

# Saccadic Eye Movements Impose a Natural Bottleneck on Visual Short-Term Memory

Sven Ohl and Martin Rolfs  
Humboldt Universität zu Berlin

Visual short-term memory (VSTM) is a crucial repository of information when events unfold rapidly before our eyes, yet it maintains only a fraction of the sensory information encoded by the visual system. Here, we tested the hypothesis that saccadic eye movements provide a natural bottleneck for the transition of fragile content in sensory memory to VSTM. In 4 experiments, we show that saccades, planned and executed after the disappearance of a memory array, markedly bias visual memory performance. First, items that had appeared at the saccade target were more readily remembered than items that had appeared elsewhere, even though the saccade was irrelevant to the memory task (Experiment 1). Second, this influence was strongest for saccades elicited right after the disappearance of the memory array and gradually declined over the course of a second (Experiment 2). Third, the saccade stabilized memory representations: The imposed bias persisted even several seconds after saccade execution (Experiment 3). Finally, the advantage for stimuli congruent with the saccade target occurred even when that stimulus was far less likely to be probed in the memory test than any other stimulus in the array, ruling out a strategic effort of observers to memorize information presented at the saccade target (Experiment 4). Together, these results make a strong case that saccades inadvertently determine the content of VSTM, and highlight the key role of actions for the fundamental building blocks of cognition.

*Keywords:* saccade, presaccadic attention, iconic memory, visual STM

Visual events often unfold rapidly before our eyes. Their immediate traces in memory allow us to reflect and act upon them when their sensory origin has disappeared from view. The capacity of visual memory is large at first—a storage known as iconic memory—but its content decays within a fraction of a second (Averbach & Coriell, 1961; Gegenfurtner & Sperling, 1993; Sperling, 1960). A handful of items survive the initial volatile phase and reach a more durable representation—visual short-term memory (VSTM)—that lasts for many seconds (Ma, Husain, & Bays, 2014).

Both selective and nonselective processes transfer information from iconic memory to VSTM (Averbach & Coriell, 1961; Gegenfurtner & Sperling, 1993). During selective transfer and the sub-

sequent maintenance of content in VSTM, informative cues can provide priorities as to which part of the scene is most relevant (Becker, Pashler, & Anstis, 2000; Griffin & Nobre, 2003; Schmidt, Vogel, Woodman, & Luck, 2002), driving a top-down selection process mediated by spatial attention (Awh, Vogel, & Oh, 2006; Fougner, 2008). But which parts of the vanished scene does the visual system retain when informative cues are missing? Here, we tested the idea that, in active observers, the targeting of rapid eye movements (saccades) determines the fate of fragile sensory traces in visual memory.

In natural vision, the eyes shift to a new location several times per second, selecting the current focus of visual and cognitive processing (Henderson & Hollingworth, 1999, 2003; McConkie & Currie, 1996). The execution of saccades appears to wipe out most iconic memory traces, and only a few attended items are maintained up until the new fixation, suggesting that transsaccadic memory relies on VSTM (Irwin, 1992; Irwin & Andrews, 1996; see Germeys, De Graef, van Eccelpoel, & Verfaillie, 2010 for a challenge of this conclusion). These previous studies, however, invariably examined transsaccadic memory only for objects that were present during saccade planning and disappeared with the onset of the saccade. With that timing, stimuli at the saccade target benefit from an increase in visual sensitivity during sensory encoding—the *presaccadic attention shift* (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs & Carrasco, 2012)—and, perhaps as a consequence, prioritized access to VSTM (Bays & Husain, 2008; Gersch, Kowler, Schnitzer, & Doshier, 2008; Irwin, 1991; Irwin & Gordon, 1998; Melcher & Piazza, 2011; Shao et al., 2010; Zhao, Gersch, Schnitzer, Doshier, & Kowler, 2012).

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Sven Ohl and Martin Rolfs, Department of Psychology, and Bernstein Center for Computational Neuroscience, Humboldt Universität zu Berlin.

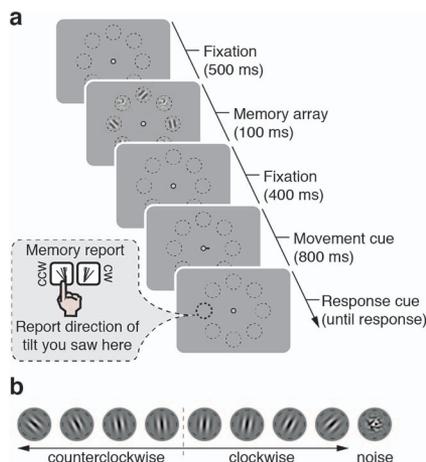
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Correspondence concerning this article should be addressed to Sven Ohl, Department of Psychology, Humboldt Universität zu Berlin, Philippstr. 13 Haus 6, 10115 Berlin, Germany. E-mail: [sven.ohl@bccn-berlin.de](mailto:sven.ohl@bccn-berlin.de)

The present study investigated to what extent the presaccadic attention shift affects visual memory beyond sensory encoding, during the consolidation and maintenance of stimulus representations. In four experiments, we assessed the impact of saccades on the memory of items that disappear from view before a saccade could even be planned. Our results provide direct, conclusive evidence that eye movements actively impose priorities on what we retain in memory and what we forget.

### Experiment 1

In a first experiment, we examined whether and how the execution of saccades affects the retention of feature information in visual memory. On each trial (Figure 1a), we presented a set of four Gabors (memory array)—tilted to a variable degree either clockwise or counterclockwise relative to vertical (Figure 1b). At the end of the trial, observers reported the orientation of one of them, identified by a response cue. On saccade trials, a movement cue, presented 400 ms after the disappearance of the memory array, prompted participants to rapidly shift gaze to one of the four locations. Importantly, the location for the saccade target was completely uninformative about the location of the response cue. Thus, the memory test location coincided with the saccade target as often as with any other item location. We hypothesized that if saccades cause an obligatory shift of memory resources toward the item that had occupied the saccade target location, we should observe higher memory performance when response cue and saccade target coincided (congruent trials) than when they did not (incongruent trials).



**Figure 1.** Experimental procedure of Experiment 1. (a) We presented a memory array consisting of four tilted Gabor patches (other locations were filled with noise patches) for 100 ms. Observers were asked to maintain those oriented Gabor patches in memory until a response cue highlighted the test location, prompting observers to report the orientation (clockwise vs. counterclockwise) of the Gabor patch initially presented at that location. During the retention interval, a movement cue instructed participants to move their eyes quickly to the indicated location. The saccade target location could be either congruent or—as in this example—incongruent with the memory test location. Importantly, the saccade target was uninformative about the memory test location, coinciding with it in only 25% of the trials. (b) Eight orientations from which each item was selected, and noise patch.

### Method

**Participants.** Five observers (ages 23–31 years; 3 female; 5 right-handed)—all naïve as to the purpose of the study—participated in seven sessions of Experiment 1 (two training and five test sessions), with at least one night between consecutive sessions. None of the five subjects had ever been trained in a similar task. We excluded one participant from the analysis as a consequence of very low performance (<60% correct trials).

In all experiments, participants received a compensation of €7 for each session. All observers had normal or corrected-to-normal vision and gave informed consent in writing prior to participation. The study was approved by Humboldt University’s ethics commission and conducted in accordance with the Declaration of Helsinki (2008).

