Oculomotor selection underlies feature retention in visual working memory

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[1]*Allgemeine und Experimentelle Psychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany; and* [2]*Graduate School of Systemic Neurosciences, Department Biologie, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany*

Hanning NM, Jonikaitis D, Deubel H, Szinte M. Oculomotor selection underlies feature retention in visual working memory. *J Neurophysiol* 115: 1071–1076, 2016. First published November 18, 2015; doi:10.1152/jn.00927.2015.—Oculomotor selection, spatial task relevance, and visual working memory (WM) are described as three processes highly intertwined and sustained by similar cortical structures. However, because task-relevant locations always constitute potential saccade targets, no study so far has been able to distinguish between oculomotor selection and spatial task relevance. We designed an experiment that allowed us to dissociate in humans the contribution of task relevance, oculomotor selection, and oculomotor execution to the retention of feature representations in WM. We report that task relevance and oculomotor selection lead to dissociable effects on feature WM maintenance. In a first task, in which an object's location was encoded as a saccade target, its feature representations were successfully maintained in WM, whereas they declined at nonsaccade target locations. Likewise, we observed a similar WM benefit at the target of saccades that were prepared but never executed. In a second task, when an object's location was marked as task relevant but constituted a nonsaccade target (a location to avoid), feature representations maintained at that location did not benefit. Combined, our results demonstrate that oculomotor selection is consistently associated with WM, whereas task relevance is not. This provides evidence for an overlapping circuitry serving saccade target selection and feature-based WM that can be dissociated from processes encoding task-relevant locations.

saccade; working memory; task relevance; visual feature

THE EFFICIENT INTERACTION with our visual environment depends on multiple processes working in parallel: selection and prioritization of parts of the visual scene, execution of rapid eye movements (saccades) to sample task information effectively, and keeping track of what is where in visual environment, even when the sensory input is not present anymore (Franconeri et al. 2013). However, the understanding of the links between those processes, visual selection, oculomotor selection, and visual working memory (WM), is limited, because they appear to be hard to dissociate from each other under experimental conditions.

It is established that the oculomotor system biases sensory processing during saccade preparation. Saccade target selection improves the detection of visual features such as shape and orientation (Deubel and Schneider 1996; Rolfs et al. 2011). The benefit at the saccade target comes at the expense of visual processing at other task-relevant locations (Deubel and Schneider 1996). These effects arise due to the oculomotor system enhancing processing in visual sensory cortex at saccade target locations (Ekstrom et al. 2008; Moore and Armstrong 2003).

The oculomotor system not only selects the immediate saccade target location but also maintains information about upcoming saccade targets (Gregoriou et al. 2012; Umeno and Goldberg 2001). Because this maintenance of spatial information can be observed in the absence of any visual input, the oculomotor system may at least partially underlie representations in spatial WM (Umeno and Goldberg 2001). This linkage also has been suggested by behavioral studies (e.g., Baddeley 1986). However, whether the oculomotor system also biases the retention of feature representations (in a similar way as it affects the perception of readily available visual information) remains unclear.

Evidence of links between oculomotor selection and visual WM is limited for several reasons. First, a location that has to be selected as saccade target is by definition also task relevant. Thus interactions between WM and saccade target selection could be driven by the task requirement to prioritize a certain location in space over the others, rather than by oculomotor selection per se. Furthermore, the oculomotor system represents task-relevant locations even during periods of fixation, when no saccade is made (Clark et al. 2012). Typical WM tasks made under fixation conditions therefore cannot distinguish whether the effects are due to visual or oculomotor selection. In the current study we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. We designed a task in which a memorized location was encoded as task relevant for one of two reasons: either to plan a delayed saccade to it (task relevant and saccade target) or to avoid making a saccade to it (task relevant but not saccade target). This allowed us to manipulate the involvement of the oculomotor system in WM. Our results demonstrate that the oculomotor system biases feature retention at saccade target locations, which is achieved by mitigating the loss of feature representations at locations to which saccades are prepared. This effect of oculomotor selection does not rely on saccade execution. We also show that information maintenance in visual WM is not mediated by mere task relevance.

