Sensory Input Matching Visual Working Memory Guides Internal Prioritization

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Abstract

Adaptive behavior necessitates the prioritization of the most relevant information in the environment (external) and in memory (internal). Internal prioritization is known to guide the selection of external sensory input, but the reverse may also be possible: Does the environment guide the prioritization of memorized material? Here we addressed whether reappearing sensory input matching visual working memory (VWM) facilitates the prioritization of other non-reappearing memorized items. Participants (total $n = 72$) memorized three orientations. Crucially some, but not all, items maintained in VWM were made available again in the environment. These reappearing items never had to be reproduced later. Experiment 1 showed that the reappearance of all but one memory item benefited accuracy and speed to the same extent as a spatial retro cue. This shows that reappearing memory-matching items allow for the dynamic prioritization of another non-reappearing memorized item. What aspects of the reappearing sensory input drive this effect? Experiment 2 demonstrated that prioritization was facilitated most if reappearing items matched VWM content in terms of both location and orientation. Sensory input fully matching VWM is likely processed more efficiently, possibly leading to stronger prioritization of other memory content. We showed the robustness of our findings in Experiment 3. We propose that the link between sensory processing and VWM is bidirectional: internal representations guide the processing of sensory input, which in turn facilitates the prioritization of other VWM content to subserve adaptive behavior.

Keywords: Visual working memory, Prioritization, Sensory input, Memory-matching

This manuscript has not yet been peer reviewed.

Public significance statement

Visual attention allows for the selective processing of objects in our environment but also the prioritization of contents held in working memory. To date, most studies have investigated the prioritization of working memory content using static displays. However, in everyday life, objects appear, disappear and reappear from our visual field within a matter of seconds. Here we investigated whether participants could leverage the dynamic nature of the world to guide working memory prioritization. In three experiments we demonstrate that humans capitalize on reappearing objects to prioritize other, non-reappearing maintained objects. Moreover, we found that whenever reappearing objects matched memory fully, prioritization of other material was most effective. Our results provide insights into how working memory prioritization may occur in more natural settings.

Introduction

The world provides us with overwhelming visual input that cannot all be processed simultaneously. Visual attention allows for the selective processing of the most relevant visual input (Carrasco, 2011; Posner, 1980). Attention cannot only select external information, but memoranda held in visual working memory (VWM) can be prioritized by attention as well. Such internal prioritization effectively enhances the fidelity of VWM representations to prepare for upcoming actions (Griffin & Nobre, 2003; Heuer et al., 2020; Koevoet, Strauch, Van der Stigchel, et al., 2023; Landman et al., 2003; Olivers et al., 2011; Olivers & Roelfsema, 2020; Souza & Oberauer, 2016; van Ede, 2020; van Ede & Nobre, 2023). Although overwhelming sensory input poses a challenge, we can leverage this input to guide us to attend the most important external information (e.g. a rapidly approaching car, see Võ et al., 2019). Here, we addressed whether sensory input may also be used to guide the prioritization of VWM content.

How could sensory input facilitate the prioritization of memorized items? Imagine you are riding your bicycle in a busy street and you want to cross the road (Figure 1). You first look to your left, and see a blue, a red and a black car approaching. These vehicles are important, and you store them into VWM for later reference. You then take a look to the right where no vehicles approach, but while doing so the blue and red car approaching from the left pass your view. The reappearance of these cars signals that now solely the black car remains relevant to cross the road safely. What happens to the memory representation of the black car? Although only cars reappeared that are now obsolete, these cars may guide one to internally prioritize the black car. This leads to the – initially counter-intuitive – proposition that you remember the remaining car better, even though it did not reappear. Here, we investigated whether memory-matching reappearing sensory input can indeed facilitate the prioritization of VWM content.