**Materials and procedure.** Observers sat in a dark room with their head positioned on a chin rest in order to minimize head movements. We recorded the positions of observers’ dominant eye (determined beforehand using a hole-in-a-card test) with an EyeLink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada). The distance between observer and screen was 57 cm. The display was a gamma-corrected Sony Trinitron CRT with a spatial resolution of  $1280 \times 800$  pixels and a refresh rate of 100 Hz. A Mac mini computer (Apple, Cupertino, CA, U.S.A.) running Matlab (Mathworks, Natick, MA, U.S.A.), Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002) controlled stimulus presentation, response collection, and online gaze control.

Participants reported the orientation of one of four Gabor patches (maximum luminance of  $113 \text{ cd/m}^2$  and minimum luminance of  $42 \text{ cd/m}^2$ ) held in memory. Each trial started with the presentation of a fixation point ( $0.6^\circ$  diameter white circle with black contour; gray background with a luminance of  $77 \text{ cd/m}^2$ ) and eight circular placeholders ( $1.96^\circ$  diameter) arranged on an imaginary circle at an eccentricity of  $6^\circ$  (Figure 1a). After 500 ms, we flashed a memory array for 100 ms, consisting of four Gabor patches (50% contrast, randomly assigned spatial frequency of 1.5 or 2.25 cycles per degree, random phase,  $0.65^\circ$  SD Gaussian envelope), each of which had one of eight possible orientations relative to vertical ( $\pm\pi/4$ ,  $\pm\pi/8$ ,  $\pm\pi/16$ , or  $\pm\pi/32$ ; Figure 1b). We determined Gabor locations randomly on each trial and filled the remaining four locations with noise patches with no orientation information (pixel noise, band-pass filtered from half to twice the spatial frequency of the Gabors, at the same contrast, enveloped in the same Gaussian window; see Rolfs & Carrasco, 2012). All stimuli then disappeared and after another 400 ms, a movement cue (black line segment,  $0.23^\circ$  long) appeared next to the fixation spot, identifying one of the placeholders as the saccade target. Participants had to move their eyes to the indicated location in less than 400 ms; otherwise the trial was aborted (see below). Another 800 ms later, a response cue (the outline of one placeholder thickened) indicated the location of one of the previously presented Gabors and participants reported whether that Gabor had been oriented clockwise or counterclockwise from vertical.

Saccade target and response cue were at the same location on 25% of all trials (congruent condition) but most often did not coincide (incongruent condition; 75% of all trials). Thus, the movement cue was not informative as to which Gabor’s orientation participants would later have to report.

In two additional control conditions, we studied memory performance when participants kept fixation in the center of the screen. In these fixation conditions, the movement cue was either replaced by a circle presented around the fixation point (neutral condition), or by the same line cue as in the saccade condition, pointing in the direction of one of the placeholders (25% congruent trials and 75% incongruent trials). In both control conditions, we instructed observers to ignore the cue and to maintain fixation.

We conducted a standard nine-point calibration (and validation) to align eye and screen coordinates before the first trial, after short breaks, and whenever necessary. Before each trial, a fixation control routine required observers' gaze position to be inside a circular region (1.5° diameter) centered on the fixation spot. Once fixation was successful for at least 200 ms, the trial started. We encouraged observers to avoid blinking before the presentation of the response cue. Blinks, delayed saccadic responses, and saccades during requested fixation periods 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 18 short blocks of 32 trials, with fixation and saccade conditions run in separate and randomly interleaved blocks. Each observer completed a total of 2,880 trials in the five test sessions (for each saccade and fixation block, 120 trials per orientation in incongruent trials; 40 trials per orientation in congruent trials; 40 trials per orientation in the neutral fixation condition). The necessary number of trials per condition was determined on the basis of a previous study using a similar task but without saccades (Murray, Nobre, Clark, Cravo, & Stokes, 2013). As the combination of a memory and a saccade task requires some training, we decided to collect a large number of trials on a smaller number of participants (Rolfs & Carrasco, 2012), resulting in a comparable number of trials per condition as in Murray et al. (2013).

**Data analysis.** We described how visual memory performance ( $y$ ) depended on the degree of stimulus tilt from vertical ( $x$ ) using psychometric functions with 3 free parameters:

$$y = \frac{\lambda}{2} + \frac{1-\lambda}{2} * \operatorname{erfc}\left(\frac{-\beta}{\sqrt{2}}(x + \gamma)\right), \quad (1)$$

where  $\lambda$  determines the asymptotes and  $\beta$  is the slope of the function. This function isolates the likelihood to forget an item (captured by  $\lambda$ ) from potential differences in the fidelity of visual memory representations (captured by  $\beta$ ) in our paradigm (adapted from Murray et al., 2013; Murray, Nobre, & Stokes, 2011). The inclusion of the  $\gamma$  parameter allowed us to estimate the slope and asymptote of each condition independently of a possible response bias (i.e., the tendency to report one direction more often than the other). This is particularly important if performance differs between the two conditions, as the expected impact of a response bias is larger when performance is low.

We obtained confidence intervals for these parameters using the following bootstrapping procedure, which simulates variability in the data at the subject level and group level. Starting on the group level, we drew 10,000 random samples, where each single bootstrap sample was created by randomly selecting  $N$  participants (with replacement) from the original pool of  $N$  participants. Each time a participant was chosen for a sample, we bootstrapped at the subject level, creating a surrogate data set by randomly drawing a value from a binomial distribution—defined by the performance

(proportion correct) and the number of trials for that individual in a given experimental condition. For each bootstrap sample, we determined the mean performance for each orientation and fitted a psychometric function to these average data, resulting in one bootstrap estimate for each of the function's parameters. Based on the 10,000 bootstrap estimates for each parameter of the function we defined 95% confidence intervals (95% CI) as the 2.5 and 97.5 percentile of the parameter distributions. To determine two-sided  $p$  values, we computed the difference between 10,000 bootstrapped samples of two conditions (e.g., congruent vs. incongruent), and determined the proportion that exceeded zero, multiplied by 2.

Similarly, for manual response times (RTs), we drew 10,000 RTs from the pool of observed RTs in a condition, for each participant in the bootstrap sample. We determined the average difference between two conditions in each bootstrap sample and computed 95% CI, and  $p$  values were based on the distribution of these differences.

For offline saccade detection, we transformed raw eye traces into 2D velocity space and classified segments exceeding median velocity by 5 SDs for a minimum duration of 8 ms as saccades (Engbert & Mergenthaler, 2006). If two consecutive saccades were separated by less than 20 ms, they were merged into a single saccade. The response saccade was defined as the first saccade that landed within a radius of 3.6° from the target's center. We excluded from further analysis trials with saccades larger than 1° executed before the response saccade. Furthermore, we rejected trials including blinks or missing eye position samples. On the basis of these criteria, a total of 11,206 trials (97%) entered the final data analysis of Experiment 1.

