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Visual Working Memory Modulates Rapid Eye Movements to Simple Onset Targets

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Abstract

Visual working memory (VWM) representations influence attention and gaze control in complex tasks, such as visual search, that require top-down selection to resolve stimulus competition. VWM and visual attention clearly interact, but the mechanism of that interaction is not well understood. Here we demonstrate that VWM representations of object features influence the spatiotemporal dynamics of extremely simple eye movements, in the absence of stimulus competition or goal-level biases. The reach of VWM therefore extends into the most basic operations of the oculomotor system.

Keywords

Visual Memory; Eye Movements; Visual Attention; Visual Perception

Visual attention requires a means to specify and keep active the properties of the to-be-attended item (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Wolfe, 1994), providing guidance to locations in the visual field that contain task-relevant features. Several theories assume that visual working memory (VWM) is the substrate of this feature template (Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995), and VWM has been found to modulate orienting when multiple objects compete for selection, with covert and overt attention biased toward items that match VWM content (Han & Kim, 2009; Hollingworth & Luck, 2009; Mannan, Kennard, Potter, Pan, & Soto, 2010; Olivers, 2009; Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Heinke, 2006). However, these biases could operate relatively late in processing at a fairly high level of the visual system, where competition is maximal (Kastner & Ungerleider, 2000). In the present study, we asked whether VWM can also modulate rapid, reflexive eye movements in the absence of stimulus competition.

Participants in the present study executed a saccade to an abrupt onset target whose color did or did not match a concurrent VWM representation. The target was the only stimulus in the display. Current theory and evidence diverge on whether VWM content should interact with such simple orienting saccades. VWM involves sustained activation of feature-specific neural populations from V1 through inferotemporal cortex (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009; Yoon, Curtis, & D'Esposito, 2006). Projections from visual cortex to the superior colliculus (SC) (Fries, 1984) and frontal eye fields (FEF) (Stanton, Bruce, & Goldberg, 1995) might allow VWM representations to influence even the most elementary oculomotor operations. However, current models of simple orienting

saccades emphasize stimulus-driven processing, with minimal influence of representations in working memory (Ludwig & Gilchrist, 2002; Mulckhuyse, van Zoest, & Theeuwes, 2008; van Zoest, Donk, & Theeuwes, 2004). For example, van Zoest et al. argued that saccades generated in less than ~200 ms are driven solely by the physical properties of the stimulus. Existing evidence on VWM-modulated orienting does not challenge this claim directly, as saccade latencies to memory-matching objects have been well over 200 ms, even when the matching object was an abrupt onset within the search array (Mannan et al., 2010). In addition, current neuro-computational theories of oculomotor control allow only for spatial biases in the modulation of saccade target selection (Kopeck & Schöner, 1995; Marino, Trappenberg, Dorris, & Munoz, 2012; Trappenberg, Dorris, Munoz, & Klein, 2001; Wilimzig, Schneider, & Schöner, 2006) and therefore do not predict that feature memory will influence orienting. Finally, stimulus competition plays a central role in theories of VWM-based selection (e.g., Desimone & Duncan, 1995), and it is not known if VWM will influence orienting when competition is eliminated. An effect of feature memory on rapid, reflexive saccades in the absence of stimulus competition and top-down selective demands would demonstrate that the influence of VWM extends into the most fundamental operations of the oculomotor system.

Experiment 1

Participants maintained a color in VWM as they executed a saccade to a target disk (Figure 1AE). First, a color patch was presented to be held in memory for a within-category discrimination test at the end of the trial. Next, a colored target disk appeared to the left or right of fixation. Participants oriented gaze to this disk as quickly as possible. The color of the target disk either matched or mismatched the color in memory. The remembered color was irrelevant to the saccade task. Participants simply directed gaze to the only visible object. These properties eliminated goal-level biases on orienting. The use of single, isolated targets allowed us to examine the effect of VWM on saccades with latencies near the limit of human capabilities.

On a subset of trials, a distractor object was included in the target display to examine the effect of VWM match in a competitive context (Figure 1F) (Walker, Kentridge, & Findlay, 1995). The distractor disk appeared simultaneously with the target, above or below central fixation. Participants were instructed to ignore the distractor and to fixate the target on the horizontal midline. The target, distractor, or neither of the two objects matched the color held in VWM.

Method

Participants—Participants were 18-30 years of age with uncorrected 20/20 vision. Twelve different participants completed each experiment (except Experiment 5, $N = 15$).

Apparatus and Stimuli—Stimuli were displayed on a 17-in CRT monitor (120 Hz refresh rate) at a viewing distance of 70 cm. The right eye was monitored by an SR Research EyeLink 1000 eyetracker. Stimuli appeared on a gray background with a white central fixation cross (0.3°).

Memory task stimuli—The central memory square subtended $1.6^\circ \times 1.6^\circ$. The color category of the square was chosen randomly from a set of three (red, green, and blue). Within the selected category, the specific color value was selected randomly from a set of four similar colors. The test display contained the memory color and a foil color (selected randomly from the remaining three colors in the category). They were assigned randomly to locations 2.5° to the left and right of center. The within-category discrimination task minimized verbal encoding.

