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 $n = 96$) 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 Experiments 3 and 4. 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 accepted for publication.

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 four 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, et al., 2024; 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.

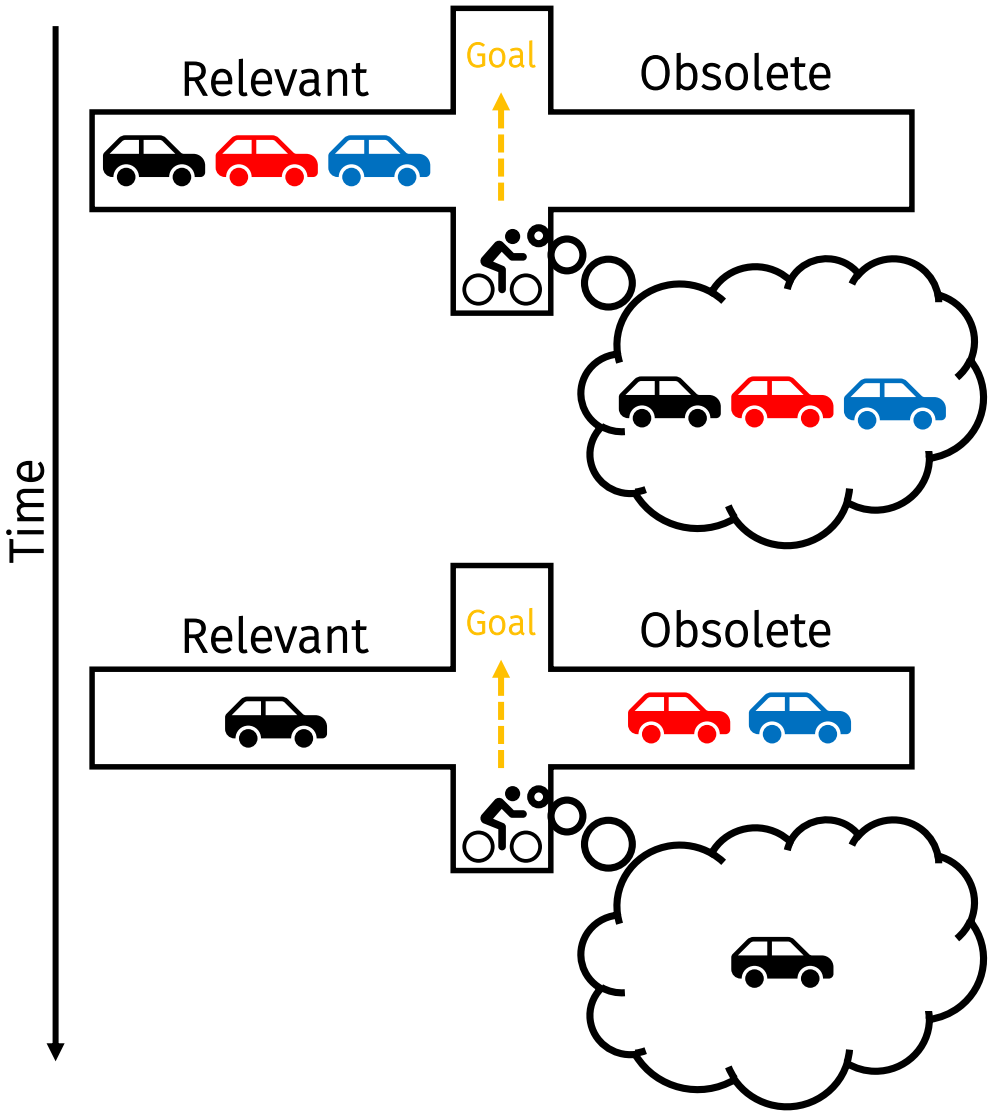

Figure 1: An example of how sensory input conveys information that might facilitate internal prioritization. In a dynamic environment, relevant information can become obsolete in a matter of seconds. When trying to cross the road, three cars are approaching from the left. Upon looking to the right where 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, et al., 2023; Koevoet, Van Zantwijk, 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 four 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) - through similar mechanisms as a retro-cue. 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/. Data for Experiments 1-3 were collected in 2023, and Experiment 4 was conducted in 2024. 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 used G*Power (v3.1) to conduct a power analysis (Faul et al., 2007). As we did not have an adequate estimate of an effect size from the previous literature for our effect of interest, we chose a medium effect size of η_p^2 = .06. To detect a main effect of this size with .80 power at an α = .05 with four conditions (within-subjects), 23 participants were required. We tested one additional participant for adequate counterbalancing (see below). The final sample size is comparable with, or even exceeds, 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 first author (D.K.) participated

in Experiments 1-3, but note that all outcomes and conclusions remain unaltered when excluding this participant unless otherwise explicitly stated. 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 $\wedge$ 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, and we report η_p^2 as a measure of effect size (as in Kumle et al., 2024).

