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Testing a Sensory Pre-activation Account of Attention Guidance from Visual Working Memory

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Abstract

Visual working memory (VWM) maintains visual information in support of ongoing cognitive functions, such as attentional guidance. Here, we tested the standard account of attention guidance by VWM, in which sensory-level pre-activation during VWM maintenance interacts with new sensory processing to enhance the relative priority of matching items. To do this, we tested, broadly, whether sensory pre-activation can support a guidance function. Participants viewed a preview color for 50 ms that they either did or did not have to remember. This was followed by a search array after a variable ISI of 0 ms to 500 ms, in 50 ms steps. A search-array item matching the preview color was either the target or a distractor, allowing us to assess attention guidance. We compared guidance by VWM (memory demand: Experiment 1) with guidance from sensory pre-activation alone (no memory demand: Experiments 2-4), focusing on the ISI range of iconic memory. In that range, sensory persistence from the preview color should have overlapped, temporally, with the appearance of the search array. If sensory pre-activation is the source of attention guidance from VWM, we predicted that sensory persistence from a physical stimulus should generate guidance qualitatively similar to that from VWM. The results disconfirmed this hypothesis, as sensory persistence alone generated no or only weak attention guidance, differing qualitatively from the robust guidance generated by VWM. The results indicate that sensory recruitment during VWM maintenance is unlikely to be central to attention guidance.

Public Significance Statement

In everyday life, people constantly guide attention and gaze toward task-relevant objects.

Working memory tends to hold the templates that implement this guidance. Here, we asked whether guidance from VWM is consistent with a relatively low-level, sensory interaction between working memory and perception. The data did not provide support for this model, suggesting instead that higher-level interactions are likely to be responsible for attention guidance by working memory.

Visual working memory (VWM) is a system that actively maintains perceptual information in the service of ongoing and near-future cognitive processes. It implements at least two component functions. First, VWM temporarily stores information for near-future use, protecting that information from decay and interference. This *maintenance* function is the focus of most research on VWM, addressing such issues as capacity and representational format (Bays & Husain, 2008; Bays et al., 2024; Curtis & D'Esposito, 2003; Luck & Vogel, 1997; van den Berg et al., 2012). Second, VWM dynamically interacts with ongoing cognitive operations to implement goal-driven behavior (Van der Stigchel & Hollingworth, 2018; van Ede, 2020; Woodman et al., 2013). This *working* function of VWM has received far less study, yet understanding interactions between VWM and other cognitive processes is central to understanding how VWM supports intelligent behavior.

One proposed interaction involves a central role for VWM in the guidance of visual attention (Hollingworth & Luck, 2009; Olivers et al., 2011; Woodman et al., 2013). Specifically, VWM can serve as a template for attention guidance, increasing the relative priority of VWM-matching items, and thus increasing the probability of attending to stimuli that are aligned with current goals. For example, when given a trial-by-trial cue indicating the properties of relevant objects, participants can largely limit selection to template-matching items (Beck et al., 2018; Williams, 1966). In fact, the relation between VWM and attention guidance appears largely automatic, such that stimuli maintained in VWM lead to guidance toward matching items when the VWM content is unrelated to, or even contrary to, the goals of the orienting task (Olivers et al., 2006; Soto et al., 2008). These effects have been observed with behavioral measures (RT), eye movements (Bahle et al., 2018; Houtkamp & Roelfsema, 2006), and the N2PC ERP component (Carlisle & Woodman, 2011; Kumar et al., 2009).

What is the mechanism of this interaction? Given the rapid and automatic nature of VWM-based attentional guidance, most researchers have assumed that the interaction between VWM and attention has a relatively early sensory locus (Desimone & Duncan, 1995; Hollingworth et al., 2013; Kiyonaga & Egner, 2013; Olivers et al., 2011; Soto et al., 2008). This view holds that when perceptual information is maintained in VWM, maintenance is supported, at least in part, by sustained activation of subpopulations of neurons in visual cortex coding the remembered value. That is, sensory representations are *pre-activated* via the process of maintaining perceptual information in VWM, with VWM imposing spatially global, feature-value-specific gain on sensory systems (Ester et al., 2009). Critically, this sensory pre-activation interacts with new visual input, facilitating sensory registration of matching stimuli. The stronger and/or more rapid sensory processing of matching stimuli increases the salience of those items in salience/priority maps controlling the allocation of attention, increasing the probability that attention and gaze will be directed to matching stimuli compared with non-matching stimuli. In sum, current theory assumes that VWM maintenance generates a spatially global, feature-value-specific signal in sensory systems that interacts with new perceptual processing to boost the relative salience/priority of matching stimuli.

This view is plausible in that it is consistent both with the assumptions of existing models of VWM maintenance and with general models of attention guidance. First, in the literature on VWM maintenance, the sensory pre-activation hypothesis holds that cortical areas for sensory processing are also recruited to maintain the same perceptual information when it is no longer visible (Adam et al., 2022; D'Esposito & Postle, 2015). This is supported by evidence that VWM content can be successfully decoded from neural activity in early sensory cortex during a delay period (Harrison & Tong, 2009; Serences et al., 2009; Xing et al., 2013). Specifically, sustained activity during VWM maintenance has been found in brain regions across V1-V4, for features including orientation and spatial location (Bannert & Bartels, 2013; Christophel et al., 2012; Harrison & Tong, 2009). More importantly, neural decoding results in VWM tasks have been directly associated with behavioral performance. For example, stimulus values decoded from early sensory cortex predict memory error in a recall task (Hallenbeck et al., 2021; Lorenc et al., 2018). Together, these results provide support for the first component of the sensory pre-activation account of VWM-attention interaction: sensory-level activation during VWM maintenance.

The sensory pre-activation hypothesis is also aligned with general models of attention that propose a role for VWM in attention guidance (Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Hamker, 2005; Wolfe, 2021). These theories propose that a key mechanism of goal-directed/top-down guidance is based on template representations, which interact with perceptual-level processing of new input to increase the relative priority of matching items. The maintenance of templates has been assumed to depend, to a significant extent, on VWM (Woodman et al., 2013). For example, in the biased-competition model, top-down control is implemented through the maintenance of goal-relevant feature values in VWM that modulate competition in perceptual cortex to favor items that match the current goal (Chelazzi et al., 1998; Desimone & Duncan, 1995; Hamker, 2004). Likewise, Wolfe's guided search model (Wolfe, 1994, 2021) assumes that template representations maintained in VWM filter perceptual processing in dimension-specific maps coding perceptual salience. For example, a goal to attend to red items would introduce a spatially global filter on the perceptual signal to enhance activity in a salience map devoted to color at the locations of red items relative to non-red items. Although Wolfe has not made explicit claims about the neural correlates of the dimension-specific salience maps, the model has typically been interpreted as claiming that these interactions occur at a relatively early perceptual level, before multi-dimensional, bound representations of objects are established at later stages of the visual system (Treisman, 1988).