MATERIALS AND METHODS

Subjects and apparatus. Eight human observers (6 females, ages 24–26 yr, 1 author) completed the experiment. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München, in accordance with German regulations and the Declaration of Helsinki. Gaze position was recorded using an EyeLink 1000 Tower Mount (SR Research, Osgoode, ON, Canada) at a sampling rate of 1 kHz. The experiment was controlled by an Apple Mac mini

computer (Cupertino, CA) with an Intel Core i5 processor (Santa Barbara, CA), and the experimental software was implemented in MATLAB (The MathWorks, Natick, MA) using the Psychophysics and Eyelink toolboxes (Brainard 1997; Cornelissen et al. 2002). Stimuli were presented at a viewing distance of 60 cm on a 21-in. gamma-linearized LaCie Electron 21/108 CRT screen (Paris, France) with a spatial resolution of 1,024 × 768 pixels and a vertical refresh rate of 120 Hz.

Stimuli and procedure. The experiment comprised three types of blocked tasks (look, avoid, and fixate) that were visually identical but differed in the pre-block instruction (Fig. 1*A*). Subjects initially fixated a central black and white bull's eye (0.35° radius) on a gray background (60 cd/m^2). The trial started once stable fixation was detected within a 2.5° radius virtual circle centered on the fixation target. Two WM items appeared peripherally at randomly selected locations (7° away from fixation, separated by an angle of 60°, 120°, or 180°). The items were black (0.5 cd/m^2)-outlined (~0.4° width) radial frequency patterns (adapted from Wilkinson et al. 1998). Each pattern (Fig. 1*B*) had a mean radius of 1.4°, a randomly selected radial frequency of 3, 4, or 5 cycles, and an angular phase (rotation angle) of 1° to 360°. The amplitude was chosen randomly between 20% and 80% of the radius. After 950 ms, the items were masked by the brief presentation (50 ms) of 4 overlaid radial frequency patterns with random amplitude, radial frequency, and angular phase. After 200 ms, a red cue (0.8° radius dot, 20 cd/m^2) was flashed for 50 ms at the location of one of the two WM items. The cue did not indicate which of the items would be probed at the end of the trial. After a delay of 800–1,200 ms, in 75% of the trials (main trials), two blue response dots (radius 0.8°, 12 cd/m^2) were presented for 1,000 ms, separated from each other by an angle of 60°, 120°, or 180°. One of the blue dots appeared at the previously cued location. In the look task, subjects saccaded toward the dot presented at the previously cued location and subsequently back to the fixation target. In the avoid task, subjects instead saccaded to the noncued dot and back to the fixation target. Subject were instructed to perform the saccade task as fast and as precisely as possible. In the fixate task, subjects ignored the blue response dots and maintained fixation, allowing us to evaluate bottom-up attentional effects induced by the presentation of the cue. Although all tasks were visually identical, task load was increased in the look and avoid tasks, because subjects additionally had to maintain the cued location to correctly perform the saccade task. In 25% of trials in all 3 tasks, catch trials were randomly interleaved in which no

blue response dots appeared and subjects maintained fixation. We probed WM by presenting one of the radial frequency patterns at its former location, which could be the cued or a noncued location. In 50% of trials the item reappeared with a changed radial amplitude. Subjects reported in a nonspeeded manner whether or not a change had occurred (same/different response). To avoid edge effects across the range, the amplitude of the probe never exceeded the range of the items to be memorized. After an initial training phase, subjects performed 30 randomly arranged blocks in 4 to 5 sessions on different days. Altogether they completed 900 trials of the look task, 900 trials of the avoid task, and 450 trials of the fixate task. To maintain a consistent level of difficulty, a threshold task (WM change detection task without eye movements) was performed before each session to determine the amplitude change corresponding to 80% correct change detection.

Data analysis. We detected saccades based on the gaze position velocity distribution (Engbert and Mergenthaler 2006). We accepted saccade trials in which we detected the saccade landing within 2.5° to the target and a return saccade to the fixation no later than 1,000 ms following target onset. We excluded trials with erroneously broken fixation (not within 2.5° from the fixation target). In total, we included 5,637 trials (78.3%) of the look task, 5,743 trials (79.8%) of the avoid task, and 3,001 trials (83.4%) of the fixate task. We computed WM performance as a percentage of correct change detection. For statistical comparisons we computed the mean values of 10,000 bootstrap samples that we drew with replacement from each condition's data set. We calculated the difference of their means and derived two-tailed *P* values from the distribution of these differences. We determined within-subject bootstrapped 95% confidence intervals (CIs) by normalizing each subject's mean across conditions and scaling the variance of the bootstrap distribution by $M/(M-1)$, where M is the number of within-subject conditions in the analysis before the bootstrap (Morey 2008).