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 ($\beta = 3.56 \pm .75$, $t = 4.73$, $p < .001$, $\eta_p^2 = .40$) and control blocks ($\beta = 2.21 \pm .77$, $t = 2.86$, $p = .013$, $\eta_p^2 = .20$) (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 ($\beta = 4.30 \pm .77$, $t = 5.58$, $p < .001$, $\eta_p^2 = .49$) and control blocks ($\beta = 2.95 \pm .80$, $t = 3.68$, $p < .001$, $\eta_p^2 = .29$), but absolute errors did not significantly differ between the reappear-two and retro cue blocks ($t = .99$, $p = .323$, $\eta_p^2 = .03$). 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 ($t = 1.79$, $p = .147$, $\eta_p^2 = .09$).

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: $\beta = 510.03 \pm 29.50$, $t = 17.29$, $p < .001$, $\eta_p^2 = .93$; retro: $\beta = 479.63 \pm 41.94$, $t = 11.44$,

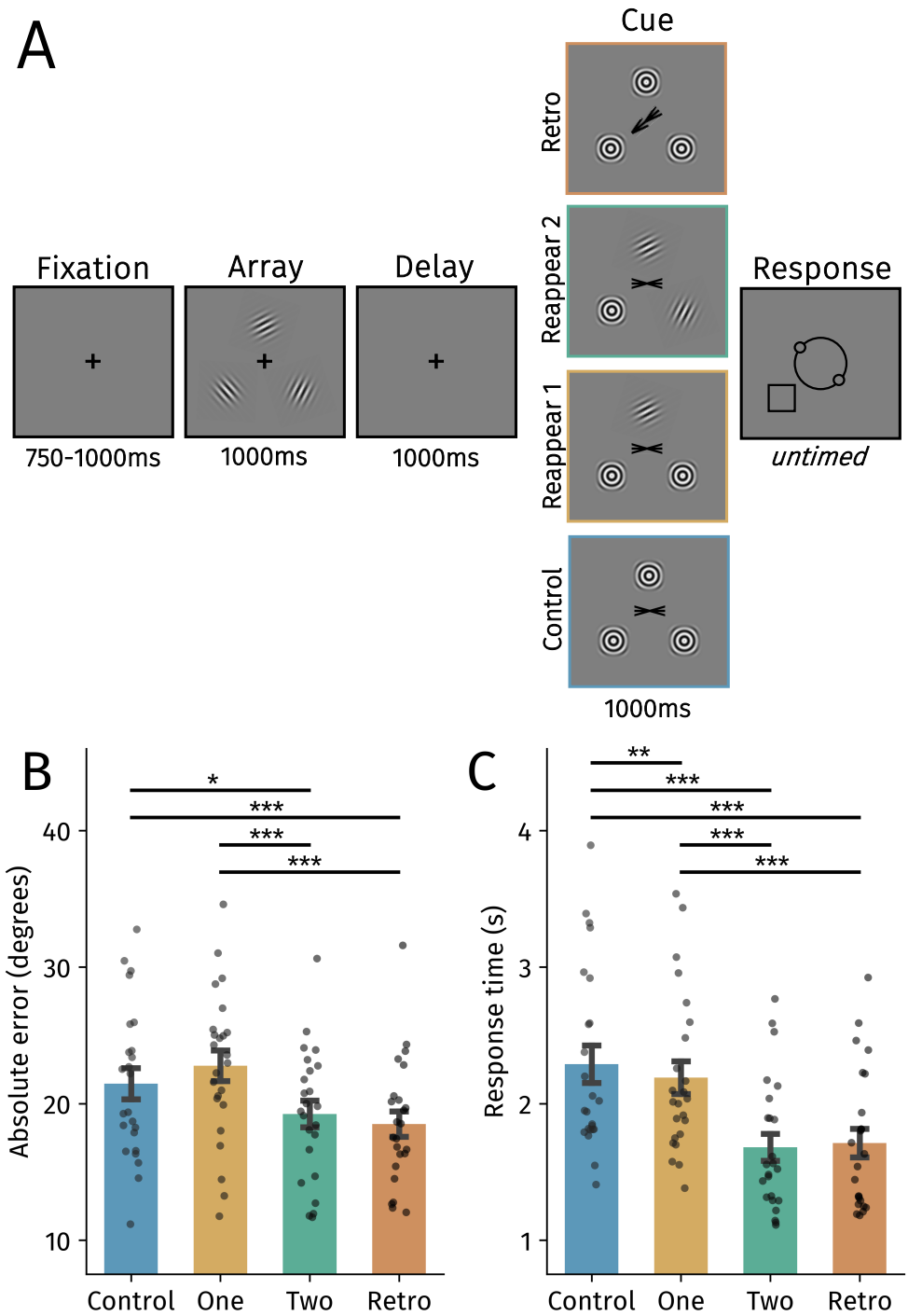

Figure 2: **a)** Trial structure of Experiment 1. After a fixation period, participants encoded the orientation of three Gabor gratings. Different cues were presented after a delay period depending on the block. In the reappear-two block, participants could infer which item should be reported because 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. Holm-corrected: $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

$p < .001$, $\eta_p^2 = .85$) and control blocks (reappear-two: $\beta = 607.27 \pm 41.95$, $t = 14.48$, $p < .001$, $\eta_p^2 = .90$, retro: $\beta = 576.86 \pm 56.93$, $t = 10.13$, $p < .001$, $\eta_p^2 = .82$). The reappear-two and retro cue blocks did not differ significantly ($t = 1.03$, $p = .30$, $\eta_p^2 = .04$), and participants responded faster in the reappear-one than in the control block ($\beta = 97.23 \pm 29.58$, $t = 3.29$, $p = .002$, $\eta_p^2 = .32$).