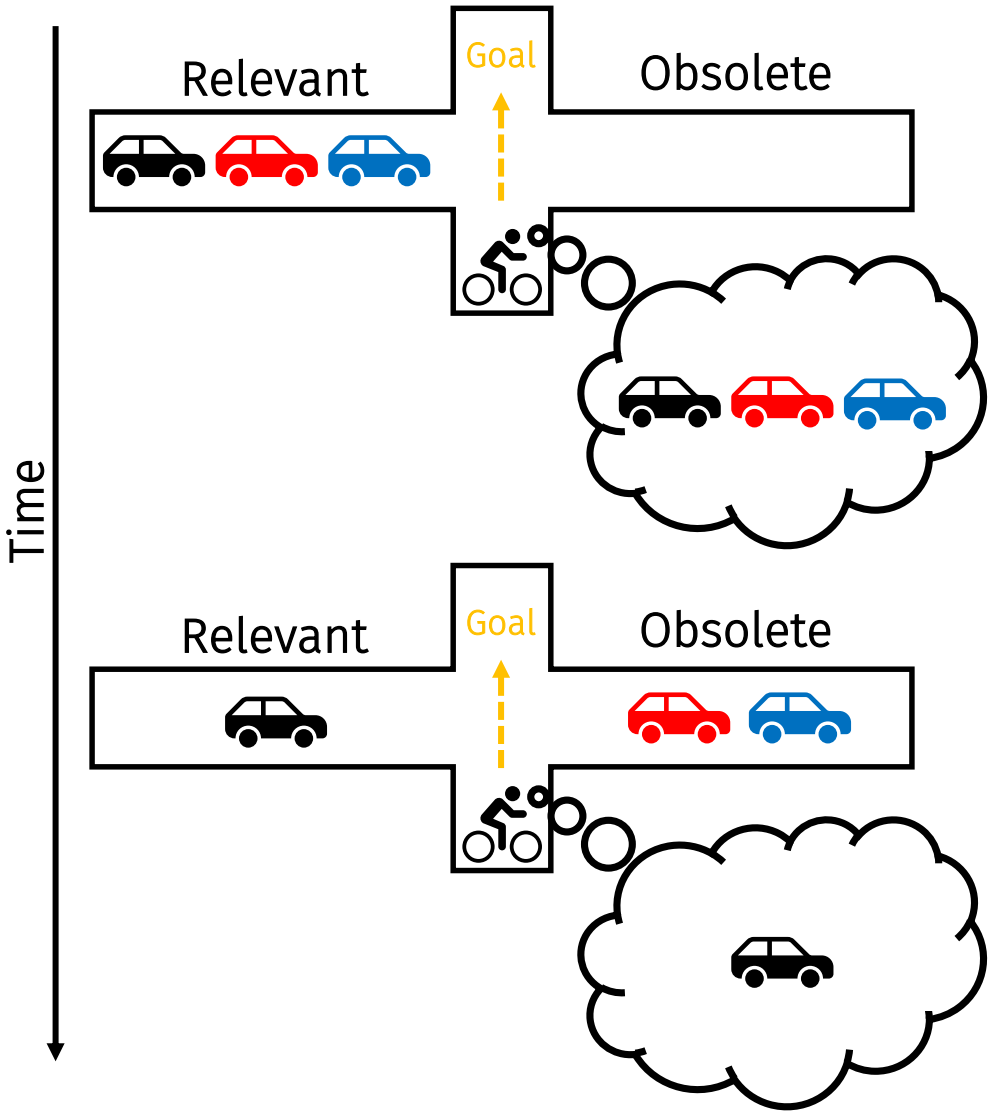

Figure 1: An example of how sensory input conveys information that might facilitate internal prioritization. In a dynamic environment, relevant information can become obsolete in a matter of seconds. When trying to cross the road, three cars are approaching from the left. Upon looking to the right where no cars are approaching, the blue and red cars pass by. The blue and red cars have now become obsolete and only the black car remains relevant to your goal of crossing the road. We here studied whether such memory-matching sensory input can be used to boost remaining VWM content through prioritization.

The idea that availability in the external world affects VWM use is well established. If relevant information is available in the environment, participants tend to not load up VWM fully (e.g. Ballard et al., 1995; Böing et al., 2023; Draschkow et al., 2021; Hoogerbrugge et al., 2023; Kvitelashvili & Kessler, 2024; Somai et al., 2020) - or

sometimes not at all (Chota et al., 2023). Instead, participants often prefer to resample to-be-memorized material and only encode one or two items at a time (Aivar et al., 2005; Ballard et al., 1995; Böing et al., 2023; Chota et al., 2023; Draschkow et al., 2021; Droll & Hayhoe, 2007; Grinschgl et al., 2021; Hoogerbrugge et al., 2024; Hoogerbrugge et al., 2023; Koevoet, Naber, et al., 2023; Kvitelashvili & Kessler, 2024; Melnik et al., 2018; Meyerhoff et al., 2021; O'Regan, 1992; Risko & Gilbert, 2016; Sahakian et al., 2023a, 2023b; Somai et al., 2020; Van der Stigchel, 2020; L. Xu et al., 2023). Put differently, participants typically prefer to simply look at externally available items over storing them in VWM, likely because this is less effortful (Risko & Gilbert, 2016; Van der Stigchel, 2020) (although sampling also has a cost, see Koevoet, Strauch, Naber, et al., 2023; Koevoet et al., 2024). In contrast, whenever external information becomes less accessible (i.e. further away or longer delay times before access), participants shift toward storing more in VWM (e.g. Draschkow et al., 2021; Hoogerbrugge et al., 2023; Sahakian et al., 2023a). These observations demonstrate that VWM use is flexibly adjusted to the constraints set by the environment.

While previous studies demonstrate a robust link between external availability and VWM encoding, the to-be-memorized material was highly stable in most tasks (Draschkow et al., 2021; Grinschgl et al., 2021; Hoogerbrugge et al., 2023; Koevoet, Naber, et al., 2023; Melnik et al., 2018; Meyerhoff et al., 2021; Sahakian et al., 2023a, 2023b; Somai et al., 2020) (but see Aivar et al., 2005; Hoogerbrugge et al., 2024; L. Xu et al., 2023). This contrasts many situations in everyday life in which the world is highly dynamic as items can appear, disappear and reappear from the visual field within a matter of seconds (Nobre & van Ede, 2023). Humans may be able to capitalize on the dynamic nature of the world by using it to prioritize relevant memorized material. Through reappearance, sensory input may facilitate operations of VWM besides encoding, such as prioritization. Here, we report three VWM experiments to directly address this possibility. We mimicked a dynamic scenario by making some but not all maintained items reappear, which may facilitate VWM prioritization of other externally unavailable content to guide goal-directed behavior (Figure 1). We hypothesized that the reappearance of maintained items that were then obsolete,

would allow for the prioritization of remaining VWM content.

Experiment 1

Methods

Transparency and openness

All data and analysis scripts are available on the Open Science Framework: https://osf.io/qzvkc/?view_only=7ab46111f1714ea5bd379b04a912355d. All data were collected in 2023. We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study. None of the experiments were preregistered.

Participants

Twenty-four participants (including the first author) with normal or corrected-to-normal vision took part in Experiment 1 (M_{age} = 24.33, range: 19-29; 8 males; 3 left-handed). We based our sample size on previous work investigating VWM prioritization (e.g. Gunseli et al., 2015; van Ede et al., 2020), and studies demonstrating the relationship between external availability and VWM use (e.g. Hoogerbrugge et al., 2024; Hoogerbrugge et al., 2023; Koevoet, Naber, et al., 2023; Somai et al., 2020). Participants reported no history of attention-deficit related disorders or autism spectrum disorder. All participants were compensated with €8 or course credits. The experimental procedure was approved by the local ethical review board (approval code: 21-0297).

Stimuli

Memory stimuli were three Gabor gratings (2.5°x2.5° in width x height; spatial frequency: 3 cpd) with a random orientation, positioned at three constant locations in a triangle at an eccentricity of 4° from the center of the screen (see Figure 2).

