

Attentional load interferes with target localization across saccades

W. Joseph MacInnes and Amelia R. Hunt

School of Psychology
University of Aberdeen
AB24 3FX

Corresponding author:

Dr Amelia R. Hunt

School of Psychology

University of Aberdeen

Aberdeen, UK AB24 2UB

Phone: +44 1224 273139

Fax: +44 1224 273426

Email: a.hunt@abdn.ac.uk

Abstract

The retinal positions of objects in the world change with each eye movement, but we seem to have little trouble keeping track of spatial information from one fixation to the next. We examined the role of attention in trans-saccadic localization by asking participants to localize targets while performing an attentionally-demanding secondary task. In the first experiment, attentional load decreased localization precision for a remembered target, but only when a saccade intervened between target presentation and report. We then repeated the experiment and included a salient landmark that shifted on half the trials. The shifting landmark had a larger effect on localization under high load, indicating that observers rely more on landmarks to make localization judgments under high than under low attentional load. The results suggest that attention facilitates trans-saccadic localization judgments based on spatial updating of gaze-centered coordinates when visual landmarks are not available. The availability of reliable landmarks (present in most natural circumstances), can compensate for the effects of scarce attentional resources on trans-saccadic localization.

Keywords: Spatial vision, remapping, visual attention, eye movements, attentional load

Abstract word count: 170

Main text word count: 4145

References: 39

Information in visual cortex is predominantly coded in retinotopic coordinates, meaning that visual input changes whenever the retina and world shift in relation to each other, as they do with each eye movement. Saccadic eye movements occur roughly three times per second during visual exploration of a scene, but they do not produce a noticeable disruption in our perception of the world around us. We experience a stable visual space around us, and our eye movements seem to move around within this world. How the visual system creates this *spatiotopic* experience based on an unstable and dynamic retinotopic input is an important component of the fundamental question of how perception is derived from retinal input.

The puzzle of how the visual system copes with saccades has a long history, and has been the subject of many recent reviews (e.g. Wurtz, 2008; Melcher and Colby, 2008; Mathot and Theeuwes, 2011). Given that we experience a spatiotopic view of the visual world, spatiotopic information must be acquired and maintained by the visual system at some level or in some form. Retinotopic coordinates have been characterized as the “native” reference frame, being more accurate and robust than spatiotopic representations (Golomb, Chun and Mazer, 2008; Golomb and Kanwisher, 2012a), and visual attention has been suggested to play a key role in encoding and maintaining information in spatiotopic coordinates. For instance, several studies have used fMRI in combination with eye movements to dissociate spatiotopic and retinotopic coding in visual maps in the brain. Of the studies that have done this, two have reported spatiotopic representations (i.e. activation of the same area of cortex irrespective of eye position) specifically in area MT (D’Avossa et al., 2007) and in LOC (McKyton and Zohary, 2007), while two others find consistent retinotopy

throughout all visual areas, including MT and LOC (Gardner, Merriam, Movshon and Heeger, 2008; Golomb and Kanwisher, 2012b). Similarly mixed results have emerged from attempts to find evidence of spatiotopic representations using perceptual measures. Some studies report trans-saccadic integration of motion signals (Melcher and Morrone, 2003) and spatiotopic aftereffects of adaptation to low-level visual features (e.g. Melcher, 2005), consistent with spatiotopic representations of these features, and others find no evidence of transsaccadic integration of visual information (e.g., Irwin, Yantis and Jonides, 1983; McKyton, Pertzov and Zohary, 2009) and aftereffects that are exclusively retinotopic (e.g., Knapen, Rolfs & Cavanagh, 2009; Wenderoth and Wiese, 2008). Spatial attention may play a role in resolving the discrepancy: Crespi et al. (2011) found that responses in MT were retinotopic when participants engaged in an attentionally-demanding task at fixation (monitoring the central fixation point for a luminance decrement), but when no central task was performed, spatiotopic coding was observed, presumably because attentional resources were available. Attention therefore may influence how space is encoded, although it is important to note that Golomb and Kanwisher (2012a) found no evidence of spatiotopic encoding in any area of visual cortex, even when spatial location was task relevant and attention was freely available for encoding stimuli in a spatiotopic reference frame.

Attention has been suggested to play a role in *saccadic remapping*. Saccadic remapping generally refers to a predictive neural response to visual stimuli that are about to be brought into a cell's receptive field by an eye movement. Duhamel, Colby & Goldberg (1992) first observed remapping in visual cells in the lateral intraparietal cortex (LIP). LIP contains a retinotopic

map with activity peaks corresponding to locations that are attended, visually salient and/or the targets of future actions or responses (e.g., Bisley and Goldberg, 2003; Goldberg, Bisley, Powell, Gottlieb, & Kusonoki, 2002). Duhamel and colleagues demonstrated that the majority of cells in LIP responded not only to stimuli in their classic receptive field, but also to stimuli just prior to an imminent saccade that would land in that cell's receptive field after that saccade was completed. Further research demonstrated that only attended locations, rather than the entire visual field, are remapped before a saccade (Gottlieb, Kusinoki & Goldberg, 1998), and Wurtz (2008) noted that remapping of a subset of attended locations is all that is really needed for visual stability to be achieved. Cavanagh, Hunt, Afraz, and Rolfs (2010) suggested an even larger role for attention in remapping. Rather than the receptive fields of visual cells shifting to receive information from the expected new receptive field location, as had been suggested by many (e.g. Melcher and Colby, 2008; Burr and Morrone, 2013), Cavanagh et al. suggested instead that pointers to attended retinotopic locations are remapped just prior to a saccade. That is, activity peaks in visual cells of areas like LIP and FEF, which correspond to attended locations, are transferred to the retinotopic coordinates in which those attended targets are expected to appear a few moments in the future on the basis of the amplitude and trajectory of the eye movement that is about to be executed. The predictive response of neurons in response to expected changes in the visual field produced by an impending saccade, under this model, reflect a shift of pointers to attended locations. Under this idea, attention is critical for remapping.

Behavioural experiments provide support for the notion that attention shifts predictively to remain focused on the expected new retinotopic locations

of targets when an eye movement is about to shift those targets across the retina. Backward visual masking can be observed when masks are placed at the future location of an attended target just prior to a saccade (Hunt & Cavanagh, 2011), and there is increased sensitivity to discriminate probes that are presented at the expected new retinotopic location of saccade targets across a sequence of saccades (Rolfs, Jonikaitis, Deubel & Cavanagh, 2011), and this shift, like the remapping in visual neurons, can be observed even before the eye movement (Jonakaitis, Szinte, Rolfs and Cavanagh, 2013). However, it is not known whether attention is strictly necessary for maintaining spatial information across saccades, or if the predictive shift serves only to keep attention focused on behaviourally relevant locations, with no consequence for accuracy of spatial representations.