RESULTS

Subjects correctly saccaded to the instructed response dot in 91.3 ± 1.8% (mean ± SE) of trials in the look task and in 90.6 ± 1.3% in the avoid task. WM performance at cued and neutral locations combined did not differ between the look and avoid task (look: 67.9 ± 0.8% vs. avoid: 67.5 ± 1.1%, *P* > 0.05) but was significantly higher in the fixate task (71.0 ±
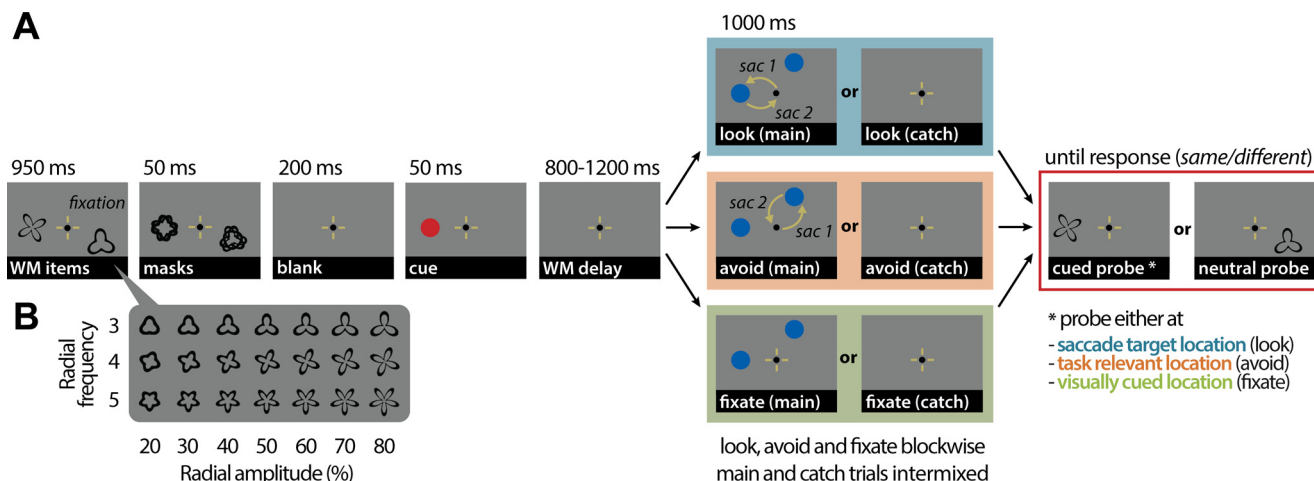

