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Saccadic selection of stabilized items in visuospatial working memory

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ABSTRACT

Saccadic eye movements prioritize the memory of visual stimuli that had previously been seen at the saccade target. In two experiments, we assessed whether this influence is limited to fragile memory traces or if saccades can also affect consolidated representations in visuospatial working memory (VSWM). To interfere with fragile memory traces, we presented visual masks at different delays following the offset of a memory array and simultaneously prompted participants to generate a saccade to one location. Masking was very effective: Memory performance was lowest right after the disappearance of the memory array and gradually increased for later mask onsets. In spite of that, memory was best for stimuli congruent with the saccade target. This advantage was largest at shortest delays and then decreased over the course of a second. Insofar as only consolidated representations survive interference from masks, we conclude that saccades exert spatially selective biases on stable representations in VSWM.

1. Introduction

A vast amount of information continuously enters the visual system. After the visual scene has disappeared from view, the plethora of information is still available as quickly decaying stimulus traces lingering in iconic memory (Averbach & Coriell, 1961; Coltheart, 1980; Sperling, 1960). Only a small fraction of this information will be consolidated and stored in stable representations that are maintained over several seconds in visual short-term memory (Cowan, 2001; Luck & Vogel, 2013; Ma, Husain, & Bays, 2014).

A core question regarding visual memory arises from the discrepancy between the unlimited (but fragile) iconic memory and capacity limited (but stable) visual short-term memory. That is, how is visual information selected from iconic memory to form continually accessible representations in visual short-term memory? One powerful selection mechanism for this transfer is the top-down guidance by attentional processes, which plays a critical role for the maintenance of memory representations (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Fougnie, 2008; Jolicoeur, 1998; Vogel, Luck, & Shapiro, 1998). A shift of attention in response to an informative cue enhances memory performance irrespective of whether cues are presented before the memory array and even during memory maintenance (Becker, Pashler, & Anstis, 2000; Gegenfurtner & Sperling, 1993; Griffin & Nobre, 2003; Kalogeropoulou, Jagadeesh, Ohl, & Rolfs, 2017; Landman, Spekreijse, & Lamme, 2003; Schmidt, Vogel, Woodman, & Luck, 2002; Souza & Oberauer, 2016). Outside the lab, however, cues informing us about what to remember may not be commonly available, suggesting that other selection mechanisms decide upon the fate of visual memory maintenance in ecologically relevant situations.

We recently proposed that saccadic eye movements constitute a powerful selection mechanism in visual memory in the absence of informative cues (Ohl & Rolfs, 2017). This adds to a series of recent studies delineating the multiple interactions between visuospatial

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working memory (VSWM) and the oculomotor system (Van der Stigchel & Hollingworth, 2018): First, the target of a saccade is preferentially selected for transfer into VSWM (Bays & Husain, 2008; Gersch, Kowler, Schnitzer, & Dosher, 2008; Henderson & Hollingworth, 2003; Irwin, 1991; 1992; McConkie & Currie, 1996; Shao et al., 2010), which may be a consequence of an automatic shift of spatial attention to the saccade target (Deubel & Schneider, 1996; Kowler & Blaser, 1995; Ohl, Kuper, & Rolfs, 2017; Rolfs & Carrasco, 2012). Second, interactions are also observed in the opposite direction, such that the oculomotor system integrates information from visual memory. For instance, the content of visual memory guides the selection of future saccade target locations (Beck, Hollingworth, & Luck, 2012), and visual search templates are reflected in the generation of involuntary microsaccades (van Loon, Olmos-Solis, & Olivers, 2017). Third, the interplay between saccades and visual memory appears critical for visual stability in the face of eye movements that change any given object's position on the retina with every saccade (for seminal review and discussion of accounts for visual stability, ranging from cancellation to calibration models, see Bridgeman, van der Heijden, & Velichkovsky, 1994). In particular, the saccade target and other visual landmarks have been assigned a pivotal role in establishing a correspondence between pre- and post-saccadic visual input (Bridgeman & Graziano, 1989; Deubel, Bridgeman, & Schneider, 1998; McConkie & Currie, 1996). These stimuli are stored in *trans*-saccadic memory—which has similar characteristics as visual short-term memory (Irwin, 1992; Irwin & Andrews, 1996)—and compared to the incoming near-foveal sensory signal during the next (post-saccadic) fixation (Deubel et al., 1998; Deubel, Koch, & Bridgeman, 2010; Deubel, Schneider, & Bridgeman, 1996; 2002). Trans-saccadic processes are not applied uniformly across the visual scene—instead they emphasize information processing near the saccade goal (Bischof & Kramer, 1968). Whereas stimulus displacements, as large as 1/3 of the saccade amplitude, introduced during a saccade often go unnoticed (Bridgeman, Hendry, & Stark, 1975), detection of *trans*-saccadic changes in the visual scene increases in the vicinity of the saccade target (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Henderson & Hollingworth, 1999; 2003). Indeed, the displacement of an entire image during the saccade elicited the percept of moving objects only near the saccade goal (Bridgeman, 1981). Finally, the fast generation of small secondary saccades that correct for errors of the primary saccade—even on the scale of microsaccades (Ohl & Kliegl, 2016; Ohl, Brandt, & Kliegl, 2011)—relies on representations in visual memory (Hollingworth & Luck, 2009; Hollingworth, Richard, & Luck, 2008), providing additional evidence for the close interaction of the oculomotor system and visual memory.

Previously we reported in a series of experiments that saccades—planned and generated after the disappearance of the memory array—affect visual memory by prioritizing stimuli presented at locations congruent with subsequent saccade targets (Ohl & Rolfs, 2017). This selection is automatic and occurs within the first second after the disappearance of the memory array. A similar spatial bias in visual memory can be induced by simply preparing a saccade to a target location, without actually executing it (Hanning, Jonikaitis, Deubel, & Szinte, 2016). We concluded, therefore, that saccadic selection in visual memory exceeds the iconic memory stage (Ohl & Rolfs, 2017). This claim was based exclusively on the time course of the saccadic influence on visual memory (Ohl & Rolfs, 2017). Whereas an influence on iconic memory traces typically occurs within < 500 ms after the disappearance of a memory array, we observed a saccadic influence on visual memory for delays that were twice as long. These results suggest that stabilized representations can be affected by saccades as well, at least for a short time window. Others have suggested, however, that representations may still be fragile in early stages of visual memory (Sligte, Scholte, & Lamme, 2008).

Here, we manipulated a representation's degree of stability in two experiments. We employed visual masks that—presented after memory array offset—interfered with fragile representations in visual memory. Using this technique, we investigated if saccades—that are planned and generated during memory maintenance—affect progressively stabilized memory representations, that is, representations that proved invulnerable to interference by visual masks presented at different delays following the offset of the memory array. Moreover, we set out to determine the time course of this potential saccadic selection mechanism for stabilized representations in VSVM. We provide further support for the notion that saccades effectively modulate the maintenance of stabilized memory representations within the first second after memory array disappearance.

2. Experiment 1

In Experiment 1, we assessed the influence of saccadic eye movements on stabilized representations in visual memory. To this end, we employed a visual masking paradigm in which the presentation of visual masks interferes with fragile traces at early memory stages (e.g., iconic memory). These masks should thus reduce the content of visual memory to a subset of stabilized representations in VSWM. Simultaneously with the masks, we presented a movement cue instructing participants to shift gaze to a target location. Using this procedure, we could investigate whether saccades exert their spatially specific bias on that subset of stabilized visual memory representations. Presenting masks and movement cue simultaneously at various delays after the offset of the memory array had two main advantages. First, it allowed us to characterize the consolidation of memory representations while introducing only one display change (i.e., the onset of visual masks and movement cue) that could potentially interfere memory performance. Second, we varied the interval between memory array offset and cue/mask delay in order to identify a critical time window in which (a) some memory representations had enough time to stabilize successfully and (b) a potential influence of saccadic eye movements could still be detected.