Mask stimuli were concentric gratings (2.5°x2.5°; 3 cpd) and were always presented at the same locations as the Gabor gratings. Arrow stimuli (0.5°x1.5°) consisted of a straight black line with two ∧ shapes either pointing toward the same direction (spatial retro cue block) or toward each other (no spatial cue; all other blocks). The response wheel (4°x4°) consisted of one larger circle on which two smaller circles were positioned. Participants rotated the orientation of these smaller circles to reproduce the memorized orientation of the stimuli using the mouse (as in Gresch et al., 2024; van Ede et al., 2020; van Ede et al., 2019). The black outline of an otherwise transparent square (2.5°x2.5°) probed the location of the item which orientation should be reported. Stimuli were presented on a gray background (RGB value: [128, 128, 128]) with a DELL U2417H monitor (1920 x 1080; 60 Hz) using PsychoPy (v2021.2.3).

Procedure

Participants were positioned approximately 60 cm from the screen in a chin- and head-rest. Trials started with a brief fixation period (750-1000 ms). Participants encoded the orientations (all random) of three Gabor gratings that were presented for 1000 ms. After the delay period (1000 ms), a cue was presented (1000 ms) that differed between blocks. In the reappear-two block, two memorized gratings reappeared in their original location which indicated that these orientations would not be probed at the end of the trial (100% valid). The reappear-one block was identical to the reappear-two block, but only one grating reappeared. The retro cue block provided participants with an arrow pointing toward the to-be-reproduced orientation. The control block was identical to the arrow cue block but there was no informative cue. To keep visual input similar across blocks, masks were always presented on locations where no gratings reappeared and a non-informative cue was shown at fixation (except in the retro cue block). After the cue phase, participants reproduced the orientation that was spatially probed (indicated by the black square) as precisely as possible by moving the mouse to turn the response wheel, and confirmed with a left mouse click. The starting position of the mouse cursor (3° eccentricity) and thus the orientation of the response wheel were randomized

on every trial. Blank inter-trial intervals varied randomly between 500-1000 ms.

Each block consisted of 60 trials and the order of blocks was counterbalanced using a balanced Latin square design across participants. To reduce fatigue, participants took a break after every block. Participants completed five practice trials of every block before the experiment.

Data Analysis

All processing and analyses were performed using custom Python (v3.9.7) scripts. Practice trials and trials with responses faster than 200 ms or slower than 6000 ms were not considered for analysis (1.1% of trials). A total of 5,697 trials were entered into the analyses.

The absolute error of the orientation report was used as a measure of accuracy (as in e.g. Gresch et al., 2024; Koevoet, Naber, et al., 2023; van Ede et al., 2020; van Ede et al., 2019). Although ultimately no participants were excluded from Experiment 1, we took two steps to ensure participants could perform the task above chance level. First, participants were excluded if the average absolute error was equal or higher than 45° in any of the conditions (as in Gresch et al., 2024). Second, across all conditions we shuffled participants' responses and calculated the averaged shuffled absolute error. We compared this shuffled absolute error to participants' actual average error 10,000 times and determined participants were better than chance if their actual responses led to lower absolute errors than the shuffled responses in at least 95% of the comparisons. No participants were excluded based on these criteria in Experiment 1, indicating that they were able to perform the task above chance level (all $p < .001$).

Accuracy and response time data were analyzed using linear mixed-effects models. We modeled by-participant intercepts and slopes of cue type effects in every model to minimize Type 1 errors (Barr, 2013) - Wilkinson notation: Outcome $\sim$ Cue type + (1 + Cue type|Participant). All p-values from the linear mixed-effects models were corrected for multiple comparisons using the Holm method.

Results

To determine if participants used reappearing items to flexibly prioritize the most relevant VWM content, we analyzed absolute errors and response times (Figure 2). If reappearing gratings guide the prioritization of the remaining material, performance should be enhanced compared with the control block.

Indeed, participants were more accurate in the reappear-two block than in the reappear-one (β = 3.56 $\pm$ .75, t = 4.73, p < .001) and control blocks (β = 2.21 $\pm$ .77, t = 2.86, p = .013) (Figure 2B). Similarly and in line with the literature (Myers et al., 2018; Souza & Oberauer, 2016; van Ede & Nobre, 2023), participants were more accurate in the retro cue condition than in the reappear-one (β = 4.30 $\pm$ .77, t = 5.58, p < .001) and control blocks (β = 2.95 $\pm$ .80, t = 3.68, p < .001), but absolute errors did not significantly differ between the reappear-two and retro cue blocks (t = .99, p = .323). This indicates that two reappearing items guide VWM prioritization in a comparable manner to traditional retro cues. In contrast, absolute errors in the reappear-one condition did not differ significantly with the control condition (t = 1.79, p = .147).

The response time analysis tells a similar story (Figure 2C): participants responded faster in the reappear-two and retro cue blocks than in the reappear-one (reappear-two: β = 510.03 $\pm$ 29.50, t = 17.29, p < .001; retro: β = 479.63 $\pm$ 41.94, t = 11.44, p < .001) and control blocks (reappear-two: β = 607.27 $\pm$ 41.95, t = 14.48, p < .001, retro: β = 576.86 $\pm$ 56.93, t = 10.13, p < .001). The reappear-two and retro cue blocks did not differ significantly (t = 1.03, p = .30), and participants responded faster in the reappear-one than in the control block (β = 97.23 $\pm$ 29.58, t = 3.29, p = .002).