## Results

Figure 2 plots the number of clockwise reports as a function of stimulus orientation, showing the expected increase in performance with increasing magnitudes of orientation. More importantly, observers performed markedly better when the saccade had targeted the memory test location (congruent) than when the saccade had targeted a different location of the array (incongruent). The benefit in memory performance at the saccade target was highly spatially tuned—it dropped sharply just one item away in the memory array (inset in Figure 2a;  $\Delta p_{0-1} = 0.074$ , 95% CI [0.049, 0.098],  $p < .001$ ). Moreover, the difference in performance between congruent and incongruent trials was not a result of a speed-accuracy trade-off. With an instruction that strongly emphasized accuracy over response time, manual RTs were highly variable and not significantly different in congruent (766 ms) and incongruent (974 ms) trials (mean  $\Delta$ response time (RT) = 208 ms, 95% CI [-346, 751],  $p > .250$ ); if anything, responses were faster in the congruent condition, which also yielded higher memory performance. Saccade latencies were indistinguishable in congruent (197 ms) and incongruent (196 ms) trials (mean  $\Delta$ SRT = 1 ms, 95% CI [-47, 50],  $p > .250$ ). Similarly, saccade amplitudes were not significantly different in congruent (5.58°) and incongruent (5.59°) trials (mean  $\Delta$ Amp = -0.01°, 95% CI [-1.315, 1.377],  $p > .250$ ).

By fitting psychometric functions to the proportion of responses as a function of orientation (Figure 2), we assessed whether saccades had an impact on the probability of forgetting an item (captured by  $\lambda$ ), the fidelity of the memory representation (cap-

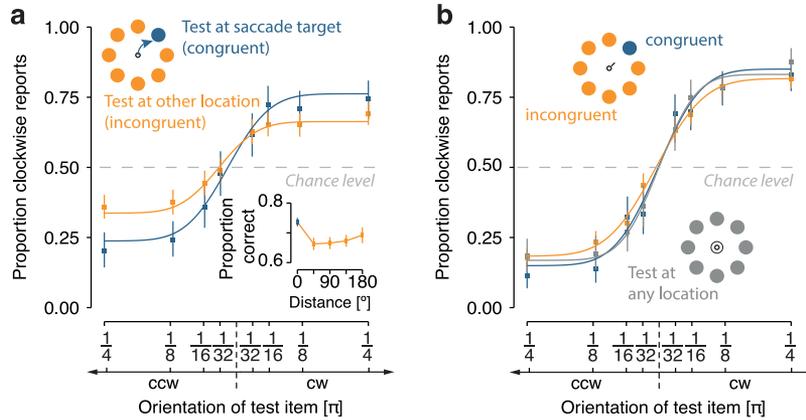


Figure 2. Results of Experiment 1. Mean proportions of clockwise reports plotted as a function of the orientation of the probed memory item. Here, psychometric functions were fitted to the average data. (a) Saccade conditions. The inset displays memory performance as a function of angular distance between memory probe and saccade target in the array. (b) Fixation conditions. Error bars are 95% CI. See the online article for the color version of this figure.

tured by  $\beta$ ), or both (see Table 1 for an overview of parameter estimates). We found that observers forgot an item much more often when they made a saccade to a different location in the display (incongruent trials), than when we probed memory at the saccade target location ( $\Delta\lambda_{\text{sac}} = 0.198$ , 95% CI [0.096, 0.303],  $p = .002$ ). This difference in memory performance was evident as a shift of the asymptotes of the psychometric functions toward chance. However, for items that observers remembered, the fidelity of the memory was the same, irrespective of whether it had been at the saccade target or elsewhere in the array. This result is evident in the slopes of the psychometric functions, which did not differ across congruency conditions ( $\Delta\beta_{\text{sac}} = 0.008$ , 95% CI [-0.067, 0.093],  $p > .250$ ). Finally, the response bias to report clockwise orientations (captured by  $\gamma$ ) was not significantly different between congruent and incongruent trials ( $\Delta\gamma_{\text{sac}} = 3.01$ , 95% CI [-0.76, 6.81],  $p = .118$ ).

In the fixation control condition (Figure 2b), the presentation of an irrelevant line cue did not result in a significant difference between the congruent and incongruent condition in any of the parameter estimates ( $\Delta\lambda_{\text{fix}} = 0.068$ , 95% CI [-0.027, 0.159],  $p = .154$ ;  $\Delta\beta_{\text{fix}} = -0.009$ , 95% CI [-0.055, 0.021],  $p > .250$ ;  $\Delta\gamma_{\text{fix}} = 0.759$ , 95% CI [-1.59, 3.10],  $p > .250$ ). The small trend for better performance in the congruent condition might reflect carry-over effects from saccade blocks, resulting from our choice to interleave short blocks of the two conditions. Neither the congruent ( $\Delta\lambda = -0.038$ , 95% CI [-0.144, 0.073],  $p > .250$ ;  $\Delta\beta = -0.012$ ,

95% CI [-0.063, 0.041],  $p > .250$ ;  $\Delta\gamma = 0.222$ , 95% CI [-2.441, 2.903],  $p > .250$ ) nor the incongruent ( $\Delta\lambda = 0.030$ , 95% CI [-0.057, 0.121],  $p > .250$ ;  $\Delta\beta = -0.022$ , 95% CI [-0.069, 0.013],  $p > .250$ ;  $\Delta\gamma = 0.967$ , 95% CI [-1.317, 3.327],  $p > .250$ ) fixation conditions differed from the neutral fixation condition, in which we presented a circular cue.

Discussion

In summary, Experiment 1 revealed a strong influence of saccades—prepared and executed at least 400 ms after the disappearance of an array of memory items—on performance in a visual memory task. Stimuli presented at the location congruent with the saccade target were more often remembered than stimuli presented at incongruent locations. This effect was observed although the saccade task was uninformative with respect to the memory task, suggesting that saccades have an obligatory impact on the formation of stable representations in visual memory. We will further substantiate this point in Experiment 4.

It is worth noting that, overall, the probability of forgetting an item ( $\lambda$ ) was smaller in fixation as compared to saccade blocks (see Table 1), indicating higher memory performance in fixation than saccade trials (see also Gersch et al., 2008). This likely reflects costs resulting from a dual task in saccade blocks—the maintenance of representations in memory and the planning of a saccadic response to an endogenous cue. Similar costs have often

Table 1  
Parameter Estimates for Psychometric Functions

Parameters	Saccade		Fixation		
	Congruent	Incongruent	Congruent	Incongruent	Neutral
$\lambda$	.475 ± .044	.674 ± .030	.299 ± .040	.367 ± .025	.337 ± .038
$\beta$	.089 ± .043	.097 ± .032	.086 ± .021	.076 ± .008	.097 ± .019
$\gamma$	2.893 ± 1.449	5.902 ± 1.289	.331 ± .963	1.073 ± .674	.098 ± .969

Note. Median of 10,000 bootstrapped parameter estimates (±SEM) in Experiment 1.

been reported (Jonikaitis, Schubert, & Deubel, 2010; Pashler, Carrier, & Hoffman, 1993) and may not be interpreted as a global detrimental effect on visual memory caused by saccades per se. Instead, the requirement to transform a symbolic cue into a saccadic motor command may draw central resources away from the memory task.

