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Visual Working Memory Adapts to the Nature of Anticipated Interference

Benchi Wang[1,2,3], Tomas Knapen[3], and Christian N. L. Olivers[3]

Abstract

■ Visual working memory has been proven to be relatively robust against interference. However, little is known on whether such robust coding is obligatory, or can be flexibly recruited depending on its expected usefulness. To address this, participants remembered both the color and orientation of a grating. During the maintenance, we inserted a secondary color/orientation memory task, interfering with the primary task. Crucially, we varied the expectations of the type of interference by varying the probability of the two types of intervening task. Behavioral data indicate that to-be-remembered features for which interference is expected are bolstered, whereas to-be-remembered features for which no interference is expected are left vulnerable. This was further supported by fMRI data obtained from visual cortex. In conclusion, the flexibility of visual working memory allows it to strengthen memories for which it anticipates the highest risk of interference. ■

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INTRODUCTION

Visual working memory (VWM) is an important but limited memory buffer that briefly and flexibly stores visual information that is relevant for an ongoing or upcoming task (Baddeley, 2003; Cowan, 2001). For VWM to be functionally useful, a critical characteristic is that its content should be relatively robust against external interference from irrelevant stimuli and tasks. Although a number of studies suggest that VWM is not entirely immune to interference from intervening tasks (e.g., Gresch, Boettcher, van Ede, & Nobre, 2021; Hakim, Feldmann-Wüstefeld, Awh, & Vogel, 2021; Bae & Luck, 2019; Feldmann-Wüstefeld & Vogel, 2019; Rademaker, Chunharas, & Serences, 2019; Souza, Rerko, & Oberauer, 2016; Clapp, Rubens, & Gazzaley, 2010; Fougnie & Marois, 2009; McNab & Klingberg, 2008; Postle, D'Esposito, & Corkin, 2005), it has been shown that VWM can also survive a large variety of intervening stimuli and tasks (Rademaker et al., 2019; Wang, Theeuwes, & Olivers, 2018, 2019; de Vries, van Driel, Karacaoglu, & Olivers, 2018; van Loon, Olmos-Solis, Fahrenfort, & Olivers, 2018; van Moorselaar et al., 2017; Bettencourt & Xu, 2016; Rerko, Souza, & Oberauer, 2014; Hollingworth & Maxcey-Richard, 2013; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2011; Vogel, Woodman, & Luck, 2006). This robustness has led to various hypotheses on how visual working memories are protected from unrelated activity, including the idea that to-be-remembered items are strengthened by directing attention to them (Souza & Oberauer, 2016), that specialized brain areas allowing for more shielded coding are being recruited (e.g., Bettencourt & Xu, 2016), or that the storage of memories occurs in more durable, connectivity-based representations (e.g., Lewis-Peacock et al., 2011; Olivers, Peters, Houtkamp, & Roelfsema, 2011).

We were interested in whether robust coding is obligatory, or can be flexibly recruited depending on its expected usefulness. Given the limited resources that characterize working memory, a maximally adaptive system should strengthen memories for which it anticipates the highest risk of interference. Conversely, information for which little interference is expected may be stored with lower fidelity. Currently, little is known on whether, and how, VWM prepares for different forms of interference. Here, we address the question to what extent VWM storage adapts to the anticipated nature of the interference.

To address this question, we ran three experiments in which we asked participants to remember both color and orientation of a grating. During the maintenance period, we inserted a secondary task that involved either color or orientation memory, with the aim of interfering with the primary task. We chose to implement a full intervening task rather than just presenting distractor stimuli to which the observer did not have to respond in order to maximize the processing of and thus the potential interference from the intervening stimuli (see, e.g., the works of Gresch et al., 2021; Wang et al. 2018; Clapp & Gazzaley, 2012, for evidence). Crucially, we varied the expectations of the type of interference by varying the probability of the two types of intervening task, beknown to participants. Experiments 1 and 2 deliver behavioral evidence that to-be-remembered features for which interference is expected are bolstered, whereas to-be-remembered features for which no interference is expected are left more

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vulnerable. Experiment 3 provides evidence that the brain protects memories against interference by momentarily increasing the strength of their representation in visual cortex.

EXPERIMENT 1

Experiment 1 provided a first test of the hypothesis that VWM adapts to the nature of the anticipated interference. We used a dual task procedure that is illustrated in Figure 1. For the primary, change-detection, task, participants were instructed to remember both the color and the orientation of a grating, as during the probe at the end of the trial, either one of these features could have changed. During maintenance, participants performed a briefer secondary change detection task, in which they saw either six randomly oriented line segments or six colored disks. These they had to remember for half a second until a probe display appeared, in which one of the elements could have changed. The crucial manipulation was the relative proportion of each type of intervening task. In the anticipated color interference condition, the intervening task was the color memory task on 80% of the trials. In the remaining 20% of trials, an orientation memory task intervened. In the anticipated orientation interference condition, these proportions were reversed. From an adaptive protection hypothesis, we predicted that primary memory would be best protected against the anticipated type of interference, whereas the other feature would be left more vulnerable. Specifically, color memory should suffer more from color interference when color interference is unexpected. Likewise, orientation memory should suffer more from orientation interference when such interference is unexpected.

Methods

Figure 1 illustrates the stimuli and task procedure.

Participants

Sample size was determined based on a study from our laboratory adopting a similar paradigm, where we observed significant interference effects for n = 15–16 (Wang et al., 2018). Here, we recruited 16 participants. One person broke off participation midway for personal reasons, resulting in 15 participants being included in the analyses (7 women and 8 men with a mean age of 23.6 years). They received monetary compensation or course credits. They all provided written informed