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 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 Beck et al., 2012; Frătescu et al., 2019; Hollingworth & Beck, 2016; J. R. Williams et al., 2022, also see Discussion). 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). It is also possible that the grating in the reappear-1 condition captured attention (Theeuwes, 1994), which caused interference during the internal prioritization process. Regardless of what may explain the lack of a benefit in the reappear-1 condition, our findings demonstrate that dynamic sensory input can facilitate the prioritization of at least one VWM representation to guide behavior.

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 $p < .001$). We chose the same sample size and number of trials per condition as in Experiment 1 for comparability, and because we did not expect to find smaller effect sizes in Experiment 2.

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 (β = 2.36 $\pm$ .86, t = 2.74, p = .019, η_p^2 = .25) and orientation blocks (β = 8.66 $\pm$ .86, t = 10.03, p < .001, η_p^2 = .81) (Figure 3B). When participants relied exclusively on spatial information, they were more accurate than when only using orientation information (β = 6.30 $\pm$ .99, t = 6.39, p < .001, η_p^2 = .64). Moreover, reports were more precise in the control compared with the orientation block (β = 7.21 $\pm$ .87, t = 8.34, p < .001, η_p^2 = .75). Accuracy in the combination and location blocks did not significantly differ from the control block (ts < 1.47, ps > .28, η_p^2s < .10).

The response time analyses complemented the accuracy findings and ruled out potential speed-accuracy trade-off effects for almost all comparisons (besides those with the control block). Participants responded fastest in the combination block (Figure 3C; location: β = 106.98 $\pm$ 30.24, t = 3.57, p < .001, η_p^2 = .35; orientation: β = 300.70 $\pm$ 30.25, t = 9.94, p < .001, η_p^2 = .81; control: β = 720.70 $\pm$ 43.92, t = 16.41, p < .001, η_p^2 = .92). 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 (β = 193.73 $\pm$ 43.91, t = 4.41, p < .001, η_p^2 = .46), indicating that location guided prioritization more effectively than orientation information in the current