## Experiment 2

In Experiment 2, we assessed the time course of the observed influence of saccadic eye movements on visual memory. Varying the delay between the offset of the memory array and the onset of the movement cue (henceforth, cue delay) from 100 to 3200 ms, we included both the iconic memory stage and VSTM. At one extreme, if saccades exert their influence exclusively on the transition of iconic memory traces to VSTM, the difference between the congruent and the incongruent condition should decay rapidly and may no longer be evident 500 ms after the memory array has disappeared (Averbach & Coriell, 1961; Coltheart, 1980; Sperling, 1960). At the other extreme, if saccades exert an influence only during maintenance in VSTM, a difference between congruent and incongruent trials should emerge with increasing cue delays (as the memory forms) and remain evident even for the longest ones. Indeed, retro-cues that explicitly inform observers about the relevance of a particular location after the disappearance of the array (Becker et al., 2000; Griffin & Nobre, 2003) selectively improve memory performance for the cued item even after many seconds (Astle, Summerfield, Griffin, & Nobre, 2012; Sligte, Scholte, & Lamme, 2008).

## Method

**Participants.** Six observers (ages 21–30 years, 4 female, 5 right-handed) participated in Experiment 2, each completing four sessions (one training and three test sessions), with at least one night between consecutive sessions. Two of them had also participated in Experiment 1.

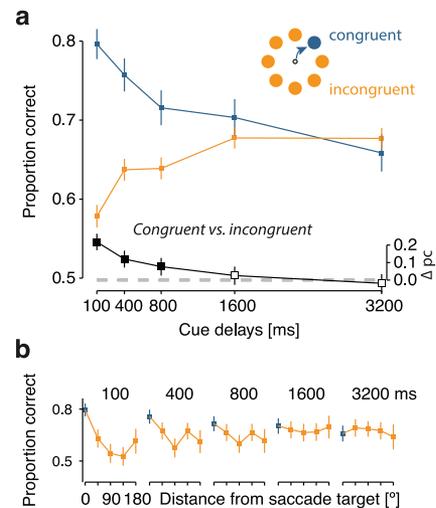
**Materials and procedure.** All aspects of the materials and procedure were identical to those in Experiment 1 with the following exceptions. First, we used five different cue delays (100, 400, 800, 1600, or 3200 ms) between the offset of the memory array and the onset of the movement cue, randomly interleaved across blocks (but constant within a block). Second, Gabor patches were randomly assigned one of two possible orientations ( $\pm\pi/4$ ). Third, we tested saccade trials only. As in the first experiment, the movement cue was completely uninformative about the location tested for memory. An experimental session consisted of 20 blocks, each consisting of 24 trials, resulting in a total of 1,440 completed trials per observer (216 trials per cue delay in incongruent trials; 72 trials per cue delay in congruent trials). During offline detection of saccades, we applied the same criteria for trial rejection as in Experiment 1; 7,815 trials (93%) entered the final data analysis of Experiment 2.

**Data analysis.** Estimates of performance differences between congruent and incongruent trials at different time points, and their confidence intervals, are based on bootstrapping ( $n = 10,000$ ; see Experiment 1). Statistical inference regarding the influence of cue delay and congruency on memory performance is based on repeated-measures analysis of variance (rmANOVA). In case of

significant interactions, we conducted additional post-hoc comparisons between specified conditions using bootstrapping. Effects on manual RTs, saccade latencies, and saccade amplitude were quantified using rmANOVAs.

## Results

We calculated memory performance as a function of cue delay, separately for congruent and incongruent trials (Figure 3). The saccadic influence on memory performance had a distinctive temporal profile. The performance difference ( $\Delta pc$ ) between congruent and incongruent trials (Figure 3a, bottom) was strongest right after the offset of the memory array ( $\Delta pc_{100} = 0.218$ , 95% CI [0.170, 0.265],  $p < .001$ ;  $\Delta pc_{400} = 0.120$ , 95% CI [0.071, 0.168],  $p < .001$ ), still evident 800 ms after the memory array had disappeared from view ( $\Delta pc_{800} = 0.077$ , 95% CI [0.026, 0.127],  $p = .004$ ), and insignificant later on ( $\Delta pc_{1600} = 0.026$ , 95% CI [-0.027, 0.077],  $p > .250$ ;  $\Delta pc_{3200} = -0.018$ , 95% CI [-0.072, 0.034],  $p > .250$ ). A two-way rmANOVA corroborated these results. Although there was no main effect of cue delay,  $F(4, 20) = 0.55$ ,  $p > .250$ , we obtained a strong effect of congruency,  $F(1, 5) = 19.11$ ,  $p = .007$ , and an interaction of the two factors,  $F(4, 20) = 6.10$ ,  $p = .002$ . That is, when we probed memory at the target of the saccade, observers' performance was best when the saccade was cued soon after the offset of the memory array, and it declined steadily for longer cue delays (congruent condition:  $\Delta pc_{1600-100} = -0.093$ , 95% CI [-0.151, -0.034],  $p = .001$ ). In stark contrast, for locations other than the saccade target, eye movements executed right after the offset of the memory array had



**Figure 3.** Results of Experiment 2. (a) Mean performance in congruent (blue [dark gray]) versus incongruent (orange [light gray]) trials is depicted as a function of cue delay (time between the disappearance of the memory array and the onset of the movement cue). The difference in memory performance ( $\Delta pc$ , bottom inset) between congruent and incongruent trials is significant when 95% CI do not overlap with zero (gray dashed line), as highlighted by filled markers. (b) Spatial specificity of the saccadic influence on memory performance. Mean performance as a function of angular distance between the memory probe location and the saccade target in the array, plotted separately for each cue delay tested. Error bars are 95% CI. See the online article for the color version of this figure.

an inhibiting effect on memory performance. In fact, for these locations, memory performance improved gradually as the cue delay increased (incongruent:  $\Delta pc_{1600-100} = 0.099$ , 95% CI [0.061, 0.138],  $p < .001$ ), reaching a level of performance similar to that at the saccade target over the course of a second.

As in Experiment 1, memory performance also depended on the angular distance between the position of the memory probe and the position of the saccade target (rmANOVA;  $F(4, 20) = 6.62$ ,  $p = .001$ ). With increasing cue delay, the advantage for the saccade target disappeared, as substantiated by a significant interaction of cue delay and distance ( $F(16, 80) = 2.73$ ,  $p = .002$ ; Figure 3b). Post hoc one-way rmANOVAs revealed a significant influence of distance for the 100 ms,  $F(4, 20) = 10.43$ ,  $p < .001$  and 400 ms cue delays,  $F(4, 20) = 3.9$ ,  $p = .017$ . For cue delays of 800 ms,  $F(4, 20) = 1.85$ ,  $p = .160$ , 1600 ms,  $F(4, 20) = 0.34$ ,  $p > .250$ , and 3200 ms,  $F(4, 20) = 0.71$ ,  $p > .250$ , the effect of distance did not reach significance. Moreover, for short cue delays, performance was somewhat higher at the location opposite the saccade target than at other incongruent locations (see also Germeys et al., 2010; White, Rolfs, & Carrasco, 2013).

The observed effects of congruency on performance were not due to a speed–accuracy trade-off. RTs were significantly faster in congruent (819 ms) than incongruent (1040 ms) trials,  $t(5) = -5.36$ ,  $p = .003$ . A rmANOVA showed that saccade latencies were equivalent for congruent (227 ms) and incongruent (229 ms) trials,  $F(1, 5) = 3.94$ ,  $p = .104$ . Saccade latencies differed significantly between cue delays,  $F(4, 20) = 15.61$ ,  $p < .001$ , independent of congruency (interaction:  $F(4, 20) = 0.23$ ,  $p > .250$ ). Saccade amplitudes ( $5.51^\circ$  in congruent and  $5.49^\circ$  in incongruent trials) were not affected by the experimental conditions (main effect of congruency:  $F(1, 5) = 0.26$ ,  $p > .250$ ; cue delay:  $F(4, 20) = 1.11$ ,  $p > .250$ ; interaction:  $F(4, 20) = 0.67$ ,  $p > .250$ ).