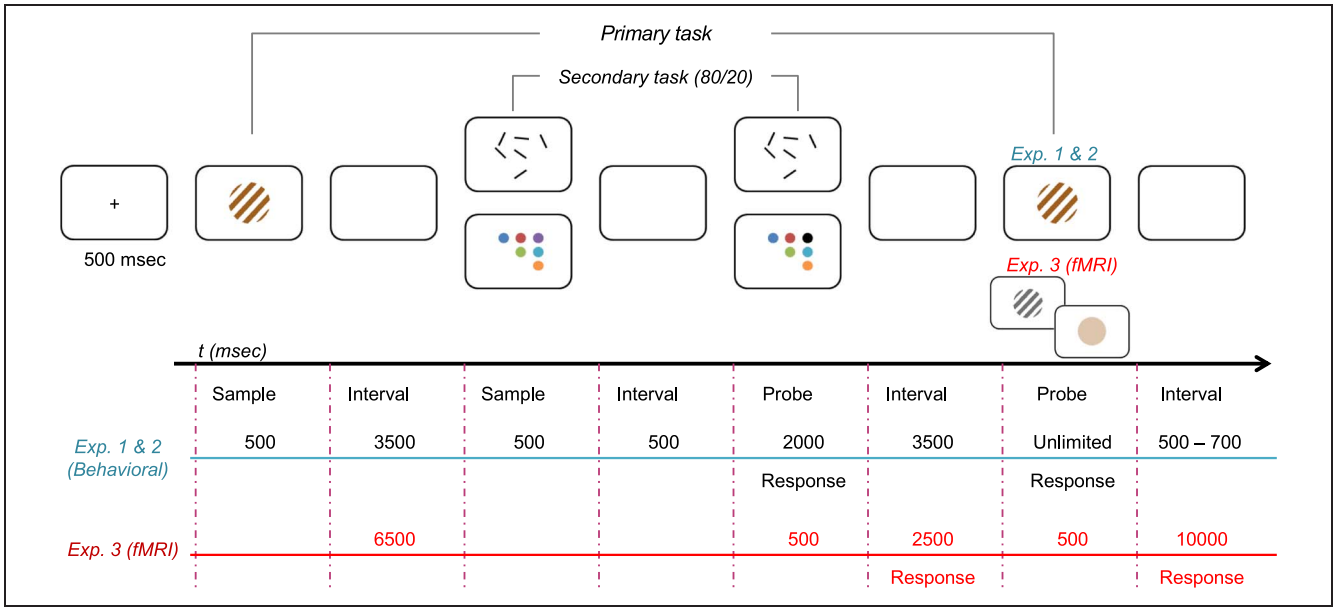


Figure 1. Illustration of the trial procedures of Experiments 1, 2, and 3. Participants are instructed to first memorize both the color and the orientation of a grating stimulus shown on a gray screen. The foreground color of the grating stimulus is randomly selected from one of two color bins centered on either 45° or 135° in CIE L*a*b color space (centered at L = 70, a = 5, b = 0 with a radius of 60; luminance: 36–44 cd/m^2), plus or minus an offset randomly selected from a range of ±10°. Its orientation is likewise randomly chosen from one of two orientation bins centered on either 45° or 135° from vertical, plus or minus an additional offset randomly selected from a range of ±10°. The additional random jitter around the canonical feature value is adopted to preclude the possibility of categorical memory and promote visual memory. The color and orientation of the test stimulus are then either both the same as the sample, or there is either a ±10° color change, or a ±15° (±30° for Experiment 2 and Experiment 3) orientation change (but never both). In between the main memorandum and test stimulus, participants are presented with either six colored disks with the colors randomly chosen from the above CIELab color set, or six randomly black oriented bars, that they are also to memorize. Their locations are randomly selected from an invisible 3 × 3 grid, 9° × 9° visual angle located in the center of the display. The presentation time for each display is different between different experiments, which can be found inside the figure. The major manipulation is in the relative proportions of the interfering task types, which is varied at the block level. In the anticipated color interference block, 80% trials have an intervening color task, 20% trials have an intervening orientation task, randomly mixed. In the anticipated orientation interference block, this is the other way around.

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consent and reported normal color vision, and normal or corrected-to-normal visual acuity. The research protocol was approved by the Scientific and Ethics Review Committee of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam (VCWE-2016-215).

Apparatus and Stimuli

The timing and recording of events and presentation of stimuli was controlled by a HP Compaq 8000 Elite computer. The stimuli were shown on a 21-in. Samsung SyncMaster color monitor with a viewing distance of approximately 70 cm. Participants were tested in a dimly lit laboratory. Stimulus presentation and response registration were controlled by custom scripts written in Python (www.python.org) with the package of PsychoPy (Peirce, 2007).

Primary memory task. Participants were instructed to first memorize both the color and the orientation of a grating stimulus shown on a gray background (17 cd/m^2). The sine-wave grating was cropped by a circular mask (radius: 4°), and its spatial frequency was 0.5 cycles per degree. The foreground color of the grating stimulus was randomly selected from one of two color bins centered on either 45° or 135° in CIE L*a*b color space (centered at $L = 70$, $a = 5, b = 0$ with a radius of 60; luminance: 36–44 cd/m^2), plus or minus an offset randomly selected from a range of ±10°. Its orientation was likewise randomly chosen from one of two orientation bins centered on either 45° or 135° from vertical, plus or minus an additional offset randomly selected from a range of ±10°. The additional random jitter around the canonical feature value was adopted to preclude the possibility of categorical memory and promote visual memory. The color and orientation of the test stimulus were then either both the same as the sample, or there was either a ±10° color change or a ±15° orientation change (but never both).

Secondary interference task. In between the main memorandum and test stimulus, participants were presented with either six colored disks (radius = 0.75°) with the colors randomly chosen from the above CIELab color set, or six randomly oriented bars (all black, length = 1.5°). Their locations were randomly selected from an invisible 3 × 3 grid, 9° × 9° visual angle located in the center of the display.

Procedure and Design

The trial sequence consisted of two change detection tasks, one embedded within the other. At the beginning of each trial, a fixation cross was shown for 500 msec. Then, a to-be-memorized grating stimulus was shown in the center of the display for 500 msec, of which participants were required to remember both color and orientation. After a 3500-msec delay, participants were presented with an array of either six colors or six orientations for 500 msec, which they were also to memorize, followed after a 500-msec blank by the same set of colors or orientations, but with one item potentially changed (50% of trials). Participants indicated whether any feature had changed or not in this intervening task by pressing the "Z" (no) or "/" (yes) key, respectively. After this response, with a maximum wait of 2000 msec, there was another 3500-msec interval, after which the test grating stimulus for the primary task was presented. Participants judged whether, compared with the original one, the grating stimulus had changed either color or orientation (never both), by pressing the "Z" (no) or "/" (yes) key. After a random intertrial interval (ITI; range: 500–700 msec), the next trial began. Only accuracy was emphasized in the instructions of the present and the following experiments.

The most important manipulation was in the relative proportions of the interfering task types, which was varied at the block level (unknown to the participants). In the anticipated color interference block, 80% trials contained an intervening color task, 20% trials contained an intervening orientation task, randomly mixed. In the anticipated orientation interference block, this was the other way around. Each block contained 300 trials and was preceded by 12 practice trials. The next crucial factor was then which type of interference was actually received—that is, the color task or the orientation task. The final factor of importance was which feature of the primary stimulus was tested for the grating task—again color or orientation. Note that the correct detection of feature changes (which we defined as a hit) will be most informative, because nonchanges cannot be uniquely attributed to color or orientation memory. For this reason, we chose to increase the proportion of change trials, such that 1/5 of the probes contained no change, 2/5 contained a color change, and 2/5 contained an orientation change. Thus, the full design comprised 2 levels of anticipated interference (color vs. orientation) × 2 levels of actual interference (color vs. orientation) × 2 types of feature being tested (again color vs. orientation). All factors were varied within participants.

Results

Primary Task Performance

The left part of Figure 2A shows the mean hit rate on the primary (grating) task, collapsed for color and orientation, as a function of whether interference was anticipated or not, and whether observers were then actually tested on the feature for which interference was anticipated or on the feature for which interference was not anticipated. The middle and right parts show the same data, but split for anticipated color and anticipated orientation interference. Note that we concentrated on hit rates (i.e., when participants correctly identify a change) because, due to the design, false alarm rates cannot be specifically attributed to color or orientation memory. Here, the average