2.1. Method

2.1.1. Participants

Ten observers (ages 20–38 years; eight female; seven right-handed) participated in five sessions of the experiment (one training and four test sessions), with at least one night between consecutive sessions. All observers had normal or corrected-to-normal vision,

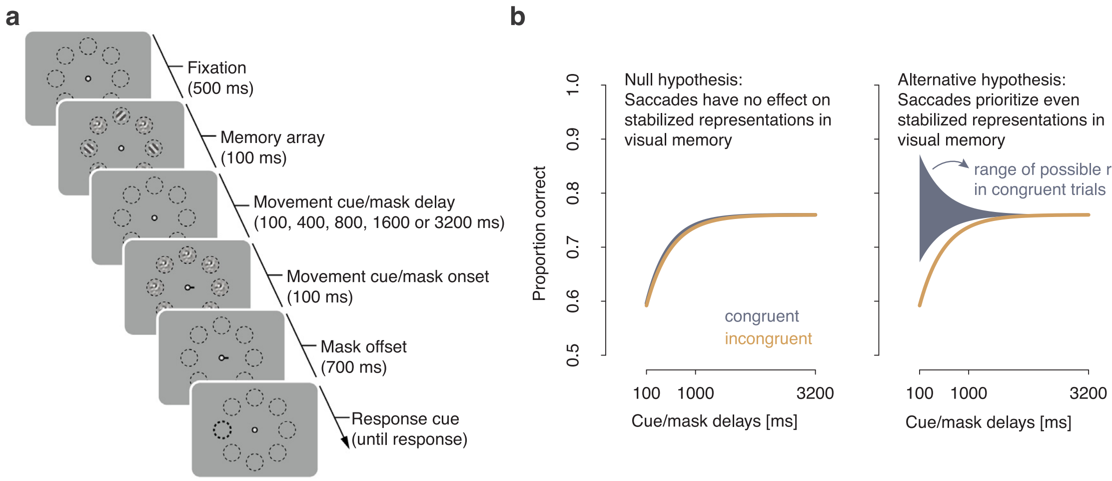

Fig. 1. Experimental procedure and hypotheses. (a) We presented a memory array consisting of four tilted Gabor patches at four randomly selected locations for 100 ms. Observers were instructed to remember their orientation for a memory test at the end of the trial. The remaining four locations contained noise patches. At varying delays during the retention interval, we presented a movement cue instructing observers to move their eyes quickly to the indicated location. Simultaneously with the movement cue, we presented visual masks (i.e., noise patches) at all eight locations. A response cue appeared 800 ms after the onset of the cue/mask display and highlighted the location for the memory test. Observers were asked to report the orientation (clockwise vs. counterclockwise) of the Gabor patch that was initially presented at that highlighted location. The saccade target location was either congruent or incongruent (as in the example trial sequence above) with the memory test location. The direction of the movement cue and memory test location were uninformative about each other, such that saccade target location and memory test location coincided in only 25% of the trials. (b) Predictions derived from the null hypothesis and alternative hypothesis for congruent (in blue) and incongruent (in orange) trials. The upper bound of the blue area mimics the results obtained in congruent trials whereas the orange line mimics memory performance in incongruent trials as observed by Ohl and Rolfs (2017), using the present paradigm but without masks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were naïve as to the purpose of the study, and gave informed consent in writing prior to participation. They received a reimbursement of 7€ for each session, plus an additional bonus of 7€ after the successful completion of all sessions. The study was approved by the ethics commission of Humboldt-Universität zu Berlin and conducted in accordance with the Declaration of Helsinki (2008).

2.1.2. Materials and procedure

Observers sat in a dark room in front of a computer screen at a distance of 57 cm. Their head was positioned on a chin rest in order to minimize small movements. We displayed visual stimuli on a gamma-linearized Sony Trinitron CRT with a spatial resolution of 1280 × 800 pixels and a temporal refresh rate of 100 Hz. We recorded the observers' dominant eye positions with an Eyelink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada). The experiment was implemented on a Mac minicomputer (Apple, Cupertino, CA, USA) running Matlab (Mathworks, Natick, MA, USA), Psychophysics toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997), and the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002).

As in our previous study (Ohl & Rolfs, 2017), observers were asked to report the orientation of one of four Gabor patches held in visual memory. At the beginning of a trial, we presented eight circular placeholders (1.96 degrees of visual angle, dva, diameter) arranged on an imaginary circle at a distance of 6 dva from a centrally presented fixation point (0.6 dva diameter white circle with black contour) on a grey background (Fig. 1a). After 500 ms of successful fixation, we presented a memory array for 100 ms that consisted of four Gabor patches (50% contrast, randomly assigned spatial frequency of 1.5 or 2.25 cycles per degree, random phase, 0.65 dva SD Gaussian envelope) at locations that were randomly selected on each trial. Critically, we randomly assigned each Gabor patch one of two possible orientations (± 22.5° from vertical). At the remaining four locations that were not occupied by Gabor patches, we presented *noise patches* without distinct orientation information (pixel noise, bandpass filtered from half to twice the spatial frequency of the Gabors, at the same contrast, 0.65 dva SD Gaussian envelope; see Rolfs & Carrasco, 2012). After removing the memory array and an additional *cue delay* of either 100, 400, 800, 1600, or 3200 ms, we presented simultaneously a *movement cue* (black line segment, 0.23° long) and *visual masks* (same noise patches as above; pixel noise bandpass filtered from half to twice the spatial frequency of the Gabors, at the same contrast, 0.65 dva SD Gaussian envelope) at the eight placeholders for 100 ms. The cue delay at which we presented the movement cue and masks was fixed in a block of trials. The movement cue appeared next to the fixation spot and identified one of the placeholders as the saccade target. We instructed observers to move their eyes to the indicated location within 400 ms. Following another delay of 800 ms, we presented a *response cue* (the outline of one randomly selected placeholder thickened) which indicated the location of one of the previously presented Gabors. Observers reported by a manual key press whether the Gabor at the highlighted location had been oriented clockwise or counterclockwise from vertical.

Assignments of the saccade target and response cue were orthogonal to each other. As a consequence, the location highlighted by the movement cue and the memory test location were the same on 25% of the trials (congruent condition) but equally often coincided with any other stimulus location (incongruent condition; 75% of all trials). Thus, the movement cue was not informative as to which

Gabor's orientation was probed for the memory test.

We aligned eye and screen coordinates by conducting standard nine-point calibration and validation procedures before the first trial and whenever necessary. Before the onset of each trial, we ran a fixation control routine that requires an observers' gaze position to be inside a circular region (1.5 dva diameter) centered on the fixation spot. The trial started only when fixation control was successful for at least 200 ms. During the experiment, we monitored for blinks, saccadic responses slower than 400 ms, and anticipatory saccades during requested fixation periods. Such events resulted in trial abort and a repetition of these trials at the end of the block in randomized order.

In each experimental session, participants completed 20 short blocks of 24 trials with different cue delays run in separate and randomly interleaved blocks. Each observer completed a total of 1920 trials in the four test sessions (96 congruent and 288 incongruent trials per cue delay). The necessary number of trials per condition was determined based on our previous study using a very similar task (Ohl & Rolfs, 2017).

2.1.3. Data analysis

For inferential statistics, we conducted repeated-measures analyses of variance (rmANOVA). Error bars are ± 1 within-subject standard error of the mean (SEM; Baguley, 2011; Morey, 2008). Post-hoc analyses of saccade latency on memory performance were conducted by logistic mixed modeling using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). We included subjects as a single random factor to the model. Saccade latency was centered for each individual participant before submitting this predictor to the model.