Although sensory pre-activation theories are the standard account of VWM-attention interactions, the empirical evidence of attention guidance from VWM does not necessarily force the conclusion of a sensory-level interaction. In addition, there are logical limitations to proposing that VWM-based sensory recruitment interacts with new perceptual input to guide attention. Specifically, the two proposed subfunctions—1) maintenance and 2) interaction with new perceptual input—are potentially at odds from a mechanistic perspective. For the maintenance function, the VWM representation needs to be buffered from new perceptual input so that it is not overwritten or distorted (Phillips, 1974). For example, when conducting natural visual search, the template representation needs to be maintained consistently in VWM despite the perceptual interference generated by multiple eye movements to different objects that may or may not match the template value. However, for the sensory-level guidance function, VWM-based sensory pre-activation would need to interact dynamically with, rather than being segregated from, new perceptual input. Currently, there is no neuro-mechanistic account of how VWM-driven sensory activation could meet the requirements of both functions within the same architecture and representational format.

Present Study

In the present study, we implemented a novel test of the sensory pre-activation hypothesis of attention guidance. This took the form of a general test of whether persistent sensory activation interacts with new perceptual processing to guide attention. The basic method is illustrated in Figure 1A. We examined attention guidance from sensory persistence generated by a physical stimulus presented immediately before a search array, and we compared this to guidance generated by VWM. In the basic paradigm, a color preview stimulus was presented for a brief duration (50 ms). This was followed by a search array in which the target or a distractor matched the preview color, and guidance was assessed by measuring the magnitude of the match effect. The ISI between the preview color and the search array varied from 0 ms to 500 ms. Moreover, the participants either had to remember the preview color, testing the magnitude of guidance generated from VWM maintenance, or they could ignore the preview color, testing the magnitude of guidance from sensory pre-activation alone.

<< Insert Figure 1 about here >>

Following a stimulus such as the preview color, there are two broad forms of sensory persistence (for reviews, see Coltheart, 1980; Irwin, 1992). *Visible persistence* is a high-capacity, retinotopic, maskable, visible trace that lasts for approximately 80-100 ms from the onset of a stimulus and integrates with new perceptual input to generate a composite percept (Di Lollo, 1980). One *sees* a brief stimulus persist after it is no longer physically present, due to the simple fact that the response of sensory neurons takes time to return to baseline levels after stimulation. *Informational persistence* is a high-capacity, retinotopic, maskable, but non-visible sensory trace that lasts approximately 200-300 ms after the offset of a stimulus and does not integrate with new perceptual input to form a composite percept (Irwin & Yeomans, 1986).

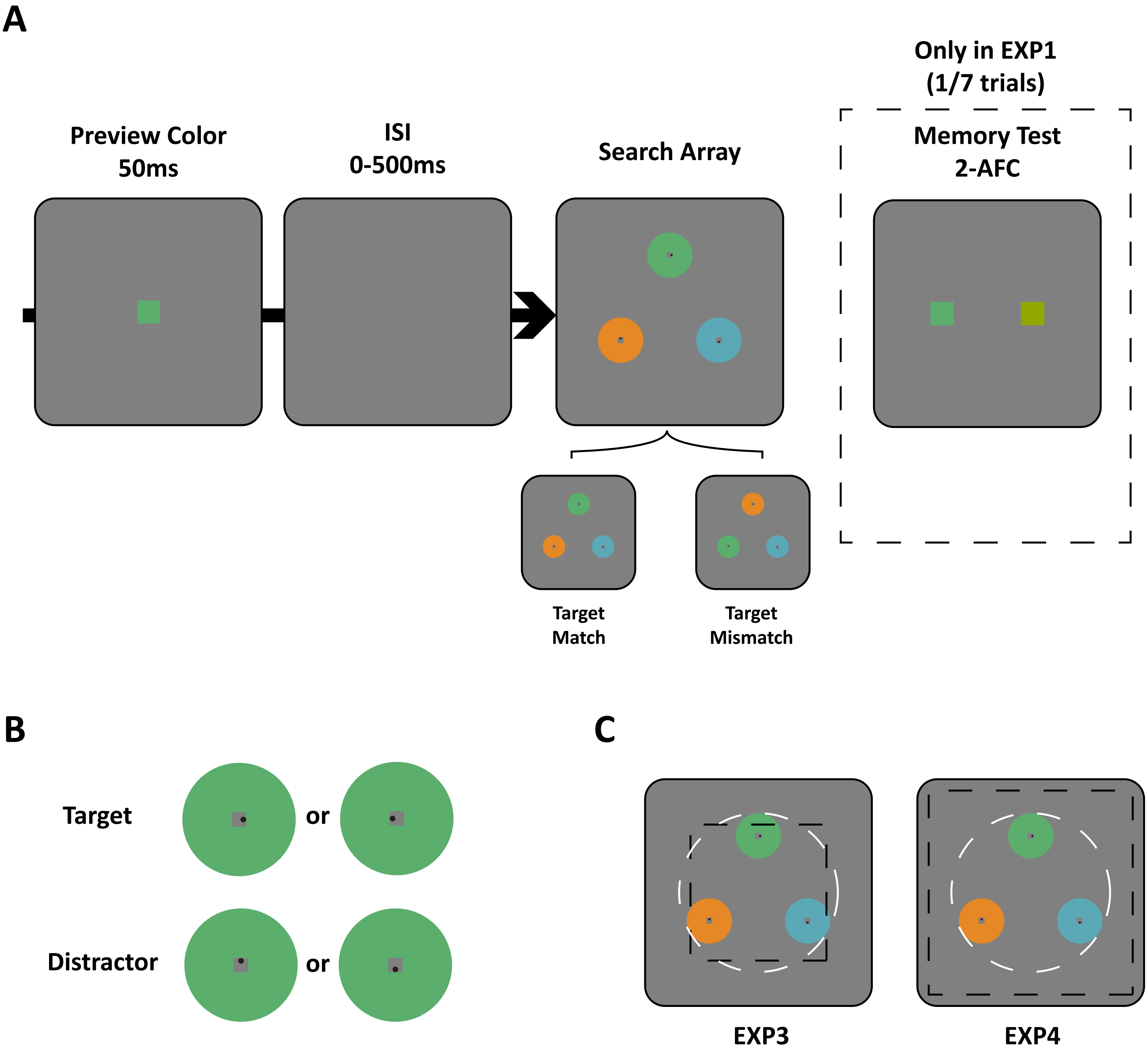

Figure 1. Illustration of the design and procedure A) in Experiments 1 and 2. On each trial, participants first saw a preview color for 50 ms. In Experiment 1, they were instructed to remember the color in preparation for a memory test that occurred on a subset of trials. In Experiment 2, there was never a memory test and thus no demand to remember the preview color. Next, there was a blank ISI that varied from 0 ms to 500 ms in 50 ms steps. Finally, participants saw either a search display or a memory test display (Experiment 1), or they always saw a search display (Experiment 2). For the search task, participants searched for a target disk with a dot that appeared at the left or right edge of the internal square (among distractors with a dot on the top or bottom). They responded manually to indicate target dot location. Each search array contained one item that matched the preview color. This item was the target on 1/3 of the trials. In Experiment 1, participants completed a color memory task on 1/7 of the trials: They discriminated the preview color from a foil color that differed from the preview color by +/- 15° in CIElab color space. B) Examples of targets and distractors in the search task. C) The relative size of the preview color square and the search array area in Experiments 3 and 4. The black dashed square showed the size of the preview color; the white dashed circle showed the possible spatial extent of the search array.

Together, these two forms of persistence are typically termed *iconic memory*, which is distinguished from VWM on several dimensions, including capacity, retinotopy, and susceptibility to perceptual interference (i.e., masking). Critically, sensory persistence is observed independently of task relevance (as observed in the masking literature) and thus the simple presentation of a visual stimulus is sufficient to generate it. Single-unit studies have demonstrated that the neural persistence supporting iconic memory is localized, at least in part, to relatively early sensory regions, such as primary visual cortex (Teeuwen et al., 2021).