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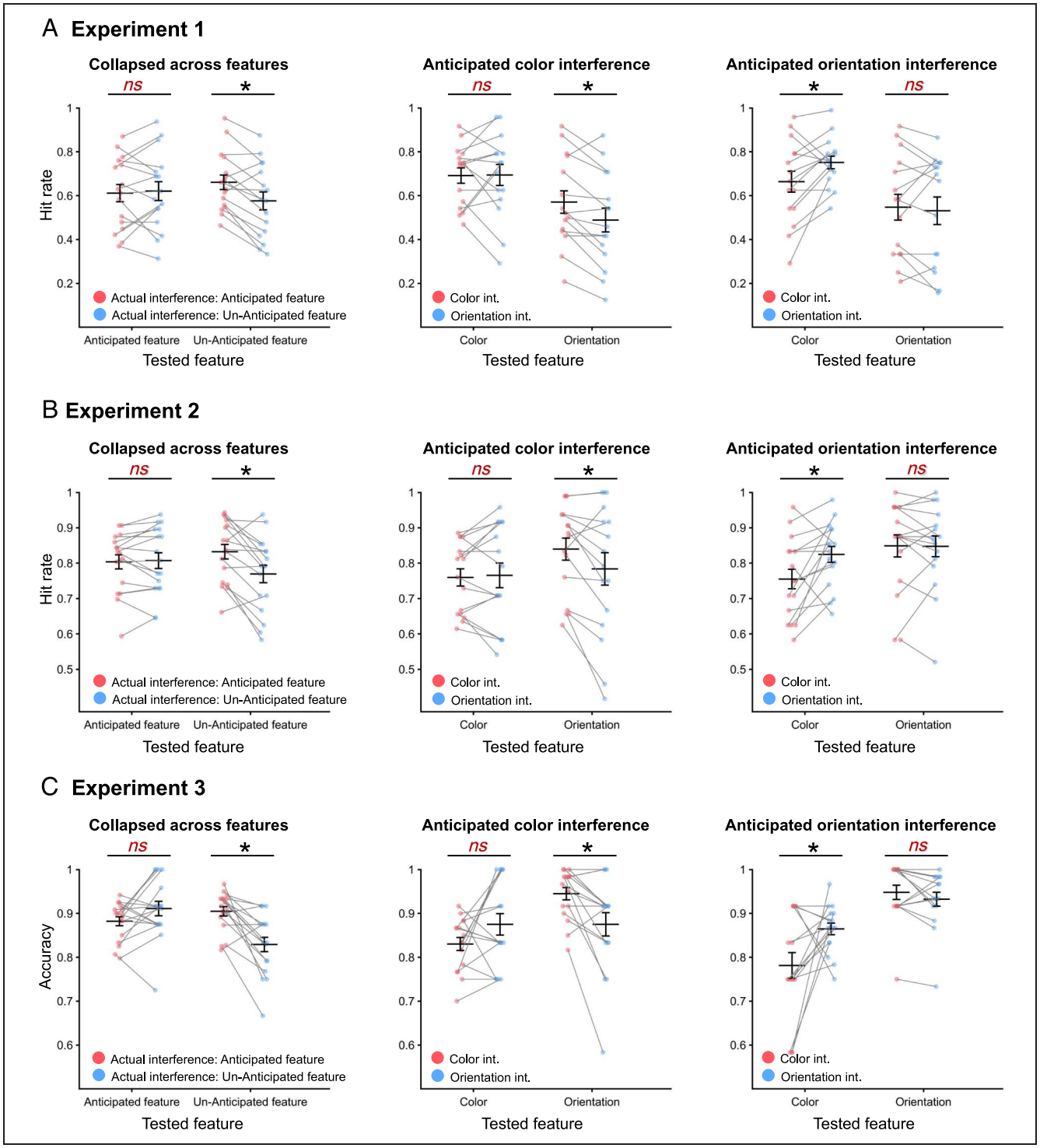


Figure 2. Behavioral results for the three experiments. Here, we observe a drop in memory performance for the unanticipated feature of the primary memory stimulus (the grating) when the interference is in the unanticipated feature dimension compared to that when the interference is in the anticipated feature. No such drop is observed when interference is in the anticipated feature dimension. This is consistent with memory for features for which no interference is expected being more vulnerable, and conversely, memory for which interference is expected is relatively more robust. The asterisks in all parts signal the significant differences between conditions. Error bars denote ±1 *SEM* across participants.

false alarm rates were 0.29 for anticipated color interference blocks and 0.25 for anticipated orientation interference blocks. Moreover, the false alarm rate did not differ between anticipated interference (0.28) and unanticipated interference (0.26), $t(14) = 0.79$, $p = .445$, $BF_{10} = 0.34$.

We performed a repeated-measures ANOVA on the data collapsed across color and orientation, with factors Actual Interference (anticipated interference vs. unanticipated interference) and Tested Feature (for which interference was anticipated vs. for which interference was unanticipated).

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This revealed a significant two-way interaction, $F(1, 14) = 9.94$, $p = .007$, partial $\eta^2 = .42$, but no main effects, both ps $> .073$. Moreover, adding the specific feature (color, orientation) as an additional factor did not result in a three-way interaction, $F < 1$. Planned comparisons revealed that when observers were tested on the feature for which interference was expected, performance did not suffer when observers indeed received interference on that feature, relative to when they received interference on the other feature, $t < 1$. In contrast, memory performance did suffer when observers were tested on the feature for which interference was unexpected, and they indeed also received interference on that feature, $t(14) = 3.86$, $p = .002$.

We performed the same analyses for each type of anticipated feature interference separately. When color interference was anticipated (Figure 2A, middle part), a repeated-measures ANOVA with factors Actual Interference (color, orientation) and Tested Feature (color, orientation) showed a significant main effect of Tested Feature, $F(1, 14) = 9.69$, $p = .008$, partial $\eta^2 = .41$, but not for Actual Interference, $F(1, 14) = 2.71$, $p = .12$, partial $\eta^2 = .16$. Memory for color was overall better than memory for orientation. Importantly, the two-way interaction between Actual Feature Interference and Tested Feature was statistically reliable, $F(1, 14) = 5.39$, $p = .036$, partial $\eta^2 = .28$. Planned follow-up comparisons revealed that orientation memory suffered from orientation interference relative to color interference, $t(14) = 3.74$, $p = .002$. In contrast, color memory did not suffer from color interference here, $t < 1$. The right part of Figure 2A shows the reverse pattern when orientation interference was anticipated. Again there was a main effect of Tested Feature, $F(1, 14) = 12.99$, $p = .003$, partial $\eta^2 = .48$, but not for the type of interference, $F(1, 14) = 2.18$, $p = .16$, partial $\eta^2 = .14$. Performance was overall better for color than for orientation. Importantly, here too, the two-way interaction was statistically reliable, $F(1, 14) = 5.48$, $p = .035$, partial $\eta^2 = .28$. Planned follow-up comparisons revealed that, here, color memory suffered from color interference, relative to orientation interference, $t(14) = 2.43$, $p = .029$. In contrast, now, orientation memory did not suffer from orientation interference, $t < 1$.

Secondary Task Performance

Figure A1A shows performance on the secondary, intervening task as a function of the different conditions. Average accuracy was between 70% and 80%, and there were no condition effects, all ps $> .122$, $0.45 < BF_{10} < 0.79$. Participants were asked to memorize six colors or orientations during the maintenance period of the main task, 70%–80% accuracy denoted that participants actually memorized about three interference items according to the classic working memory (WM) capacity estimate (Cowan, 2001).

Discussion

The results are consistent with the hypothesis that VWM adaptively anticipates interference. We find that memory of a feature (color or orientation) suffers more from interference, which is defined within the same dimension than from interference defined within a different dimension, but only when such interference is unanticipated. That is, color memory suffers more from color interference than from orientation interference when observers expect orientation interference, but not when they expect color interference. Likewise, orientation memory suffers more from orientation interference than from color interference, unless observers can expect such orientation interference. Thus, observers appear to protect their memory against anticipated interference within the same feature dimension.

EXPERIMENT 2

Although the pattern of results of Experiment 1 matched the predictions, performance for specifically orientation was quite low at close to 0.5 hit rate. This may have resulted in potential floor effects. In addition, this could prevent adequate memory decoding in the subsequent fMRI version of the experiment that we wished to run (see Experiment 3). In Experiment 2, we therefore sought to replicate the findings, while making the orientation memory test easier, by increasing the orientation difference.

Methods

Sixteen participants (12 women and 4 men with a mean age of 22.3 years) participated. The method was the same as in Experiment 1 except that now the test stimulus could carry a $\pm 30°$ orientation change, instead of a $\pm 15°$ orientation change. The research protocol was approved by the Scientific and Ethics Review Committee of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam.