In order to detect saccadic eye movements, we transformed raw eye positions into 2D velocity space offline and then classified successive eye positions as saccades if they exceeded the median velocity by 5 SDs for at least 8 ms (Engbert & Mergenthaler, 2006). We merged two saccadic events into a single saccade if they were separated by < 20 ms. We classified the first saccade that landed within a radius of 3.6 dva from the center of the saccade target (i.e., 60% of the target's eccentricity) as the response saccade. We excluded trials based on four rejection criteria: Trials that included saccades with an amplitude > 1 dva before execution of the response saccade, trials that included blinks, trials that included anticipatory saccades (i.e., shorter latency than 80 ms), or trials with missing samples in the recordings of eye position. A total of 17,456 trials (91%) entered the final data analysis. The data are publicly available through the Open Science Framework at https://osf.io/4tkra/.

2.2. Results

The goal of the present study is to test whether a saccadic influence on maintenance in visual memory is restricted to the most fragile representations in iconic memory or, alternatively, whether saccades can also change the priority among stabilized representations at consolidated stages of VSVM. We presented visual masks at various delays following the offset of the memory array. The presentation of visual masks at early delays is expected to cause the strongest interference with memory maintenance, such that only items chosen for spontaneous transfer from iconic memory to VSVM will escape the detrimental influence of the visual mask (Gegenfurtner & Sperling, 1993; Vogel, Woodman, & Luck, 2006). The rationale of the present experiment is to study the time course of the saccadic influence on increasingly stabilized representations in visual memory by varying the onset of the movement cue (i.e., the signal to make a saccadic eye movement to a target location) simultaneously with the visual mask. In one possible scenario, memory performance increases with increasing cue/mask delay (due to interference by masking) but is not further modulated by a saccadic eye movement (Fig. 1b, left panel). In this scenario, saccades would only stabilize the most fragile memory representations. Alternatively, visual masks may still limit access to VSVM, but saccades prioritize stimuli presented at the location congruent with the saccade target. This scenario would suggest that a saccadic influence on visual memory (cf. Ohl & Rolfs, 2017) extends to more stabilized memory representations (Fig. 1b, right panel).

We computed memory performance as a function of cue/mask delay, separately for both congruent and incongruent trials (Fig. 2). Masking strongly affected performance: Recall improved with increasing delay between memory array offset and presentation of the cue/mask in both congruent and incongruent trials. On top of this, saccades exerted a clear influence on visual memory performance with a distinct temporal profile. The difference in visual memory performance (Δpc) between congruent and incongruent trials (Fig. 2a) was strongest right after the offset of the memory array ($\Delta pc_{100} = 0.081$, $CI_{95\%} = [0.035\ \ 0.127]$, $p = 0.003$; $\Delta pc_{400} = 0.045$, $CI_{95\%} = [0.003\ \ 0.086]$, $p = 0.039$), and decreased steadily over time ($\Delta pc_{800} = 0.036$, $CI_{95\%} = [-0.011\ \ 0.082]$, $p = 0.120$; $\Delta pc_{1600} = 0.019$, $CI_{95\%} = [-0.023\ 0.062]$, $p > 0.250$; $\Delta pc_{3200} = 0.002$, $CI_{95\%} = [-0.042\ 0.045]$, $p > 0.250$). A two–way repeated –measures analysis of variance (rmANOVA) corroborated these findings. We observed a significant main effect of cue/mask delay ($F(4, 36) = 13.01$, $p < 0.001$) and a significant effect of congruency ($F(1, 9) = 7.97$, $p = 0.020$). The interplay of cue/mask delay and congruency was further substantiated by a significant interaction between the two factors ($F(4, 36) = 3.33$, $p = 0.020$). That is, in incongruent trials, memory performance was worst when we presented visual masks (and the movement cue) right after memory array offset, and performance increased steadily for longer delays. At the same time, the memory benefit for congruent trials was largest for the shortest movement cue/mask delay, and it decreased for longer delays until performance in congruent and incongruent trials reached a similar level.

We further examined the spatial specificity of the saccadic influence on visual memory by relating memory performance to the angular distance between saccade target and memory test location. Running a 5 (angular distance) × 5 (cue/mask delay) rmANOVA revealed a significant influence of the angular distance ($F(4, 36) = 3.11$, $p = 0.027$) and of cue/mask delay ($F(4, 36) = 17.97$, $p < 0.001$). Spatial specificity of the saccadic influence on visual memory was not further substantiated by a significant interaction between cue/mask delay and distance ($F(16, 144) = 0.90$, $p > 0.250$; Fig. 2b), implying that spatial priorities set by saccades during

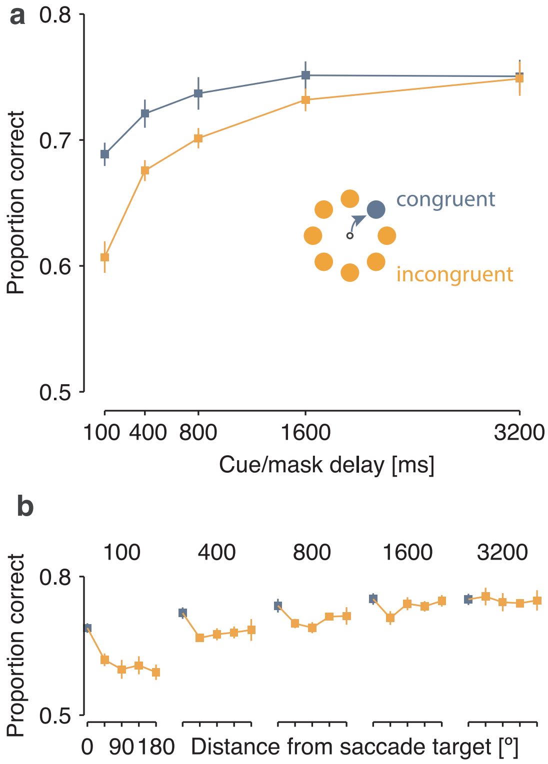

Fig. 2. Results of Experiment 1. (a) Mean performance in congruent (blue) and incongruent (orange) trials is depicted as a function of cue/mask delay. (b) Mean memory performance is displayed as a function of angular distance between the location of the memory probe and the saccade target. The spatial specificity of the saccadic influence is shown for each cue/mask delay separately. Error bars represent ± 1 SEM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

memory maintenance are observed throughout the different cue delays. Taking a closer look at the results displayed in Fig. 2b reveals an interesting pattern, in which items presented at a location next to the saccade target appears to have suffered most from the saccade (in particular for cue/mask delays from 400 to 1600 ms). However, post-hoc t-tests did not support a statistically significant difference in mean memory performance at the various incongruent locations (all *ps* > 0.1). Note, however, that a similar increase in memory performance at the location opposite to the saccade target, as compared to memory performance at intermediate locations, has been repeatedly documented in studies using a circular arrangement of stimulus locations (Germeys, De Graef, Van Eccelpoel, & Verfaillie, 2010; Ohl & Rolfs, 2017; White, Rolfs, & Carrasco, 2013).

The observed influence of saccades on visual memory performance was not due to a speed-accuracy tradeoff. Manual reaction times were significantly faster in congruent (757 ms) than incongruent (951 ms) trials ($t(9) = -3.32$, $p = 0.009$). Analyses regarding saccade parameters, using an additional 2 (congruency) × 5 (cue/mask delay) rmANOVA, showed that saccade latencies were not statistically different in congruent (235 ms) and incongruent (235 ms) trials ($F(1, 9) = 0.74$, $p > 0.250$). Saccade latencies differed significantly between cue delays ($F(4, 36) = 16.97$, $p < 0.001$; 236 ms for delay_{100}, 222 ms for delay_{400}, 229 ms for delay_{800}, 238 ms for delay_{1600}, and 250 ms for delay_{3200}), but were independent of congruency (interaction: $F(4, 36) = 1.97$, $p = 0.120$). Analyses of saccade amplitude (5.72 dva in congruent and 5.71 dva in incongruent trials) showed no significant influence by any experimental condition (main effect of congruency: $F(1, 9) = 0.002$, $p > 0.250$; cue delay: $F(4, 36) = 1.03$, $p > 0.250$; interaction: $F(4, 36) = 0.17$, $p > 0.250$).