Saccade task stimuli—The saccade display contained only the target on 75% of trials (target-only trials) and the target plus a distractor on 25% (distractor-present trials). The target (1° diameter) appeared on the horizontal midline. Direction (left/right) was selected randomly, and eccentricity was selected randomly within a range (4.61°–7.06°). Target color was drawn either from the memory category (*target match*) or randomly from one of the two remaining categories (*no match*). In the former case, the color from the matching category was either an *exact match* for the remembered color or an *inexact match*. On inexact match trials, the saccade target color became the foil color in the memory display. This was designed to make it counterproductive to intentionally attend to the color of the target for the purpose of aiding memory for the initial color square.

On distractor-present trials, the target was accompanied by a 0.66°-diameter distractor disk placed 1.3° above or below the fixation cross (randomly determined). In the *target-match* condition, the target matched the memory category (exact or inexact), and the distractor did not. In the *distractor-match* condition, the distractor matched the memory category (exact or inexact), and the target did not. In the *no-match* condition, neither the target nor the distractor matched the memory category.

For both targets and distractors, the results were identical for exact and inexact matches, and all analyses collapsed this variable.

Procedure—Each trial began with central fixation. After a delay of 400 ms, the color memory square appeared for 300 ms, followed by a blank (fixation cross only) delay of 700 ms (long enough to eliminate sensory persistence of the memory color stimulus, Irwin & Yeomans, 1986). Then, the saccade display appeared. Participants were instructed to execute a saccade to the target as rapidly as possible and to avoid fixating the distractor if one appeared. Targets always appeared on the horizontal midline, so there was never a reason to make a vertical eye movement.

When a fixation was detected in the target region, the target display remained visible for 200 ms before the appearance of the test display. Participants pressed one of two buttons to indicate which of the two test squares matched the color of the memory square.

After 18 trials of practice, participants completed 384 experiment trials. There were 288 trials of target only (144 no-match, 144 match) and 96 trials of distractor present (32 no-match, 32 distractor-match, 32 target-match), randomly intermixed.

Data Analysis—A combined velocity ($> 30^\circ/\text{s}$) and acceleration ($> 8000^\circ/\text{s}^2$) threshold was used to detect saccades. Trials were eliminated if the eyes were $> 1^\circ$ from central fixation when the target stimulus appeared (8.0% of trials across all experiments) or if saccade latency was > 500 ms or < 60 ms (4.4% of trials across all experiments).

Results

Target-only Trials—VWM content influenced both the spatial and temporal properties of saccade execution (Figure 2A). First, we assessed horizontal landing error (absolute distance of the saccade landing position from the center of the target). Saccades landed closer to the target when it matched the color value in VWM than when it did not [mean error = -0.76° and 0.87° , respectively, $t(11) = 2.78, p = .02$], with saccades to nonmatching targets tending to land shorter. Equivalent results were obtained when using the signed error instead of absolute error.

In addition, saccades to VWM-matching targets had shorter latencies than saccades to non-matching targets [mean latencies = 148 ms and 159 ms, respectively, $t(11) = 7.22, p < .001$].

Distractor-present Trials—Forty-seven percent of saccades landed closer to the distractor than to the target when the *distractor* matched the remembered color (11.5% landed within 1.5° of the distractor center). Only 15.2% of saccades landed closer to the distractor when neither object matched color memory (2.0% within 1.5°). When the *target* matched color memory, only 6.0% of saccades landed closer to the distractor (0.5% within 1.5°). All pairwise contrasts were reliable, $ps < .05$. Saccade latency exhibited a complementary pattern of results (supplementary materials).

Experiment 2

To generate even more rapid saccades, the fixation cross was removed 100 ms before saccade target onset. For target-only trials, the same numerical pattern of saccade landing error was observed (Figure 2B) but did not reach significance [mean error = .86° for target match and .90° for no match, $t(11)=1.21, p=.25$]. Replicating Experiment 1, saccade latency for VWM-matching targets was lower than for non-matching targets (mean latencies=125 ms and 136 ms, respectively, $t(11)=2.83, p=.02$). Thus, VWM influenced oculomotor processes occurring within 150 ms of target onset. The distractor-present results replicated those from Experiment 1 (supplementary materials).

Experiments 3-5

We conducted three control experiments (details in supplementary materials).

Experiment 3: Incidental memory for color

To rule out the possibility of a strategic bias to orient gaze toward a matching color, color was made an incidental feature of the remembered object. Participants remembered the orientation of a colored, star-shaped object. In the test display, participants discriminated the original star from a foil differing by 10° of orientation. Because color had no relationship with memory task (orientation discrimination), there was no incentive to attend to any particular color in the saccade display.

For target-only trials, there was a reliable effect of color match on the latency of the orienting saccade but no reliable effect on landing error. The distractor-present trials replicated the Experiment 1 results in full.