The question of the role of attention in maintaining information about a target's locations across saccades is complicated by the fact that there are many reference frames in which a target's location could be encoded. Egocentric frames of reference include head- and hand-centric coordinates in addition to gaze-centric frames, while allocentric frames of reference include environment landmarks and their relation to spatial objects of interest. The encoding of spatial position is primarily retinotopic or gaze-centered even in parietal cortex (e.g. Batista, Buneo, Snyder & Anderson, 1999; Buneo, Jarvis, Batista and Anderson, 2002), but behaviourally we are clearly capable of using information from many frames of reference to guide our actions. Saccades are more accurate when environment landmarks are present (Deubel, 2004) as is localization with reaching to current (Conti & Beaubaton, 1980) and remembered target locations (Krigolson & Heath, 2004). Online adjustments to reaching are also improved by

landmarks when the reaching limb is visible (Coello & Grealy, 1997) although this results in longer reach times to incorporate the additional coordinate system (Krigolson, Clark, Heath & Binstead, 2007). Gaze-centered coordinates have been shown to contribute to localization of targets even in the presence of landmarks (Schütz, Henriques, and Fiehler, 2013), suggesting the two sources of input may be flexibly combined into a single representation of target location. Tasks in which locations must be remembered for later report will also engage spatial working memory processes, which also have been argued to depend on attention (Awh & Jonides, 2001). How these different mechanisms of spatial perception combine to give us a unitary perception of a given location is an interesting question that we will return to in the discussion.

The current experiments examined the role of attention in keeping track of locations across saccades by measuring localization performance under conditions of high and low attentional load. A location probe was presented in the periphery at the beginning of each trial. Participants then monitored a stream at fixation for an easy or difficult target, and the stream remained at center or shifted to the left or right, eliciting a saccade. The remembered location of the probe was indicated using the mouse. If attention contributes to remapping, as the framework of Cavanagh et al (2010) and results from Crespi et al. (2011) suggest, diverting attention away from a target should degrade the spatial representation of it, particularly when a saccade is executed that shifts it from one retinotopic position to another. The pattern of errors can shed light on the nature of the contribution of attention. For example, a modest increase in the distribution of errors will indicate a general loss of fidelity in the representation of location. An increase in the number of extreme errors would indicate an

occasional but total failure to maintain a representation. A bias in errors that is related to the direction of the eye movement will suggest a systematic failure in accounting or compensating for the eye movement. Given the alternative reference frames for encoding location information reviewed above, we expect diverting attention will result in a modest decrease in the accuracy of localization rather than a catastrophic breakdown. We attempt to limit the use of environmental cues for encoding location information by presenting stimuli on an OLED display in a darkened room in Experiment 1. In Experiment 2 we attempt to measure the contribution of environmental cues to localization directly by presenting and by manipulating landmarks.

Experiment 1

Method

Participants. Six students or members of staff at the University of Aberdeen volunteered for the study and gave informed consent to participate. All had normal or corrected-to-normal vision. The study was approved by the School of Psychology ethics committee at the University of Aberdeen.

Apparatus. Stimuli were presented on a 61cm Sony Trimeter OLED monitor and were controlled by an Apple Mac Pro (2.93 GHz, 6GB Ram, OS 10.6.4) using PsychToolbox 3 (Brainard, 1997). The OLED monitor was used to minimize ambient light, and background pixels were measured at 0.00 cd/m² while central stimuli were being displayed. All remaining light sources in the experiment room were extinguished. To disrupt dark adaptation during the experiment, each trial began with a bright screen (17.1 cd/m²) instructing participants to press the space bar.

Stimuli and Procedure. Six blocks of 30 trials (three blocks at high load and three blocks of low load) were completed, in a different random order for each participant. See Figure 1 for an illustration of the display and Figure 2 for an example timeline from a single trial. Two tasks were performed: a vernier acuity stream task to manipulate attention, and a localization task to measure spatial memory for a probe.

Vernier acuity task. A stream of pairs of vertical line segments was shown one at a time, with each pair presented for 100 ms followed by a temporal gap of 500 ms. All vernier pairs were grey (0.4 cd/m^2), had a total vertical height of 0.5° and separated with a mid-vertical gap of 0.27° . Participants were instructed to respond with a keyboard press whenever the lines on the screen were not aligned. Load was manipulated by misaligning the vernier line segments less in the high load (0.038°) than in the low load (0.35°) condition (see Figure 1), so that misalignments in the low load stream were easier to detect and therefore required less attention. The stream lasted for six seconds, and each vernier pair had an independent 15% chance of being a misaligned (target) pair. Vernier targets were never presented immediately prior to a shift in the stream's location to prevent saccadic influence on the vernier task (Cai, Pouget, Schlag-Rey & Schlag, 1997). The vernier stream was equally likely to remain in its initial central location (1/3 of trials) or shift to the left (1/3) or right (1/3) by 7° . Stream shift occurred 3s after trial onset, and 1s after the probe had been removed. Participants were instructed to follow the stream when it shifted and continue with responses to the vernier task. To prevent participants from localizing the probe relative to the central stream location, we applied a random variance of 1.0° to the initial stream location, and also to the second stream

location in the saccadic shift conditions. The load manipulation was blocked and eight practice trials prior to each block prepared participants to expect easy or difficult targets. Block order was randomized across participants. The independent probability of stream targets meant most trials had fewer than two targets. We included only these trials in the analysis.

Localization task. Simultaneous with the onset of the first element in the vernier task, a localization probe (a small light grey (0.4 cd/m^2) circle, 0.2° in diameter) was presented for 2s in the upper half of the screen. Placement of the probe was randomly selected to be within an 8° (non-rendered) square, with a minimum distance of 1.2° above the vernier stream. Participants were instructed to remember the location of the probe, but not to look at it. Once the vernier stream was finished, the mouse cursor re-appeared at a random location on the screen and participants were instructed to use the mouse to select the remembered location of the probe on the screen by clicking on it. Feedback on the Vernier task was given to participants during practice trials, but no feedback was given on the localization task.

Analysis. Trials were excluded if participants failed to respond to a vernier target (13%) or if the localization error exceeded three standard deviations from the mean (1%). Participants missed more vernier targets in the difficult condition (21%) than the easy condition (4%) ($t(5) = 11.9, p < .001$). All statistics were run using the R statistics package using the type III AOV function for ANOVAs.

Results

Error in localization was measured as the Euclidean distance in visual degrees between actual and reported probe location. The overall mean error

was 2.21° ($sd=1.22$). Results were subjected to a within-subjects ANOVA with Load (high or low) and Saccade (saccade or no saccade) as factors. There was a main effect of Saccade ($F(1,5) = 19.5$, $p=.007$, $\eta^2_G=.24$), reflecting greater localization errors after making a saccade, however this was qualified by a significant interaction between Load and Saccade ($F(1,5)=16.2$), $p=.010$, $\eta^2_G=.13$), due to the saccade effect being significant only in the high load condition ($t(1,5)=7.4$, $p<.001$, $d=3.7$) and the load effect being significant only in the saccade condition ($t(1,5)=2.6$, $p=.048$, $d=1.6$, see Figure 3 for the interaction, and Figure 4 (a,b) for the distribution of localization responses). This interaction was consistent across all participants in that everyone showed larger costs of high load in the saccade condition as compared to the no saccade condition. No other effects were significant.