Based on the results reported above, we claim that saccadic eye movements prioritize even consolidated representations in VSVM. However, it may be argued that the simultaneous presentation of visual masks and movement cue entail a different cascade of processing steps than the one assumed here. In fact, presentation of a movement cue will prompt observers to prepare a saccade by shifting attention to the indicated location prior to saccade onset (e.g., presaccadic shift of attention), which in turn may protect the saccade target from visual masking. Note, however, that this reverses the order of events we assumed. Indeed, in this scenario, saccades would protect memory representations from visual masking irrespective of a representation's degree of stability. Importantly, we can test this alternative mechanism as it predicts that saccades with shorter latency will be more likely to protect memory representations from masking during early cue/mask delays.

We ran a logistic mixed model (LMM) to test the hypothesis that shorter saccade latencies improve visual memory performance in congruent trials. More specifically, the LMM includes cue/mask delay (contrast-coded with a delay of 100 ms set as baseline), congruency (contrast-coded with *incongruent trials* set as baseline), the interaction cue/mask delay × congruency, centered saccade latency (i.e., subtracting the mean from all latencies), the interaction saccade latency × congruency, the interaction saccade

Table 1
Results of logistic mixed model.

	Coefficient	SE	p-value
Intercept	0.46	0.139	< 0.001
Delay 400	0.30	0.060	< 0.001
Delay 800	0.43	0.060	< 0.001
Delay 1600	0.59	0.061	< 0.001
Delay 3200	0.73	0.065	< 0.001
Congruency	0.36	0.086	< 0.001
Saccade latency	–0.05	0.858	> 0.250
Delay 400 × congruency	–0.13	0.126	> 0.250
Delay 800 × congruency	–0.17	0.125	0.177
Delay 1600 × congruency	–0.25	0.125	0.043
Delay 3200 × congruency	–0.34	0.132	0.011
Delay 400 × latency	–0.75	1.280	> 0.250
Delay 800 × latency	–0.02	1.293	> 0.250
Delay 1600 × latency	0.06	1.333	> 0.250
Delay 3200 × latency	–3.55	1.366	0.009
Congruency × latency	–0.83	1.612	> 0.250
Delay 400 × congruency × latency	1.03	2.554	> 0.250
Delay 800 × congruency × latency	2.40	2.532	> 0.250
Delay 1600 × congruency × latency	1.28	2.622	> 0.250
Delay 3200 × congruency × latency	–0.18	2.707	> 0.250

latency × cue/mask delay, and their three-way interaction as fixed effects (Table 1).

The intercept of the LMM reflects a baseline condition of memory performance at a cue/mask delay of 100 ms in incongruent trials for a saccade with mean latency. For incongruent trials, memory performance at each cue/mask delay was significantly better than the baseline delay of 100 ms (all bs > 0.30, all ps < 0.001). Memory performance at a cue/mask delay of 100 ms was significantly higher in congruent than in incongruent trials ($b = 0.36$, $SE = 0.086$, $p < 0.001$). This benefit for congruent trials was significantly smaller only at later cue delays of 1600 ms ($b = –0.25$, $SE = 0.125$, $p = 0.043$) and 3200 ms ($b = –0.34$, $SE = 0.132$, $p = 0.011$). Critically, there was no significant influence of saccade latency on memory performance at a cue/mask delay of 100 ms in incongruent trials ($b = –0.05$, $SE = 0.858$, $p > 0.250$). Moreover, the estimated influence of saccade latency in congruent and incongruent trials was not statistically significant ($b = –0.83$, $SE = 1.612$, $p > 0.250$). Similarly, saccade latency had no significant effect on memory performance at delays of 400, 800, and 1600 ms (all $p > 0.250$), and three-way-interactions of delay × congruency × latency were not statistically significant (all $p > 0.250$). Saccade latency only showed a significant effect on memory performance at the latest cue/mask delay of 3200 ms ($b = –3.55$, $SE = 1.366$, $p = 0.009$), which was not significantly different in congruent trials ($b = –0.18$, $SE = 2.707$, $p > 0.250$).

Above, we developed the argument that if saccades protect fragile memory traces from masking, then performance should be affected by saccade latency (i.e., earlier saccades come rescue fragile representations). Based on the absence of an effect of saccade latency, we argued that saccades influenced robust representations in VSVM (i.e., representations that were still available in memory despite the presentation of a visual mask). Based on the same reasoning, however, saccade latency should affect fragile representations in iconic memory when no interfering visual mask is presented—the faster a saccade the more likely it can stabilize fragile content in quickly decaying (and capacity-unlimited) iconic memory. To substantiate this claim, we reanalyzed data from a previously published experiment that is identical to the present experiment apart from the lack of visual masks and a different set of observers (Experiment 2 in Ohl & Rolfs, 2017). The absence of a visual mask in this experiment resulted in a common pool of fragile and stabilized representations in visual memory, in particular at early cue delays. We predicted, therefore, a significantly larger influence of saccade latency in the experiment without visual masks than in the present experiment in which visual masks were displayed.

Again, we ran a LMM including congruency, saccade latency, and experiment (coding: 0 = present study; 1 = experiment 2 from Ohl & Rolfs, 2017; importantly, saccade latencies were not significantly different between the two experiments $t(14) = 0.48$, $p > 0.250$ and saccade latency distributions in both experiments had similar standard deviations (across trials and collapsed over subjects); Experiment 1: $SD = 44.4$ ms; Experiment 2 from Ohl and Rolfs, 2017: $SD = 47.5$ ms) at the shortest cue delay of 100 ms (Table 2 and Fig. 3). We refrained from adding all cue delays as a factor to the model in order to reduce the model complexity (i.e., removing 4-way interactions) and ran an additional model for a cue delay of 400 ms instead (see Table 2 and Fig. 3). Again, we observed significantly higher memory performance in congruent trials of the present experiment ($b = 0.36$, $SE = 0.086$, $p < 0.001$). In the experiment without visual mask, this congruency effect was larger ($b = 0.79$, $SE = 0.169$, $p < 0.001$). Moreover, saccade latency did not affect memory performance in any condition of the experiment with visual masks. However, we observed a significant three-way interaction of saccade latency × congruency × experiment ($b = –12.56$, $SE = 3.960$, $p = 0.002$). In line with our hypothesis, this means that faster saccades improved memory performance in congruent trials of the experiment without masking. At a cue delay of 400 ms (Table 2), we observed the same three-way interaction ($b = –8.18$, $SE = 3.624$, $p = 0.024$), corroborating a significant influence of saccade latency in a paradigm without visual masks.

Table 2
Results of logistic mixed model across two experiments.

	Coefficient	SE	p-value
cue delay of 100 ms			
Intercept	0.45	0.111	< 0.001
Congruency	0.36	0.086	< 0.001
Saccade latency	1.39	1.003	0.166
Experiment (0 = present study)	−0.14	0.184	> 0.250
Congruency × saccade latency	−0.99	1.742	> 0.250
Congruency × experiment	0.79	0.169	< 0.001
Saccade latency × experiment	1.96	1.899	> 0.250
Congruency × latency × experiment	−12.56	3.960	0.002
cue delay of 400 ms			
Intercept	0.74	0.127	< 0.001
Congruency	0.23	0.091	0.014
Saccade latency	−1.68	1.165	0.150
Experiment (0 = present study)	−0.16	0.210	> 0.250
Congruency × saccade latency	0.25	2.038	> 0.250
Congruency × experiment	0.25	0.169	0.145
Saccade latency × experiment	2.04	1.996	> 0.250
Congruency × latency × experiment	−8.18	3.624	0.024