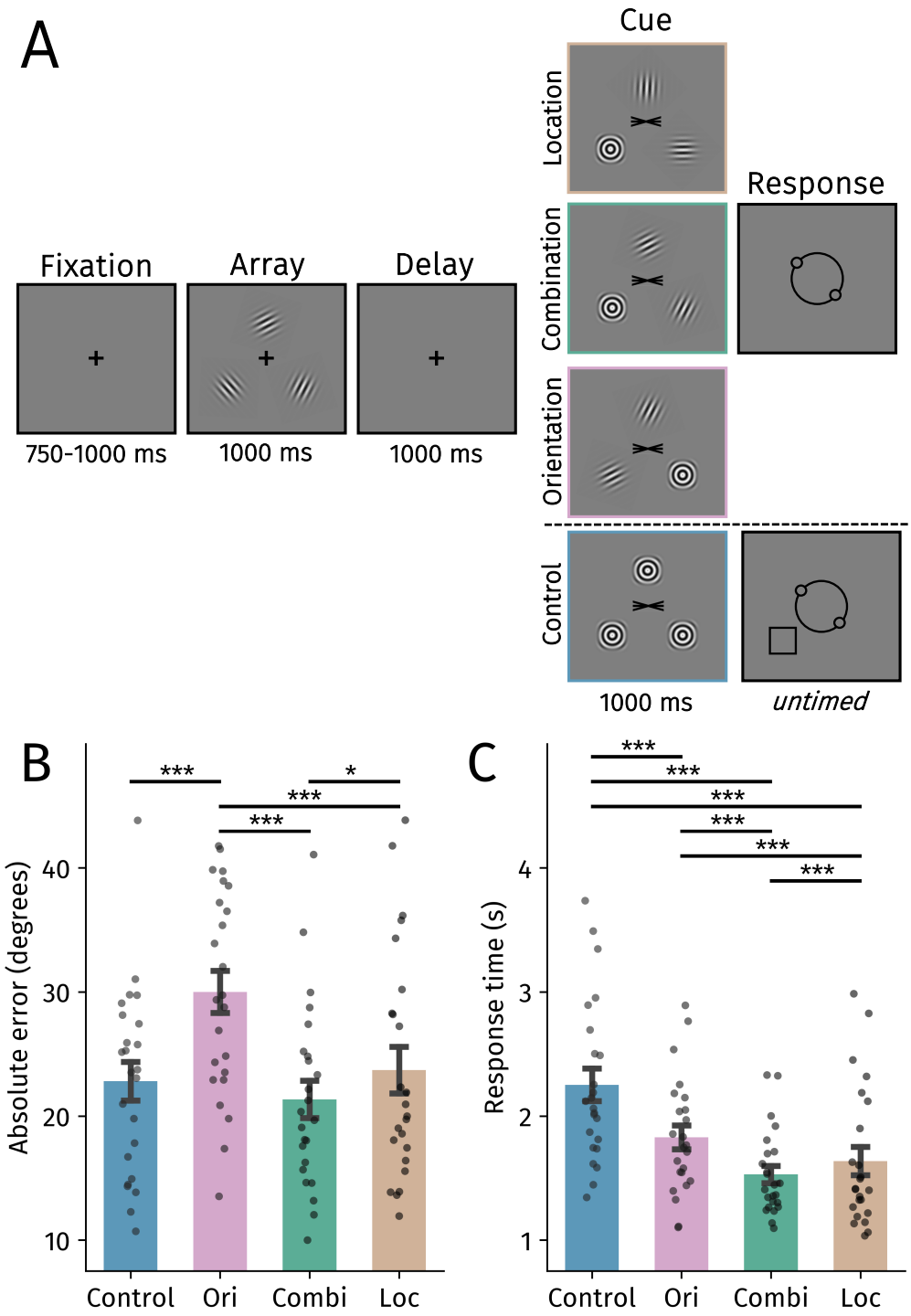

Figure 3: **a)** Trial structure of Experiment 2. In this example, the bottom left orientation ('\') has to be reproduced. In the combination block, participants deduced which item should be reported using a combination of location and orientation information from the cue. In contrast, participants could 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. Holm-corrected: $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

task.[1] Response times were slower in the control than in the orientation (β = 420.00 $\pm$ 30.28, t = 13.87, p < .001, η_p^2 = .89) and location blocks (β = 613.73 $\pm$ 60.14, t = 10.21, p < .001, η_p^2 = .82).

Our results show that reappearing items matching VWM guide the prioritization of the remaining maintained grating most effectively. 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. Another possibility is that the inclusion of the orientation block may have encouraged participants to encode orientations unbound to their spatial locations, and this encoding strategy may have extended to 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 probe during recall). Second, we controlled for a potential effect of low-level visual adaptation by briefly presenting masks after the encoding phase.

