2344–2352. <http://dx.doi.org/10.1152/jn.2001.86.5.2344>
- Vasquez, B., & Danckert, J. (2008). Direction specific costs to spatial working memory from saccadic and spatial remapping. *Neuropsychologia*, *46*, 2344–2354. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.03.006>
- Wang, X., Fung, C. C., Guan, S., Wu, S., Goldberg, M. E., & Zhang, M. (2016). Perisaccadic receptive field expansion in the lateral intraparietal area. *Neuron*, *90*, 400–409. <http://dx.doi.org/10.1016/j.neuron.2016.02.035>
- Wexler, M., & Collins, T. (2014). Orthogonal steps relieve saccadic suppression. *Journal of Vision*, *14*, 1–9. <http://dx.doi.org/10.1167/14.2.13>
- AQ: 11 Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*, 233–235. <http://dx.doi.org/10.1038/nature06860>
- Zirnsak, M., Steinmetz, N. A., Noudoost, B., Xu, K. Z., & Moore, T. (2014). Visual space is compressed in prefrontal cortex before eye movements. *Nature*, *507*, 504–507. <http://dx.doi.org/10.1038/nature13149>

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