To assess potential bias in direction of localization errors, we repeated the Load * Saccade ANOVA above, except we separated the Saccade factor into three levels (left, right and no saccade) and used the signed horizontal error as the dependent measure of localization accuracy. There was no significant effect of the Saccade Direction factor, and no interaction with Load ($F(1,5) < 1$). We also analyzed the standard deviation of localization error using a two (Load) x three (Left, Right or No Saccade) ANOVA. There was a trend towards greater standard deviation on saccade trials ($F(1,5)=4.3$, $p = .093$) but no effect of load or interaction (both $F(1,5) < 1$). See Figure 4a and 4b for an illustration of the distributions of errors. Together these results suggest horizontal saccades increase the distribution of horizontal errors, but the direction (left/right) of the saccade does not influence localization in any systematic way.

The results therefore confirmed the prediction that attentional load disrupts localization, specifically on saccade trials. The saccade did not introduce significant errors to localization in the low-load task ($t(1,5) < 1.0$), presumably because spatial attention was maintained on the remembered location of the target when that location shifted across the retina as a consequence of the saccade. With diminished availability of attention, the saccade increased localization errors. The increase in localization error can be best characterized as a general loss of the fidelity of horizontal position information.

Experiment 2

In a second experiment, instead of eliminating landmarks, we presented and explicitly manipulated a salient landmark, in the form of a border around the probe location (Figure 1). We shifted the border during the saccade on some of the trials. The degree to which the border shift disrupts localization should reveal the degree to which the probe location was encoded relative to the border location. To implement this manipulation we needed to monitor eye position. The eye monitor itself emits visible light, making it impossible to eliminate other landmarks besides the border we introduced. Therefore in this experiment we are primarily interested in comparing the effect of shifting the border under high- and low-load conditions. If attentional load impairs the updating of retinal coordinates across a saccade, participants may rely on the border more. If so, shifting the border during a saccade would consequently disrupt localization more under high load than under low load conditions. This should result in a three-way interaction between load, the saccade, and the border shift, with the greatest error induced by shifting the border during a saccade under high load.

Materials and Methods

Participants. Twelve students or members of staff at the University of Aberdeen gave informed consent to participate in two sessions of 45 minutes each. All had normal or corrected-to-normal vision.

Apparatus. Eye movements were monitored using an EyeLink 1000 (SR Research, Mississauga, Canada) in the desktop configuration, sampling eye position at a rate of 1000Hz. The head was stabilized in a chin rest 65cm from a 61cm CRT monitor with a refresh rate of 100Hz.

Stimuli and Procedure. The trials matched Experiment 1, with the exception of the following. An explicit landmark was displayed on half the trials, in the form of a 10° dark grey ($.45 \text{ cd/m}^2$) square border surrounding the range of possible probe locations (see Figure 1). The border appeared simultaneously with the onset of the probe and vernier stream and remained on the screen until the end of the trial. On half of the trials in which the border was presented, it shifted 1.0° up or down while on the other half of the trials, it remained in the same position. On saccade trials, the shift was triggered when the start of the saccade was detected. On no-saccade trials the shift occurred at the midpoint of the vernier stream (3s). The probe location was at least 1.2° from the border edge to prevent the shift from overlapping the probe. Each session consisted of four blocks of 48 trials (two blocks of each difficulty level in a randomized order). The horizontal distance between vernier lines was set to $.033^\circ$ (high load) and $.23^\circ$ (low load). Each block was preceded by 16 practice trials. The instructions to participants were the same as Experiment 1, and no explicit instructions were given regarding the border. There were no differences between the two sessions and data were combined for analysis.

Analysis. Trials were excluded if 1) participants moved their eyes greater than 1.5° away from the vernier stream while the probe was visible (2.7%); 2) participants failed to respond to a vernier target (17.7%); 3) short saccades or delays in saccade detection and the monitor refresh rate led to the border shift occurring after the end of the saccade (1.4%); 4) the trial timed out without a probe response (0%). Average number of excluded trials was 21%. One participant was replaced for having more than 50% excluded trials. Participants missed more vernier targets in the high load condition (22%) than the low load condition (12%) ($t(11) = 5.2, p < .001, d = 2.5$).

Results

To assess whether participants made use of the border in localization, we first compared localization errors on trials with no border against those with a stable (non-shifting) border. Error in localization as measured by the mean Euclidean distance between actual and reported probe location was subjected to a within-subjects ANOVA with Environment (border present vs. absent), Load (high vs. low) and Saccade (saccade vs. no saccade) as factors. There was a significant effect of Environment ($F(1,11) = 31.6, p < .001, \eta^2_G = .57$) with a visible, stable border reducing localization error by 0.45°. There was also a main effect of Saccade ($F(1,11) = 10.0, p = .009, \eta^2_G = .10$) with saccades resulting in a 0.13° increase in errors compared to no saccade. There were no other main effects or interactions. This analysis provides evidence that participants were using the border to reduce their error. To corroborate that this reduction in error was due to a general restriction of variability, we also examined the standard deviations, and observed a similar a reduction in standard deviation with a border present ($F(1,11) = 8.2, p = .015, \eta^2_G = .12$). No other main effects or interactions were

significant. The absence of an interaction between saccade and load is in contrast with Experiment 1, however, unlike in Experiment 1, here there were visible landmarks in all conditions so participants could compensate for the effect of shifts by using existing environmental landmarks.

Having established that a stable border improved accuracy in localizing the target, we went on to examine the effect of shifting the border. Trials in which a border was present were subjected to a within-subjects ANOVA with Environment (shift vs. no shift), Load (high vs. low), and Saccade (saccade vs. no saccade) as factors. There was a main effect of Environment ($F(1,11)=7.1, p=.022, \eta^2_G=.09$) with larger errors on shift trials. There was also a main effect of Saccade, with larger errors than with no saccade ($F(1,11)=5.1, p=.045, \eta^2_G=.07$). Finally, we observed the critical three-way interaction (Figure 5) predicted above (Environment x Load x Saccade, $F(1,11)=5.1, p=.045, \eta^2_G=.03$) reflecting an increased cost of shifting the border in mid saccade under high load (cost = $.17^\circ$) than under low load (cost = $.05^\circ$), see Figure 5. Planned t-tests showed that the difference between border shift and no-shift conditions was significant only during saccades under high load ($t(11)=2.7, p=.021, d=0.7$). Under low load and with no saccade, this difference was not significant (all p 's $>.1$). The results therefore demonstrate an effect of shifting the border only during a saccade and under high load conditions. Scarce attentional resources may lead to a failure to register or compensate for the border shift, and also perhaps encourage a strategy of using allocentric instead of retinotopic coordinates to encode and report the target's remembered location. Note that shifting the border did not remove the advantage of including it in the first place (see Figure 5; the

difference between border and no border was significant in all conditions (all p 's $<.01$).

To mirror the analyses in Experiment 1, we also assessed whether there were systematic left or right biases associated with left or right saccades, by repeating the Load x Environment x Saccade ANOVA with saccade direction separated into three levels (left, right, and no saccade), using signed horizontal localization error as the dependent variable. Similar to Experiment 1, there was no effect of saccade direction ($F(1,11) < 1.0$), and no interactions involving saccadic direction (see Table 1 for values). We also applied the same ANOVA but with the standard deviation of the error as the dependent variable. The three-way interaction was the only significant effect ($F(1,11)=14.8$, $p = .003$, $\eta^2_G = .03$) and replicates the results using mean Euclidean error reported above: The spread of localization responses is greatest when the border shifts during a saccade under high load.