Fig. 1. Design and stimuli. *A*: task design. Subjects memorized 2 randomly chosen radial frequency patterns. Shortly afterward, a cue (red dot) was presented at the location of one of the working memory (WM) items. After a delay period, in 75% of the trials (main trials) 2 response targets (blue dots) appeared, one at the cued location and another at a new location. Subjects saccaded to the cued location and back to the center in the look task, or saccaded to the uncued location and back to the center in the avoid task. In the fixate task, subjects maintained fixation. Within all tasks, in 25% of the trials (catch trials) no response targets appeared and subjects kept central fixation. We probed WM by presenting one WM item at its former location with the same or a changed amplitude. *B*: WM items. The probe amplitude was either identical or increased/decreased relative to the pattern shown previously. Radial frequency was task irrelevant.
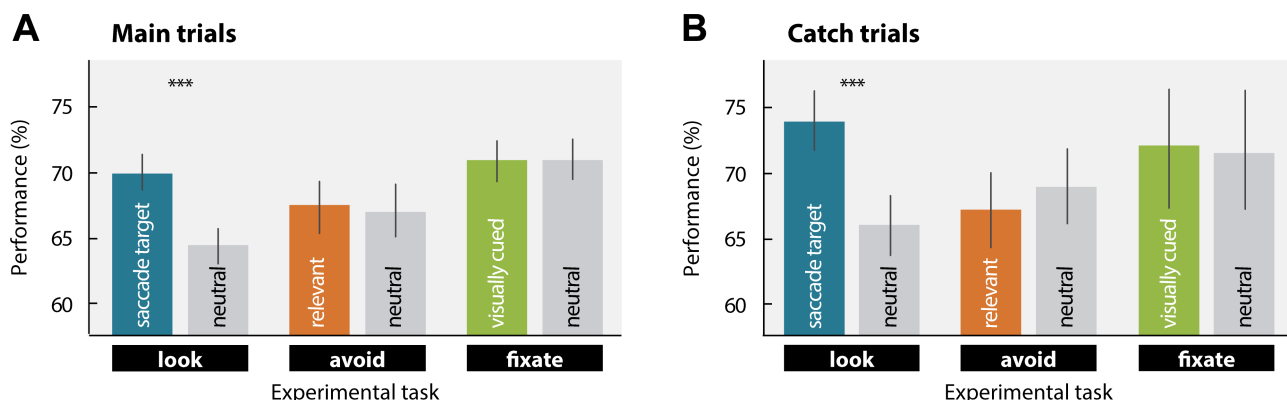
Fig. 2. WM performance for the different tasks and cueing conditions in the main trials (*A*) and the catch trials (*B*). Error bars indicate within-subject 95% confidence intervals (CIs). ***$P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

1.1%, $P < 0.001$). This suggests a comparably increased task load in both eye movement tasks. Average saccade latencies did not differ between look and avoid task (look: 272 ± 18 ms vs. avoid: 272 ± 14 ms, $P > 0.05$), which furthermore suggests a comparable task load in the two eye movement tasks. We compared WM performance at cued and neutral locations. In the main trials of the look task, that is, when subjects prepared and executed a saccade toward the cued location, WM performance was superior at the saccade target compared with neutral locations (Fig. 2*A*; saccade target: $69.8 \pm 5.7\%$ vs. neutral: $64.3 \pm 6.2\%$, $P < 0.001$). In contrast, WM performance at task-relevant vs. neutral locations (avoid task) did not differ (Fig. 2*A*; task relevant: $67.4 \pm 5.7\%$ vs. neutral: $66.9 \pm 5.1\%$, $P > 0.05$). The absence of a performance difference between cued and neutral locations in the fixate task rules out that attentional effects due to bottom-up attentional cueing induced the benefit at the saccade target in the look task (Fig. 2*A*; visually cued: $70.9 \pm 7.0\%$ vs. neutral: $70.8 \pm 6.0\%$, $P > 0.05$). Thus, with identical visual input in all three tasks, the cued location was only superior when a saccade was prepared toward it.

The question arises whether saccade execution per se can account for the WM advantage at the saccade target. Analysis of the catch trials in the look task, in which subjects prepared a saccade but finally kept fixation, showed a very similar pattern of results (Fig. 2*B*; saccade target: $74.1 \pm 5.3\%$ vs. neutral; $66.1 \pm 6.4\%$, $P < 0.001$), indicating that oculomotor selection was sufficient for the WM advantage. The decisive role of oculomotor selection as opposed to saccade execution also was observed in the avoid task. In 15% of the trials, the saccade target appeared at the uncued location, which was later probed for WM (to increase statistical power, we doubled the likelihood of the appearance of a response dot at the location of the uncued WM item). Simply executing a saccade (that could not be prepared over the WM delay) did not lead to a WM advantage at the saccade target (avoid task: memory probe at saccade target: $65.8 \pm 5.6\%$ vs. memory probe elsewhere: $67.0 \pm 5.1\%$, $P > 0.05$). This demonstrates that the advantage was mediated by oculomotor selection rather than saccade execution.