## Discussion

We delineated the time course of a saccadic influence on visual memory representations, and found a strong difference for stimuli congruent versus incongruent with the saccade target location up to 800 ms after the disappearance of the memory array. This time course suggests a saccadic influence on a stage that exceeds what is typically regarded as iconic memory (<500 ms after the offset of the array). However, depending on the experimental setup, traces in iconic memory can persist for more than one second (Irwin & Thomas, 2008), which complicates the definition of a clear-cut temporal border between iconic memory and VSTM. Indeed, iconic memory and VSTM might simply represent two states of a single process—the time-consuming formation of a stable memory representation. From that perspective, saccades may provide very strong cues as to what information should be selected for VSTM, and they might outperform the efficiency of cues for covert attention that have been used in traditional studies of iconic memory.

In line with this idea, Rolfs and Carrasco (2012) found that visual sensitivity increases much more rapidly when observers prepare a saccade to a cued location than when they are shifting attention covertly. Alternatively, saccades may affect representations that have already been selected for VSTM (nonselective transfer; Gegenfurtner & Sperling, 1993), but not yet reached a durable format.

## Experiment 3

In Experiment 3, we examined whether saccades stabilize fragile traces in visual memory. To this end, we varied the interval between movement cue and response cue while keeping the interval between memory array offset and movement cue fixed at 400 ms. In Experiments 1 and 2, this interval between memory array and movement cue yielded a strong memory performance benefit for stimuli that had been presented at the location congruent with the saccade target. Therefore, if saccades stabilize fragile representations in visual memory, we expect that varying the delay between movement cue onset and response cue should not affect the benefit for stimuli presented at the same location as the saccade target—even if that delay spans several seconds. Alternatively, if saccades reactivate a representation for a short moment without stabilizing it, we expect that the difference between congruent and incongruent trials would diminish at longer delays between the movement cue and the response cue.

## Method

**Participants.** Nine observers (ages 19–33; 3 male; 8 right-handed) participated in Experiment 3, each completing four sessions (one training and four test sessions), with at least one night between consecutive sessions. Four of them had previously participated in an experiment combining an eye movement and a visual memory task.

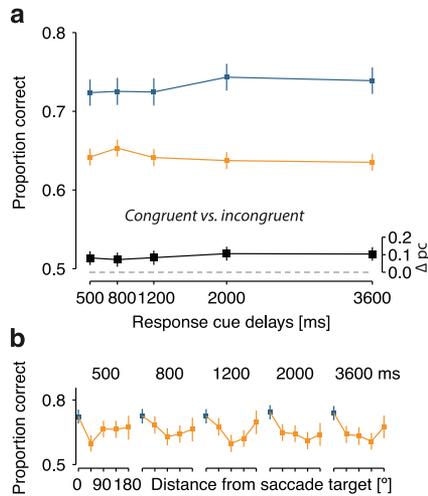
**Materials and procedure.** All aspects of the materials and procedure were identical to those in Experiment 2 with one exception. We varied the interval between movement cue and response cue (500, 800, 1200, 2000, or 3600 ms) while using a fixed interval of 400 ms between memory array offset and movement cue onset. Note that, because of the 400 ms interval available for the execution of the saccade, this choice of intervals resulted in total trial durations that were identical to those in Experiment 2.

As in the first two experiments, the movement cue was completely uninformative about the location tested for memory. An experimental session consisted of 20 blocks, each consisting of 24 trials, resulting in a total of 1,440 completed trials per observer (288 trials per cue delay in incongruent trials; 72 trials per cue delay in congruent trials). During offline detection of saccades, we applied the same criteria for trial rejection as in Experiment 1; 12,579 trials (97%) entered the final data analysis of Experiment 3.

**Data analysis.** As before, estimates of performance differences between congruent and incongruent trials for different response cue intervals, and their confidence intervals, are based on bootstrapping ( $n = 10,000$ ). Statistical inference regarding the influence of the response-cue delay and congruency on memory performance is based on rmANOVA, followed by post-hoc bootstrapping of differences in specified conditions. Effects on manual RTs, saccade latencies, and saccade amplitude were quantified using rmANOVAs.

## Results

We evaluated memory performance as a function of response-cue delay, separately for congruent and incongruent trials (Figure 4). As in the previous experiment, memory performance was higher in congruent than incongruent trials. Importantly, this dif-



**Figure 4.** Results of Experiment 3. (a) Mean performance in congruent (blue [dark gray]) versus incongruent (orange [light gray]) trials is depicted as a function of response-cue delay. (b) Spatial specificity of the saccadic influence on memory performance for each response-cue delay tested. Conventions as in Figure 3. Error bars are 95% CI. See the online article for the color version of this figure.

ference between congruent and incongruent trials remained at a constant level across all tested delays. A two-way rmANOVA corroborated this result. We observed a strong main effect of congruency,  $F(1, 8) = 41.37, p < .001$ , but no effect of the response-cue delay,  $F(4, 32) = 0.10, p > .250$ , nor an interaction of the two factors,  $F(4, 32) = 0.40, p > .250$ .

As in Experiments 1 and 2, we quantified the spatial specificity of the saccadic influence on memory performance by evaluating the impact of the angular distance between the position of the memory probe and the position of the saccade target. In a two-way rmANOVA, we observed a main effect of angular distance,  $F(4, 32) = 13.41, p < .001$ . Again, neither the influence of the response-cue delay,  $F(4, 32) = 0.32, p > .250$ , nor the interaction between the two factors were significant,  $F(16, 128) = 1.30, p = .209$ .

The performance differences observed in Experiment 3 could not be explained by a speed–accuracy trade-off. RTs were significantly faster in congruent (665 ms) than incongruent (823 ms) trials,  $t(8) = -5.69, p < .001$ . Saccade latencies (188 ms in congruent and 189 ms in incongruent trials) did not depend on congruency,  $F(1, 8) = 0.78, p > .250$ . As in Experiment 2, saccade latencies differed significantly between response-cue delays,  $F(4, 32) = 5.08, p = .003$ ; saccade latencies increased slightly with longer delays (from 184 ms for shortest delay to 192 for longest response-cue delay). The interaction between response-cue delay and congruency was marginally significant,  $F(4, 32) = 2.35, p = .075$ —clearly a spurious effect, as congruency is based on the response cue, that is, information provided after the eye movement. Again, saccade amplitudes ( $5.75^\circ$  in congruent and  $5.74^\circ$  in incongruent trials) did not vary with experimental conditions (congruency:  $F(1, 8) = 0.38, p > .250$ ; response-cue delay:  $F(4, 32) = 1.85, p = .144$ ; interaction:  $F(4, 32) = 1.34, p > .250$ ).

## Discussion

The results of Experiment 3 were clear-cut: we observed a strong benefit for stimuli presented at locations congruent with the saccade target, which was independent of the interval between the movement cue and the response cue. Thus, increasing the retention interval did not decrease the performance difference, providing strong evidence for the hypothesis that saccades stabilize visual memory traces.