To our knowledge, all previous studies on VWM-based attention guidance have used memory-item-to-search-array ISIs of 700 ms or more to eliminate possible contamination by guidance from sensory persistence. Here, we included very short ISIs to examine whether the sensory pre-activation generated by a physical stimulus would interact with the processing of the search display to guide attention. In our method, the very shortest ISI of 0 ms should fall within the range of visible persistence, and ISIs up to approximately 250 ms should fall within the range of informational persistence. We compared attention guidance from a task-irrelevant preview stimulus, assessing the effect of sensory pre-activation alone, to attention guidance under the same design when participants had to remember the preview stimulus for a memory test. If sensory pre-activation and interaction with new sensory processing is the principal mechanism by which VWM guides attention, then we predicted that sensory pre-activation from a physical stimulus should generate robust attention guidance that is comparable to attention guidance generated from VWM. In fact, given that the degree of sensory pre-activation from a physical stimulus is likely to be considerably stronger than that generated by VWM—the former has a stage in which the persisting activity is visible, whereas the latter does not—one might reasonably predict that, if attention guidance has a sensory locus, guidance from persisting physical stimulation should be more robust than that generated by VWM alone.

The broad predictions are illustrated in Figure 2. Under the hypothesis that sensory pre-activation supports attention guidance (Figure 2A), we predicted robust guidance at the shortest ISIs, both with and without a VWM demand. However, after the period of sensory persistence (200-300 ms), we then predict that guidance should diminish to near floor levels without a VWM demand, but with a VWM demand, it should continue at longer ISIs (at perhaps a reduced level). Under the hypothesis that sensory pre-activation does not support attention guidance (Figure 2B), we predicted that without a VWM demand, there should be no or minimal guidance across the range of ISI. With a VWM demand, however, there should be robust guidance, although the implementation of this guidance may be delayed (perhaps by 50-100 ms, Vogel et al., 2006) by the process of consolidating the preview color into VWM.

<< Insert Figure 2 about here >>

Experiments 1 and 2

Participants completed the visual search task illustrated in Figure 1A. In Experiment 1, participants were required to remember the preview color in preparation for a subset of trials on which a color memory test was presented instead of the search array. The preview color was unpredictive of the target item in the search array, and thus there was no incentive to use the preview color to guide search. In Experiment 2, there was never a memory test, and thus participants could ignore the preview color. In this latter case, the preview color generated sensory pre-activation in the form of sensory persistence, but since the preview stimulus was

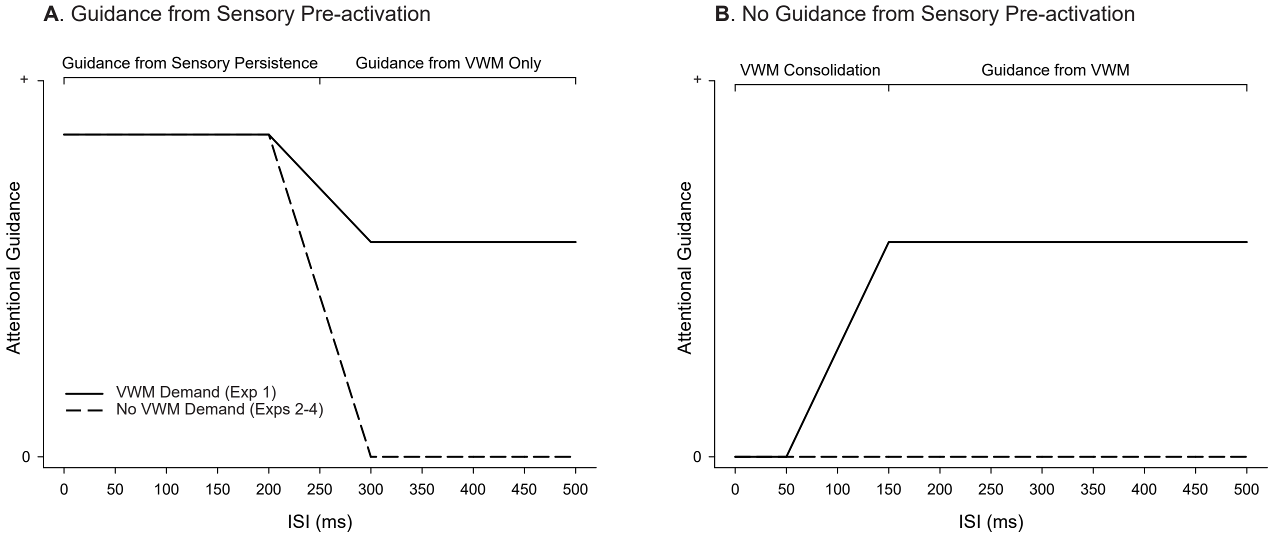

Figure 2. Predicted results under the hypothesis that sensory pre-activation supports attention guidance (A) and under the hypothesis that sensory pre-activation does not support attention guidance (B). In the experiments, attention guidance was operationalized as the difference between RT when the item matching the preview color was the target versus a distractor (match effect).

not task relevant and there was no memory demand, we could dissociate sensory pre-activation from VWM maintenance. Experiment 1 served as a baseline, quantifying guidance by VWM across a range of ISI that included a period of sensory persistence (for short ISIs) and a period driven by VWM alone (for longer ISIs). This pattern of guidance was compared with the pattern of guidance generated in Experiment 2 from sensory pre-activation alone.

Method

Transparency and Openness. We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study, and the study follows JARS (Appelbaum et al., 2018). The experiment code, data, and analysis code are available at https://osf.io/y9kpc/?view_only=5a17243ea83f4abeb1e4e9ac4bb95dcf. This study's design and its analysis were not pre-registered.

Participants. Twenty-four participants (Experiment 1: 19 females and 5 males; Experiment 2: 16 females and 8 males) were recruited for each experiment from the University of Iowa SONA participant pool, with an age range of 18-30 years old. All participants reported normal or corrected-to-normal vision. The study procedures were approved by the University of Iowa Institutional Review Board.

The sample size of 24 was determined by the effect size of the VWM-based attentional guidance effect: i.e., RT difference between trials with a memory-matching distractor and trials with a memory-matching target. This effect was observed using similar stimuli in Hollingworth and Bahle (2020b), with an effect size of η_p^2 = 0.643, which indicates that N=7 would be sufficient to ensure 80% power at α = .05. Since the present design included an additional manipulation of inter-stimulus interval (ISI) and a cross-experiment comparison, we set a recruiting goal N = 24 in both Experiment 1 and Experiment 2.

Apparatus. The stimuli were presented on an LCD monitor (resolution: 1920 × 1080 pixels) with a refresh rate of 100 Hz at a viewing distance of 60 cm, maintained by a forehead rest. Manual responses were collected via the keyboard. The experiment was implemented in PsychoPy software.

Stimuli. All stimuli were presented against a grey background (R:128, G:128, B:128). Stimulus colors were chosen from a CIELab color wheel (L = 65, a = 20, b = 30). The sizes of the stimuli are reported in degrees visual angle.

The preview color square (2° × 2°) was randomly chosen from the color wheel and displayed at the center of the grey background.