[1] Note that our task does not offer a fair comparison between orientation and location information. As there were only three different locations, it may have been easier to use this information to guide internal prioritization compared with orientation which had 180 different orientations throughout the task. Thus, although participants seemed to not be able to use the isolated orientation information to guide internal prioritization here, it may be possible that in other designs orientation information may be used more effectively.

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 $p < .001$). As we aimed to replicate the main findings from Experiments 1 and 2, we chose the same sample size and number of trials per condition as in those experiments.

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 ($\beta = 4.23 \pm .92$, $t = 4.60$, $p < .001$, $\eta_p^2 = .48$) and responded faster ($\beta = 612.69 \pm 48.84$, $t = 12.55$, $p < .001$, $\eta_p^2 = .87$) in the combination compared with the control block.

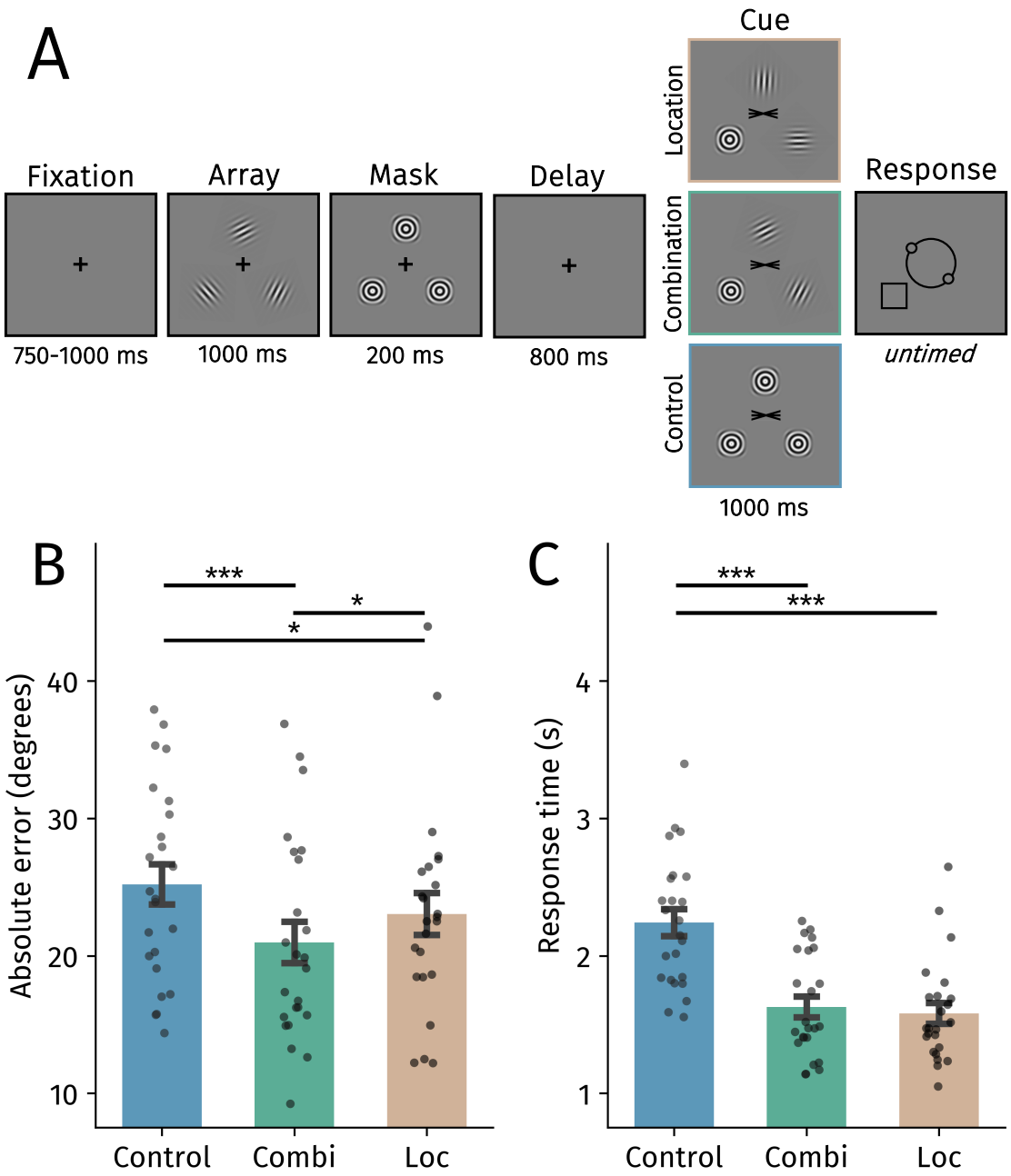

Figure 4: **a)** Trial structure of Experiment 3. **b)** Mean absolute error in degrees across block types. **c)** Average response times across block types. Black points reflect individual participants. Error bars represent SEM. *Abbreviations:* Combi = Combination, Loc = Location. Holm-corrected: *$p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

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, η_p^2 = .22). Location information did, however, also facilitate VWM prioritization as reports were more precise (β = 2.16 $\pm$ 1.07, t = 2.03, p = .043, η_p^2 = .15)[2] and faster in the location block than in the control block (β = 659.52 $\pm$ 68.52, t = 9.63, p < .001, η_p^2 = .80). Response times did not significantly differ between the location and combination blocks (t = 1.48, p = .138, η_p^2 = .09). Together, Experiment 3 replicated the main findings from the previous experiments and ruled out low-level visual adaptation as a possible confound.

There were two caveats remaining when interpreting the results from Experiments 1-3. Firstly, it is possible that participants prioritized the singleton mask stimulus without considering the reappearing gratings. Although unlikely, as we found consistent differences between location and combination conditions, we wanted to rule out this possibility experimentally. Second, it remained possible that differences in task performance between the location and combination conditions were caused by interference. Such interference could have occurred because 'new' orientation information was presented when gratings reappeared in the location but not the combination condition.

Experiment 4