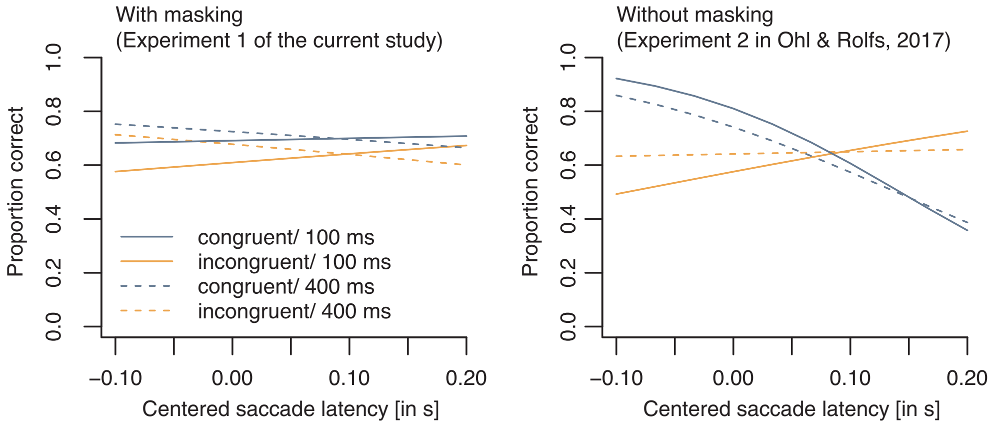

Fig. 3. Linear mixed model predictions displaying the influence of saccade latency (centered around the mean; in seconds) on memory performance. Predictions are based on the fixed effects of the LMM, showing predictions in congruent (blue) and incongruent (orange) trials for movement cue delays of 100 ms (solid lines) and 400 ms (dashed lines) in the present experiment with masks (left panel) vs. data from Ohl and Rolfs (2017, their Experiment 2; right panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Discussion

In Experiment 1, we tested whether saccades affect stabilized representations in VSVM. To this end, we presented masks and movement cue simultaneously at various points in time after memory array offset and determined memory performance as a function of a stimuli's congruency with the saccade target location. Memory performance was superior for stimuli congruent with the saccade target—a benefit that decreased with increasing cue/mask delays. Additional analyses showed that saccade latency was not associated with memory performance when presenting masks in Experiment 1. In the absence of visual masks (cf. Ohl & Rolfs, 2017; their Experiment 2), however, shorter saccade latencies can improve visual memory performance. These analyses support our conclusion that masking interfered effectively with fragile representations in visual memory, leaving only stabilized representations in memory that were further modified by saccadic eye movements. Nevertheless, the current experimental design comes at a cost as the simultaneous presentation of the masks and the movement cue imposes the additional analysis regarding saccade latency in order to distinguish between competing interpretations. Moreover, it assumes that enough variance in saccade latencies exists to detect a possible influence of saccade latencies on memory performance in Experiment 1. To overcome these limitations, it is possible to separate the presentation of masks and movement cue within the short time window in which both masking and saccades affect visual memory performance. In a second experiment, therefore, we presented the movement cue after the masks, which allowed us to directly assess the question whether saccades affect stabilized representations in visual memory.

3. Experiment 2

In Experiment 2, we created an additional condition in which masks and movement cue were temporarily separated. This is to ensure that the programing of saccades—as prompted by the movement cue—cannot interfere with the visual masking itself. More specifically, in this new condition masks were presented shortly (i.e., 100 ms) after memory array offset while the movement cue was presented 400 ms after the disappearance of the memory array (i.e., 300 ms after mask onset). We compared memory performance in this condition to memory performance when masks and movement cue were presented simultaneously—as in Experiment 1—either 100 ms or 400 ms after memory array offset. Given the results of Experiment 1, we derived specific hypotheses for the conditions with simultaneous onset of masks and movement cue: Observers should show (1) an increase in memory performance when masks are presented later during the trial, (2) an overall benefit for stimuli at locations congruent with the saccade target, and (3) that this benefit decreases over time. Critically, when saccades affect stabilized representations in VSWM—as we concluded from Experiment 1—we should observe a memory benefit for stimuli congruent with the saccade target location even if masks and movement cue are separated in time.

3.1. Method

3.1.1. Participants

Ten observers (ages 21–31; five female; nine right-handed) participated in two sessions of Experiment 2, with at least one night between the two sessions. Before running a test session, participants completed a short training for the experiment that comprised one block with 32 trials.

3.1.2. Materials and procedure

In Experiment 2 we presented visual stimuli on a gamma-linearized VIEWPixx /3D (VPixx Technologies Inc., Saint Bruno, QC, Canada), running in CRT-equivalent scanning-backlight mode (luminance in a range of 0–100 cd/m^2; pixel response time ~1 ms). Spatial resolution was set to 1920 × 1080 pixels with a vertical refresh rate of 120 Hz. The experiment was controlled by a DELL Precision T3600 (Debian GNU Linux 8), using Matlab (Mathworks, Natick, MA, USA), including the Psychophysics (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and the Eyelink toolboxes (Cornelissen et al., 2002).

The procedure was identical to Experiment 1 with two exceptions. First, we included two simultaneous cue/mask delays of 100 ms and 400 ms after memory array onset. Second, we added a new condition in which masks and movement cue were separated in time (i.e., masks were presented 100 ms and the movement cue 400 ms after memory array offset). The three conditions were presented in separate, randomly interleaved mini-blocks. In Experiment 2, one session consisted of 18 blocks, with 32 trials in each block, resulting in a total of 1,152 trials per participant (96 trials per delay in congruent trials, 288 trials per delay in incongruent trials).

3.1.3. Data analysis

Data analysis was identical to the analysis of Experiment 1. After pre-processing the data, a total of 10,209 trials (88.6%) entered the final data analysis of Experiment 2.

3.2. Results

In Experiment 2, we tested the influence of saccadic eye movements on memory performance when masks and movement cue were presented simultaneously and compared it to a new condition in which the mask's offset preceded the onset of the movement cue by 300 ms. Critically, separating masks and movement cue in time allowed us to test a saccadic influence on stabilized memory representations when the oculomotor program cannot interfere with the masking itself. We computed memory performance for saccade-target-congruent and incongruent trials as a function of the cue/mask delay (Fig. 4a). The two conditions in which masks and movement cue were presented simultaneously at either 100 ms or 400 ms after array offset replicate the general pattern of results from Experiment 1. Memory performance was best when masks where presented at a later point in time ($pc_{100/100} = 0.60$, $pc_{400/100} = 0.59$, $pc_{400/400} = 0.64$), and we observed better memory for stimuli congruent with the saccade target location ($\Delta pc_{100/100} = 0.064$, $CI_{95\%} = [0.003\ 0.125]$, $\Delta pc_{400/400} = 0.057$, $CI_{95\%} = [0.024\ 0.090]$). In contrast to Experiment 1, the memory benefit in congruent trials did not seem to decrease between the shortest delays at 100 ms and 400 ms. Critically, when masks preceded the onset of the movement cue, we still observed the predicted memory benefit for stabilized representations that were congruent with the saccade target location ($\Delta pc_{400/100} = 0.068$, $CI_{95\%} = [0.024\ 0.112]$).

A two-way rmANOVA corroborated these results. We observed a significant main effect of cue/mask delay ($F(2, 18) = 4.03$, $p = 0.036$) and a significant main effect of congruency ($F(1, 9) = 16.14$, $p = 0.003$). Post-hoc comparisons revealed a marginally significant difference in memory performance between the $delay_{100/100}$ and $delay_{400/400}$ ($t(9) = 2.20$, $p = 0.055$), and significantly better memory performance in the $delay_{400/400}$ as compared to the $delay_{400/100}$ ($t(9) = 2.79$, $p = 0.021$). The difference between the two early mask onset conditions, $delay_{100/100}$ and $delay_{400/100}$, was not significant ($t(9) = 0.68$, $p > 0.250$). In contrast to Experiment 1, we did not observe a significant interaction between cue/mask delay and congruency ($F(2, 18) = 0.11$, $p > 0.250$), suggesting that the advantage for congruent stimuli was similar at these early points in time after memory array offset.