We also analyzed the data for direction-specific effects of border shift. The Load x Environment x Saccade ANOVA was repeated with Environment shift split into three levels (Up, Down, No shift), Saccade returned to two levels (Saccade/No Saccade) and with signed vertical error as the dependent measure. There was a main effect of Environment ($F(2,22) = 43.0$, $p < .001$, $\eta^2_G = .38$) with downward shift (-.90) and no shift (-.71) showing a downward bias and upward shift (.09) showing a slight upward bias. Environment also interacted with Load ($F(2,22) = 3.5$, $p = .048$, $\eta^2_G = .03$): this was largely due to the upward bias for upward border shifts being eliminated under load (see Table 1, the load effect when the border shifted up was marginal $t(11)=2.0$, $p=.072$, and it was not significant for the stable and downward-shifting border). This analysis

demonstrates a tendency for localization errors to follow the direction of the border shift (seen in Table 1 and Figure 4e and 4f), but it is not error consistent with the shift direction of the border per se that is increased by load. Rather, there is a small increase in a downward bias when the border shifts under load (see Table 1 for values).

Horizontal Error	Saccade Left	No Saccade	Saccade Right
Low load	0.08	0.05	0.14
High load	-0.05	0.09	0.15
Vertical Error	Border shift down	No shift	Border shift up
Low load	-0.80	-0.77	0.26
High load	-1.00	-0.67	-0.08

Table 1. Experiment 2 directional biases. The effect of Load on directional localization error (in degrees visual angle) is shown for saccade direction (first two lines) and for border shift direction (last two lines). For horizontal error, rightward signed errors are positive and leftward signed errors are negative. For vertical errors, upward signed errors are positive and downward signed errors are negative.

Saccade errors did not differ between load conditions. There was no difference in the number of eye movements which missed the new stream location ($t(11) < 1.0$), and the standard deviations of the landing position of saccades to the stream were virtually identical under high load (1.2°) and low load (1.2°), ($t(11) < 1.0$).

Discussion

In the absence of environmental cues (Experiment 1), trans-saccadic localization accuracy was diminished by the attentional load manipulation, suggesting the ability to maintain precise location information across saccades depends, in part, on the availability of attentional resources. There was also a

marked increase in localization errors when we shifted the border under high attentional load in Experiment 2. Our interpretation of this pattern of results is that, under low load, participants were able to rely on both remapped retinotopic and allocentric coordinates in localizing the target, leading performance to be robust against shifts in landmarks. Under high load, however, the ability to remap was degraded, and participants had to rely more heavily on an allocentric strategy. When the border shifted, this allocentric strategy, together with a diminished ability to use retinotopic coordinates, led to an increase in errors relative to when the border was stable. The general idea that the availability of attention can influence the frame of reference in which a target is encoded or updated is consistent with Crespi et al. (2011), who came to a similar conclusion based on fMRI activity.

As seen in the distribution of localization responses under load (Figure 4), the increase in localization error on saccade trials was not due to a systematic spatial bias. That is, moving the eyes to the left or right led to a general loss in the precision with which the target's horizontal location was represented, rather than a failure to compensate for the specific direction of the retinal shift. That said, saccades were exclusively horizontal in our experiment, and the loss of precision associated with saccades was only observed in the horizontal dimension, and not in the vertical dimension. Thus the saccade appears to increase errors along the same plane as the saccade, but not necessarily in (or against) the same direction.

Likewise, there was an overall localization bias toward the direction of the border shift, consistent with the target locations being encoded or reported in reference to the border. However, the size of the bias was smaller than the

border shift itself, and what increased under load was not error in the direction of the border shift per se, but the overall distribution of errors, as well as the tendency to report the target location as lower on the screen than it actually was. Perhaps participants were aware that the border had shifted even on saccade trials, but not confident about the direction in which it shifted, leading to uncertainty about the target location. Responses tend to be biased away from extreme values under uncertainty (e.g., Radvansky, Carlson-Radvansky and Irwin, 1995), which could lead to a downward bias in this context. Had the border shift been completely masked by the saccade (for example, if the shift were smaller or in the same direction as the saccade), more errors consistent with the direction shift would certainly have been observed, and this component of the error may have interacted with load.

The distribution of errors is also not consistent with an occasional but total breakdown in the ability to remember the location of the probe; this would lead to an increased number of trials with very large errors in the high-load condition. Instead, we observe a modest increase in the spread of errors around the correct response. An increase in the overall variance of responses on high-load trials suggests a general loss of fidelity in the representation of target location on high-load trials relative to low-load trials, leading to less precise location judgments on average. The increase in variance is consistent with a study by Golomb and Kanwisher (2012b), in which a similar increase in the variance of localization in spatiotopic coordinates over retinotopic coordinates was observed. It should also be noted that they did not find an effect of landmarks in their experiment. However, unlike in our experiment, they used

single points as landmarks rather than a border, and other environmental cues (e.g. monitor edge) were available to observers in all conditions.

As discussed in the introduction, attention has been suggested to play a key role in supporting spatial vision across saccades (Cavanagh et al., 2010). However, it is important to also consider that attention has been shown to be reliably and obligatorily allocated to a saccade goal immediately prior to a saccade being executed (e.g. Hoffman and Subramanian, 1995; Deubel, Schneider and Bridgeman, 1996). How would this pre-saccadic shift of attention to the saccade goal influence localization performance in our experiment? The attentional load task appeared at screen center, and then shifted to the left or right to cue the eye movement. Attention would presumably be diverted to the new fixation location just before the saccade was executed, and this would be true in both the high-load condition and in the low-load condition, regardless of how much attention was actually needed to detect the vernier targets. If the attention needed to detect the vernier targets were the same as the attention required to program and execute the eye movement (as Deubel et al., 1996, suggests), then the shift of attention to the saccade target would have *reduced* the difference between high- and low-load on saccade trials, rather than increased it, as we observed. It is possible that both of these effects exist simultaneously in the results, but the effect of diminished attention to the target on peripheral localization is stronger and carries the interaction.

Attention has also been argued to play a key role in the maintenance of information in spatial working memory (Awh and Jonides, 2001). Directing attention towards the remembered location of a spatial probe led to both faster reaction time to detect a target appearing there, and better accuracy in

remembering the location of the probe relative to when attention was directed to a different location (Awh, Jonides and Reuter-Lorenz, 1998). These authors argue that spatial attention is involved in the rehearsal of information in spatial working memory. Although we did not observe an effect of the probe on localization performance in the absence of a saccade here, it is important to note that this does not directly contradict the results of Awh et al (1998) because the experiments are substantially different: the most important difference is that the attention target and the probe were always in different locations in our experiment. Had we included a condition in which they were in the same location, localization performance would probably have improved.