Results

Primary Task Performance

The left part of Figure 2B shows the mean hit rate on the primary (grating) task, collapsed for color and orientation, as a function of whether interference was anticipated or not, and whether observers were then actually tested on the feature for which interference was anticipated or on the feature for which interference was not anticipated. The middle and right parts show the same data, but split up for anticipated color and anticipated orientation interference. We again concentrated on hit rates, whereas the average false alarm rates were 0.31 and 0.28 for anticipated color interference and anticipated orientation interference blocks, respectively. Moreover, the false alarm rate did not differ for anticipated interference (0.29) and unanticipated interference (0.29), $t(15) = .14$, $p = .893$, $BF_{10} = .26$.

We again observed a significant two-way interaction between Actual Interference and Tested Feature, $F(1, 15) =$

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11.07, $p = .005$, partial $\eta^2 = .87$. Moreover, adding the Specific Feature (color, orientation) as an additional factor to the ANOVA did not result in a three-way interaction, $F < 1$. Consistent with Experiment 1, planned comparisons revealed that when observers were tested on the feature for which interference was expected, performance did not suffer when observers indeed received interference on that feature, relative to when they received interference on the other feature, $t < 1$. In contrast, memory performance did suffer when observers were tested on the feature for which interference was unexpected, and they indeed also received interference on that feature, $t(15) = 3.56$, $p = .003$.

We performed the same analyses for each type of anticipated feature interference separately. When color interference was anticipated (Figure 2B, middle part), there was now no effect of Tested Feature, $F(1, 15) = 1.62$, $p = .222$, partial $\eta^2 = .1$, indicating that color and orientation memory was now of approximately equal difficulty. There was also no overall effect of Type of Actual Interference, $F(1, 15) = 2.03$, $p = .175$, partial $\eta^2 = .12$. Importantly, the two-way interaction was reliable, $F(1, 15) = 10.04$, $p = .006$, partial $\eta^2 = .4$. As in Experiment 1, orientation memory suffered from orientation interference relative to color interference, $t(15) = 3.74$, $p = .002$. In contrast, color memory did not suffer from color interference here, $t < 1$. The right part of Figure 2B shows the reverse pattern when orientation interference was anticipated. Here too, there was no main effect of tested feature, $F(1, 15) = 2.99$, $p = .1$, partial $\eta^2 = .17$, suggesting equal difficulty for color and orientation. There was a main effect for Interference, $F(1, 15) = 4.68$, $p = .047$, but this was further modulated by the two-way interaction, $F(1, 15) = 4.92$, $p = .042$, partial $\eta^2 = .25$. Planned follow-up comparisons revealed that, here, color memory suffered from color interference, relative to orientation interference, $t(15) = 2.59$, $p = .021$. In contrast, orientation memory did not suffer from orientation interference, $t < 1$.

Secondary Task Performance

Figure A1B shows performance on the secondary intervening task as a function of the different conditions. There were no condition effects, all $ps > .103$, $.26 < BF_{10} < .87$.

Here, orientation memory performance was on par with color memory performance. This did not change the crucial pattern of results, which was overall much the same as in Experiment 1. Memory for a feature suffered from unanticipated interference defined within the same dimension, compared with a different dimension. In contrast, anticipated interference had little effect. Experiment 2 then paved the way for Experiment 3, which sought to find neural evidence for flexible anticipation of interference.

EXPERIMENT 3

Our behavioral experiments indicate that observers protect their memory against anticipated interference within the same feature dimension. In Experiment 3, we sought to find signatures of such protection in the patterns of fMRI responses. Are visual memories represented differently when interference is expected, and if so, how do they differ?

A priori, there are a number of possibilities of how memories could be protected against interference. First, under what we will refer to as the strengthened activation account, it could enhance the pattern of activation associated with the threatened feature, so that it becomes more robust against the new input (e.g., Todd & Marois, 2004). Second, under what we will call the silent memory account, more passive storage mechanisms could be involved, enabling features to be maintained in patterns of connectivity rather than activity, for example, through synaptic plasticity (Lewis-Peacock et al., 2011; see the work of Olivers et al., 2011, for a review of the behavioral support). Such connectivity patterns might be more robust against interference than activity patterns (Mallett & Lewis-Peacock, 2019). Third, under what we refer to as a cortical transfer account, it is possible that other or additional brain areas are selectively being recruited for the threatened interference (Christophel, Iamshchinina, Yan, Allefeld, & Haynes, 2018), which are more robust against interference. Most notably, Xu and colleagues (Xu, 2018, 2020; Bettencourt & Xu, 2016) have argued that, in the face of interference, VWM relies primarily on representations in parts of the intraparietal sulcus (IPS), whereas early visual areas deal with the new sensory input. Naturally, none of these possibilities are mutually exclusive. Nor do these possibilities exclude even more, as yet unknown mechanisms.

To address these questions, we performed pattern classification analyses on fMRI activity patterns measured in early visual cortex and IPS. Both ROIs were mapped separately using visual field mapping and WM localizer tasks.

Methods

We aimed for the fMRI experiment to replicate the behavioral findings of Experiments 1 and 2, and therefore chose to match the statistical power and recruit another group of 16 participants (12 women and 4 men with a mean age of 21.4 years). The research protocol was approved by the Scientific and Ethics Review Committee of the University of Amsterdam (2016-EXT-7216).

Main Task

The procedure was the same as in Experiment 2 except for the following. The timing of events was changed slightly. At the beginning of each trial, a fixation cross was shown for 500 msec. The grating stimulus was then presented for 500 msec followed by a blank interval of 6500 msec. Then, the displays for the intervening task appeared, with 500 msec for the first display, a 500-msec delay, and then the second display for 500 msec, after which participants

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could respond during a 2500-msec interval. Afterward, the test stimulus was presented for 500 msec, which was either a gray grating (when probing orientation, 50% trials), or a filled colored disk of equal size as the grating stimulus (when probing color, 50% trials). In the first case, observers had to indicate whether it was of the same orientation as the memory item, and, in the second case, whether it was of the same color. The ITI was 10 sec, and the total duration for each trial was 22 sec.

The two interference anticipation conditions (anticipate color interference vs. anticipate orientation interference) were tested in different runs, in counterbalanced order, with each condition including six runs of 24 trials each. Within each run, 20 trials (83.3%) contained an intervening task carrying the anticipated feature, four trials (16.7%) contained an intervening task carrying the unanticipated feature, and these were randomly mixed.

Localizer Tasks

We adopted the procedures used previously to determine the superior IPS region, which has been shown to be involved in VWM storage (Bettencourt & Xu, 2016; Xu & Chun, 2006). For each trial, one, two, three, four, or six real-world objects were presented sequentially at the center of the gray screen followed by a short interval. Observers had to judge whether a probe object presented at the center had been shown in the original display(s). Memory materials were randomly chosen from 16 distinctive objects, with each subtending 5° × 5° of visual angle. Each trial lasted 6 sec, consisting of a fixation display (500 msec), a sample sequence including eight possible stimulus presentation slots (100 msec each, followed by 50-msec interval, for a total of 1,150 msec), a blank interval (1000 msec), a probe display (2000 msec), and a feedback display (1350 msec). We also had blank fixation trials (6 sec, i.e., set size was 0). Trial presentation order was pseudorandom and balanced for in a run. Participants completed two runs, with each run containing 72 trials (12 per set size).

To identify and delineate V1–V3, we performed a separate population receptive field mapping session, using a stimulus design and analysis procedures based on those from the work of van Es, Theeuwes, and Knapen (2018). We altered the stimulus to subtend up to 12 degrees of eccentricity. Subjects performed a single, simple change-detection task at fixation throughout this experiment, of which we acquired four repetitions of 317 sec each. Taking the resulting population-receptive field estimates, we visualized polar angle on the cortical surface for each observer and delineated the boundaries between the visual field maps of V1–V3 using pycortex (Gao, Huth, Lescroart, & Gallant, 2015).