Experiment 4: Priming control

To rule out an account in terms of passive priming (Bichot & Schall, 2002; McPeck & Keller, 2001), participants viewed the initial color patch but were instructed to ignore it. No memory test was administered at the end of the trial. Participants were told that the color square simply indicated that the trial was about to begin. All color-match effects were eliminated, demonstrating that the results of previous experiments were not due to priming.

Experiment 5: Eliminating a demand to process distractors

Distractor-present trials were removed, eliminating any experimental-level demand to discriminate the target from a distractor. In addition, to reduce target location predictability, the target eccentricity range was expanded (between 3.03° and 7.06°). Participants completed 400 trials, 200 match and 200 no match. The VWM effects on landing error and latency observed in Experiment 1 were replicated in full.

Discussion

These results demonstrate that even the most rapid and simple saccade targeting processes depend on a close integration of object information maintained in VWM and sensory input. VWM modulation is not limited to situations in which stimulus competition must be resolved, and it is not limited to longer-latency saccades. Four considerations point to a visual-sensory locus of interaction between VWM and orienting observed in the present study. First, other sources of saccade modulation were not functional: Goal-level biases were controlled, as was spatial attention prior to target onset (target position was unpredictable). Second, an effect on saccades generated in less than 150 ms is consistent with a modulation of initial sensory input into oculomotor regions. Third, visual neurons in SC and FEF are not, themselves, color-selective; color-memory effects are therefore likely to be generated within color-sensitive sensory systems that project to SC and FEF (White, Boehnke, Marino, Itti, & Munoz, 2009). Finally, evidence of feature-specific VWM activation in early visual cortex (Harrison & Tong, 2009; Serences et al., 2009) renders initial sensory modulation plausible. Facilitated sensory processing of memory-matching targets would then lead to the more rapid and/or more accurate computation of the endpoint of the saccade. This same mechanism would increase the *relative* salience of an object in a competitive context, leading to the observed advantage for memory-matching targets and distractors in the distractor-present trials. These processes are analogous to feature-based attention mechanisms that modulate sensory processing at both attended and unattended locations (Zhang & Luck, 2009), extending these effects to automatic consequences of VWM maintenance.

The results contrast with earlier evidence that rapidly generated saccades are driven solely by the physical properties of the stimulus (Ludwig & Gilchrist, 2002; Mulckhuyse et al., 2008; van Zoest et al., 2004). They indicate that the initial perceptual “salience” of a stimulus (i.e., the efficiency of the sensory response and/or the strength of the sensory signal) is a joint property of an object's physical attributes and the match between those attributes and the content of VWM. Other authors have resisted this type of explanation in the context of evidence that rapid saccades deviate toward distractors matching features of a target (Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). Mulckhuyse et al. argued that initial perceptual salience is equivalent for stimuli that match or do not match a target template, but subsequent inhibition of the distractor is impaired when it shares target features. In this view, template properties do not influence initial salience; they only guide the later resolution of competition. Such an account cannot apply to the present results, because in the main condition, only a target was present; there was no competition and no demand for inhibition. Thus, the present data provide strong evidence that the initial perceptual salience of a stimulus is influenced by the strategic maintenance of object features.

Do the present data constitute an early effect of top-down, *goal-level* factors on orienting? VWM content was orthogonal to task goals, and thus the effects here cannot be described as goal directed; rather, there appears to be an obligatory interaction between the content of VWM and target processing. However, the current dissociation between VWM content and the features of the target is somewhat artificial. Under normative conditions, VWM will represent the target template, and the same mechanism observed here would facilitate rapid orienting to a target. Thus, the present results are consistent with theories of selection stressing that attentional orienting—including extremely rapid orienting—is contingent on a representation of target features (Folk, Remington, & Johnston, 1992).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Figure 1.

A-D. Sequence of events on a sample trial of Experiment 1. Participants began by fixating a central cross (not displayed). A color memory square was presented for 300 ms (A), followed by central fixation for 700 ms (B). A single target object was then presented to the left or right of fixation, and participants executed a saccade to that object as quickly as possible (C). After the target was fixated, there was a 200-ms delay before the presentation of the memory test stimuli (D). Participants selected the color alternative that matched the original memory color. The eye icons show horizontal fixation position throughout the trial. **E.** Saccade task stimuli in the two memory match conditions for the target-only trials. **F.** Saccade task stimuli in the three memory match conditions in the distractor-present trials.

A: Experiment 1, Target-only Trials **C: Experiment 1, Target + Distractor Trials** **B: Experiment 2, Target-only Trials** **D: Experiment 2, Target + Distractor Trials** **Figure 2.**

A and B. Distributions of horizontal landing position error (left) and eccentricity (right) for the target-only trials in Experiments 1 (A) and 2 (B). Vertical dotted lines show the range in which the target could appear. **C and D.** Distributions of horizontal landing position eccentricity for the distractor-present trials in Experiments 1 (C) and 2 (D). Solid vertical lines show the position of the distractor object.