Although our data do not speak directly to the relationship between spatial working memory and spatial updating across saccades, it is interesting to speculate about the shared role of attention in both processes. In our experiment, holding a spatial location in working memory is required in both saccade and no-saccade conditions. Unique to the saccade condition is that the representation of the probe location must account for the shift in eye position (in the absence of environmental cues in Experiment 1), and perhaps integrate eye position information with other cues such as available visual landmarks (such as those presented in Experiment 2). If rehearsal of spatial information and spatial updating both depend on attention, performing both simultaneously would degrade spatial representations more than performing either alone. Indeed, limited attention is a plausible explanation for the strong interference with spatial working memory that is observed when eye movements are performed during the retention interval (e.g. Pearson and Sahraie, 2003). An interesting recent study by Golomb and Kanwisher (2012a) measured how precisely

observers were able to localize remembered targets in either retinotopic or spatiotopic coordinates and found that the retinotopic memory is more precise, and over multiple saccades, the spatiotopic memory degrades while the retinotopic memory does not. This too suggests that it is not the saccade *per se* that interferes with spatial working memory, but the combination of spatial working memory and spatial updating to compensate for saccades (which is not required for localization in retinotopic coordinates). Many experiments designed to understand spatiotopic representations, like the present one, involve spatial working memory in some form or another, because of delays between the target presentation and report. This raises for future research an important and interesting question of how remapping operates within spatial working memory and how this relates to remapping that does not involve memory.

Remapping in single-cell studies has been shown to begin around 100ms before saccade onset (Duhamel et al., 1992) and this is mirrored in the putative perceptual effects of remapping (Hunt & Cavanagh, 2009). Based on this, the critical period for disrupting localization by distracting attention may be immediately before and during the eye movement itself. In our experiment, we engaged attention in the stream task around this time, and we can tentatively suggest that precision in the representation of the target's location decreased for this reason. However, the stream task also began well before the saccade was elicited and persisted after it was completed. An open question is when exactly around the time of the saccade that manipulations of attention have their biggest impact on localization, to better specify the role of pre-saccadic and post-saccadic mechanisms.

Our results suggest attention contributes to spatial updating of gaze-centered coordinates across saccades, but we do not claim that attention is *not* necessary for encoding targets in environmental coordinates. The target probe and the border were presented at the same time as the stream began, allowing for encoding of the target's position relative to the border from the outset of the trial. The border then remained present on the screen for the duration of the trial. Increasing load did not have any impact on the degree to which the border benefited localization; one might have expected larger benefits of landmarks under conditions of high load if landmarks provide a compensatory route through which localization information that was lost during remapping can be retrieved. However, in the second experiment we made no effort to eliminate other environmental landmarks in addition to the border around the localization target (we did not attempt this because the eye monitor itself emits visible light, making it impossible to both monitor eye movements and also eliminate all environmental cues). It is therefore likely that even without the explicit border surrounding the target, participants were able to compensate by using the edges of the monitor itself to localize the target instead. It is also likely that the presence of the border around the remembered target location at the time of response constrained the participants to respond within this border, thereby reducing error. A contribution of response bias to the effect of landmark presence on localization error could also explain why there was no interaction of this effect with attentional load. A final point is that the benefit of the landmark was substantial, and the shifts in the border location introduced relatively small errors, and only under load. Had we used larger or more frequent border shifts, this may have dissuaded participants from using the frame. If participants tried

to actively ignore the border because it was consistently unreliable, interactions of the presence of the landmark with the load manipulation may have been observed.

The results of Experiment 1 demonstrate that the ability to keep track of locations in spatial coordinates across saccades in an environment devoid of landmarks is dependent, at least in part, on attention. Given how unusual an environment completely devoid of landmarks is in everyday life, it is unlikely that failures in attention would routinely give rise to a loss of spatial information. The results of Experiment 2 suggest that participants were able to augment location information based on remapping of retinotopic coordinates by using environment-based cues, which is consistent with previous studies (Lemay, Bertram, & Stelmach, 2004; Schütz et al., 2013; but see Sheth & Shimojo, 2004). This means that as long as there are multiple frames of reference through which participants can encode and recall the target's location, it is possible to compensate when one becomes less reliable or available.

Conclusions

Our results provide support for a model of remapping that is based on shifts of spatial attention that precede the saccade (Cavanagh et al., 2010). Previous work pointed in a similar direction – for example, showing that attention shifts to remain focused on the retinotopic coordinates of currently-attended targets as the eyes move (Hunt and Cavanagh, 2011; Rolfs et al., 2011), and that remapping at the neural level is applied only to attended targets (Gottlieb et al., 1998). While previous results show that attention shifts to keep track of targets, and that attended targets are remapped, they fall short of showing that location information across saccades depends, to any extent, on attention. Here we have

demonstrated that limiting the availability of attention degrades the precision of location judgments, specifically when a saccade intervenes between the initial presentation and the localization response. Our findings also emphasize that remapping is one of many sources of location information. Under most conditions, the strategy of using relative environmental coordinates to encode target locations will provide an additional useful cue to spatial layout across saccades.

Acknowledgements

This research was supported by grants from the BBSRC (BB/H01280X/1) and the James S McDonnell Foundation (both to A.R.H). The authors would like to thank Kelly Norman for assistance with data collection, and the members of the Perception and Attention theme at the University of Aberdeen for feedback and discussion.

References

- Awh E, Jonides J (2001) Overlapping mechanisms of attention and spatial working memory. *Trends Cogn Sci* 5: 119-126.
- Awh E, Jonides J, Reuter-Lorenz PA (1998). Rehearsal in spatial working memory. *J Exp Psych: Hum Percept Perform* 24: 780-790.
- Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. *Science* 285: 257–260.
- Bisley J, Goldberg ME (2003) Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299: 81-86.
- Brainard DH (1997) The Psychophysics Toolbox, *Spat Vis* 10: 433-436.
- Buneo CA, Jarvis MR, Batista AP, Andersen RA (2002) Direct visuomotor transformations for reaching. *Nature* 416: 632–636.

Burr DC, Morrone MC (2013) Constructing stable maps of the world. *Perception* 41: 1355–1372.

Cai RH, Pouget A, Schlag-Rey M, Schlag J (1997) Perceived geometrical relationships affected by eye-movement signals. *Nature* 386: 601-604.

Cavanagh P, Hunt AR, Afraz A, Rolfs M (2010) Visual stability based on remapping of attention pointers. *Trends Cogn Sci* 14: 147-153.

Coello Y, Grealy M (1997) Effect of size and frame of visual field on the accuracy of an aiming movement. *Perception* 26: 287–300.

Conti PD, Beaubaton D (1980) Role of structured visual field and visual reafference in accuracy of pointing movements. *Percept Mot Skills* 50: 239–244.

Crespi S, Biagi L, d'Avossa G, Burr DC, Tosetti M, Morrone MC (2011) Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS ONE* 6(7): e21661. doi:10.1371/journal.pone.0021661

d'Avossa G, Tosetti M, Crespi S, Biagi L, Burr DC, Morrone MC (2007) Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nat Neurosci* 10: 249-255.

Deubel H (2004) Localization of targets across saccades: Role of landmark objects. *Vis Cogn* 11: 173-202.