As in Experiment 1, we further examined the spatial specificity of the saccadic influence on visual memory (Fig. 4b). In all conditions, we see a strong profile with best performance at the saccade target location. Moreover, we observed an increase in

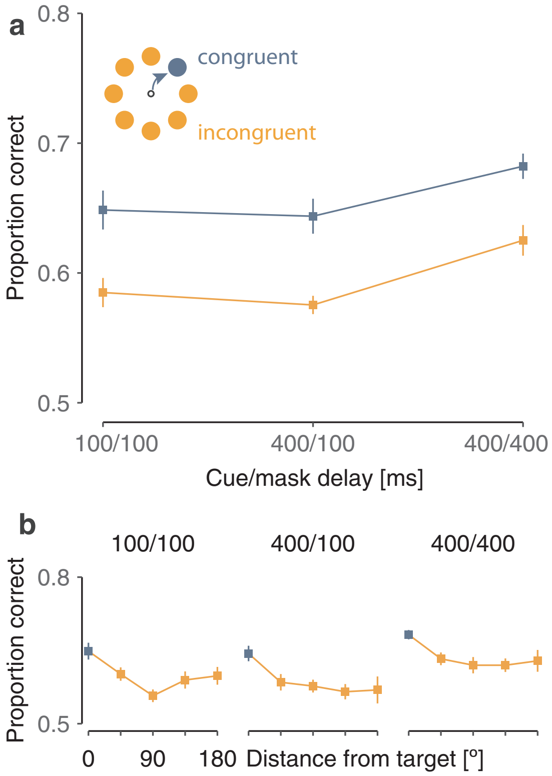

Fig. 4. Results of Experiment 2. (a) Mean performance in congruent (blue) and incongruent (orange) trials is depicted as a function of three different cue/mask delays. (b) Mean memory performance is displayed as a function of angular distance between the location of the memory probe and the saccade target. The spatial specificity of the saccadic influence is shown for each cue/mask delay separately. Error bars represent ± 1 SEM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

memory performance for the location opposite to the saccade target in the shortest cue/mask delay. A 5 (angular distance) × 3 (cue/mask delay) rmANOVA corroborated these findings. We observed a significant main effect of angular distance ($F(4, 36) = 4.86$, $p = 0.003$) and of cue/mask delay ($F(2, 18) = 4.78$, $p = 0.022$). As in Experiment 1, there was no additional modulation by the interaction between angular distance and cue/mask delay ($F(8, 72) = 0.24$, $p > 0.250$).

Next, we tested whether improved memory performance at the saccade target location could be accounted for by a speed-accuracy tradeoff. This was not the case. In fact, manual reaction times were significantly faster in congruent (765 ms) as compared to incongruent (981 ms) trials ($t(9) = -4.95$, $p < 0.001$). Furthermore, using a 2 (congruency) × 3 (cue/mask delay) rmANOVA, we assessed whether saccade parameters varied between congruent and incongruent trials for the different cue/mask delays. Mean saccade latency did not statistically differ between congruent (239 ms) and incongruent (238 ms) trials ($F(1, 9) = 1.54$, $p = 0.246$). While saccade latencies differed between cue/mask delays ($F(2, 18) = 48.95$, $p < 0.001$) with fastest latencies for delay$_{400/100}$ (208 ms) followed by delay$_{400/400}$ (240 ms) and delay$_{100/100}$ (264 ms), there was no significant interaction between congruency and cue/mask delay ($F(2, 18) = 1.83$, $p = 0.189$). Mean saccade amplitudes were the same for congruent (5.61 dva) and incongruent (5.61 dva) trials; there was neither a significant influence of congruency ($F(1, 9) = 0.002$, $p > 0.250$) nor cue/mask delay ($F(2, 18) = 0.85$, $p > 0.250$). We observed a significant interaction between congruency and cue/mask delay ($F(2, 18) = 3.70$, $p = 0.045$). However, those mean amplitudes did not reveal a meaningful pattern (congruent delay$_{100/100}$ 5.52 dva, congruent delay$_{400/400}$ 5.58 dva, congruent delay$_{400/100}$ 5.72 dva, incongruent delay$_{100/100}$ 5.58 dva, incongruent delay$_{400/400}$ 5.65 dva, incongruent delay$_{400/100}$ 5.60 dva) and they all remained in a very small amplitude range between 5.52 dva and 5.72 dva. Thus, neither a speed-accuracy tradeoff, nor meaningful differences in saccade parameters could account for the better memory performance when items were congruent with the location of the saccade target.

3.3. Discussion

In Experiment 2, we presented a new condition in which saccades were prompted after presentation of the visual masks. Given the temporal gap between masks and movement cue we ensured that a saccadic influence and the influence of the masks were clearly separated in time. Even under these conditions, we observed better memory performance for stimuli congruent with the saccade target location as compared to any other equidistant location. These results thus support the conclusion from Experiment 1 that saccades prioritize even stabilized representations in visual memory.

4. General discussion

VSVM is capacity-limited and thus requires a selection of information that will be granted access to this prioritized state. Here, we demonstrate that saccades constitute an effective selection mechanism that prioritizes representations in visual memory that have reached a durable format. This finding provides additional support for the close interactions between visual memory and the oculomotor system and actions more generally, including movements such as grasping or pointing (Heuer & Schubö, 2017; Heuer, Crawford, & Schubö, 2017).

Saccades are preceded by a mandatory shift of attention to the saccade target location that occurs even if performance would benefit from a deployment of attention away from the saccade target (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007; Ohl et al., 2017). Indeed, superior memory performance at the saccade target is likely to be the consequence of this pre-saccadic attention shift. However, a shift of pre-saccadic attention as the potential cause for the present findings does not imply that the mechanisms of overt and covert attention on visual memory are identical. Importantly, in the present study the movement cue was entirely uninformative with respect to the location of the stimulus to be recalled. This is in contrast to the frequently used *retro*-cueing paradigm in which observers covertly shift attention in response to an informative, endogenous cue that is presented during memory maintenance (Griffin & Nobre, 2003; Landman et al., 2003). Thus, saccades automatically prioritize the memory representation congruent with the saccade target location, whereas endogenous covert attention allows observers to strategically use the information provided by the cue to optimize memory performance. These wilful influences on visual memory are very likely mediated through different mechanisms. Accordingly, the time course of the saccadic influence on visual memory is rather restricted as compared to the long time window over which covert attention shifts (following a *retro*-cue) affect memory performance (Astle, Summerfield, Griffin, & Nobre, 2012; Ohl & Rolfs, 2017).

A distinction between the role of saccadic eye movements and covert shifts of attention is not exclusively derived from behavioural evidence in visual memory tasks—a dissociation of covert attention and saccade preparation has also been suggested based on their distinct neural implementations, and their influence's different time course on visual processing (for a detailed discussion see Rolfs & Carrasco, 2012). The literature on covert attention shifts in response to a *retro*-cue has identified a number of candidate mechanisms—for instance, the strategic removal of uncued representations, or the enhancement of memory representations that is dependent on cue validity (for review see Souza & Oberauer, 2016). In that respect, saccades represent an additional, ecologically valid selection mechanism that effectively prioritizes the maintenance of stabilized memory representations in the absence of informative cues. Thus, complementary research on *retro*-cueing and action-related influences on memory constitute a very promising line of research for a fine-grained behavioural decomposition of top-down influences (e.g., pre-saccadic attention vs. endogenous attention) on early visual memory.