Together, these analyses show that participants were able to use the reappearing gratings to prioritize the most relevant VWM content. More specifically, when two gratings reappeared, participants responded more accurately and faster in a comparable fashion to a traditional spatial retro cue. However, whenever one grating reappeared, accuracy remained somewhat comparable (but decreased numerically) although responses were faster compared with the control condition. In terms of our aforementioned example (Figure 1), this implies that humans can prioritize the black car whenever the blue and red cars have passed. If instead only the blue

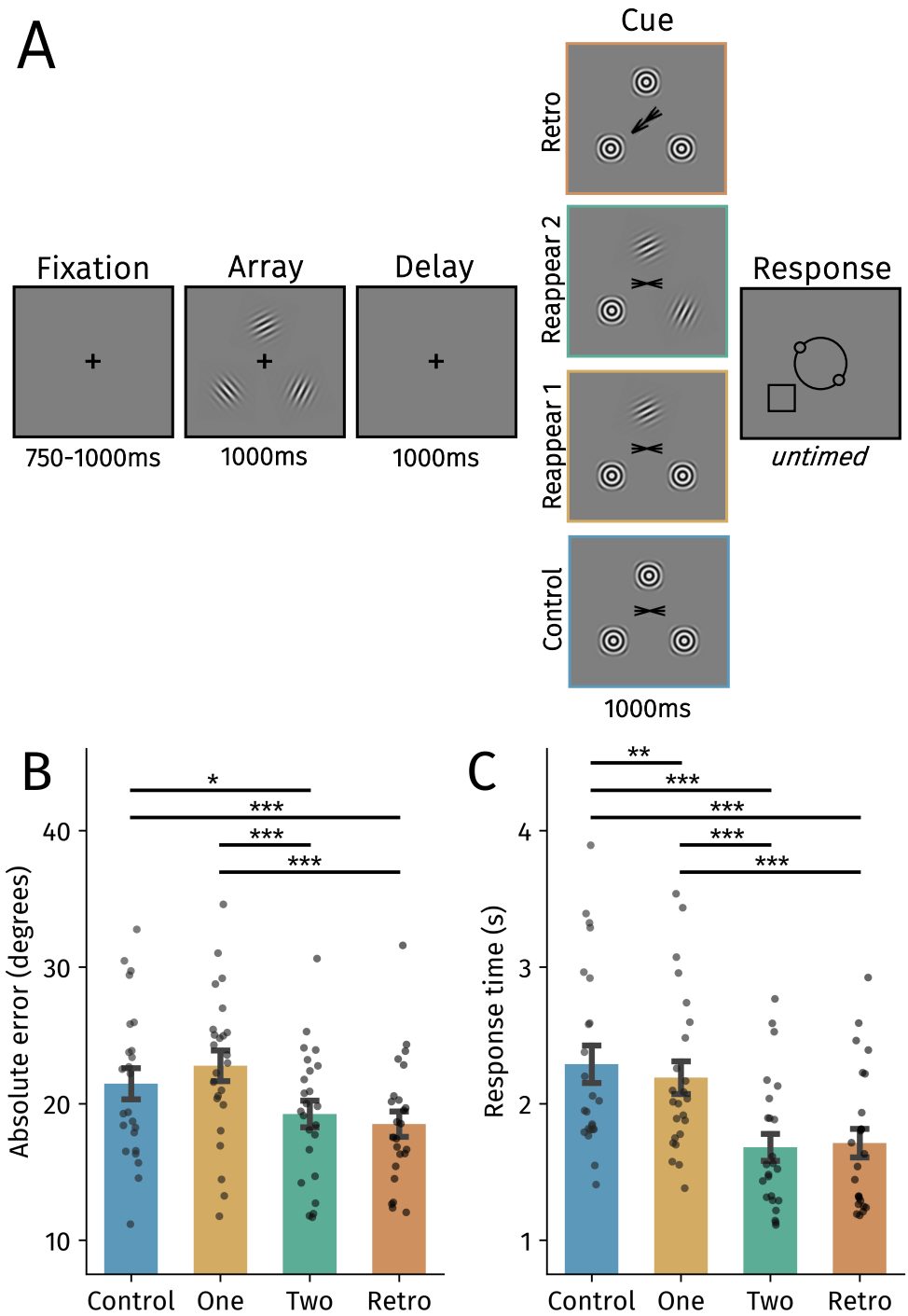

Figure 2: **a)** Trial structure of Experiment 1. After a fixation period, participants encoded the orientation of three Gabor gratings. Different cues were presented after a delay period depending on the block. In the reappear-two block, participants could infer which item should be reported because the reappearing stimuli would never be probed at the end of the trial. The reappear-one block left participants with two remaining options of possible orientations to report. Using an arrow cue, participants shifted attention toward the to-be-probed item in the retro cue block. Lastly, participants did not receive any information during the cue phase in the control block. **b)** Mean absolute error in degrees across block types. **c)** Average response times across block types. Black points reflect individual participants. Error bars represent SEM. *$p < .05$, **$p < .01$, ***$p < .001$.

car has passed, behavior is not guided effectively by internally focusing on both the black and red car. These results are generally in line with the idea that only a single item held in VWM can guide behavior at a time (Olivers et al., 2011; van Moorselaar et al., 2014) (but see Frătescu et al., 2019; Hollingworth & Beck, 2016). Moreover, these findings may indicate that participants used the reappearing items to internally attend other non-reappearing items instead of dropping (or forgetting) the reappearing items (see Discussion). Thus, whenever the dynamic sensory input facilitates the prioritization of one, but not multiple VWM representations, behavior is guided effectively.

Experiment 2

The data from Experiment 1 showed that participants were able to use reappearing items to prioritize remaining VWM content. These reappearing items consisted of two main features: an orientation and a location. Many studies suggest that VWM predominantly employs spatial reference frames whenever possible - even when location is task-irrelevant (e.g. Draschkow et al., 2022; Foster et al., 2017; Luria et al., 2016; Treisman & Zhang, 2006; van Ede et al., 2019), which may suggest that participants predominantly used location information to guide prioritization in Experiment 1. Nonetheless, orientation information matching VWM content may also contribute to the prioritization process.