Deubel H, Schneider WX, Bridgeman B (1996) Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res* 36: 985-996.

Duhamel JR, Colby CL, Goldberg ME (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90–92.

Gardner JL, Merriam EP, Movshon JA, Heeger DJ (2008) Maps of visual space in human occipital cortex are retinotopic, not spatiotopic. *J Neurosci* 28: 3988-3999.

- Goldberg ME, Bisley J, Powell KD, Gottlieb J, Kusunoki M (2002) The role of the lateral intraparietal area of the monkey in the generation of visual saccades and visuospatial attention. *Ann N Y Acad Sci* 956: 205–215.
- Golomb, JD, Chun, MM, Mazer, JA (2008) The native coordinate system of spatial attention is retinotopic *Jour of Neur*, 28(42): 10654-10662.
- Golomb JD, Kanwisher N (2012a) Higher level visual cortex represents retinotopic, not spatiotopic, object location. *Cereb Cortex* 22: 2794-2810.
- Golomb JD, Kanwisher N (2012b) Retinotopic memory is more precise than spatiotopic memory. *Proceed Nat Acad Sci* 109: 1796-1801.
- Gottlieb J, Kusunoki M, Goldberg M (1998) The representation of visual salience in monkey parietal cortex. *Nature* 391: 481-484.
- Hoffman JE, Subramaniam B (1995) The role of visual attention in saccadic eye movements. *Percept Psychophys* 57: 787-795.
- Hunt AR, Cavanagh P (2011) Remapped visual masking. *J Vis* 11: 1-8.
- Hunt AR, Cavanagh P (2009) The perceived direction of gaze shifts before the eyes move. *J Vis* 9: 1-7.
- Irwin DE, Yantis S, Jonides J (1983) Evidence against visual integration across saccadic eye movements. *Percept Psychophys* 34: 49-57.
- Jonikaitis D, Szinte M, Rolfs M, Cavanagh P (2013) Allocation of attention across saccades. *J Neurophysiol* 109: 1425-1434.
- Radvansky GA, Carlson-Radvansky LA, Irwin DE (1995) Uncertainty in estimating distances from memory. *Mem Cognit* 23:596-606.
- Knapen T, Rolfs M, Cavanagh P (2009) The reference frame of the motion aftereffect is retinotopic. *J Vis* 9: 1-6.

- Krigolson O, Heath M (2004) Background visual cues and memory-guided reaching. *Hum Mov Sci* 23: 861–877.
- Krigolson O, Clark N, Heath M, Binsted G (2007) The proximity of visual landmarks impacts reaching performance. *Spat Vis* 20: 317–336.
- Lemay M, Bertram BM, Stelmach GE (2004) Pointing to an allocentric and egocentric remembered target. *Motor control* 8: 16-32.
- Mathôt S, Theeuwes J (2011) Visual attention and stability. *Philos Trans R Soc Lond B Biol Sci* 366: 516-527.
- McKyton A, Zohary E (2007) Beyond retinotopic mapping: the spatial representation of objects in the human lateral occipital complex. *Cereb Cortex* 17: 1164-1172.
- McKyton A, Pertzov Y, Zohary E (2009) Pattern matching is assessed in retinotopic coordinates. *J Vis* 9: 1-10.
- Melcher DE, Colby CL (2008) Trans-saccadic perception. *Trends Cogn Sci* 12: 466-476.
- Melcher DE (2005) Accumulation and persistence of memory for natural scenes. *J Vis* 6: 8-17.
- Melcher D, Morrone MC (2003) Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nat Neurosci* 6: 877-881.
- Pearson D, Sahraie A (2003) Oculomotor control and the maintenance of spatially and temporally distributed events in visuo-spatial working memory. *Quart J Exp Psychol* 56 1089-1111.
- Rolfs M, Jonikaitis D, Deubel H, Cavanagh P (2011) Predictive remapping of attention across eye movements. *Nat Neurosci* 14: 252-256.
- Schütz I, Henriques DYP, Fiehler K (2013) Gaze-centered spatial updating in delayed reaching even in the presence of landmarks. *Vision Res* 87: 46-52.

Sheth BR, Shimojo S (2004) Extrinsic cues suppress the encoding of intrinsic cues. *J Cogn Neurosci* 16: 339–350.

Wenderoth P, Wiese M (2008) Retinotopic encoding of the direction aftereffect. *Vision Res* 48: 1949-1954.

Wurtz RH (2008) Neuronal mechanisms of visual stability. *Vision Res* 48: 2070–2089.

Figure Captions

Figure 1 Screen layout and timeline for Experiment 1. All environmental cues were eliminated and the localization target was removed prior to the shift to the second stream.

Figure 2. Screen layout and sequence of events for Experiment 2. In the second experiment, the environment marker onset simultaneously with the probe and Vernier stream and its shift was triggered by the onset of the saccade that was executed in response to the stream moving to the left or right.

Figure 3 The effect of Load and Saccade on localization error (mean Euclidean distance between the actual probe location and the reported location) in Experiment 1. The interaction is significant.

Figure 4 Spatial distribution of responses to the probes split by saccade condition and collapsed across load. Data are shown separately for A) Experiment 1 horizontal errors, B) Experiment 1 vertical errors, C) Experiment 2 horizontal errors for saccade directions D) Experiment 2 vertical errors by saccade directions, E) Experiment 2 horizontal errors for shift directions F) Experiment 2 vertical errors by shift directions. There are no biases in distribution due to saccadic direction, but observed cost of saccades to localization error seems mostly in the horizontal direction. There is also a

slight downward bias in both experiments, but this bias reverses for upward environment shifts.

Figure 5 Localization error (Euclidean distance) in Experiment 2. When comparing stable to sifting environment, the error is highest when the environment shifts during a saccade and the attention system is under load. 'No environment' bars indicate the baseline condition, and note that environment shifts do not entirely remove the advantage of including the environment in the first place.