Training Task for Multivoxel Pattern Analysis

To train the classifier on color and orientation, in this training task, on each trial, a grating stimulus with the same colors and orientations as in the main task was presented four times sequentially at the center of the screen, where each pattern was presented for 600 msec followed by a 1500-msec interval. Participants had to memorize both the color and orientation, and then to judge whether one of the grating stimuli had different color or orientation compared with the remaining three by pressing the corresponding keys. The ITI was 8.4 sec. In total, participants completed four runs of 16 trials each. The change happened in 50% of the trials.

fMRI Data Acquisition and Analysis

All MRI data were acquired on a Philips Achieva 3 T scanner (Philips Medical Systems), equipped with a 32-channel head coil. T1-weighted and T2-weighted images were acquired for each participant with isotropic resolution of 1 mm. Whole-brain EPIs were acquired in 44 transverse slices, with an isotropic voxel size of 2.7 mm (SMS factor 4, in-plane -SENSE- acceleration factor 1.5, 700-msec repetition time [TR], 30-msec echo time, 55° flip angle, 80 × 80 matrix, 216-mm field of view).

We used fMRIPrep (Esteban et al., 2019) to preprocess the functional scans. Based on the estimated susceptibility distortion, an unwarped BOLD reference was calculated for a more accurate coregistration with the anatomical reference. The BOLD reference was then coregistered to the T1-weighted images. All EPI images were slice-time-corrected, motion-corrected (within and between scans), and high-pass-filtered (three cycles per run).

Voxel Selection

To select voxels in the superior IPS ROI, we followed the analysis adopted in the study by Bettencourt and Xu (2016). MRI data from the superior IPS localizer task was entered in a parametric multiple regression analysis with the parametric modulation coefficient for each set size weighted by each participant's corresponding VWM capacity calculated using Cowan's *K* (Cowan, 2001). Superior IPS was identified as a region showing significant increases in activation with increasing memory load, intersected with the superior parietal ROI generated by Freesurfer's automatic parcellation (following the work of Bettencourt & Xu, 2016; Xu & Chun, 2006). This resulted in an ROI of 195 (±110) voxels, on average, across all participants. Participants were asked to memorize six colors or orientation during the maintenance period of the main task; 70%–80% accuracy denoted that participants actually memorized about three interference items according to the classic capacity estimate (Cowan, 2001).

For V1–V3, we selected the top 120 voxels in each ROI (i.e., V1, V2, and V3) that were the most active during the simple memory task (i.e., the superior IPS localizer task). This voxel selection procedure was predetermined based on earlier studies (Bettencourt & Xu, 2016; Harrison & Tong, 2009; Kamitani & Tong, 2005). These voxels were then combined together to form a single ROI for V1–V3.

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Multivoxel Pattern Analysis

Multivoxel pattern analysis (MVPA) was used in the present experiment to decode the color and orientation of the grating stimulus in both occipital and parietal brain regions. A linear support vector machine was trained by using the training data set from the above-described independent training session, and then was used to classify the orientation and the color of the grating stimulus on each trial from the main experiment's test data set, where classification of color and classification of orientation were conducted separately, so chance level was 50%. For each ROI, training the classifier was done on the average percentage signal change in a time window from 5.6 to 11.2 sec (TRs 8–16; from trial onset in the training task), as we deemed this time window to most likely reflect sustained maintenance activity (see Figure A4 for BOLD response and MVPA decoding accuracy collapsed across features in the training task, respectively). We adopted a similar method as in a previous study (Harrison & Tong, 2009) to select the time window for the test data set, that is, 3.5–7 sec (TRs 5–10; see Figure A3). We selected the first time point (3.5 sec) to account for the hemodynamic lag of the BOLD response, given that, at this time, the BOLD response started rising after presenting the grating stimulus (i.e., the magnitude of BOLD signal was significantly larger than 0 after this time point in both superior IPS and V1–V3, all ps $< .001$). The end time point (7 sec) was selected in a conservative way to avoid any contamination from the interference task, which was presented at a time of 7.5 sec. For completeness, we will also present the full time series. As a check following a reviewer's suggestion, we also performed the same analyses on normalized data in which we z-scored the data points per TR before submitting them to the classifier. This yielded the same pattern of findings. The analysis was programmed in Python using the *Scikit-learn* package (www.scikit-learn.org).

Results

Behavioral Results

Primary task performance. The left part of Figure 2C shows the mean accuracy on the primary (grating) task, collapsed for color and orientation, as a function of whether interference was anticipated or not, and whether observers were then actually tested on the feature for which interference was anticipated or on the feature for which interference was not anticipated. The middle and right parts show the same data, but split up for anticipated color and anticipated orientation interference. We again observed a significant two-way interaction between actual interference and feature tested, $F(1, 15) = 26.26, p < .001$, partial $\eta^2 = .64$. Moreover, adding the specific feature (color, orientation) as an additional factor did not result in a three-way interaction, $F < 1$. Consistent with the previous experiments, planned comparisons revealed that when observers were tested on the feature for which interference was expected, performance did not suffer reliably when observers indeed received interference on that feature, relative to when they received interference on the other feature, $t(15) = 1.89, p = .078$. In contrast, memory performance did suffer reliably when observers were tested on the feature for which interference was unexpected, and they indeed also received interference on that feature, $t(15) = 4.34, p < .001$.

When using hit rates and false alarm rates as the measurement separately, such protection for anticipated feature still held, both ps $> .059$; in contrast, memory performance did suffer reliably when observers were tested on the feature for which interference was unexpected, and they indeed also received interference on that feature, both ps $< .036$ (see Figure A2).

We performed the same analyses for each type of anticipated feature interference separately. When color interference was anticipated (Figure 2C, middle part), there was a main effect for tested feature, $F(1, 15) = 5.95, p = .028$, partial $\eta^2 = .28$, but there was no overall effect of type of actual interference, $F < 1$. Performance was slightly better for testing orientation than color. Importantly, the two-way interaction was reliable, $F(1, 15) = 8.42, p = .011$, partial $\eta^2 = .36$. As in Experiments 1 and 2, orientation memory suffered from orientation interference relative to color interference, $t(15) = 3.19, p = .006$. In contrast, color memory did not suffer from color interference here, $t(15) = 1.7, p = .109$. The right part of Figure 2C shows the reverse pattern when orientation interference was anticipated. Here too, there was a main effect of tested feature, $F(1, 15) = 33.21, p < .001$, partial $\eta^2 = .69$, but not for actual interference type, $F(1, 15) = 2.29, p = .151$, partial $\eta^2 = .13$. This was further modulated by the two-way interaction, $F(1, 15) = 10.46, p = .006$, partial $\eta^2 = .41$. Planned follow-up comparisons revealed that, here, color memory suffered from color interference, relative to orientation interference, $t(15) = 2.27, p = .039$. In contrast, orientation memory did not suffer from orientation interference, $t(15) = 1.45, p = .169$.