This latter possibility is supported by neural and psychophysiological evidence. For instance, sensory recruitment models posit that working memory and perception recruit the same low-level sensory brain areas (Chota & Van der Stigchel, 2021; Christophel et al., 2017; Harrison & Tong, 2009; Serences, 2016; Serences et al., 2009) (but see Y. Xu, 2020, 2023). Neuroimaging and pupillometric studies have supported this notion by revealing enhanced responses to visual stimuli matching the content of VWM, regardless of their location (Gayet et al., 2017; Olmos-Solis et al., 2018; Wilschut & Mathôt, 2022) (also see Karabay et al., 2024). Moreover, what is stored in VWM guides attention (Olivers et al., 2006; Soto et al., 2008), accelerates access

to awareness (Ding, Naber, Paffen, Gayet, et al., 2021; Ding, Naber, Paffen, Sahakian, et al., 2021; Gayet et al., 2013), and affects eye-movements (Hollingworth et al., 2013; Silvis & Van der Stigchel, 2014). Gayet et al. (2017) suggested that VWM pre-activates neuronal populations responsible for visual perception, leading to enhanced processing of matching visual input. Through such memory-driven pre-activation, reappearing items matching memory in terms of both orientation and location may be processed deeper and/or faster than reappearing items not matching the memorized orientations. Enhanced sensory processing of the fully memory-matching reappearing items could make it easier to deduce which orientation should be reported, leading to more effective VWM prioritization. In Experiment 2, we investigated which aspects - orientation, location or a combination - of reappearing items facilitate VWM prioritization most effectively.

Methods

The methods in Experiment 2 were identical to Experiment 1 unless specified explicitly.

Participants

Twenty-seven participants with normal or corrected-to-normal vision took part in Experiment 2. Three participants were excluded for not performing above chance level (see Methods Experiment 1). This left a final sample of twenty-four participants (including the first author) as in Experiment 1 (M_{age} = 23.00 (range: 18-30), 8 males, 6 left-handed) that were able to perform the task above chance level (all $p < .001$).

Procedure

Participants completed four blocks containing differing cues: combination, orientation, location and control (Figure 3). One difference from the first experiment is that the spatial probe (the black square) in the response screen was removed for all blocks besides the control block. We removed this probe in the cue blocks because

1) this ensured participants had to use the cues to deduce which orientation should be reported, 2) the spatial probe may induce reliance on location information, and 3) the probe would likely confuse participants in the orientation cue block due to inconsistent positions of the gratings during the encoding and cue phases.

The combination block was identical to the reappear-two block in Experiment 1, but there was no spatial probe. The location block was similar but although two stimuli reappeared in congruent locations, they now had a random orientation. This way participants could only use the location and not the orientation information to infer which item should be reported. In contrast, in the orientation block two stimuli reappeared with an identical orientation as before but now in a random location. Here, participants relied exclusively on the orientation information and not the location to deduce which orientation should ultimately be reported. The control block was identical to Experiment 1.

After discarding trials (0.5%) with very fast (<200 ms) or very slow (>6000 ms) response times, 5,790 trials were retained for the analyses.

Results

If both the orientation and location information from the reappearing gratings facilitate prioritization, performance should be best in the combination block compared with the other blocks wherein items reappeared. Absolute errors were indeed smaller in the combination than in the location ($\beta = 2.36 \pm .86$, $t = 2.74$, $p = .019$) and orientation blocks ($\beta = 8.66 \pm .86$, $t = 10.03$, $p < .001$) (Figure 3B). When participants relied exclusively on spatial information, they were more accurate than when only using orientation information ($\beta = 6.30 \pm .99$, $t = 6.39$, $p < .001$). Moreover, reports were more precise in the control compared with the orientation block ($\beta = 7.21 \pm .87$, $t = 8.34$, $p < .001$). Accuracy in the combination and location blocks did not significantly differ from the control block ($ts < 1.47$, $ps > .28$).

The response time analyses complemented the accuracy findings and ruled out potential speed-accuracy trade-off effects for almost all comparisons (besides those