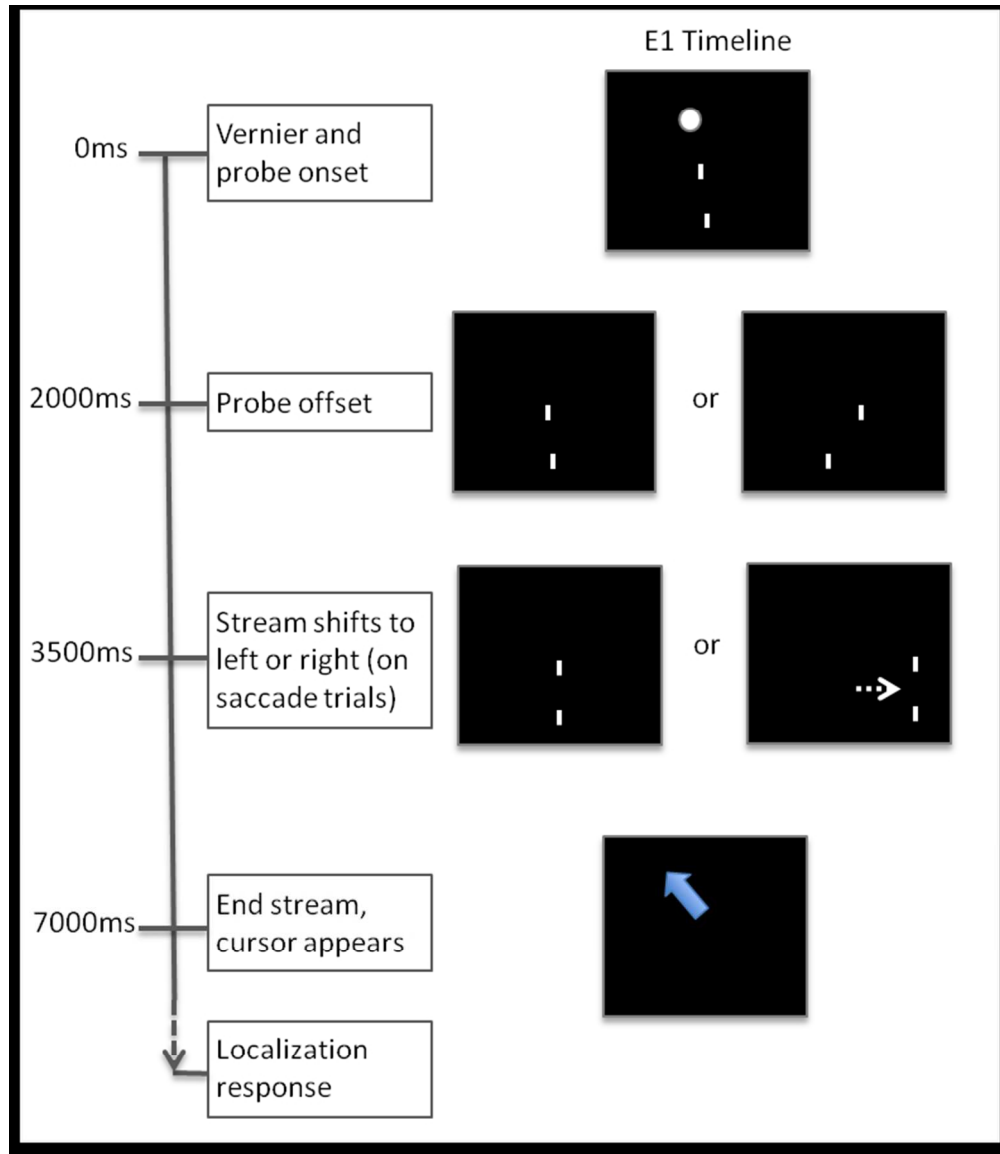


Figure 1. Screen layout and timeline for Experiment 1. All environmental cues were eliminated and the localization target was removed prior to the shift to the second stream.
134x154mm (150 x 150 DPI)

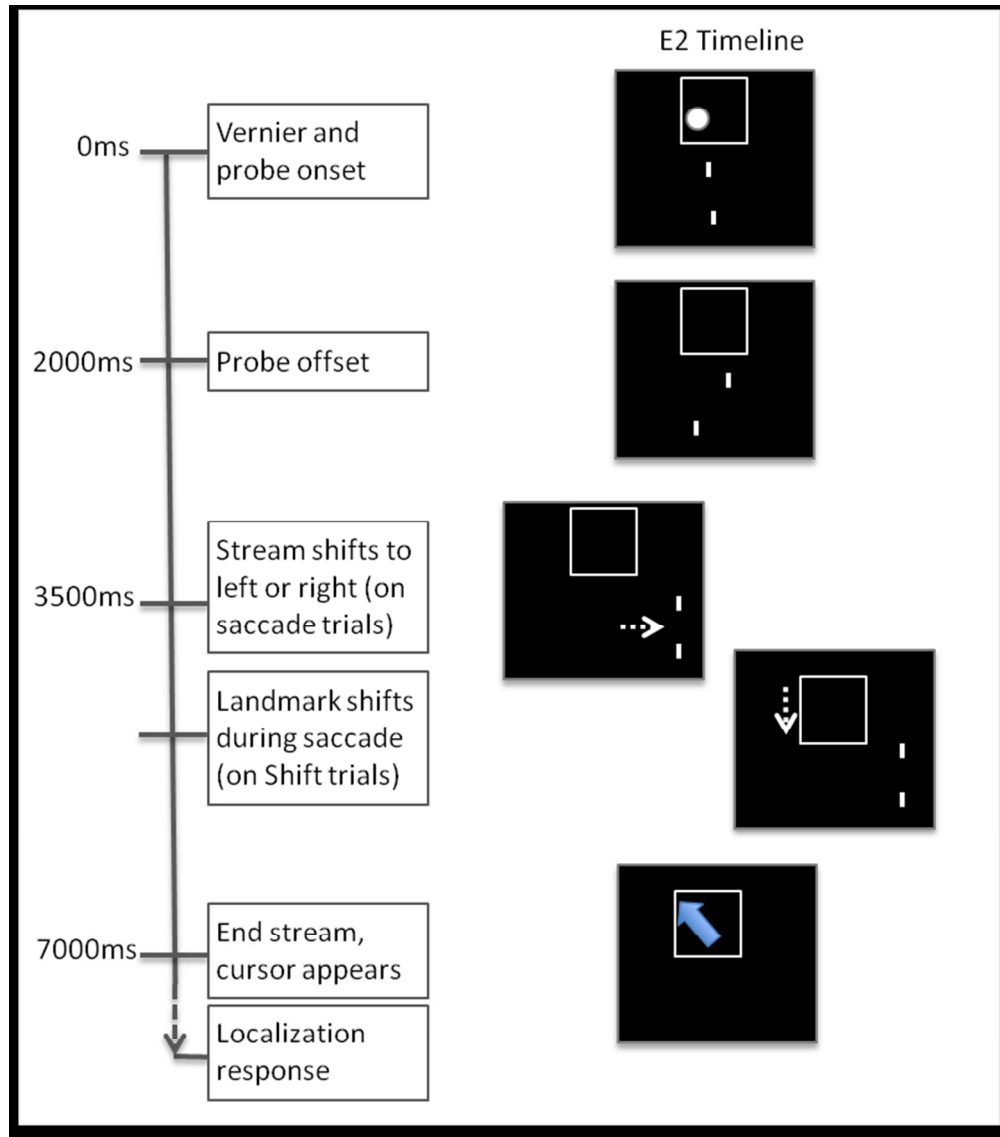


Figure 2. Screen layout and sequence of events for Experiment 2. The environment marker onset simultaneously with the probe and Vernier stream and its shift was triggered by the onset of the saccade that was executed in response to the stream moving to the left or right.
136x154mm (150 x 150 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