The results reported thus far suggest that saccades exert their effect on memory involuntarily, even if observers gain no apparent strategic advantage from prioritizing the item at the saccade target over other items in the array. Experiment 4 will test this idea more directly.

## Experiment 4

In a final experiment, we assessed the time course of the saccadic influence on visual memory when the saccade target location was far less likely (1/10 of all trials) to be probed for the memory test than every single other item location in the display (3/10 of all trials each). We explicitly informed participants about this contingency. A performance benefit for congruent trials—with the movement cue representing an anticue for the memory task—would lend strong support for the claim of an inadvertent saccadic influence on visual memory representations.

## Method

**Participants.** Eight observers (ages 21–31; 7 right-handed) participated in Experiment 4, each completing six sessions (one training and five test sessions), with at least one night between consecutive sessions. Two of them had previously participated in an experiment combining an eye movement and a visual memory task.

**Materials and procedure.** All aspects of the materials and procedure were identical to those in Experiment 2 with the following exceptions. First, we used three rather than five different cue delays (100, 400, or 1600 ms) between the offset of the memory array and the onset of the movement cue. Second, the saccade target coincided with the memory test location in only 10% of the trials, rendering the target of the saccade 1/3 as likely as any other stimulus location for the memory test. We explicitly informed observers about this contingency.

An experimental session consisted of 20 blocks, each consisting of 24 trials, resulting in a total of 2,400 completed trials per observer (720 trials per cue delay in incongruent trials; 80 trials per cue delay in congruent trials). During offline detection of saccades, we applied the same criteria for trial rejection as in Experiment 1; 17,629 trials (92%) entered the final data analysis of Experiment 4.

**Data analysis.** Estimates of performance differences between congruent and incongruent trials for different cue delays, and their confidence intervals, are based on bootstrapping ( $n = 10,000$ ). Statistical inference regarding the influence of cue delay and congruency on memory performance is based on rmANOVA. We followed up significant interactions using additional post-hoc bootstrapping of differences in specified conditions. Effects on manual RTs, saccade latencies, and saccade amplitude were quantified using rmANOVAs.

## Results

As in the previous experiments, the saccadic influence on memory performance had a distinctive temporal profile. The performance difference between congruent and incongruent trials (Figure 5a, bottom) was strongest shortly after the memory array offset ( $\Delta pc_{100} = 0.156$ , 95% CI [0.122, 0.191],  $p < .001$ ), was reduced (but still significant) 400 ms after the memory array had disappeared from view ( $\Delta pc_{400} = 0.044$ , 95% CI [0.004, 0.081],  $p = .030$ ), and insignificant thereafter ( $\Delta pc_{1600} = 0.014$ , 95% CI [-0.025, 0.054],  $p > .250$ ). A two-way rmANOVA mirrored the results from Experiment 2. Although there was no main effect of cue delay,  $F(2, 14) = 2.42$ ,  $p = .125$ , we obtained a strong effect of congruency,  $F(1, 7) = 15.42$ ,  $p = .006$ , and an interaction of the two factors,  $F(2, 14) = 20.48$ ,  $p < .001$ . Observers' performance was best at the location congruent with the saccade target when the saccade was cued soon after the offset of the memory array, and it declined for longer cue delays (congruent condition:  $\Delta pc_{1600-100} = -0.096$ , 95% CI [-0.146, -0.045],  $p < .001$ ). Locations incongruent with the saccade target showed the opposite pattern. Here, saccades executed right after the offset of the memory array inhibited memory performance as compared to longer cue delays (incongruent:  $\Delta pc_{1600-100} = 0.046$ , 95% CI [0.027, 0.065],  $p < .001$ ).

As in the previous experiments, performance was also a function of the angular distance between the saccade target and the memory test location,  $F(4, 28) = 7.00$ ,  $p < .001$ . There was no main effect for cue delay,  $F(2, 14) = 0.96$ ,  $p > .250$ , but a significant interaction of distance and cue delay,  $F(8, 56) = 9.79$ ,  $p < .001$ . That is, the advantage for the saccade target decreased with increasing cue delays (Figure 5b). Post-hoc one-way rmANOVAs revealed a significant influence of distance for the 100 ms cue delay,  $F(4, 28) = 15.24$ ,  $p < .001$  and a marginally significant

influence at 400 ms cue delay,  $F(4, 28) = 2.22$ ,  $p = .093$ . For a cue delay of 1600 ms the effect of distance did not reach significance,  $F(4, 28) = 0.79$ ,  $p > .250$ .

The performance differences observed in Experiment 4 could not be explained by a speed-accuracy trade-off. RTs were not significantly different in congruent (757 ms) and incongruent (810 ms) trials,  $t(7) = -1.54$ ,  $p = .167$ . Saccade latencies were similar for congruent (230 ms) and incongruent (231 ms) trials,  $F(1, 7) = 0.002$ ,  $p > .250$ , but differed significantly between cue delays,  $F(2, 14) = 7.77$ ,  $p < .005$ , with the shortest latency (217 ms) for an intermediate delay of 400 ms, followed by the shortest delay of 100 ms (234 ms) and the longest delay of 1600 ms (241 ms). There was no interaction between cue delay and congruency,  $F(2, 14) = 1.19$ ,  $p > .250$ . Again, saccade amplitudes (5.50° in congruent and 5.49° in incongruent trials) were largely unaffected by experimental conditions. A rmANOVA did not reveal significantly different amplitudes for congruent versus incongruent trials,  $F(1, 7) = 0.10$ ,  $p > .250$ . However, in contrast to Experiment 2 there was a small trend of decreasing amplitudes with increasing cue delay,  $F(2, 14) = 3.55$ ,  $p = .057$ . The interaction between congruency and cue delay did not reach significance,  $F(2, 14) = 1.74$ ,  $p = .211$ .

## Discussion

The results of this experiment support the conclusion that saccades protect the memory of items at their targets in an obligatory fashion; their impact remains strong even when a stimulus congruent with the saccade target is far less likely to be tested than any other stimulus in the memory array and participants are explicitly informed about this fact. This involuntary effect of saccades on visual memory suggests that—in active vision—they play a key role in deciding upon the fate of information in the transition from iconic memory to stable representations in VSTM.

### General Discussion

The present study shows that goal-directed eye movements have significant impact on the content of visual memory. In four experiments, we asked observers to plan and execute saccades after the disappearance of an array of oriented stimuli, and then probed their memory for the orientation of one of the items. Despite the fact that the movement target did not predict the probe location, observers remembered an item most readily (Experiment 1) when it had been presented at the target of the saccade (congruent trials), and often forgot the items seen at other locations (incongruent trials). This relative advantage for the congruent location was spatially highly circumscribed—performance dropped sharply just one item away from the movement target (Experiments 1–4).

The impact of saccades on memory performance was largest soon after the disappearance of the visual array (Experiment 2), when quickly decaying memory traces compete for access into more stable representations in VSTM (Gegenfurtner & Sperling, 1993). Early in this sensitive phase, visual information lingers in iconic memory, which decays within a few hundred milliseconds after the disappearance of a stimulus (Averbach & Coriell, 1961; Coltheart, 1980; Sperling, 1960). Interestingly, we observed a saccadic influence for as long as 800 ms after the disappearance of the array, exceeding what is typically considered the iconic memory stage. At that point, however, representations in VSTM may still be fragile (Sligte et al., 2008).