Experiment 4 aimed to address these two issues. First, we increased the total number of locations and removed the mask stimulus on the to-be-probed location. This ensured that participants could not selectively prioritize the mask stimulus, but instead had to use the reappearing stimuli. Second, we included a condition where two mask stimuli appeared on locations that were never probed. This condition could not cause feature-based interference because no new orientations were presented during the cue period.

[2] Note that this effect was non-significant when excluding the first author's data, t = 1.69, p = .09.

Methods

The methods in Experiment 4 were identical to Experiment 3 unless specified explicitly.

Participants

Twenty-eight participants with normal or corrected-to-normal vision took part in Experiment 4. Four participants were excluded for not performing above chance level (see Methods Experiment 1). This left a final sample of twenty-four participants as in Experiments 1-3 (M_{age} = 22.13 (range: 19-28), 4 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 5A): the location and combination blocks from Experiment 2 and 3, and a masks condition. In the masks condition, two mask stimuli without orientation information reappeared. As in the previous experiments, orientations that originally occupied these locations were never probed at the end of the trial. This allowed us to test whether or not the memory-match effect was solely driven by the interference caused by 'new' gratings in the location condition. Another important task design difference is that stimuli could now be presented in six, instead of three different locations compared with the previous experiments. Moreover, no stimulus was now presented on the to-be-probed location. This ensured that participants could not selectively prioritize the mask stimulus without considering the reappearing gratings.

We increased the number of trials per condition to 75, slightly increasing statistical power. As in the previous experiments, we discarded trials (0.76%) with very fast (<200 ms) or very slow (>6000 ms) response times. The analysis included 5,359 trials in total. Note that for the response time analysis, the model did not converge when including by-participant random slopes, and we therefore fit this model as follows, Wilkinson Notation: Response time $\sim$ Cue Type + (1|Participant) (as recommended

by Barr, 2013).

Results

In Experiment 2 and 3, we observed that participants were more accurate in the combination than in the location combination condition. Using an improved design that addressed possible caveats, we replicated the same pattern (β = 4.69 $\pm$ .77, t = 6.11, p < .001, η_p^2 = .62) (Figure 5B). Ruling out a speed-accuracy trade-off, participants responded faster in the combination than in the location condition (β = 127.44 $\pm$ 23.11, t = 5.51, p < .001, η_p^2 = .57) (Figure 5C).