To investigate the temporal dynamics of the effect, we binned the trials according to their WM delay duration in a 150-ms moving average. If oculomotor selection actually is the underlying factor, we hypothesized that the advantage at the saccade target would vary with the time allocated to oculomotor selection. Indeed, the analysis of the look task showed a

decline of WM performance over time at nonsaccade targets (Fig. 3*A*; 800–950 ms: $66.7 \pm 2.1\%$ vs. 1,050-1,200 ms: $62.0 \pm 2.3\%$, $P < 0.001$). In contrast, WM performance at the saccade target remained stable between the shortest and the longest delay (Fig. 3*A*; 800–950 ms: $69.5 \pm 2.1\%$ vs. 1,050-1,200 ms: $72.3 \pm 2.3\%$, $P > 0.05$). Maintaining a location as a motor target thus seems to diminish the decay of feature representations held at the intended motor goal.

Our previous analysis suggested that oculomotor selection mediates the advantage at the saccade target. We reasoned that a poor selection should result in a slower saccade execution,
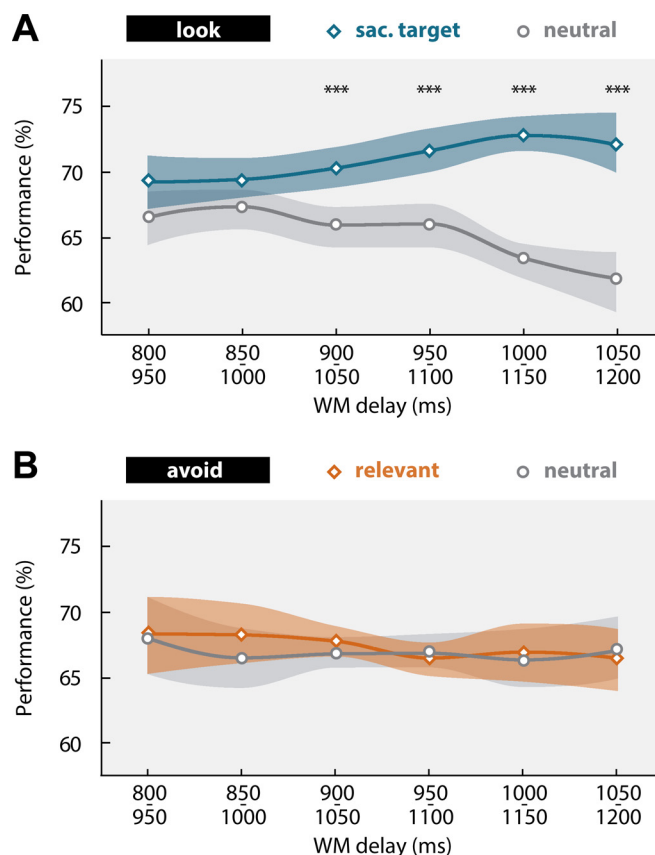

Fig. 3. WM performance as a function of memory delay (binned in 5 time windows) in the look task (*A*) and the avoid task (*B*) for main and catch trials combined. Colored areas indicate within-subject 95% CIs. ***$P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

hence longer saccade latencies. Therefore, we split the data according to the latency of the first saccade into three latency terciles. Indeed, the WM advantage at the saccade target disappeared in the last latency tercile, that is, for the slowest initiated saccades (Fig. 4A; saccade target: 66.6 ± 4.7% vs. neutral: 66.3 ± 4.7%, $P > 0.05$), confirming the need of an effective oculomotor selection for the improved retention of feature information at the saccade target. Importantly, saccade latencies did not differ between short and long WM delays in either the look task (800–950 ms: 270 ± 19 ms vs. 1,050-1,200 ms: 266 ± 15 ms, $P > 0.05$), nor in the avoid task (800–950 ms: 272 ± 15 ms vs. 1,050-1,200 ms: 268 ± 14 ms, $P > 0.05$). This rules out the possibility that the pronounced benefit for well-prepared saccades can be explained in terms of a longer WM delay, and thus preparation time.

DISCUSSION

In the current study we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. In contrast to the saccade target location in the look task, the task-relevant location in the avoid task did not entail a saccade plan toward it, and any mechanisms actively maintaining that location did not interact with WM representations. Our results thus demonstrate that oculomotor selection, and not task relevance per se, mediates the retention

Fig. 4. WM performance as a function of saccade latency (binned in 3 terciles) for the main trials of the look task (*A*) and the avoid task (*B*). Histograms at *bottom* illustrate pooled (cued and uncued) distributions of saccade latencies. Colored areas indicate within-subject 95% CIs. ***$P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

of feature information at the saccade target. This is achieved by mitigating the loss of feature representations at locations marked as saccade targets, an effect due to saccade target selection, even without concomitant saccade execution.