For the search task, the array consisted of three colored disks, each with a radius of 2°. The three disks were evenly spaced around a virtual circle around central fixation with a radius of 5.0°. The angular position of the first disk was chosen randomly, with the angular positions of the two additional disks each offset by 120°. One of the disks had a color identical to the preview square. For the other two disks, three colors were chosen at 90°, 180°, and 270° from the preview color in the circular color space. Two of these three colors were randomly selected for inclusion in the search array, assigned randomly to the remaining two disks. Inside each disk, there was a grey square in the center (0.5°× 0.5°). One of the disks (target) had a black dot with a radius of 0.1° that appeared at the left or right edge of the internal square. For the other two disks (distractors), the black dot appeared at the top edge or bottom edge of the internal square. The target and distractor attributes are illustrated in Figure 1B. The target feature was very small for two reasons: 1) to ensure that target detection required object fixation, maximizing sensitivity to guidance effects (Hollingworth & Bahle, 2020a) and 2) to ensure that participants could not guide attention based on the target attribute and thus would not form a guidance template for that feature that could potentially interfere with color-based guidance.

For the memory test display, two colored squares (2.06° × 2.06°) were displayed, 4.0° to the left and right of the screen center. One of the squares had the same color as the memory color square, whereas the other square's color was offset by +/- 15° around the color wheel, randomly selected. The two squares were randomly assigned to either the left or right locations. Note that the difficult discrimination task encouraged participants to encode the specific color value rather than a color category label. The use of VWM to support this type of fine-grained perceptual discrimination has been proposed to depend on relatively low-level sensory recruitment (Adam et al., 2022; Park & Serences, 2022).

Procedure. For Experiment 1, each trial started with a presentation of a central fixation point for 500 ms. Then, the preview color square was displayed for 50 ms. Participants were instructed to remember the color. After 0-500 ms ISI (in 50 ms steps), participants either completed the search task (6/7 of the trials) or the memory task (1/7 of the trials). In the search task, the search array was displayed after the ISI. Participants searched for the disk with a dot that appeared at the left or right edge of the internal square, pressing the 'Q' key to indicate a left dot or the 'P' key to indicate a right dot. They were instructed to make their response as quickly and as accurately as possible. On 1/3 of the search trials, the disk with the target attribute matched the preview color (memory-match condition). For the remaining 2/3 of search trials, the target attribute appeared in one of the other two disks in the array (memory-mismatch condition). In the memory task, two colored squares were displayed after a 0-500 ms (in 50 ms steps) ISI, and participants responded to indicate whether the left square (‘Q’ key) or the right square (‘P’ key) matched the preview color from the beginning of the trial. For both tasks, a text message (“incorrect”) was displayed when participants made an incorrect response. Note that because the matching color did not predict the target in the search array, participants had no incentive to attend to the matching item; the effects of match were therefore incidental, and such incidental guidance by VWM has been documented extensively (Beck et al., 2018; Olivers et al., 2006; Olivers et al., 2011; Soto et al., 2005; Soto et al., 2008). Further, because the memory test and search trials in Experiment 1 were separated, participants could not improve their memory performance by strategically attending the matching item in the search array, again ensuring that observed guidance from VWM was incidental.

For Experiment 2, the procedure was identical, except there were no memory test trials, and thus no demand to remember the preview color. Participants were instructed that the color square appearing at the beginning of the trial indicated that the search task was about to begin.

Before the main session of each experiment, participants completed a practice session of 16 trials, selected randomly from the full design. In the main session of Experiment 1, there were 770 trials. These were divided between search trials (660) and memory test trials (110). For the search trials, there were 60 trials for each of the 11 levels of ISI. For each ISI, 20 of the trials were memory match, and 40 were memory mismatch. The 770 trials were divided into 10 equivalent blocks of 77 trials each. Within each block, trials from the various conditions (including search and memory test trials) were randomly intermixed. Experiment 2 had the same structure, except there were no memory test trials. The 660 search trials were divided into 10 equivalent blocks of 66 trials each. The entire experiment took approximately 60 minutes (Experiment 1) or 50 minutes (Experiment 2).

Results

We first report accuracy in the search task and in the memory task of Experiment 1. We then report the primary analyses examining guidance effects on search RT.

Search and Memory Test Accuracy. In Experiment 1, visual search accuracy was 99.00% for the memory-match condition and 97.43% for the memory-mismatch condition, which differed reliably, $t(23) = 5.63$, $p < 0.001$, $d_z = 1.15$. In Experiment 2, visual search accuracy was 98.64% for the memory-match condition and 98.44% for the memory-mismatch condition, which did not differ reliably, $t(23) = 1.12$, $p = 0.27$, $d_z = 0.23$. Note that the reliable accuracy difference in Experiment 1 was in the same direction as the RT results and thus does not raise concern about a speed-accuracy tradeoff. The average accuracy for the memory task in Experiment 1 was 74.96%, collapsing across ISI (there were too few trials at each ISI to include this as a factor).

Search RT. The primary dependent measure was mean RT in the search task. To eliminate outliers, we used a two-step RT trimming procedure. First, we excluded trials with an RT below 250 ms (not possible to have discriminated the target attribute and thus reflecting anticipatory responses) or above 3000 ms (likely to have reflected a lapse in task engagement), resulting in the removal of 0.10% of correct trials in Experiment 1 and 0.14% in Experiment 2. Second, we eliminated RTs more than 2.5 standard deviations from the participant's mean in each condition, resulting in the removal of 1.77% of the remaining trials in Experiment 1 and