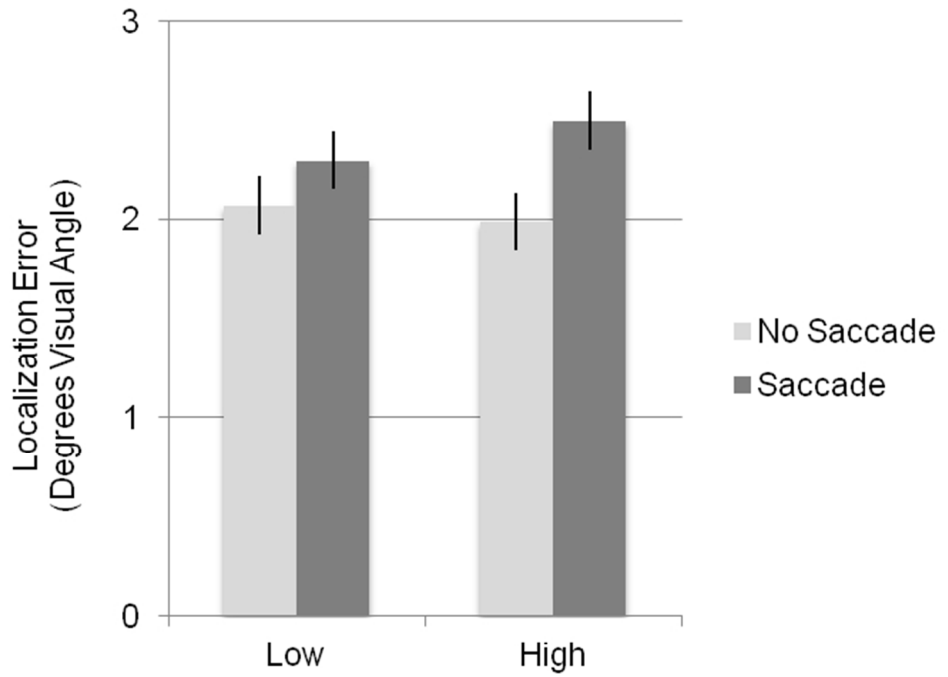


Figure 3 The effect of Load and Saccade on localization error (mean Euclidean distance between the actual probe location and the reported location) in Experiment 1. The interaction is significant.
119x90mm (150 x 150 DPI)

Review

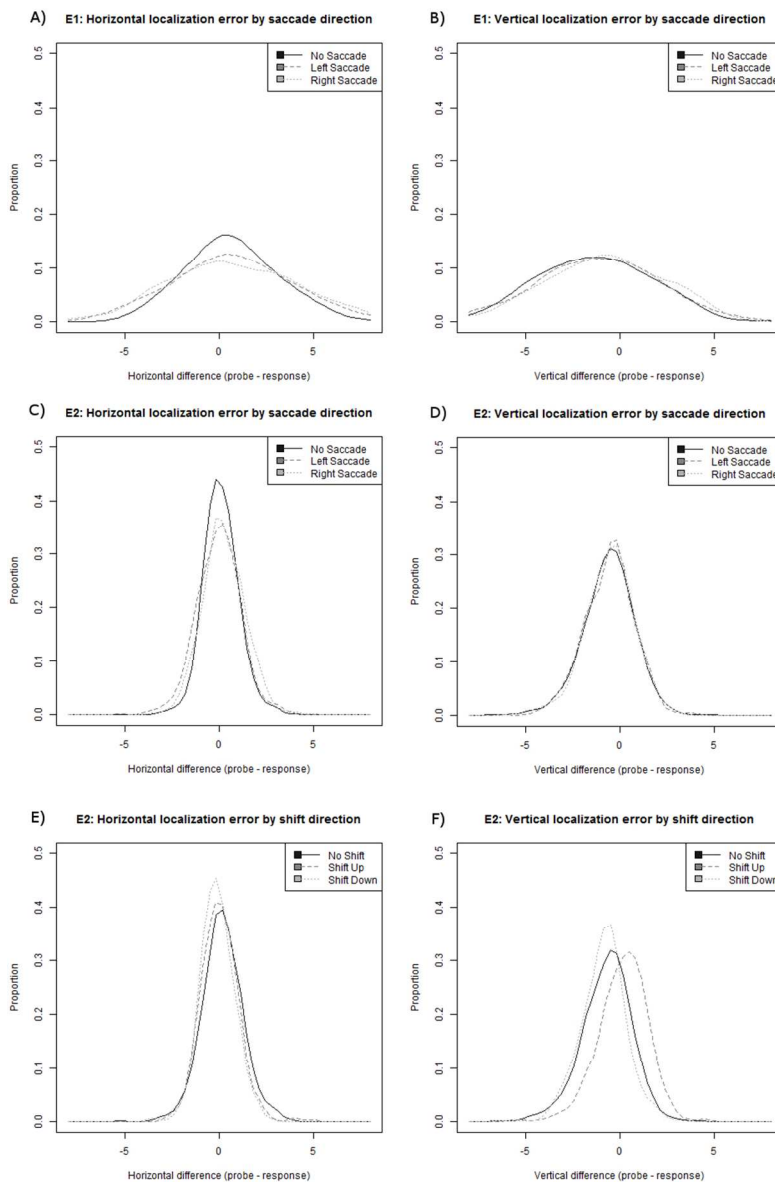


Figure 4. Spatial distribution of responses to the probes split by saccade condition and collapsed across load. Data are shown separately for A) Experiment 1 horizontal errors; B) Experiment 1 vertical errors; C) Experiment 2 horizontal errors by saccade directions; D) Experiment 2 vertical errors by saccade directions; E) Experiment 2 horizontal errors by border shift directions F) Experiment 2 vertical errors by border shift directions. There are no biases in distribution due to saccadic direction, but observed cost of saccades to localization error are mostly in the horizontal direction. In vertical error, there is a slight downward bias in both experiments, but this bias reverses for upward environment shifts.

338x508mm (72 x 72 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

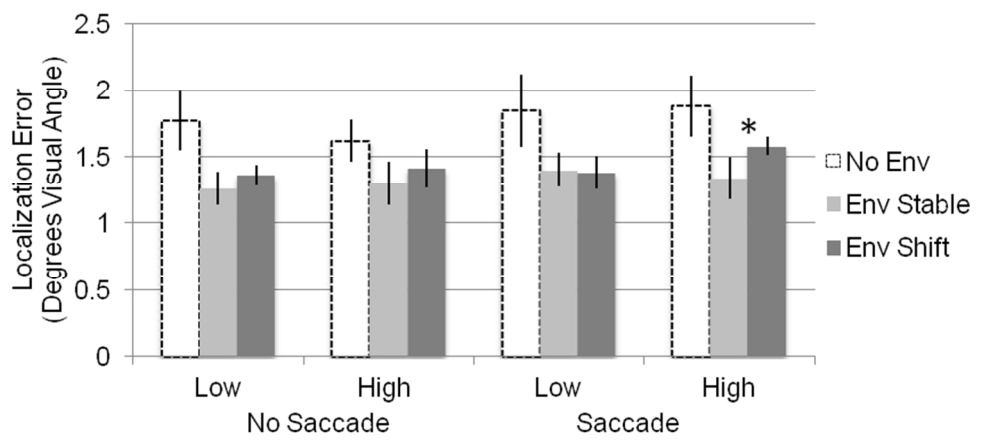


Figure 5. Localization error (Euclidean distance) in Experiment 2. When a border is present, error is highest when the border shifts during a saccade and the attention system is under load. "No environment" bars indicate the baseline condition.
148x69mm (150 x 150 DPI)

Peer Review