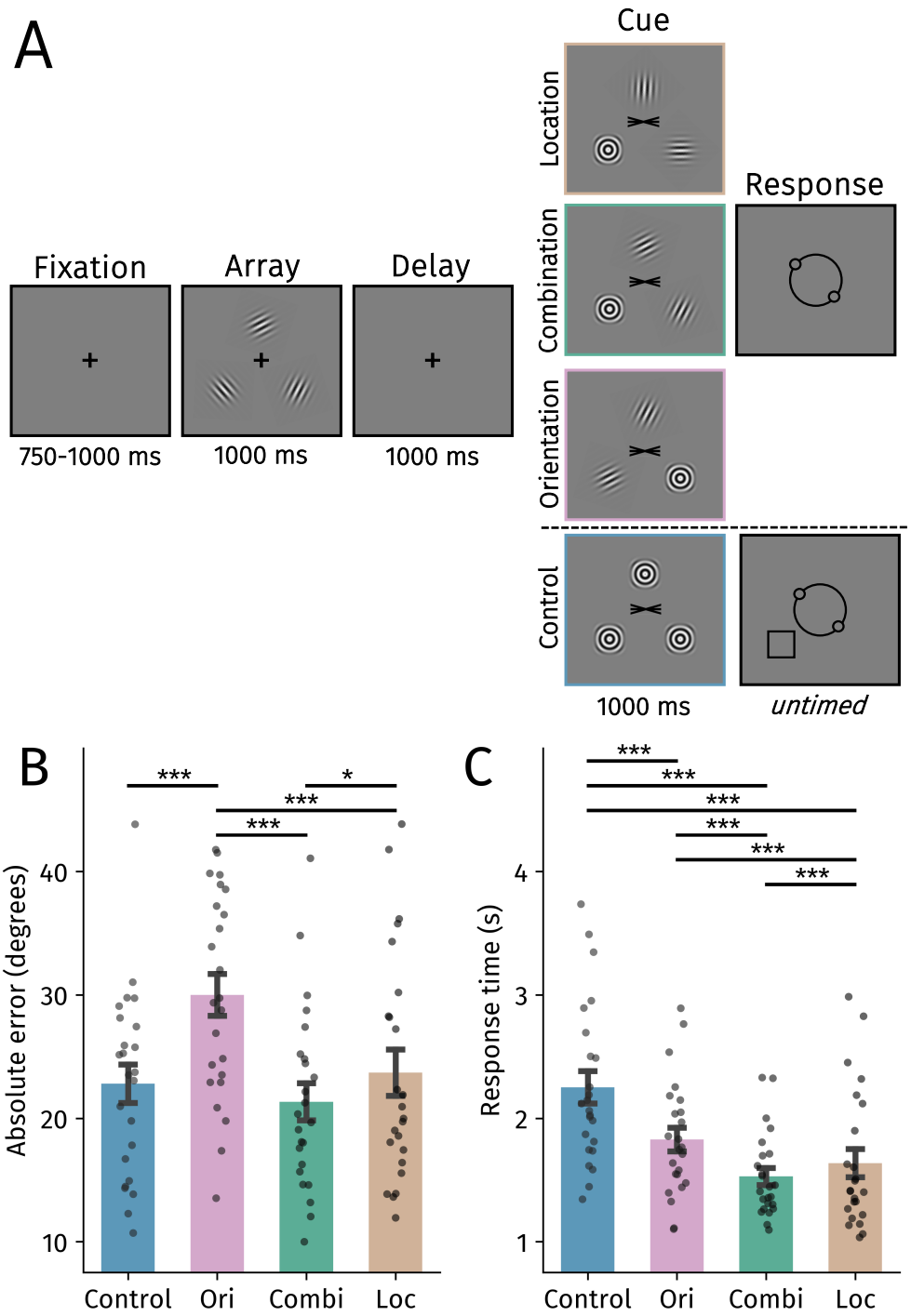

Figure 3: **a)** Trial structure of Experiment 2. In this example, the bottom left orientation ('\') has to be reproduced. In the combination block, participants deduced which item should be reported using a combination of location and orientation information from the cue. In contrast, participants could only use the location or the orientation information in the other experimental blocks. Participants used a spatial probe during the response screen to infer what item should be reported in the control block.. **b)** Mean absolute error in degrees across block types. **c)** Average response times across block types. Black points reflect individual participants. Error bars represent SEM. *Abbreviations:* Ori = Orientation, Combi = Combination, Loc = Location. $^{**}p < .01$, $^{***}p < .001$.

with the control block). Participants responded fastest in the combination block (Figure 3C; location: $\beta = 106.98 \pm 30.24$, $t = 3.57$, $p < .001$; orientation: $\beta = 300.70 \pm 30.25$, $t = 9.94$, $p < .001$; control: $\beta = 720.70 \pm 43.92$, $t = 16.41$, $p < .001$). This is in line with the accuracy analysis, and again indicates that a combination of orientation and location information facilitates VWM prioritization most effectively. Additionally, responses were faster during the location block compared with the orientation block ($\beta = 193.73 \pm 43.91$, $t = 4.41$, $p < .001$), indicating that location guided prioritization more effectively than orientation information in the current task.[1] Response times were slower in the control than in the orientation ($\beta = 420.00 \pm 30.28$, $t = 13.87$, $p < .001$) and location blocks ($\beta = 613.73 \pm 60.14$, $t = 10.21$, $p < .001$).

Our results show that reappearing items matching VWM guide the prioritization of the remaining maintained grating most effectively. This strikingly occurred even though reappearing items indicated that they would never be probed at the end of the trial. A combination of location and orientation information led to enhanced accuracy and speed when compared with the other blocks wherein gratings reappeared. Location was more effective than orientation information in facilitating VWM prioritization. In contrast to Experiment 1, we did not observe a difference in accuracy between the control and combination blocks. We suspected that this may be attributed to the spatial probe (i.e. black square) during the response screen in the control block but not in the other blocks. Participants may have used this probe as a spatial pointer to facilitate task performance when compared with the other blocks. We addressed this, and other remaining issues, in Experiment 3.

Experiment 3

Experiment 3 aimed to address two issues. First, we assessed the robustness of the main findings from the first two experiments (while always including the spatial

[1]We note that our task does not offer a fair comparison between orientation and location information because 180 different orientations were possible but only 3 different location options. Participants likely use orientation information more effectively in another, more comparable context. This importantly did not affect the comparison between the combination and location blocks.

probe during recall). Second, we controlled for a potential effect of low-level visual adaptation by briefly presenting masks after the encoding phase.

Methods

The methods in Experiment 3 were identical to Experiment 2 unless specified explicitly.

Participants

In Experiment 3, twenty-five participants with normal or corrected-to-normal vision took part. One participant was excluded for not performing above chance level (see Methods Experiment 1). This left a final sample of twenty-four participants (including the first author) as in Experiment 1 and 2 (M_{age} = 22.08 (range: 19-27), 3 males, 1 left-handed) that were able to perform the task above chance level (all $p < .001$).

Procedure

The experiment consisted of three blocks (Figure 4): the control, location and combination blocks from Experiment 2. To control for adaptation effects, masks were presented for 200 ms after memory array offset. Furthermore, the black square probe was included in all blocks to enhance comparability between them.

Trials (0.34%) with very fast (<200 ms) or very slow (>6000 ms) response times were discarded. 4,305 trials were retained for the analyses.

Results

In Experiment 1 we observed that whenever two memory-matching gratings reappeared, participants were more accurate and faster when reproducing the cued orientation. We replicate both of these findings (Figure 4): participants were more precise ($\beta = 4.23 \pm .92$, $t = 4.60$, $p < .001$) and responded faster ($\beta = 612.69 \pm 48.84$, $t = 12.55$, $p < .001$) in the combination compared with the control block.