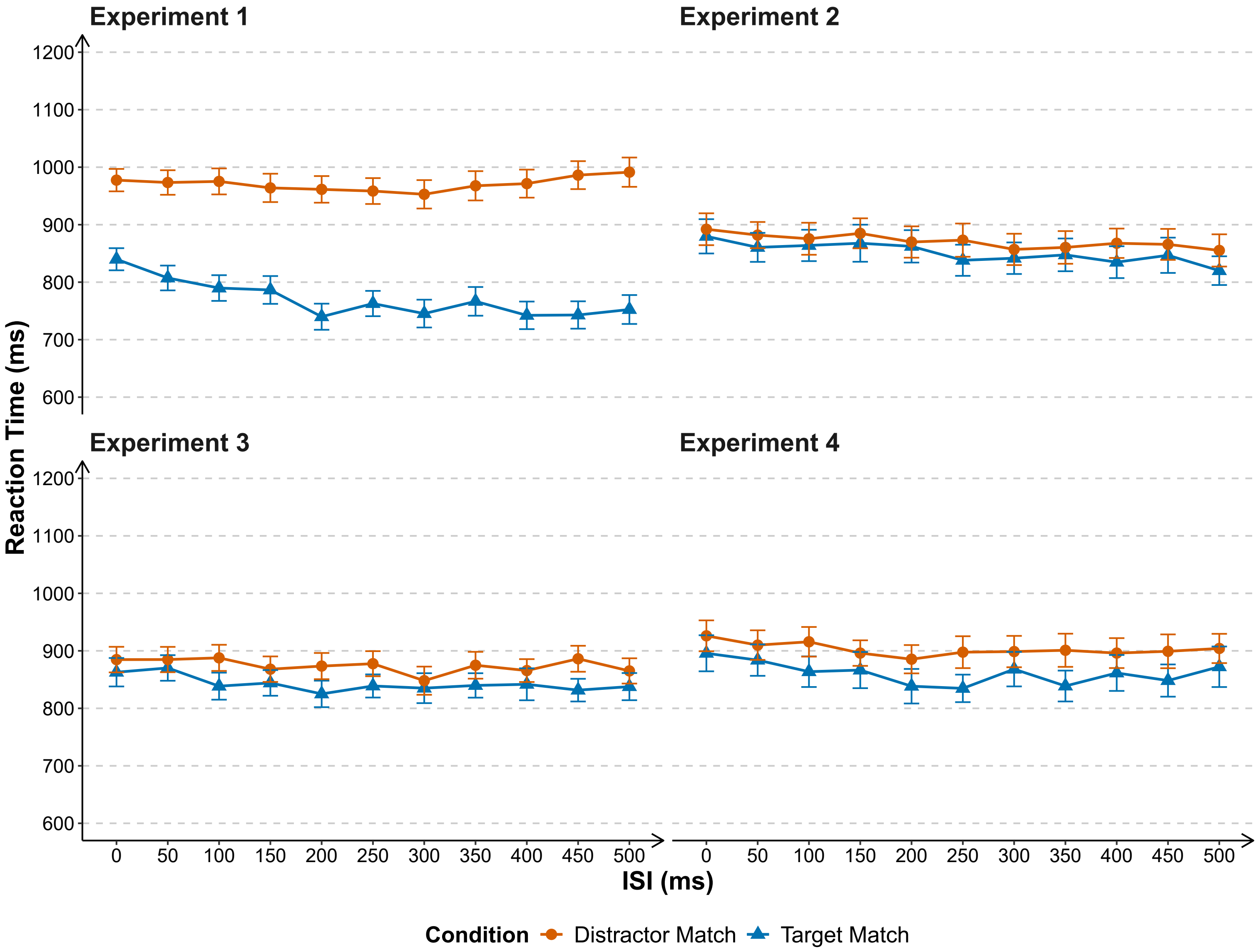

Figure 3. Mean RT results in Experiments 1-4 as a function of VWM-match condition and ISI. Error bars are standard errors of the means.

1.42% in Experiment 2. The mean RT results as a function of ISI and memory match are displayed in Figure 3.

<< Insert Figure 3 about here >>

To index the guidance effect, we calculated the difference in mean RT between the memory-match condition and the memory-mismatch condition, at each ISI. We term this difference a *match effect*, which reflects the extent to which attention was guided by the preview color value during visual search. This is equivalent to a validity effect in the standard literature on attentional cuing. Then, in each experiment, we used a linear mixed effect (LME) approach to evaluate the match effect and how it changed as a function of ISI. A linear model was used, since the addition of a quadratic term did not improve the fit of the model in either experiment. The fixed effect structure of the model contained the intercept and slope for the effect of ISI on the match effect. In addition, we compared the pattern of guidance with and without a memory demand by including experiment as a fixed effect. The random effect structure contained a random participant intercept and a random participant slope for ISI. The analyses were conducted using the lme4 package (version 1.1-37) in R (version 4.4.3).

The mean match effect results and model fits are presented in Figure 4. In Experiment 1, the mixed-effects analysis indicated that there was a significant match effect of 155.81 ms when ISI was 0 ms, $t(30.05) = 6.84$, $p < 0.001$, Cohen's $d = 2.49$. The slope effect was also significant, $t(23.39) = 6.84$, $p < 0.001$, Cohen's $d = 2.11$. With each 1 ms increase in ISI, the match effect was predicted to increase by 0.18 ms. In other words, when the ISI increased to 500 ms, the match effect was predicted to be 245.81 ms.

<< Insert Figure 4 about here >>

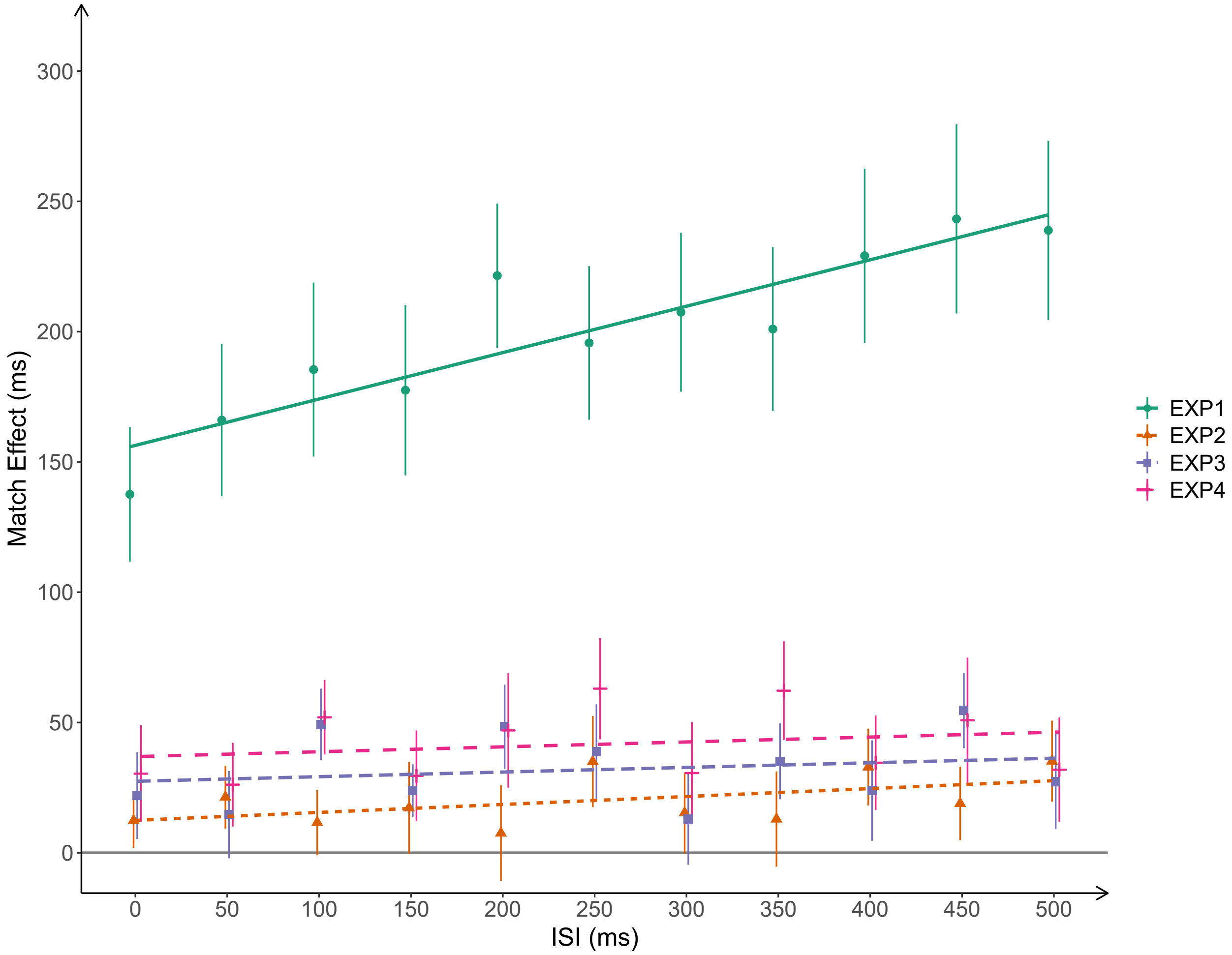

Figure 4. Mean VWM-match effect (VWM-mismatch RT minus VWM-match RT) as a function of ISI in Experiments 1-4. Plotted values are the observed means. Lines are the model predicted means. Error bars are standard errors of the means.