Secondary task performance. Figure A1C shows performance on the secondary, intervening task as a function of the different conditions. There were no condition effects, both ps $> .49$, $0.26 < BF_{10} < 0.32$.

fMRI Decoding Results

Figure 3A shows support vector machine decoding accuracy for the grating stimulus during the delay before the interfering task (the time window of interest) in both early visual cortex (V1–V3; left part) and superior IPS (right part). Interestingly, in V1–V3, when observers anticipated color interference, decoding accuracy for color was above chance, $t(15) = 2.42, p = .029$, whereas we observed no such above-chance decoding for orientation, $t(15) = 0.17$, $p = .867$. Conversely, when observers anticipated orientation interference, decoding accuracy for orientation was

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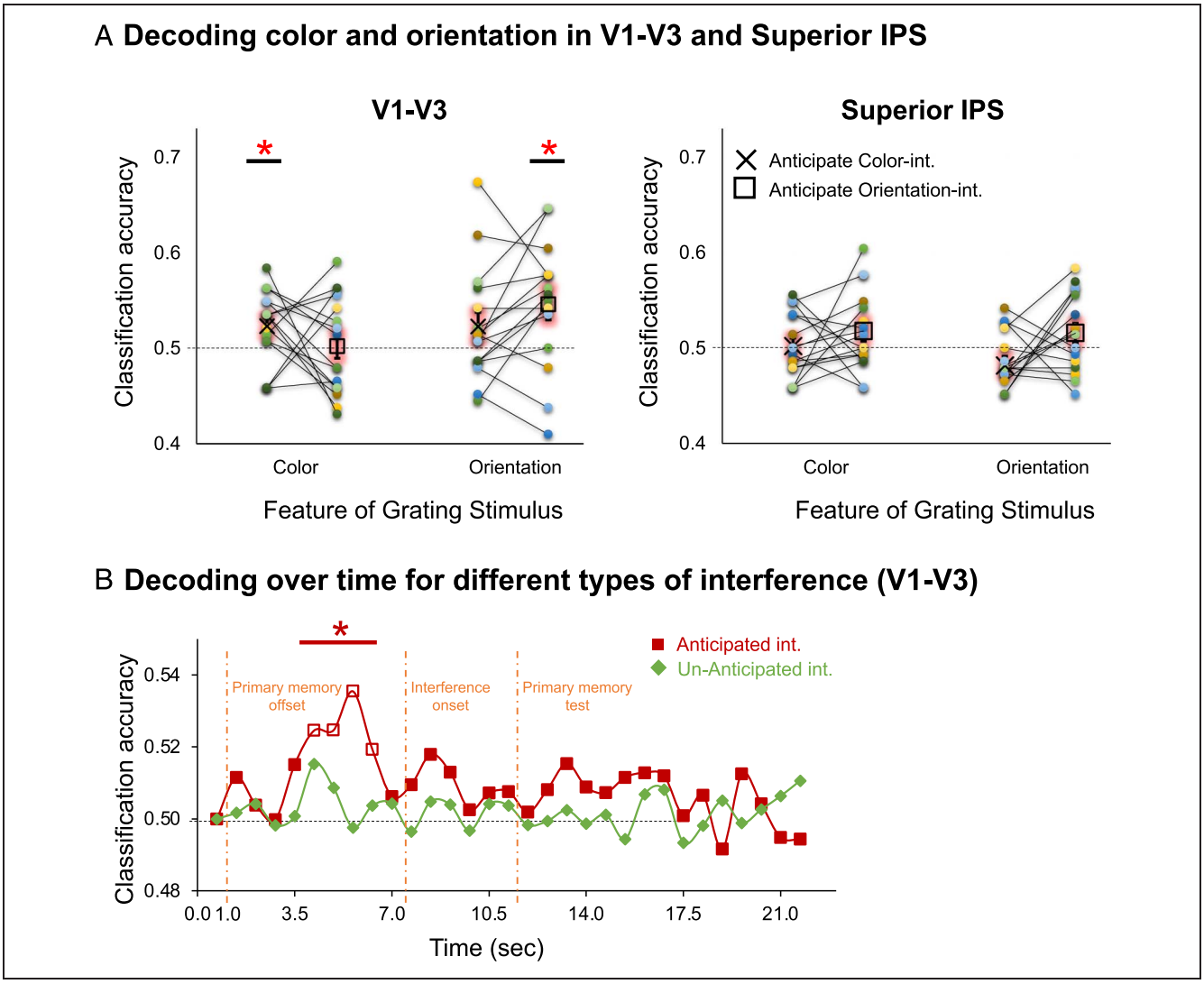


Figure 3. fMRI decoding results. (A) Decoding accuracy for the TR 5–10 epoch for color and orientation features as a function of which feature is anticipated to suffer from interference. The asterisks signal the significant difference relative to chance level. (B) It shows temporal pattern of decoding accuracy for anticipated and unanticipated interference conditions. The open symbols during the initial delay period before interference represent significant differences relative to chance level. All error bars denote ±1 *SEM*.

above chance, $t(15) = 2.83$, $p = .013$, but not for color, $t(15) = 1.51$, $p = .152$. The same analysis on superior IPS yielded no above-chance decoding of feature information, regardless of which type of interference was anticipated, all ps $> .08$ (see Figure 3A left part).[1]

Figure 3B shows the full time series of classification performance in V1–V3, collapsed for color and orientation (see Figure A5 for the decoding accuracy of each of the features separately). To further explore when the effect shown in Figure 3A occurred, we conducted a further analysis to decode features over time. As can be seen in Figure 3B, only when a feature was anticipated to be interfered with did decoding accuracy rise above chance, specifically from 3.2 sec ($TR = 6$) to 6.3 sec ($TR = 9$) after stimulus offset of the grating stimulus, all ps $< .04$ (uncorrected). After false discovery rate correction for the first 10 time points up to the interference, decoding accuracy rose above chance from 3.2 sec ($TR = 6$) to 5.6 sec ($TR = 8$). Figure A3 in the appendix presents the univariate fMRI response in each of the ROIs. This yielded no condition differences.

Discussion

Both the behavioral and the imaging data support the idea that observers preemptively adapt their visual memory to the type of anticipated interference. The behavioral pattern mimics that of Experiments 1 and 2, with stronger interference from unanticipated secondary stimulation. This again suggests that features for which interference is expected are represented more robustly. The brain activity pattern confirms this idea, as it revealed a shift in which feature is represented most strongly in early visual cortex, depending on which type of interference is anticipated. That is, above-chance color classification emerged when color interference was expected, whereas orientation information emerged when orientation interference

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was expected. As such, the imaging data support a strengthened activation account, under which the cognitive system protects visual memories by enhancing their activity patterns. However, we point out that although we provide positive evidence for such an account, it does not exclude other accounts in terms of connectivity or cortical transfer. With regard to the latter, however, we found no evidence that IPS serves as the backup site for to-be-shielded memories. We will return to this in the General Discussion section.

Note that overall, classification performance with regard to the stimulus features was rather weak, with decoding accuracy for the nonthreatened feature hardly rising above chance levels. We are unsure why our experiment was less sensitive on this aspect than similar VWM experiments in the literature. One factor is that fMRI studies of VWM have mostly used orientation, whereas here, we used both color and orientation. As Figure A5 shows, especially the decoding of color was suboptimal when no color interference was expected. However, successful MVPA decoding of color has been reported in the past (e.g., Serences, Ester, Vogel, & Awh, 2009, who focused on V1 only). What may have been less optimal here is that observers were asked to memorize both the color and the orientation for each stimulus. Having to memorize a conjunction may have either weakened or transformed the representation for each of the constituent features, resulting in reduced decoding performance (Fougnie, Asplund, & Marois, 2010; Seymour, Clifford, Logothetis, & Bartels, 2009, 2010).

GENERAL DISCUSSION

Three experiments provided evidence for an adaptive strengthening of features stored in VWM in anticipation of interference. The results showed that memory for color or orientation suffered from interference caused by a secondary task for which the stimuli defined within the same dimension, unless this interference was predicted. Experiment 3 in addition provided evidence that threatened features could be successfully decoded from fMRI-related activity, whereas features for which interference was less likely could not be decoded.