Earlier studies have demonstrated links between task relevance and WM. In particular, asking subjects to select one of several objects maintained in WM was shown to increase the probability of its correct retrieval (e.g., Griffin and Nobre 2003; Souza et al. 2014). However, this work cannot dissociate effects of task relevance and oculomotor selection. Because the oculomotor system also represents spatial selection during periods of fixation (Clark et al. 2012), the reported beneficial effects of visual selection on WM could be mediated not only by the selection of task-relevant locations but also by the covert oculomotor selection of these task-relevant locations. In our study, the measurement of WM performance at the cued location in the avoid task allowed us to disentangle task relevance and oculomotor selection. In the avoid task, the cue only informed the subjects about where not to look but did not provide information about the future saccade target location. However, the cued location still was task relevant, because the selection of the correct saccade target after the delay was not possible without maintaining it in spatial memory. Therefore, this task uniquely provides a paradigm in which a stimulus is task relevant but to which it can be safely assumed that oculomotor selection does not occur. Because we did not find a WM benefit at these task-relevant nonsaccade targets, the frequently reported link between task relevance and WM is likely based on oculomotor programs.

The impact of oculomotor programming on feature WM has been investigated by earlier work (Bays and Husain 2008; Melcher and Piazza 2011; Shao et al. 2010). In line with our results, improved WM performance at the saccade target compared with neutral locations has been reported. However, by cueing the saccade target location before or together with the presentation of the WM material, these studies investigated encoding rather than retention. Because in visually guided saccade tasks sensory discrimination is best at the saccade target and worse at nontarget locations (Deubel and Schneider 1996; Rolfs et al. 2011), the observed WM benefits and costs in earlier studies cannot be clearly attributed to links between oculomotor selection and WM. They also could arise due to subjects being able to discriminate, perceive, and thus encode features at saccade target locations better than at nontarget locations. For this reason, we cued the saccade target location only after the WM items disappeared and were masked, ruling out any sensory explanation of oculomotor selection on feature-based WM. Furthermore, those earlier studies again cannot distinguish between task relevance and oculomotor selection, since in their designs selected saccade target locations also were task relevant.

Our findings from the fixate task are important for the interpretation of earlier work linking task relevance, oculomotor selection, and WM. We observed that performance decreased at both cued and noncued locations in the avoid task compared with the fixate task (Fig. 2). This suggests that adding a further task (preparing/executing saccades vs. keeping fixation) increases the task difficulty, leading to the overall decrease in WM performance. Therefore, earlier work cannot rule out that the impaired WM performance in saccade vs. fixation tasks is due to a general increase in task load instead
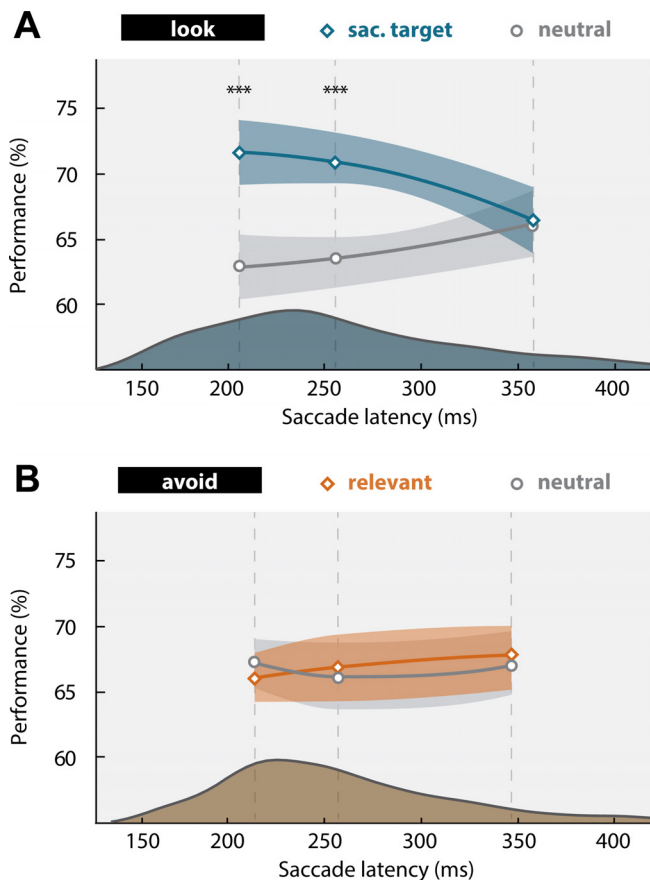
of oculomotor selection (Hale et al. 1996; Lawrence et al. 2001; Lawrence et al. 2004; Pearson and Sahraie 2003; Postle et al. 2006). Our results, in contrast, are unbiased from task-load effects, because we compared WM at saccade target vs. neutral locations within the same task. The look and avoid tasks, furthermore, were matched in terms of visual input and task load. Thus the preserved WM performance at saccade goal locations (but not at task-relevant locations) can only be explained by the beneficial effect of saccade target selection. It is interesting to note that the WM benefit at the saccade target became pronounced only with longer WM delays. Figure 3*A* shows that the performance difference between saccade goal and neutral locations was significant only for delays of 900 ms and longer. Given the predictable WM delay of 800 to 1,200 ms, this may indicate that subjects delayed their saccade preparation until shortly before the temporal interval where the saccade target could be expected. Alternatively, the time course of our effect may rely on slow memory processes: as shown by previous work, the effect of postcues on WM necessitates time to evolve (e.g., Souza et al. 2014).