We then turned to the masks condition. The masks cue provided the same spatial information as the other conditions, but did not match the content held in memory and could not cause interference by introducing new orientation information. This allowed us to determine whether or not the memory-match effect was driven by the interference caused by 'new' gratings (Figure 5). Participants were more accurate in the masks compared with the location condition (β = 4.03 $\pm$ 1.13, t = 3.58, p < .001, η_p^2 = .36), and response accuracies did not differ significantly between the masks and combination conditions (β = .66 $\pm$ .92, t = .72, p = .47, η_p^2 = .02).

As for response times, we found no differences between the masks and location conditions (β = 36.51 $\pm$ 23.13, t = 1.58, p = .11, η_p^2 = .10). By contrast, participants responded faster in the combination than in the masks condition (β = 90.93 $\pm$ 23.11, t = 3.94, p < .001, η_p^2 = .40).

Together, these results indicate that the accuracy difference between the location and combination conditions were, at least in part, driven by interference caused by new orientation information. Nevertheless, response times revealed that reappearing gratings that matched VWM still guided internal prioritization most effectively even when controlling for interference. Based on the four experiments reported above, we conclude that reappearing items matching VWM guide the internal prioritization of another non-reappearing item most effectively.

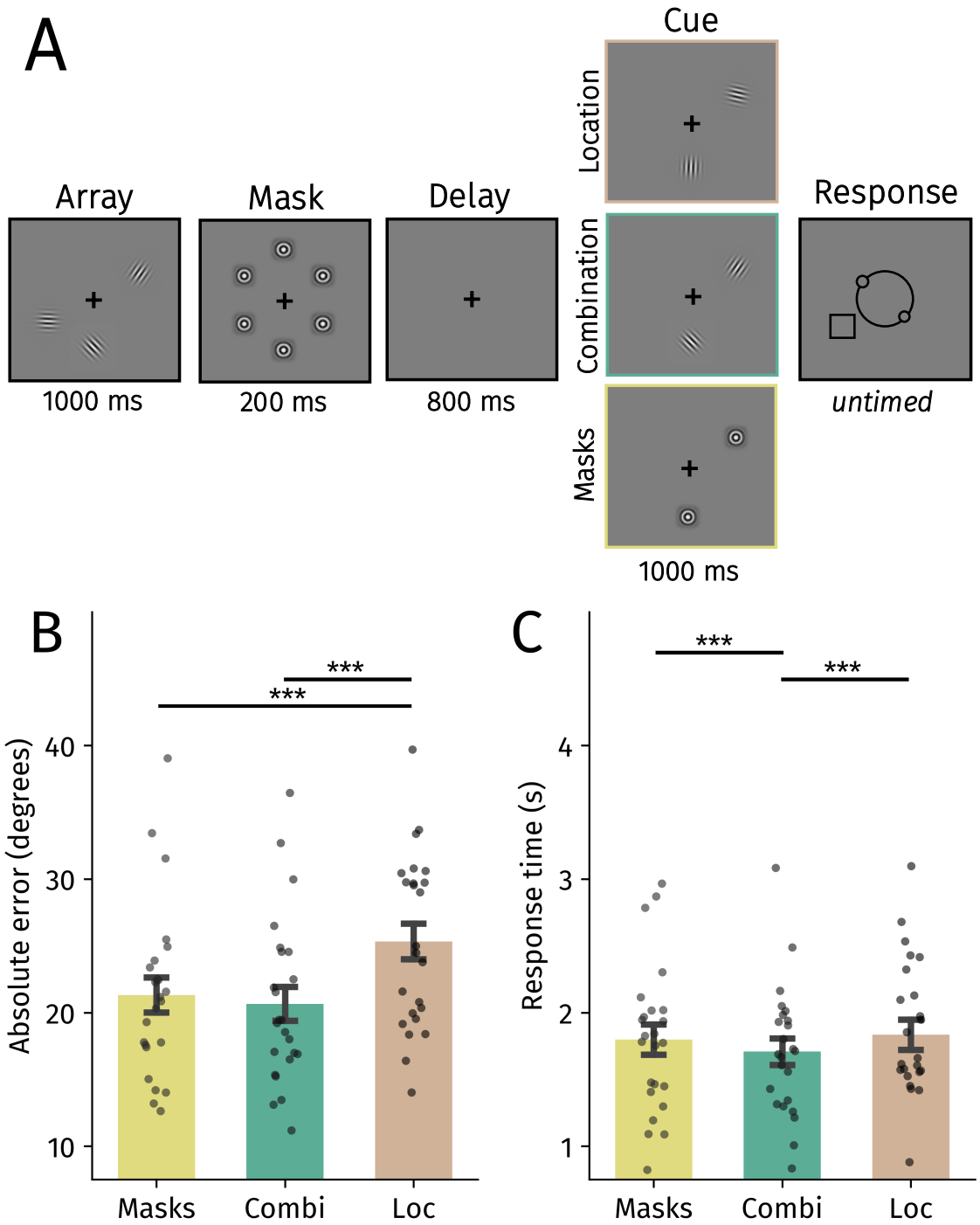

Figure 5: **a)** Trial structure of Experiment 4. **b)** Mean absolute error in degrees across block types. **c)** Average response times across block types. Black points reflect individual participants. Error bars represent SEM. *Abbreviations:* Combi = Combination, Loc = Location. Holm-corrected: ***$p < .001$.

Discussion

We report four 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 and 3, 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). Experiment 4 demonstrated that although a part of the findings from previous experiments may be attributed to the reappearance of items with novel orientation, reappearing items that match memory contents guided VWM prioritization most effectively. 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. Our findings are reminiscent of spatial and visual change-detection tasks that manipulated the similarity between the study and probe displays (Hollingworth, 2006, 2007; Jiang et al., 2000; Udale et

al., 2018). Jiang et al. (2000) found that performance was best when probe displays were most similar to memorized locations or colors. These results dovetail with the current findings from Experiments 2-4, as sensory input matching (visual) working memory content boosted performance. We extend these findings by presenting cues well before participants are able to respond, tapping into an internal prioritization process that prepares for upcoming behavior instead of the retrieval process itself. Together, 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 guide which remaining item should be prioritized. This explanation also captures the results from Experiment 4 as interference caused by presenting novel orientations accounts for the observed accuracy benefits in the combination compared with the location conditions (also see Bays et al., 2024; Oberauer, 2002). In-