In Experiment 2, the mixed-effects analysis indicated that there was not a significant match effect when ISI was 0 ms, *t*(41.51) = 1.60, *p* = 0.12, Cohen's *d* = 0.50. The slope effect was also not significant, *t*(50.52) = 1.11, *p* = 0.27, Cohen's *d* = 0.31.

We compared the results in Experiment 1 and Experiment 2 by including experiment as a fixed effect. The match effect in Experiment 2 was 142.16 ms lower than in Experiment 1 when the ISI was 0 ms, and this difference was significant, *t*(35.89) = -5.02, *p* < 0.001, Cohen's *d* = -1.68. Moreover, the slope in Experiment 2 was also significantly lower than in Experiment 1, *t*(46.44) = -3.23, *p* < 0.01, Cohen's *d* = -0.95. With each 1 ms increase in ISI, the match effect was predicted to be 0.15 ms lower in Experiment 2 compared to Experiment 1. In other words, when ISI was 500 ms, the match effect was predicted to be 217.15 ms lower in Experiment 2 compared with Experiment 1.

Discussion

In Experiment 1, we observed a robust match effect based on the search-irrelevant content of VWM. The match effect was observed across the range of ISIs, from 0 ISI to 500-ms ISI. Moreover, the magnitude of the match effect increased reliably with increasing ISI, from approximately 150 ms at 0 ISI to approximately 250 ms at 500-ms ISI. The results much more closely conform to the prediction that sensory pre-activation does not support attention guidance (Figure 2B). Specifically, the results from Experiment 1 indicate that the period of maximum sensory pre-activation (immediately following the preview color) does not necessarily produce the maximum guidance effect. Instead, the later period of maintenance, outside the range of sensory persistence, produced the largest match effect. Given that this latter period would have reflected VWM maintenance alone, the pattern of results in

Experiment 1 indicates that consolidation of the preview color into VWM is likely to be necessary to obtain maximum guidance of attention.

The results of Experiment 2 were striking in comparison. When there was no demand to remember the preview color, there was no reliable match effect. Critically, there was no reliable match effect even in the ISI range where visible and informational persistence of the preview color should have been present. Together, the results suggest that sensory pre-activation (of the type generated from a physical stimulus) does not necessarily play a central role in attention guidance and does not appear to be responsible for the type of interaction that produces robust guidance from VWM.

One unanticipated finding was that we observed a reliable guidance effect in Experiment 1, with a memory demand, even at the shortest ISI of 0 ms, which might appear inconsistent with the idea that consolidation into VWM is necessary for robust guidance. However, it is possible that some degree of consolidation, allowing for guidance, can be implemented more rapidly than we had assumed (and as depicted in Figure 2B). In addition, the very shortest ISIs in Experiment 1 also produced the longest overall search times (see Figure 3). Thus, the initiation of search may have been delayed by the consolidation process itself at these ISIs.

Experiments 3 and 4

In Experiment 2, we found that sensory pre-activation from a physical stimulus was not sufficient to guide attention robustly. However, the preview color stimulus was relatively small and did not overlap the locations where the search array would appear. Physical overlap is not necessary for robust guidance from VWM (as observed in Experiment 1), but it is possible that a low-level interaction requires time for value-specific activity to propagate to other locations in the visual field (Ester et al., 2009). That is, sensory activation may be sufficient to guide attention but not at the shortest ISIs used in Experiment 2 when there is no spatial overlap and insufficient time for activity to propagate spatially. In addition, the method in Experiments 1 and 2 might have induced apparent motion from the preview to the search stimulus. Specifically, color correspondence between the preview stimulus and the matching item in the search array could have led to apparent motion between these two items (Hein & Moore, 2012), and such feature correspondence effects have been shown to be influenced by the content of VWM (Hein et al., 2021). Thus, apparent motion may have influenced attention to a greater extent when the preview color was maintained in VWM.[1]

To eliminate both possible explanations for the results of Experiments 1 and 2, in Experiments 3 and 4, we replicated Experiment 2 but increased the size of the preview color stimulus (see Figure 1C). In Experiment 3, we increased the size of the preview color without fully overlapping the array locations, and in Experiment 4 we increased it further so that it was larger than the array, with the preview color fully overlapping the locations where the search items would appear. In addition to addressing the issue of physical overlap, the extreme difference in size between the preview stimulus and the color-matching item in the search array constituted a salient feature discontinuity that should have prevented any experience of apparent motion (Hein & Moore, 2012).

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[1] Although apparent motion in the Experiment 1 and 2 displays is theoretically possible, it is strongly limited by the correspondence challenge introduced by the change in the number of visible objects. We note that inspection of the displays at each ISI by the two authors revealed no experience of apparent motion.

Method

Participants. In each of the experiments, 24 new participants (Experiment 3: 16 females and eight males; Experiment 4: 18 females and six males) were recruited from the University of Iowa SONA participants' pool, between 18-30 years old. All participants reported normal or corrected-to-normal vision.

Apparatus, Stimuli and Procedure. The apparatus, stimuli, and procedures were the same as in Experiment 2, except that the size of the preview color square was increased from 2° X 2° (Experiment 2) to 12° × 12° (Experiment 3) or 18° × 18° (Experiment 4).

Results

Search Accuracy. In Experiment 3, overall visual search accuracy was 98.52% for the memory-match condition, and 98.25% for the memory-mismatch condition, which did not differ reliably, $t(23) = 1.62$, $p = 0.12$, $d_z = 0.33$. In Experiment 4, overall visual search accuracy was 98.47% for the memory-match condition, and 98.26% for the memory-mismatch condition, which did not differ reliably, $t(23) = 1.13$, $p = 0.27$, $d_z = 0.23$.

Search RT. We used the same two-step RT trimming method as in Experiment 1. For the first step, we excluded 0.08% (Experiment 3) and 0.12% (Experiment 4) of the correct trials. For the second step, we further excluded 1.11% (Experiment 3) and 1.59% (Experiment 4) of the remaining trials. The mean RT results as a function of ISI and memory match are displayed in Figure 3.

We used the same LME approach as in Experiment 1. The match effect results are presented in Figure 4. In Experiment 3, the mixed-effects analysis indicated that there was a significant match effect of 26.76 ms when ISI was 0 ms, $t(49.37) = 2.88$, $p < 0.01$, Cohen's $d =$

0.82. However, the slope effect was not significant, $t(50.16) = 0.55$, $p = 0.59$, Cohen's $d = 0.16$. In Experiment 4, the mixed-effects analysis indicated that there was a significant match effect of 36.96 ms when ISI was 0 ms, $t(49.37) = 2.25$, $p < 0.05$, Cohen's $d = 0.73$. However, the slope effect was not significant, $t(73.25) = 0.67$, $p = 0.51$, Cohen's $d = 0.16$.