Our imaging data cannot confirm the idea that specifically IPS serves as a protective VWM buffer. Bettencourt and Xu (2016) raised the hypothesis that when interference is expected, observers may temporarily withdraw VWM representations from visual cortex and rely on more robust IPS-based representations instead (see Xu, 2020, for the most recent advocacy of this idea). Contrary to this, we observed a transient enhancement of the threatened feature in visual cortex, whereas IPS revealed no evidence for the memorized features here. We are careful to point out that this does not mean that IPS plays no role in VWM, as there is a vast literature suggesting that it is a central part of VWM functioning. However, as Xu (2020) point out, it may be representing control processes more than content. That said, we essentially report a null finding here, and any interpretation with regard to the role of IPS in our experiment should be made with care.

Working memory serves to maintain not only the current task goal but also prospective goals for future tasks (Lewis-Peacock et al., 2011; Olivers et al., 2011). When serving for future tasks, as shown in this study, the memory is surviving an intervening stimulus or task, which is seen as one defining characteristic of working memory (Engle, Tuholski, Laughlin, & Conway, 1999; Miller, Erickson, & Desimone, 1996). Here, we showed an adaptive strengthening of features stored in VWM in anticipation of within-dimension interference. When the distractors (colors) were in the same feature dimension of one of the original memory target's features (color), people could strengthen their memory for such feature when they expected the interference from the same dimension. This is consistent with data from recent visual search studies, showing that people flexibly adjust the target features that they are looking for depending on the expected interference from distractors (Boettcher, van Ede, & Nobre, 2020; Lee & Geng, 2020; Geng & Witkowski, 2019).

An important question is how this robustness is achieved and at which processing stage. We speculate that here, it happened during memory encoding or consolidation, as our imaging data suggest that this process is quite an early and transient modulation. One possibility is then an actual enhancement of the memory, expressed as the enhanced likelihood and/or precision of encoding. Behaviorally, with our current design, we cannot determine whether interference anticipation led to improved memory, as there was no condition without interference to compare to. In a comparison that comes closest, we found that memory for a feature that had encountered anticipated within-dimension interference was no better than memory for the same feature but which had encountered interference from a different dimension. For example, memory performance for color when color interference was expected and received was no different from memory performance for color when orientation interference was anticipated and received. Although this could be interpreted as a lack of enhancement, it could also be interpreted as the enhancement being just strong enough to overcome the interference. A second way of protecting against interference is by inhibiting the interfering stimulus. Recently, Gresch et al. (2021) investigated this option. They presented an interfering stimulus during the delay of a VWM task and found that interference was reduced when the time of onset of the interference was predictable compared to when it was variable. They further found that this advantage for a predictable interference was the same regardless of whether observers had to actively process the interfering stimulus (i.e., for a secondary task, and thus could not inhibit it) or could just ignore it. This latter finding suggests that the shielding of the memory does not occur through suppression of the interfering stimulus. Note that also in our experiment, observers have to actively process the interfering stimuli for the additional task they had to perform. Hence it is unlikely that inhibition played a role in

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protecting the memory against the interference. Third, shielding may occur through recoding the memory into "accessory," activity-silent connectivity patterns that may allow for more durable storage while people perform an intervening task (e.g., van Loon et al., 2018; Wolff, Jochim, Akyürek, & Stokes, 2017; van Moorselaar, Theeuwes, & Olivers, 2016; Lewis-Peacock et al., 2011). Note that such activity-silent patterns are difficult to pick up using fMRI, which may have contributed to the rather weak and transient decoding results in our study. Note further that the various options are not mutually exclusive. Both enhancement and recoding may be recruited to protect a memory. In fact, the initial enhancement may be part of the transition to a more durably engrained silent memory trace. Finally, another possibility is that the representation is strengthened after, rather than during encoding. Future studies will have to distinguish between these possibilities.

To maximize the potential for interference, we opted for an additional task in which observers had to attend to and memorize the intervening stimuli. One may ask whether the additional task is necessary to trigger protective mechanisms, or whether the presentation of the stimuli as such is sufficient. In addition, when a task is necessary, does it have to be a memory task or would other tasks also suffice? Although these are relevant questions, the design of our studies precludes an answer. However, in two previous studies (Wang et al., 2018, 2019) we used a similar intervening task to test whether VWM representations become vulnerable to interference. This was then compared with a passive viewing condition in which the stimuli were presented, but there was no associated task. We found interference under the first scenario, but not the second. This is consistent with other findings indicating that an active task at least strengthens, or increases the likelihood, of interference (e.g., see the works of Gresch et al., 2021; Wang et al., 2018; Clapp & Gazzaley, 2012, for evidence). However, in our earlier study, the intervening stimuli were not directly related to the main memorandum. That is, whereas observers had to remember a color or orientation for the primary task, the secondary task involved memorizing letters. Thus, it remains to be tested whether protective mechanisms are necessary for feature-specific stimulus interference.

In conclusion, we find that robust coding of stimulus features in VWM is not obligatory. Instead, we report more evidence for the flexibility of VWM, as it strengthens memories for which it anticipates the highest risk of interference, while it leaves memories that are less at risk and more vulnerable to interference.

APPENDIX A

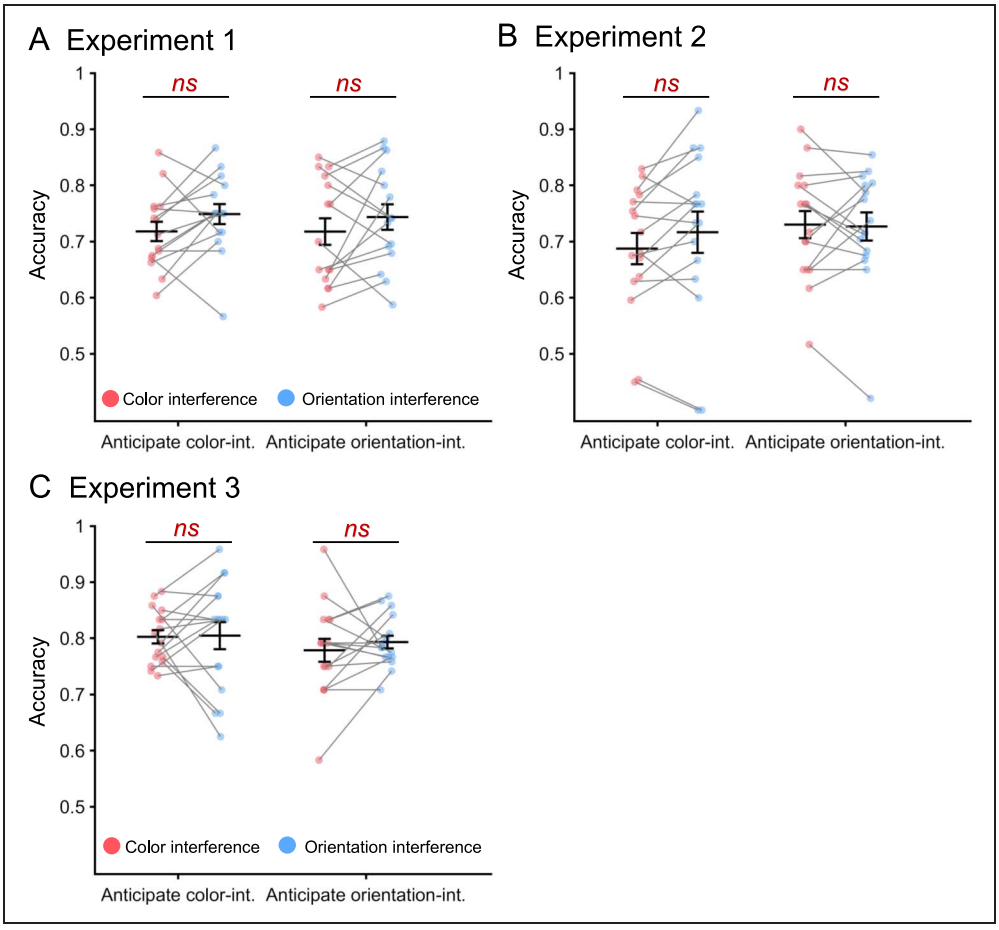


Figure A1. Memory performance on the secondary, intervening task. Error bars denote ±1 *SEM* across participants.