We observed that oculomotor selection consistently interacts with feature WM, whereas task relevance per se does not. In line with this finding, there is evidence that processes associated with maintaining task relevant locations that are not encoded as saccade targets differ from those maintaining saccade targets. A neurophysiological study reported that separate neuronal populations in the frontal eye fields (FEF) encode allowed (look task) and avoided (avoid task) locations (Hasegawa et al. 2004). Human functional magnetic resonance imaging (fMRI) data also suggest that different areas might represent these locations, with the FEF encoding saccade target locations in the look task and the parietal cortex encoding task-relevant locations in the avoid task (Curtis et al. 2004, 2005). This has led to suggestions of two distinct selection processes: prospective selection, involving oculomotor selection, and retrospective selection, which does not involve oculomotor selection (Curtis et al. 2004, 2005). Our findings suggest that only prospective selection interacts with feature-based WM representations.

In support of different mechanisms underlying representations of saccade target and task-relevant locations, an earlier study with a design similar to ours also observed different effects of oculomotor selection and spatial selection in look and avoid tasks (Dhawan et al. 2013). This study reported improved perceptual discrimination at saccade target locations in the look task and reduced discrimination at task-relevant locations in the avoid task. In the current study we did not observe a corresponding reduction in WM performance at task-relevant locations. However, our effects on WM are hard to compare with this earlier study, which focused on spatial selection during the presaccadic period close to saccade execution. Nevertheless, both studies likewise reveal a different pattern of processing associated with task-relevant locations and saccade targets, which is in line with the proposal that location maintenance differs in look and avoid tasks (Curtis et al. 2005).

In summary, we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. Our findings suggest that oculomotor selection, and not execution, biases both visual selection and WM benefits at saccade target locations, with a corresponding cost at nonsaccade target locations. We show that oculomotor selection is consistently associated with WM, whereas task relevance is not. This effect is presumably mediated by an overlapping circuitry serving saccade target selection and spatial WM maintenance, and it is likely dissociable from circuits maintaining target locations that do not constitute saccade targets.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

N.M.H., D.J., H.D., and M.S. conception and design of research; N.M.H. performed experiments; N.M.H. and M.S. analyzed data; N.M.H., D.J., H.D., and M.S. interpreted results of experiments; N.M.H. and M.S. prepared figures; N.M.H. and D.J. drafted manuscript; N.M.H., D.J., H.D., and M.S. edited and revised manuscript; N.M.H., D.J., H.D., and M.S. approved final version of manuscript.

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