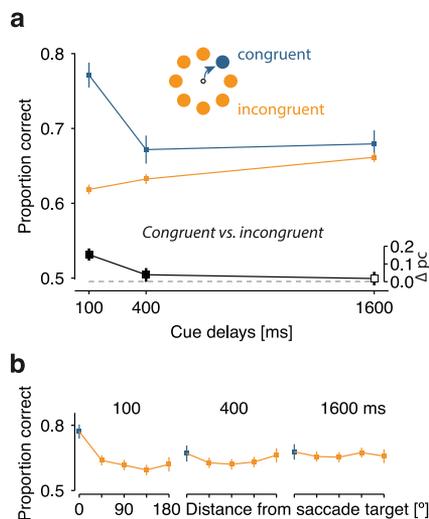


Figure 5. Results of Experiment 4. (a) Mean performance in congruent (blue [dark gray]) versus incongruent (orange [light gray]) trials is depicted as a function of cue delay. (b) Spatial specificity of the saccadic influence on memory performance for each cue delay tested. Conventions as in Figure 3. Error bars are 95% CI. See the online article for the color version of this figure.

Indeed, saccades appear to impose spatial priorities on the transition from volatile sensory traces in iconic memory to durable representations in VSTM. Once a saccade has imposed these priorities during the sensitive period, the observed difference in memory performance remains highly stable across several seconds (Experiment 3). In contrast, if a saccade is prepared and executed only after extended retention intervals, the execution of saccades may generally benefit memory performance (Williams, Pouget, Boucher, & Woodman, 2013), but their spatially specific impact was no longer observed (Experiment 2). The timing of saccades relative to stimulus offset is thus critical to understand their contribution to visual memory. Because humans shift gaze about 2 to 3 times per second, the period of their impact outlasts the duration of naturally paced fixations. Saccades will therefore play a key role in forming the content of visual memory in active observers.

The saccadic influence on memory performance was observed despite the fact that the movement cue was unrelated to the memory task and therefore did not provide any strategic advantage in allocating memory resources to the stimulus congruent with the saccade target. This contrasts with the impact of retro-cues of covert attention, which can be used strategically to either remove noncued stimuli or enhance memory representations as a function of cue validity (Souza & Oberauer, 2016). We found a substantial memory benefit for stimuli at locations congruent with the saccade target even if the saccade target was the least important for the memory task (Experiment 4). This requires that setting priorities in visual memory is an inadvertent consequence of saccades and suggests that they form a natural bottleneck, selectively funneling information from iconic memory to a stable representation in VSTM. Whereas this information would likely be behaviorally relevant in natural vision, our experiments show that the impact of saccades on memory is automatic and trumps observers' knowledge about the irrelevance of the memories at a saccade target location.

Across all experiments, we found that memory performance did not monotonically decrease with distance from the saccade target. Instead, performance dropped sharply just one or two items away from the saccade target, but then rose to an intermediate level for stimuli presented opposite to it, especially for short cue delays. This ski-jump pattern of performance is reminiscent of center-surround suppression in attentional processing (Cutzu & Tsotsos, 2003), and remarkably consistent with the results of recent studies of presaccadic attention (White et al., 2013) and transsaccadic memory (Germeys et al., 2010). Similar spatial profiles of performance have also been observed in tasks requiring fixation (see Cutzu & Tsotsos, 2003, for a review). For instance, Tse, Sheinberg, and Logothetis (2003) mapped out detection performance in a change-blindness paradigm in response to an exogenous cue, and observed a consistent enhancement at the location opposite to it. The mechanisms leading to these surprising behavioral benefits are not clear at present and provide an interesting question for future research (see Rolfs, Engbert, & Kliegl, 2004, for one hypothesis).

### The Role of Presaccadic Attention Shifts

How do saccades exert these strong influences on visual memory performance? Saccade planning shapes the spatial deployment of visual attention, increasing visual sensitivity at the movement target before saccade onset (Rolfs & Carrasco, 2012) at the ex-

pense of all other locations (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). This presaccadic attention shift is likely to mediate the impact of saccades on visual memory. However, unlike the results in previous studies of transsaccadic memory (e.g., Bays & Husain, 2008; Gersch et al., 2008; Irwin, 1991; Irwin & Gordon, 1998; Melcher & Piazza, 2011; Shao et al., 2010), the present findings cannot be explained by enhanced visual sensitivity. Presaccadic shifts of attention facilitate the sensory encoding of visual stimuli at the saccade target only if they are presented while movement preparation is underway (Deubel, 2008; Rolfs & Carrasco, 2012). Here, we obtained significant congruency effects when saccade preparation could not start until 800 ms after the disappearance of the visual array.

It is well known that attention affects visual processing beyond sensory encoding. In studies of iconic memory, response cues presented just after the offset of a memory array draw attention to a subset of stimuli allowing for their immediate read-out (Averbach & Coriell, 1961; Coltheart, 1980; Gegenfurtner & Sperling, 1993; Sligte et al., 2008; Sperling, 1960). Moreover, studies using retro-cues show consistently that the voluntary deployment of attention results in a performance benefit for the relevant item in VSTM (Astle et al., 2012; Becker et al., 2000; Griffin & Nobre, 2003; Murray et al., 2013; Rerko, Souza, & Oberauer, 2014; Sligte et al., 2008). Our results are different from these previous findings in two important ways. First, the influence of saccades on visual memory is inadvertent. That is, in stark contrast to immediate response cues or retro-cues, which inform the observer (during a memory retention interval) about the relevant test location, the impact of saccades on visual memory occurred despite the fact that the movement target was uncorrelated to the test location (or even the least relevant location in the display; Experiment 4). Thus, whereas the saccade was cued explicitly, observers had no strategic advantage in prioritizing the target of the eye movement for the memory task. Indeed, the uninformative cue by itself (fixation condition in Experiment 1) had no significant effect on performance. Therefore, the generation of a saccade, or merely its preparation, not a willful, strategic deployment of attention, brings about an inadvertent spatial bias in visual memory. Second, the time course of the effect of voluntary attention on memory maintenance is distinct from the saccadic influence observed here. Whereas retro-cues increase memory performance when presented many seconds after the offset of the memory array (Astle et al., 2012; Sligte et al., 2008), we found that saccades affect memory performance only within the first second.

In general, the temporal dynamics of saccade-related effects on visual processing differ strongly from those of endogenous shifts of attention. Whereas the voluntary deployment of attention affects visual processing no sooner than 300 ms after a cue, saccade preparation enhances processing at the saccade target within 60 ms following the onset of a movement cue and 100 ms before saccade onset (Rolfs & Carrasco, 2012). These differences in temporal dynamics could be interpreted as a general dissociation between covert attention and saccade preparation (Belopolsky & Theeuwes, 2009; Hunt & Kingstone, 2003), an idea that received further support from the finding of distinct neural implementations in the frontal eye fields and the superior colliculus (Gregoriou, Gotts, & Desimone, 2012; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Juan, Shorter-Jacobi, & Schall, 2004; Thompson, Biscoe, & Sato, 2005). An alternative interpretation is that the deployment of

covert attention necessitates observers to fixate at the same time, which may require the selection process to be slow and controlled (but not genuinely different). Moreover, there are elementary differences between fixation and saccade tasks that impede any comparison of mechanisms involved in a memory task. Memory performance is typically deteriorated by the presentation of a new stimulus (Broadbent & Broadbent, 1981; Landman, Spekreijse, & Lamme, 2003). That is, in a fixation task, a cue can cause general interference but at the same time increase memory performance for the cued item. The presentation of a go signal in a saccade task also constitutes a source of interference, similar to the cue in the fixation task. However, in the saccade task, the execution of the saccade itself will lead to additional visual interference, because visual transients at new retinotopic locations will be generated once the eyes land. In other words, in a saccade task, additional visual interference might affect memory performance, and a saccade-related effect on visual memory might result from a very different strategy to stabilize memory representations as compared to the deployment of covert attention in a fixation task. A full understanding of memory, therefore, requires studying it in active observers.