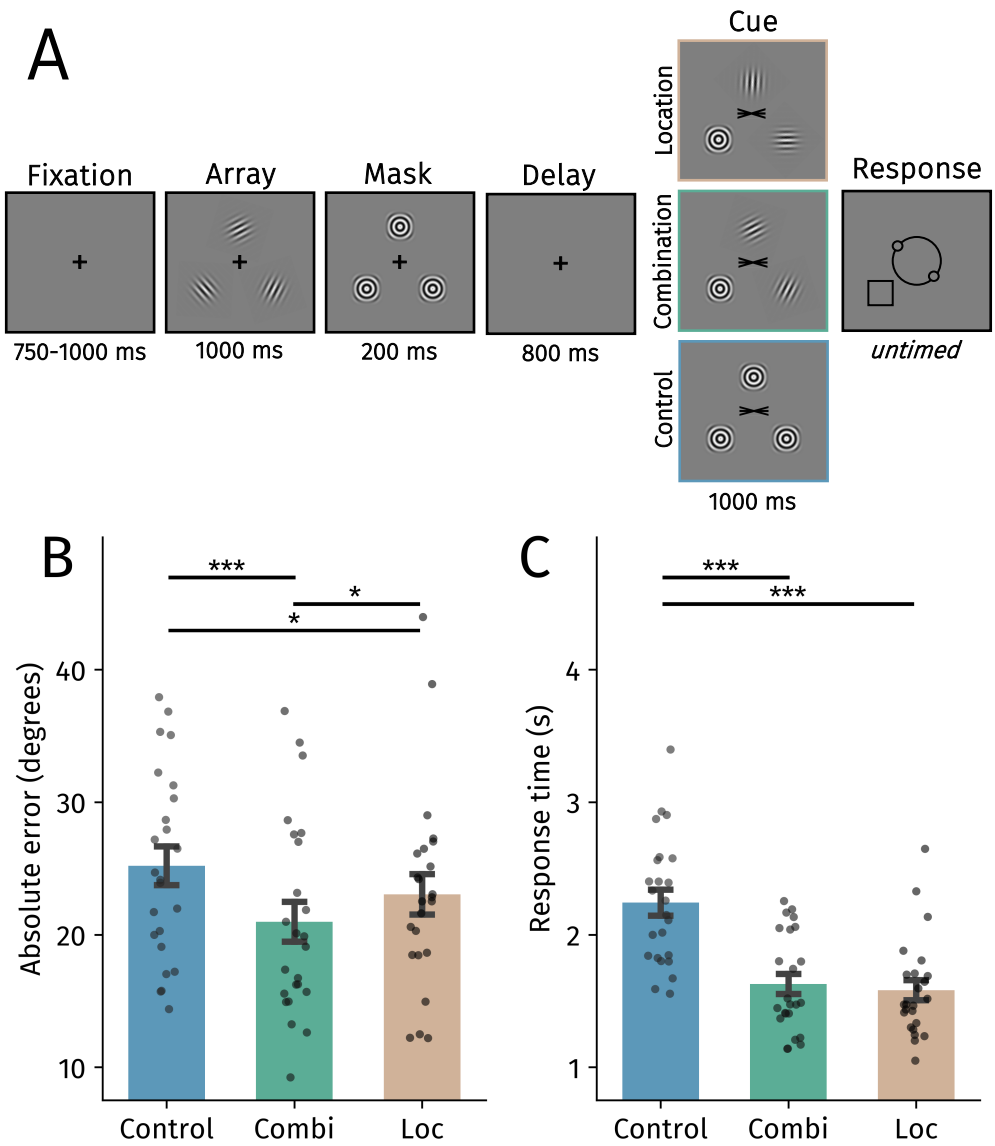

Figure 4: **a)** Trial structure of Experiment 3. **b)** Mean absolute error in degrees across block types. **c)** Average response times across block types. Black points reflect individual participants. Error bars represent SEM. *Abbreviations:* Combi = Combination, Loc = Location. *$p < .05$, ***$p < .001$.

Experiment 2 demonstrated that especially gratings matching memory in terms of both location and orientation facilitated VWM prioritization. In line with this, responses were more accurate in the combination compared with the location condition (β = 2.07 $\pm$ .82, t = 2.53, p = .023). Location information did, however, also facilitate VWM prioritization as reports were more precise (β = 2.16 $\pm$ 1.07, t = 2.03, p = .043) and faster in the location block than in the control block (β = 659.52 $\pm$ 68.52, t = 9.63, p < .001). Response times did not significantly differ between the location and combination blocks (t = 1.48, p = .138). Together, Experiment 3 replicated the main findings from the previous experiments and ruled out low-level visual adaptation as a possible confound.

Discussion

We report three experiments that investigated whether memory-matching reappearing sensory input facilitated the prioritization of another non-reappearing memorized item. Experiment 1 showed that reappearing memorized items facilitated the prioritization of a single remaining relevant item held in VWM. The beneficial effects on performance elicited by the reappearing items were comparable to a spatial retro cue. In Experiment 2, we went a step further and asked what aspects of reappearing items guide VWM prioritization most effectively. We observed that items matching VWM in both orientation and location guided internal prioritization most strongly (compared with only the orientation or location). We showed the robustness of these findings in Experiment 3. Our results demonstrate that humans leverage the dynamic nature of sensory input to guide the prioritization of the most relevant VWM content.

VWM is typically studied by briefly presenting to-be-encoded material, and subsequently removing this information from the environment (e.g. Luck & Vogel, 1997; Vogel et al., 2006). A more recent line of work instead leaves to-be-memorized items externally available indefinitely to resemble more stable environments (Ballard et al., 1995; Böing et al., 2023; Chota et al., 2023; Draschkow et al., 2021; Grinschgl et al.,

2021; Hoogerbrugge et al., 2023; Koevoet, Naber, et al., 2023; Meyerhoff et al., 2021; O'Regan, 1992; Risko & Gilbert, 2016; Sahakian et al., 2023a, 2023b; Somai et al., 2020; Van der Stigchel, 2020). Here we combined these approaches by using sensory input which appeared, disappeared and reappeared within a matter of seconds to mimic a more dynamic daily-life situation (Figure 1). We observed that humans capitalize on the reappearance of maintained items to boost another non-reappearing representation held in memory. This shows that the external world affects VWM operations beyond encoding, revealing that the environment is used to flexibly update the priority of memory content.