We further compared the results of Experiments 3 and 4 with those in Experiment 1 (working memory demand). The match effect in Experiments 3 and 4 were, respectively, 129.05 and 118.85 ms lower than in Experiment 1, and both differences were significant (Experiment 3: $t(53.89) = -5.00$, $p < 0.001$, Cohen's $d = -1.36$; Experiment 4: $t(53.89) = -4.66$, $p < 0.001$, Cohen's $d = -1.27$). Moreover, the slopes in Experiments 3 and 4 were also significantly lower than in Experiment 1 (Experiment 3: $t(95.46) = -3.83$, $p < 0.001$, Cohen's $d = -0.78$; Experiment 4: $t(95.46) = -3.82$, $p < 0.001$, Cohen's $d = -0.78$). With each 1 ms increase in ISI, the match effect was predicted to be 0.16, and 0.16 ms lower in Experiments 3 and 4, respectively, compared to Experiment 1. When ISI was 500 ms, the match effect was predicted to be 209.05 and 198.85 ms lower in Experiments 3 and 4, respectively, compared with Experiment 1.

Discussion

In Experiments 3 and 4, we continued to observe a pattern of guidance from sensory pre-activation that was qualitatively different from the pattern observed for guidance by VWM. This was observed even though the preview color was made substantially larger and, in Experiment 4, fully overlapped the locations where the search array items would appear. Unlike Experiment 2, we did observe a reliable guidance effect in both experiments (of approximately 25-40 ms, on average), but the magnitude of these effects did not approach the magnitude of the effect observed with a VWM demand in Experiment 1 (150-250 ms, on average). Moreover, the pattern of increasing match effect with increasing ISI in Experiment 1 was not observed in either Experiment 3 or 4. Consistent with Experiment 2, these results indicate that sensory pre-activation (again, of the type generated by a physical stimulus) is unlikely to be the substrate of the interaction generating robust attentional guidance from VWM.

In Experiments 3 and 4, it is theoretically possible that integration masking occurred at certain ISIs, where the preview stimulus and search array could be potentially integrated, retinotopically, into a single representation at SOAs below 80-100ms (Di Lollo, 1980). However, since Experiment 2 produced very similar results to Experiments 3 and 4, and since there was no retinotopic overlap in Experiment 2, it is unlikely that integration masking (or any other form of retinotopic masking) played an important role in the current study.

General Discussion

In the present study, we examined whether sensory pre-activation interacts with subsequent perceptual processing to increase the priority of matching items, biasing attention. This type of mechanism is the standard account of how attention is guided by VWM: sensory recruitment during the maintenance stage of VWM leads to sensory pre-activation of the remembered value, which facilitates the subsequent perceptual processing of matching stimuli, increasing their salience and priority for attentional selection. In Experiment 1, we quantified the guidance generated by a preview color that had to be remembered for a memory test. Attention was biased robustly toward memory-matching items in a subsequent search array. However, the magnitude of the guidance effect was not maximized at preview-to-search-array ISIs where sensory persistence of the preview color should have been maximal. Instead, the largest guidance effect was observed at the longest ISIs, where any sensory pre-activation should have depended on VWM maintenance alone, and sensory activity based on the preview color should have been strongly attenuated (i.e., outside the temporal range of visible and informational persistence). Thus, the results suggest that consolidation into VWM plays an important role in the guidance of attention and that sensory activation per se may not be central to the mechanism of guidance.

In Experiments 2, 3, and 4, we eliminated the memory demand but retained the preview color, testing whether sensory pre-activation alone is sufficient to guide attention. In Experiment 2, using the same stimuli as in Experiment 1, we failed to observe reliable guidance of attention, even at ISIs within the “iconic memory” range of visible and informational persistence. In Experiments 3 and 4, the preview color was made physically larger and, in Experiment 4, fully overlapped the locations of the search array items. Although we observed reliable guidance of attention, the magnitude did not approach that observed with a memory demand. The qualitatively different patterns of results, with and without a memory demand, indicate that the type of robust guidance generated by VWM is unlikely to depend on sensory activity, at least sensory activity of the type generated by a physical stimulus.

There are two possible explanations for the present results. First, despite the present results, the critical mechanisms of interaction between VWM and attention *do* depend substantially on sensory level pre-activation, but the type of pre-activation generated by VWM operates in a qualitatively different manner than sensory pre-activation from a physical stimulus. Second, the critical mechanisms of interaction between VWM and attention *do not* depend substantially on sensory level pre-activation, contrary to current theory. Both possibilities have major theoretical implications. We discuss them in turn.

First, we consider the possibility that sensory pre-activation from a physical stimulus and sensory pre-activation from VWM-based sensory recruitment are functionally different vis-à-vis the type of interaction that leads to attention guidance. In this possibility, sensory pre-activation may still be central to attention guidance, but the present experiments without a memory demand did not engage the necessary type of sensory pre-activation. Adopting this possibility depends on two assumptions. First, one would need to demonstrate that sensory recruitment from VWM and sensory activation from physical stimuli are indeed qualitatively different. This would be consistent with the idea that sensory-level activation from VWM is maintained in a separate format from new perceptual processing. For example, Rademaker et al. (2019) argued that the sensory information and VWM information are both maintained in the visual cortex, but by different populations of neurons. Some previous evidence also suggests that representations of VWM content can be rotated in cognitive space relative to sensory input (Libby & Buschman, 2021). Second, it would be necessary to demonstrate that VWM-based sensory recruitment, relative to physical stimulation, preferentially interacts with new perceptual processing to increase the salience of matching items. As discussed in the Introduction, these two requirements are not obviously compatible. That is, a form of sensory-level memory maintenance that is distinct and buffered from perceptual processing (so that it is not overwritten or distorted by new perceptual input) and potentially maintained via a distinct population of sensory-level neurons would appear to be necessarily isolated from sensory processing in a manner that would limit the possibility for it to interact robustly with sensory processing to modulate salience. Thus, although we cannot eliminate this possibility, it appears plausible only with a complex (and at this point, highly speculative) architecture of sensory-level maintenance and interaction.

The second possibility is that guidance of attention from VWM does not depend centrally on a sensory-level interaction. This is broadly consistent with general accounts of the neural substrates of VWM maintenance that highlight higher-level cortical representation (such as that localized to parietal and prefrontal cortex) rather than sensory recruitment (Xu, 2017). In this view, although VWM can be decoded from sensory-level activity under some circumstances, this activity is largely epiphenomenal, playing a limited role in the maintenance or working functions of VWM. A major source of evidence for this account, discussed by Xu (2017), is the fact that VWM is quite strongly resistant to perceptual-level masking: i.e., isolated from new perceptual input. In fact, this was a defining feature of VWM, distinguishing it from iconic memory (Phillips, 1974). Whereas visible and informational persistence are strongly disrupted by trailing perceptual input, VWM is only moderately affected or unaffected (Bettencourt & Xu, 2016; Pashler, 1988; Phillips, 1974). Specifically, a plausible candidate region for the interaction between VWM and attention is posterior parietal cortex (PPC), which maintains perceptual information that is abstracted from low-level sensory representation. Such a representational format, since it is not tied to specific retinotopic coordinates, could provide robust retention in the face of potentially interfering perceptual input (Xu, 2018) and implement spatially broad modulation of input to priority maps. This format would also be consistent with the finding that templates for attention guidance tend to be broadly tuned in color space, following a “good-enough” principle that allows for efficient attentional guidance across variation in perceptual input (Yu et al., 2023).