Here and in our previous study (Ohl & Rolfs, 2017), we established a spatially selective bias for representations congruent with the saccade target location. It remains an open question, however, if performance is enhanced for stimuli congruent with the later saccade target location, or alternatively, whether congruent stimuli are simply protected while stimuli at incongruent locations suffer from saccade-related interference. In tasks that include a movement cue prompting a saccadic response, we typically observe a general cost as compared to trials without saccadic eye movements (Schut, Van der Stoep, Postma, & Van der Stigchel, 2017; Experiment 1 in Ohl & Rolfs, 2017). Such general costs may result from the experimental paradigm itself, as it requires observers to perform two tasks at the same time (i.e., a motor and a memory task). In line with this idea, a general memory benefit occurs in tasks without a movement cue when observers are allowed to freely move their eyes during the retention interval (Williams, Pouget, Boucher, & Woodman, 2013).

Typically, perceptual benefits due to pre-saccadic attention shifts have been conceptualized as enhanced performance which follows the logic of findings reporting neural enhancement in visual cortex to stimuli presented at the saccade target (Moore, Tolias, & Schiller, 1998). However, neural enhancement does not necessarily imply enhanced behavioural performance (Zénon & Krauzlis, 2012). In line with this alternative view, recent behavioural findings in a perceptual task suggest that saccades suppress stimuli at non-target locations instead of enhancing performance at the saccade target (Khan, Blohm, Pisella, & Munoz, 2015). Based on a reanalysis of our previously published data (Ohl & Rolfs, 2017), we showed that faster saccades during short retention intervals increase the probability that unstable memory traces at a high capacity stage are protected. However, our present data suggests that protection is not the whole story. Our finding that faster saccades during the same short retention intervals did not affect memory performance after masking unstable memory traces suggests an additional effect of saccades that goes beyond a mere protection from visual interference. A recent study has shown that saccade preparation (i.e., oculomotor selection as opposed to saccade execution) is sufficient to observe superior memory performance for stimuli congruent with the saccade target location (Hanning et al., 2016). Interestingly, that study also reported effects of saccade latency on visual memory performance, suggesting that an effective selection of the saccade target is required for the superior performance for stimuli in the memory array congruent with the location of the saccade target. Dissociating between the different accounts how saccade latency may affect visual memory constitutes an interesting question for future research as it points to two different sources for the implementation of the saccadic influence (e.g., what processing stage is affected by saccades; how efficient was selection of the saccade target).

The rationale of the present study is based on the assumption that visual masking decreases memory performance by interfering with a memory representation that has not been fully stabilized. Note that this conclusion does not imply that we advocate a visual memory model in which a representation necessarily enters consecutive memory stages. In fact, there is strong evidence for a processing account of visual memory in which temporal integration possesses a critical role (Di Lollo, 1980). An alternative account of masking's detrimental influence on memory performance holds that masking slows down short-term consolidation (Nieuwenstein, Potter, & Theeuwes, 2009; Wyble, Potter, Bowman, & Nieuwenstein, 2011). This idea emerged from the attentional blink paradigm in which observers are asked to detect stimuli with defined characteristics within a rapidly presented stream of stimuli (Jolicoeur & Dell'Acqua, 1998; Shapiro, Arnell, & Raymond, 1997). In this task, detection performance is typically hampered for secondary target stimuli that follow in close temporal proximity after the first target stimulus. It is assumed that consolidation of the first target requires attention, which in turn slows down the processing of the second target (Nieuwenstein et al., 2009; Wyble et al., 2011). Thus, masking may influence memory performance by either interfering with a fragile representation or by slowing down memory consolidation. Ricker and Sandry (2018) directly tested the two accounts of masking in a recent serial visual memory paradigm, and observed that masking is indeed effective through both mechanisms. However, the rate of consolidation did not depend on the interval between stimulus and masks—consolidation was only slower when masks were present as compared to a condition without masks. Moreover, memory performance for the first stimulus during serial visual presentation did not improve with increasing time for consolidation. Thus, in the present study it is unlikely that slowing down of the consolidation process played a major role—we displayed stimuli in one display (as opposed to serial presentation) and observed a strong dependence of memory performance on the interval between memory array offset and mask onset.

A recent line of research supports the view of dynamic middle- and long-term memory systems in which an already consolidated memory representation enters again a fragile state after its reactivation (Nader & Hardt, 2009). In a second step, the reconsolidation of such representations may modify the strength of the initial memory association—underlining the dynamical character of this memory model, which is in contrast to the idea of a permanent representation once after completed consolidation. The influence of visual transients—resulting from saccades, blinks, or blank screens—on visual performance (e.g., in a change detection task) demonstrate the vulnerability of visual representations in response to such transients, in particular for task-irrelevant aspects of the visual scene (Dornhoefer, Unema, & Velichkovsky, 2002). Thus, saccades in the present study may have caused a transient state in which the reconsolidation of memory representations was biased to the action goal, prioritising stimuli congruent with the saccade target at the cost of all other stimuli.

Research on active vision has repeatedly demonstrated how action-relevant locations are prioritized during visual perception (Rolfs, 2015). Moreover, there is strong neurophysiological evidence that retinotopically organized oculomotor regions involved in saccade preparation modulate neural responses in early visual cortex, thus providing a plausible neural mechanism for saccade-related effects on vision and memory (Merrikhi et al., 2017; Moore & Zirnsak, 2017; Noudoost, Chang, Steinmetz, & Moore, 2010). Such a feedback-driven boost of activity in early visual cortex is well-suited to select memory representation that reside in retinotopically organized visual areas (Harrison & Tong, 2009; Pasternak & Greenlee, 2005; Serences, Ester, Vogel, & Awh, 2009) within a distributed neural network underlying visual working memory (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017).

In summary, we have provided additional evidence that saccades impact visual memory and replicated that this impact decays within a second after the disappearance of the sensory event. Our data suggest that saccades select even among stabilized representations in VSWM, inadvertently emphasizing those whose location coincided with the movement target. Faster saccades can stabilize traces in iconic memory while saccade latency had no effect on the subset of stabilized representations that were immune to visual interference. These results add to a growing body of evidence that actions constitute an ecologically valid mechanism that limits the amount of information processed in a capacity-limited visual system, shaping how we perceive and remember the world around us.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.concog.2018.06.016.

References

Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception & Psychophysics, 74*(1), 146–162.

Averbach, E., & Coriell, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal, 40*(1), 309–328.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences, 5*(3), 119–126.

Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience, 139*(1), 201–208.

Baguley, T. (2011). Calculating and graphing within-subject confidence intervals for ANOVA. *Behavior Research Methods, 44*(1), 158–175.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48.

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science, 321*(5890), 851–854.

Beck, V. M., Hollingworth, A., & Luck, S. J. (2012). Simultaneous control of attention by multiple working memory representations. *Psychological Science, 23*(8), 887–898.

Becker, M. W., Pashler, H., & Anstis, S. M. (2000). The role of iconic memory in change-detection tasks. *Perception, 29*(3), 273–286.

Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychologische Forschung, 32*, 185–218.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.

Bridgeman, B. (1981). Cognitive factors in subjective stabilization of the visual world. *Acta Psychologica, 48*, 111–121.

Bridgeman, B., & Graziano, J. A. (1989). Effect of context and efference copy on visual straight ahead. *Vision Research, 29*(12), 1729–1736.

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research, 15*(6), 719–722.

Bridgeman, van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioural and Brain Sciences, 17*(2), 247–292.

Castet, E., Jeanjean, S., Montagnini, A., Laugier, D., & Masson, G. S. (2006). Dynamics of attentional deployment during saccadic programming. *Journal of Vision, 6*, 196–212.

Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The distributed nature of working memory. *Trends in Cognitive Sciences, 21*(2), 111–124.

Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics, 27*(3), 183–228.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers, 34*(4), 613–617.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24*(1), 87–114.

Currie, C. B., McConkie, G. W., Carlson-Radvansky, L. A., & Irwin, D. E. (2000). The role of the saccade target object in the perception of a visually stable world. *Perception & Psychophysics, 62*(4), 673–683.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*(12), 1827–1837.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research, 38*, 3147–3159.

Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Research, 50*(2), 249–259.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research, 36*(7), 985–996.

Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *Progress in Brain Research, 140*, 165–180.