We repeatedly found that especially reappearing items fully matching memory facilitated VWM prioritization most effectively (compared with items only matching in orientation or location). The sensory recruitment model of VWM provides an explanation for this observation. The sensory recruitment account proposes that the perception and maintenance of sensory information recruits the same low-level sensory areas (D'Esposito, 2007; Gayet et al., 2018; Scimeca et al., 2018). Indeed, early visual areas are involved in perception as well as VWM (Harrison & Tong, 2009; Serences et al., 2009), and neural and pupil responses to visual input matching VWM content are enhanced (Gayet et al., 2017; Olmos-Solis et al., 2018; Wilschut & Mathôt, 2022) (also see Karabay et al., 2024). Maintaining material in VWM may pre-activate neuronal populations involved in processing specific visual features, leading to an enhanced neural response to matching input (Gayet et al., 2017). In the context of the current data, memorized orientations could have pre-activated orientation and spatially sensitive neurons during maintenance. Whenever items completely matching these pre-activated neuronal patterns reappear, they may be processed more efficiently compared with reappearing items that do not (fully) match these pre-activated patterns. In turn, enhanced processing of the reappearing material may help deduce which remaining item should be prioritized. This would indicate that the confluence of internal and external signals enable one to prioritize the most relevant information in the environment and memory.

Besides pre-activation through maintenance, another attentional process may

have contributed to the boosted prioritization when fully memory-matching items reappeared. In van Ede et al. (2020), subtle gaze biases revealed that visual input during maintenance containing features (e.g., color or orientation) of items held in VWM can automatically 'capture' internal attention (see Ester & Nouri, 2023; Theeuwes, 1994) - even when these retro cues were uninformative. Such internal attentional capture possibly also occurred in our task, facilitating the use of reappearing items which led to enhanced prioritization. However, one could also argue the opposite for both the internal attentional capture and pre-activation accounts: If the reappearing items are processed more deeply or automatically captured attention, this could distract from the most relevant VWM content that should be prioritized. We consider the latter possibility unlikely since reappearing items fully matching memory instead boosted performance in our experiments. The reappearing items were temporarily task-relevant, and became obsolete only after extracting the relevant information. Thus, processing the reappearing items more efficiently aids the extraction of useful information to deduce which item should be reported, leading to stronger prioritization of VWM content. Together, through the pre-activation of shared neural substrates and/or internal attentional capture, we posit that processing the reappearing items more deeply and rapidly is beneficial for performance.

Let us briefly revisit the aforementioned example of crossing the street (Figure 1): our results indicate that seeing the red and the blue car moving from left to right, facilitates the prioritization of the memorized black car. As van Ede and Nobre (2023) argue, many retro cue experiments may not reflect how memorized material is prioritized in natural settings, as one seldom receives explicit spatial or feature-based cues indicating what VWM content is most relevant. One way that memories may be prioritized more naturally is based on temporal expectations (Heuer & Rolfs, 2023; Nobre & van Ede, 2023; van Ede et al., 2017). Being able to predict *when* to act upon a specific representation allows to prioritize that representation which enhances its fidelity and protects it from interference (Gresch et al., 2022; Gresch et al., 2021; van Ede et al., 2017). In addition to temporal expectations, we here introduce another way how VWM prioritization may manifest itself in daily life: humans capitalize on

the dynamic nature of sensory input to prioritize VWM content.

Our findings open a number of intriguing questions. Investigating potential similarities and discrepancies between the here newly introduced reappearing-item cue and more traditional retro cues may shed light on how VWM content is prioritized in more natural situations. For example, what is the fate of the reappearing maintained items? It is possible that participants either selectively forget the reappearing items, or prioritize remaining material without dropping VWM content (Souza et al., 2014; Williams et al., 2013; Williams & Woodman, 2012). The current data cannot fully dissociate between these options because cues indicated to-be-reproduced items with full validity. However, the reappear-one condition from Experiment 1 provides a clue into this issue: If participants dropped reappearing items, one would expect a benefit in this condition compared with the control condition. In contrast, no clear benefit was found as absolute errors were not significantly affected (and numerically even increased). This indicates that instead of forgetting, participants likely used the reappearing items to internally attend another non-reappearing item held in memory, which is thought to be limited to a single representation (e.g. Olivers et al., 2011; van Moorselaar et al., 2014), but this remains to be tested more directly. Moreover, it is possible that reappearing items may retain relatively strong memory traces when compared with uncued items in designs with traditional retro cues because the items physically reappear, which may refresh the memory traces. These hypothesized stronger memory traces may manifest themselves in more accurate and faster responses when probing uncued items (i.e. less costs of cueing), having relatively strong biasing effects on reports of cued items, or even improving long-term memory representations. Other open questions concern how other types of information that dynamic sensory input is able to communicate such as temporal order may be used to guide VWM prioritization (as in Figure 1; also see Heuer & Rolfs, 2023).

Here, we investigated if, and how, reappearing task-irrelevant sensory input facilitates VWM prioritization. By demonstrating that humans capitalize on the dynamic nature of the world to prioritize VWM content, we advance our understanding of

how memory prioritization may occur in more natural settings. Together, we propose that the relationship between VWM and sensory processing is bidirectional: VWM drives the selection of sensory input, which in turn guides the prioritization of the most relevant memory representations.

Acknowledgments: We thank Daan Gerits for his help with data collection for Experiments 2 and 3, thank Surya Gayet for his help with the design of Experiment 3, and thank Daryl Fougnie for valuable discussions. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement n° 863732).

Competing interests: The authors have no competing interests to declare.

Data and code availability: Analyses scripts and data are available via the Open Science Framework: https://osf.io/qzvkc/?view_only=7ab46111f1714ea5bd379b04a912355d.

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