In a related effort, Gersch et al. (2008) investigated the influence of saccade generation on performance in a visual memory task and arrived at conclusions similar to ours. In their task, observers had to execute a sequence of saccades along a color-cued saccade path. At some point during the movement sequence, an array of letters was presented between two successive saccades and, at the end of a trial, a probe highlighted one location in the array for which observers had to report from memory the corresponding letter. As in our study, better memory performance was observed at locations that coincided with the saccade path as compared to off-path locations, with highest memory performance at the upcoming saccade target. However, whereas the memory probe location was entirely uncorrelated to the targets of the saccades, the saccade path did have a special status, because of its explicit color-cuing throughout the trial (including a different color of the response cue for on-path stimuli) and the low total number of possible paths (eight) with several hundred repetitions of each of them over the course of >100 2-hr sessions per participant. These factors in Gersch et al.'s experimental design choices are likely to engage other attentional selection mechanisms that will affect memory performance—including saliency-based selection, feature-based attention, sequence learning, and contextual cueing—and render a direct explanation of their results in terms of a saccadic impact on memory difficult. The fact that they found a strong memory benefit for on-path stimuli even in fixation trials (with no saccades) supports this conclusion. In contrast, our paradigm was specifically designed to isolate the impact of saccades on memory representations while controlling for any other selection mechanisms.

### A Relation Between Saccades and the Capacity of VSTM?

Studies of VSTM capacity have consistently suggested that an average of three to four objects can be remembered (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001)—a finding that has been conceptualized in different versions of the slot model (Luck & Vogel, 2013; Zhang & Luck, 2008). However, observers show strong interindividual differences in their capacity ranging from

one to six objects (Cowan, 2001; Vogel et al., 2001; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), and capacity limits may depend on the stimuli used in memory experiments (Brady, Störmer, & Alvarez, 2016). These findings raise questions about the origin of the large variability in visual memory capacity. An alternative view is that limits arise as a consequence of finite resources that can be distributed flexibly across items (Bays & Husain, 2008). Interindividual differences in capacity could then be modeled as variability in the availability of resources, or differences in individuals' strategies in the allocation of resources to stimuli. In this framework, saccades would be an effective (perhaps even the most effective) way to shift resources to item locations.

On the basis of our results, we may speculate that interindividual differences in visual memory capacity relate to differences in saccadic behavior. In natural environments, we generate two to three saccades per second. With each saccade, information at the saccade target is selectively favored during visual processing and prioritized for the transition into VSTM. In one possible scenario the number of saccades that are planned and executed in a retention period would be positively correlated with memory capacity. Interestingly, multiple saccades can be programmed in parallel, with attention being allocated to each movement target prior to the onset of the movement sequence (Baldauf & Deubel, 2008). Thus, the more previous stimulus locations the eyes visit (or intend to visit), the more items would undergo the transition into VSTM. Interindividual differences in memory capacity could therefore reflect interindividual differences in the ability to program a number of saccades in parallel. Although this potential relationship is exciting, it would not provide evidence for a causal influence of saccades on memory capacity. Indeed, it could well be the other way around: The number of locations one can store in VSTM might well limit the number of saccades programmed in parallel. It is worth noting that, in our experiments, saccades were triggered by the presentation of a movement cue. The time course and overall profile of saccade-related influences on visual memory might be different when observers are allowed to freely move their eyes without any constraints on fixation behavior. Indeed, in one such paradigm, it has been observed that observers spontaneously moved their eyes to locations that have previously been occupied by stimuli from the memory array (Williams et al., 2013). Moreover, memory performance was better when participants were allowed to move their eyes as compared to a condition with enforced fixation.

### Potential Neural Mechanisms

To reach a better understanding of the observed link between saccade planning and visual memory, we may hypothesize the mechanisms involved at the neural level. Saccade preparation influences visual processing massively and throughout early visual cortex (e.g., Moore, Tolias, & Schiller, 1998; Saber, Pestilli, & Curtis, 2015). This influence prioritizes the processing of visual information at the movement target before the eyes move and is thus thought to underlie presaccadic shifts of attention (Rolfs & Carrasco, 2012). Indeed, the deployment of spatial attention and the selective transfer of information from iconic memory into VSTM appear to rely on the same neural architecture, involving a fronto-parietal network and early visual cortex (Ruff, Kristjánsson,

& Driver, 2007). Moreover, it is now commonly believed that the neural mechanisms underlying the processing of sensory information also maintain it in VSTM. This sensory-recruitment hypothesis received support from studies showing memory-specific activity in the primary visual cortex of monkeys (Supér, Spekreijse, & Lamme, 2001) and successful decoding of attended features in memory from fMRI signals in early visual areas (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). Thus, early visual cortex could provide the crucial interface between visual memory and the oculomotor system. Interestingly, sensory recruitment may only be necessary for the storage of precise visual information, such as a particular color or the exact orientation of a tilted stimulus (Harrison & Tong, 2009). For categorical judgments such as the one used in the present experiments (clockwise vs. counterclockwise), sensory recruitment is no longer necessary once the observer has made a categorical decision. We speculate, therefore, that the observed impact of saccades on visual memory was limited to a short-lived period of sensory recruitment, when an analogue representation of oriented stimuli formed iconic and fragile VSTM. For longer time intervals, orientations could be stored as abstract labels (see also Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992), beyond retinotopic visual areas and, thus, unsusceptible to saccadic influences.

### Summary and Conclusion

In summary, our results suggest that saccades inadvertently alter the probability with which visual stimuli undergo the transformation from a fragile sensory memory signal into a stable representation in VSTM, constraining models that consider both visual memory and processes underlying saccade generation (e.g., Schneegans, Spencer, Schoner, Hwang, & Hollingworth, 2014). In natural vision, when saccade targets contain information that is important to the current behavioral goals, this goal-directed memory may protect information that is currently most relevant and might otherwise be lost across the saccade. Indeed, the loss of visual memory at behaviorally irrelevant locations may be a small price to pay, or even beneficial when processing resources are limited.

Over the last years, research on visual memory has strongly focused on delineating the mechanisms underlying its limitations during fixation (Luck & Vogel, 2013; Ma et al., 2014). Previous studies have established close links between saccade preparation and sensory encoding, and between covert attention and visual memory performance. Our experiments provide explicit evidence for the impact of eye movements on stages of visual processing that go beyond sensory encoding. Indeed, saccades may provide a natural bottleneck in the selection of information for VSTM. These results open new avenues for future research and may provide fertile ground for research on memory in the active observer.

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