Di Lollo, V. (1980). Temporal integration in visual memory. *Journal of Experimental Psychology: General, 109*(1), 75–97.

Dornhoefer, S. M., Unema, P. J. A., & Velichkovsky, B. M. (2002). Blinks, blanks and saccades: How blind we really are for relevant visual events. *Progress in Brain Research* (pp. 119–131). Elsevier Science B. V.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, 103*(18), 7192–7197.

Fougnie, D. (2008). The relationship between attention and working memory. In N. B. Johansen (Ed.). *New Research on Short-Term Memory* (pp. 1–45). Nova Science Publishers, Inc.

Gegenfurtner, K. R., & Sperling, G. (1993). Information transfer in iconic memory experiments. *Journal of Experimental Psychology: Human Perception and Performance, 19*(4), 845–866.

Germeys, F., De Graef, P., Van Eccelpoel, C., & Verfaillie, K. (2010). The visual analog: Evidence for a preattentive representation across saccades. *Journal of Vision, 10*(10), 1–28.

Gersch, T. M., Kowler, E., Schnitzer, B. S., & Dosher, B. A. (2008). Visual memory during pauses between successive saccades. *Journal of Vision, 8*(16), 1–18.

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*(8), 1176–1194.

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology, 115*(2), 1071–1076.

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature, 458*(7238), 632–635.

Henderson, J. M., & Hollingworth, A. (1999). The role of fixation position in detecting scene changes across saccades. *Psychological Science, 10*(5), 438–443.

Henderson, J. M., & Hollingworth, A. (2003). Eye movements and visual memory: Detecting changes to saccade targets in scenes. *Perception & Psychophysics, 65*(1), 58–71.

Heuer, A., & Schubö, A. (2017). Selective weighting of action-related feature dimensions in visual working memory. *Psychological Bulletin & Review, 24*(4), 1129–1134.

Heuer, A., Crawford, J. D., & Schubö, A. (2017). Action relevance induces an attentional weighting of representations in visual working memory. *Memory & Cognition, 45*(3), 413–427.

Hollingworth, A., & Luck, S. J. (2009). The role of visual working memory (VWM) in the control of gaze during visual search. *Attention, Perception & Psychophysics, 71*(4), 936–949.

Hollingworth, A., Richard, A. M., & Luck, S. J. (2008). Understanding the function of visual short-term memory: Transsaccadic memory, object correspondence, and gaze correction. *Journal of Experimental Psychology: General, 137*(1), 163–181.

Irwin, D. E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology, 23*(3), 420–456.

Irwin, D. E. (1992). Memory for position and identity across eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 18*(2), 307–317.

Irwin, D. E., & Andrews, R. V. (1996). Integration and accumulation of information across saccadic eye movements. *Attention and Performance XVI: Information Integration in Perception and Communication, 16*, 125–155.

Jolicoeur, P. (1998). Modulation of the attentional blink by on-line response selection: Evidence from speeded and unspeeded task decisions. *Memory & Cognition, 26*(5), 1014–1032.

Jolicoeur, P., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation. *Cognitive Psychology, 36*, 138–202.

Kalogeropoulou, Z., Jagadeesh, A. V., Ohl, S., & Rolfs, M. (2017). Setting and changing feature priorities in visual short-term memory. *Psychonomic Bulletin & Review, 24*(2), 453–458.

Khan, A. Z., Blohm, G., Pisella, L., & Munoz, D. P. (2015). Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *European Journal of Neuroscience, 41*(12), 1624–1634.

Kleiner, M., Brainard, D. H., Pelli, D. G., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception, 36*(14).

Kowler, E., & Blaser, E. (1995). The accuracy and precision of saccades to small and large targets. *Vision Research, 35*(12), 1741–1754.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897–1916.

Landman, R., Spekreijse, H., & Lamme, V. A. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research, 43*(2), 149–164.

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences, 17*(8), 391–400.

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience, 17*(3), 347–356.

McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance, 22*(3), 563–581.

Merrikhi, Y., Clark, K., Albarran, E., Parsa, M., Zirnsak, M., Moore, T., & Noudoost, B. (2017). Spatial working memory alters the efficacy of input to visual cortex. *Nature Communications, 8*, 1–10.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*(14), 1–16.

Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual Review of Psychology, 68*(1), 47–72.

Moore, T., Tolias, A. S., & Schiller, P. H. (1998). Visual representations during saccadic eye movements. *Proceedings of the National Academy of Sciences, 95*(15), 8981–8984.

Morey, R. D. (2008). Confidence intervals from normalized data: A correction to Cousineau (2005). *Tutorial in Quantitative Methods for Psychology, 42*(2), 61–64.

Nader, K., & Hardt, O. (2009). A single standard for memory: The case for reconsolidation. *Nature Reviews Neuroscience, 10*(3), 224–234.

Nieuwenstein, M. R., Potter, M. C., & Theeuwes, J. (2009). Unmasking the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 35*(1), 159–169.

Noudoost, B., Chang, M. H., Steinmetz, N. A., & Moore, T. (2010). Top-down control of visual attention. *Current Opinion in Neurobiology, 20*(2), 183–190.

Ohl, S., & Kliegl, R. (2016). Revealing the time course of signals influencing the generation of secondary saccades using Aalen’s additive hazards model. *Vision*

Research, 124, 52–58.

Ohl, S., & Rolfs, M. (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 43*(5), 736–748.

Ohl, S., Brandt, S. A., & Kliegl, R. (2011). Secondary (micro-)saccades: The influence of primary saccade end point and target eccentricity on the process of post-saccadic fixation. *Vision Research, 51*(23–24), 2340–2347.

Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision, 17*(13), 1–11.

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience, 6*(2), 97–107.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Ricker, T. J., & Sandry, J. (2018). The relationship between masking and short-term consolidation during recall from visual working memory. *Annals of the New York Academy of Sciences,* 1–11.

Rolfs, M. (2015). Attention in active vision: A perspective on perceptual continuity across saccades. *Perception, 44*(8–9), 900–919.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience, 32*(40), 13744–13752a.

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & Psychophysics, 64*(5), 754–763.

Schut, M. J., Van der Stoep, N., Postma, A., & Van der Stigchel, S. (2017). The cost of making an eye movement: A direct link between visual working memory and saccade execution. *Journal of Vision, 17*(6), 1–20.

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science, 20*(2), 207–214.

Shao, N., Li, J., Shui, R., Zheng, X., Lu, J., & Shen, M. (2010). Saccades elicit obligatory allocation of visual working memory. *Memory & Cognition, 38*(5), 629–640.

Shapiro, K. L., Arnell, K. M., & Raymond, J. E. (1997). The attentional blink. *Trends in Cognitive Sciences, 1*(8), 291–296.

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS ONE, 3*(2), e1699.

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception & Psychophysics, 78*(7), 1839–1860.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs, 74*(11), 1–29.

Van der Stigchel, S., & Hollingworth, A. (2018). Visuospatial working memory as a fundamental component of the eye movement system. *Current Directions in Psychological Science, 27*(2), 136–143.

van Loon, A. M., Olmos-Solis, K., & Olivers, C. N. L. (2017). Subtle eye movement metrics reveal task-relevant representations prior to visual search. *Journal of Vision, 17*(6), 1–15.

Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 24*(6), 1656–1674.

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance, 32*(6), 1436–1451.

White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research, 85*, 26–35.

Williams, M., Pouget, P., Boucher, L., & Woodman, G. F. (2013). Visual–spatial attention aids the maintenance of object representations in visual working memory. *Memory & Cognition, 41*(5), 698–715.

Wyble, B., Potter, M. C., Bowman, H., & Nieuwenstein, M. (2011). Attentional episodes in visual perception. *Journal of Experimental Psychology: General, 140*(3), 488–505.

Zénon, A., & Krauzlis, R. J. (2012). Attention deficits without cortical neuronal deficits. *Nature, 489*(7416), 434–437.