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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; Fougny, 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, & Doshier, 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 VSWM. 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,

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