More recent work has argued for a functional sensory recruitment account by demonstrating that 1) sensory-level activity can survive subsequent perceptual inference under some circumstances (Bahmani et al., 2018), 2) that new sensory input can systematically bias memory in a way that is perhaps more subtle than masking but that nevertheless indicates a sensory locus for memory maintenance and an interaction between this maintenance and new perceptual processing (Hallenbeck et al., 2021; Lorenc et al., 2018; Rademaker et al., 2019), and 3) that memory maintenance can systematically bias conscious perception (Teng & Kravitz, 2019). With respect to the present question of attention guidance, the first line of evidence does not solve the basic problem of "segregation yet interaction" posed above; a form of sensory recruitment is buffered from new sensory processing could support a maintenance function but could not obviously support an interactive function. The second line of evidence does indicate interaction, but not in the direction needed to account for attention guidance. The third line of evidence could potentially indicate some degree of interaction between sensory recruitment and new sensory input, but this depends on the problematic assumption that conscious visual perception has a sensory locus; if VWM representation in higher-level cortical areas can influence conscious perception directly, then the results cannot support the inference of a sensory-level interaction. Moreover, recent work shows that some effects of VWM on conscious perception are likely to be caused, instead, by interactions within VWM itself during perceptual decision processes (Niu & Hollingworth, 2025a).

Another line of evidence, based on eye-tracking and EEG, suggests that VWM can influence attention allocation in a relatively rapid manner, potentially suggesting a sensory locus of interaction. For example, eye-tracking results have shown that VWM-match can influence the landing position of saccades that are generated in the range of 90-150 ms latency (Hollingworth et al., 2013). EEG evidence also demonstrates that VWM-matched items can trigger stronger selection-related ERP components (Kumar et al., 2009). Although rapid influences can be consistent with early sensory effects, they do not necessarily force this conclusion. For example, neural evidence demonstrates that frontal eye fields (FEF) can process information during the first sweep of sensory processing, with activation of FEF sometimes occurring even earlier than activation of primary sensory cortex (Kirchner et al., 2009; Paus, 1996).

How does the present work relate to other studies that have used preview manipulations in visual search? The only directly related work comes from studies that have examined the phenomenon of visual marking, in which a preview of a subset of distractor items leads to improved visual search efficiency (Braithwaite et al., 2005; Braithwaite et al., 2007). In these studies, the color of the suppressed items in the preview led to suppression of items matching that color in the full search array. This can be conceptualized as the application of a guidance template, but one that is negative (specifying distractor values) as opposed to the positive guidance observed here. In contrast to the present results, where we found that positive guidance from VWM was implemented at the shortest possible ISIs, Braithwaite et al. (2007) found that negative guidance was fully expressed at only a much longer ISIs of at least 1,000 ms. This finding is consistent with evidence suggesting that, whereas positive templates can be established proactively, negative templates are not implemented directly through VWM but require an additional process of template recoding (Beck & Hollingworth, 2015; Prakash & Hollingworth, in press).

There are several additional issues raised by the present results. First, the magnitude of the guidance effect in Experiment 1 was not detectably asymptotic within the range ISIs used. This is surprising, given evidence that consolidation into VWM can be as efficient as 50 ms per item (Vogel et al., 2006), and our participants had only one item to remember. Longer consolidation times may have been necessary given the precise color information required in the present discrimination task, compared with the categorical information required in Vogel et al. Additional work with a larger range of ISIs will be necessary to characterize the relationship between consolidation time and guidance magnitude and to examine how the function might change with differences in task design, such as different requirements for memory precision. Second, we observed a small but reliable guidance effect based on sensory persistence alone in Experiments 3 and 4. Again, the magnitude of the effect did not approach that generated by a memory demand, but it calls for explanation, nonetheless. One possibility is that sensory pre-activation alone does indeed interact with new sensory input to guide attention, but that this effect is relatively weak and is insufficient to account for the observed guidance effect from VWM. Another possibility, however, is that despite its irrelevance the search task, participants encoded the preview color into VWM on some proportion of trials due to lapses in control (or simple curiosity). Given the magnitude of the VWM-match effect in Experiment 1, even a relatively small proportion of such trials could have been sufficient to generate the effects observed in Experiments 3 and 4.

In sum, the present study does not eliminate a sensory pre-activation account of attention guidance, but it does raise substantial explanatory hurdles that such an account would need to clear. Specifically, one would need to explain how sensory recruitment by VWM is functionally separated from new sensory processing yet preferentially interacts with new sensory processing to guide attention. The present results, showing that strong sensory pre-activation from a physical stimulus fails to generate robust attention guidance, instead support a more straightforward conclusion: that attention guidance operations are unlikely to depend on sensory pre-activation from VWM-based sensory recruitment. In addition to the implications for understanding the functional role of sensory recruitment, the results also have implications for theories of attention control and visual search, suggesting that feature-based biases and filtering are unlikely to be implemented at an early sensory level.

Constraints on Generality

Our study included mainly young adult, Caucasian undergraduates, with an overrepresentation of females. We recommend cautious generalization of our findings to children or to aging populations, as there are well-documented developmental differences in working memory processes across the lifespan. Among young adults, however, there is no published evidence to indicate differences in fundamental cognitive mechanisms of attention and VWM as a function of gender, ethnicity, or cultural background.

Author Notes

Zexuan Niu, and Andrew Hollingworth, Department of Psychological and Brain Sciences, The University of Iowa. Both authors contributed to conceptualization, investigation, and visualization methodology, formal analysis, writing of original draft, and review and editing. Niu was responsible for data curation.

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The experiment code, data, and analysis code are available at (Niu & Hollingworth, 2025b): https://osf.io/y9kpc/?view_only=5a17243ea83f4abeb1e4e9ac4bb95dcf.

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Figure Captions

Figure 1. Illustration of the design and procedure A) in Experiments 1 and 2. On each trial, participants first saw a preview color for 50 ms. In Experiment 1, they were instructed to remember the color in preparation for a memory test that occurred on a subset of trials. In Experiment 2, there was never a memory test and thus no demand to remember the preview color. Next, there was a blank ISI that varied from 0 ms to 500 ms in 50 ms steps. Finally, participants saw either a search display or a memory test display (Experiment 1), or they always saw a search display (Experiment 2). For the search task, participants searched for a target disk with a dot that appeared at the left or right edge of the internal square (among distractors with a dot on the top or bottom). They responded manually to indicate target dot location. Each search array contained one item that matched the preview color. This item was the target on 1/3 of the trials. In Experiment 1, participants completed a color memory task on 1/7 of the trials: They discriminated the preview color from a foil color that differed from the preview color by +/- 15° in CIElab color space. B) Examples of targets and distractors in the search task. C) The relative size of the preview color square and the search array area in Experiments 3 and 4. The black dashed square showed the size of the preview color; the white dashed circle showed the possible spatial extent of the search array.

Figure 2. Predicted results under the hypothesis that sensory pre-activation supports attention guidance (A) and under the hypothesis that sensory pre-activation does not support attention guidance (B). In the experiments, attention guidance was operationalized as the difference between RT when the item matching the preview color was the target versus a distractor (match effect).

Figure 3. Mean RT results in Experiments 1-4 as a function of VWM-match condition and ISI. Error bars are standard errors of the means.

Figure 4. Mean VWM-match effect (VWM-mismatch RT minus VWM-match RT) as a function of ISI in Experiments 1-4. Plotted values are the observed means. Lines are the model predicted means. Error bars are standard errors of the means.