deed, seeing novel orientations during the memory prioritization process caused interference, which could be due to the overlapping neural circuitry in perception and memory (Gayet et al., 2017; Gayet et al., 2018; Harrison & Tong, 2009; Serences et al., 2009), and this finding dovetails with work on distraction in VWM (e.g. Lorenc et al., 2021; Lout et al., 2023; van Moorselaar et al., 2015; Vogel et al., 2006; Wilschut & Mathôt, 2022). Moreover, as the above pre-activation account would predict, prioritization was most effective (i.e. faster responses) when reappearing fully matched VWM compared with when they had no new orientations. Together, this indicates 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 memory-matching 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 guided the prioritization process most effectively 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 infer 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. However, the underlying internal prioritization mechanism do not necessarily differ between retro-cues, temporal expectations or the currently employed cues. It is indeed possible that the above examples are different ways to inform the same internal prioritization process to facilitate adaptive behavior.

Our findings open a number of intriguing questions. Although the underlying internal prioritization mechanism may not differ, investigating potential similarities and discrepancies between the here newly introduced reappearing-item cues 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 prioritized remaining material without dropping VWM content (Souza et al., 2014; M. Williams et al., 2013; M. 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 selectively 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 some have hypothesized to be limited to a single representation (e.g. Olivers et al., 2011; van Moorselaar et al., 2014) - although note this idea has been challenged (Beck et al., 2012; J. R. Williams et al., 2022) and the number of VWM representations guiding attention may be task-dependent (Frătescu et al., 2019; Wang et al., 2024). Future work may tackle whether forgetting plays a role by either implementing invalidly cued trials, as well as independently manipulating set size and the number of reappearing items. 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. Additionally, it would be interesting to investigate whether the timecourse of internal prioritization would differ between more traditional retro-cues and reappearing-item cues. If participants would use higher level reasoning (e.g. deduction) when extracting the relevant information from the reappearing items, the prioritization process may occur relatively slowly when compared with selecting items from VWM based on their features or locations. Other open questions concern how reappearing items are used when their properties change across trials (i.e. mixed design) and how other types of information that reappearing items are able to convey, such as temporal order, may be used to guide VWM prioritization (as in Figure 1; also see Heuer & Rolfs, 2023).

We note that we primarily recruited highly-educated young adults for the current study. It remains to be investigated if the reported effects generalize to individuals with different demographic characteristics (e.g. lower education or older age).

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, 3 and 4, 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/.

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