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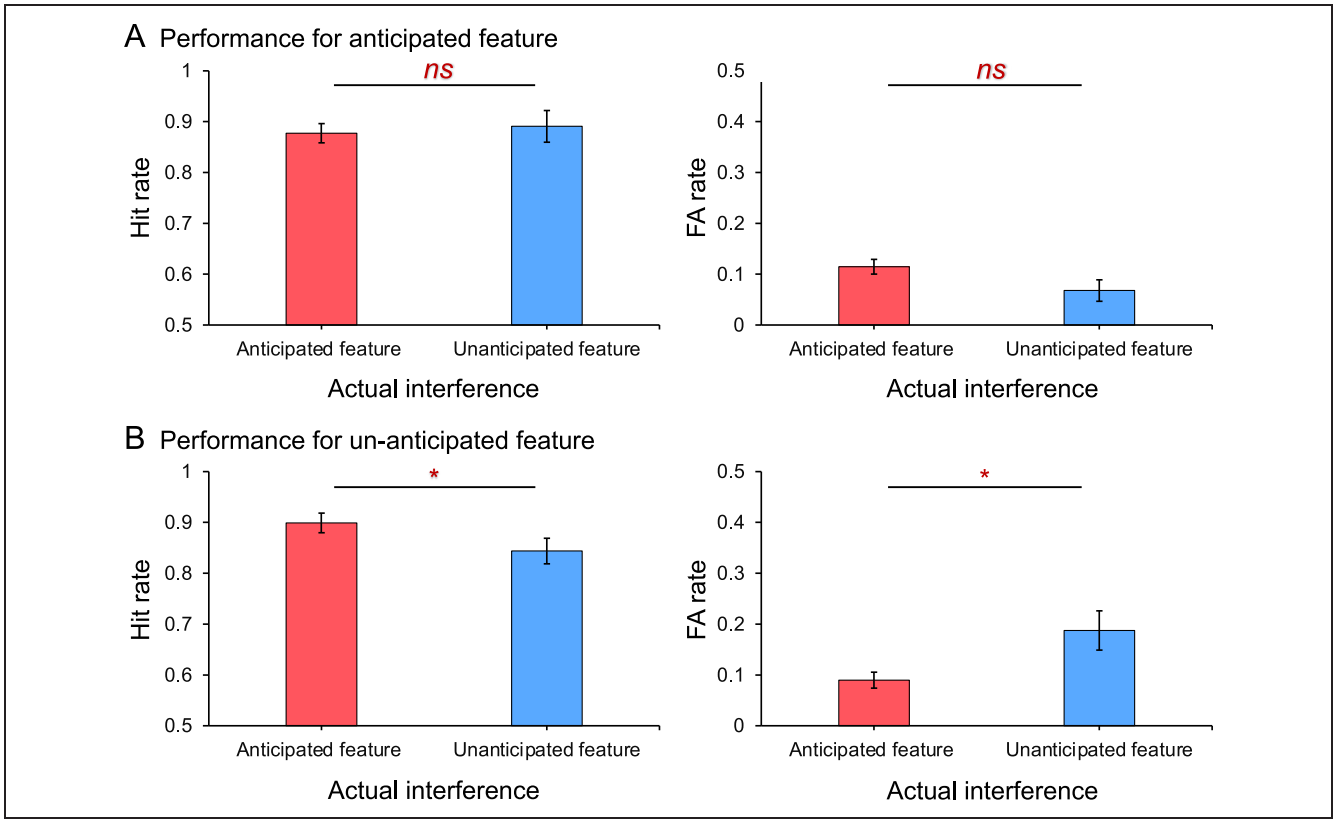


Figure A2. Hit and false alarm rates in Experiment 3. Error bars denote ±1 *SEM* across participants.

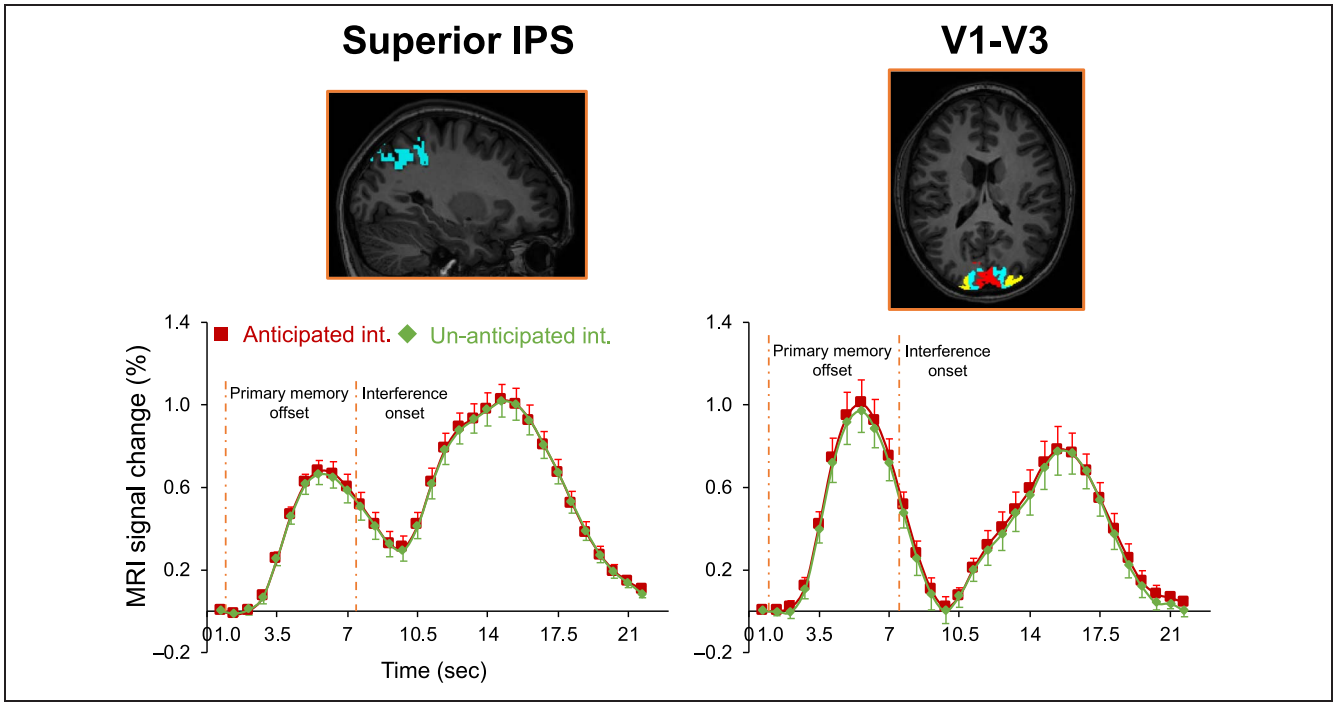


Figure A3. fMRI BOLD response for different conditions in the main task. Gray shaded region marks the time window for extracting the test data in MVPA analysis. Error bars denote ±1 *SEM*.

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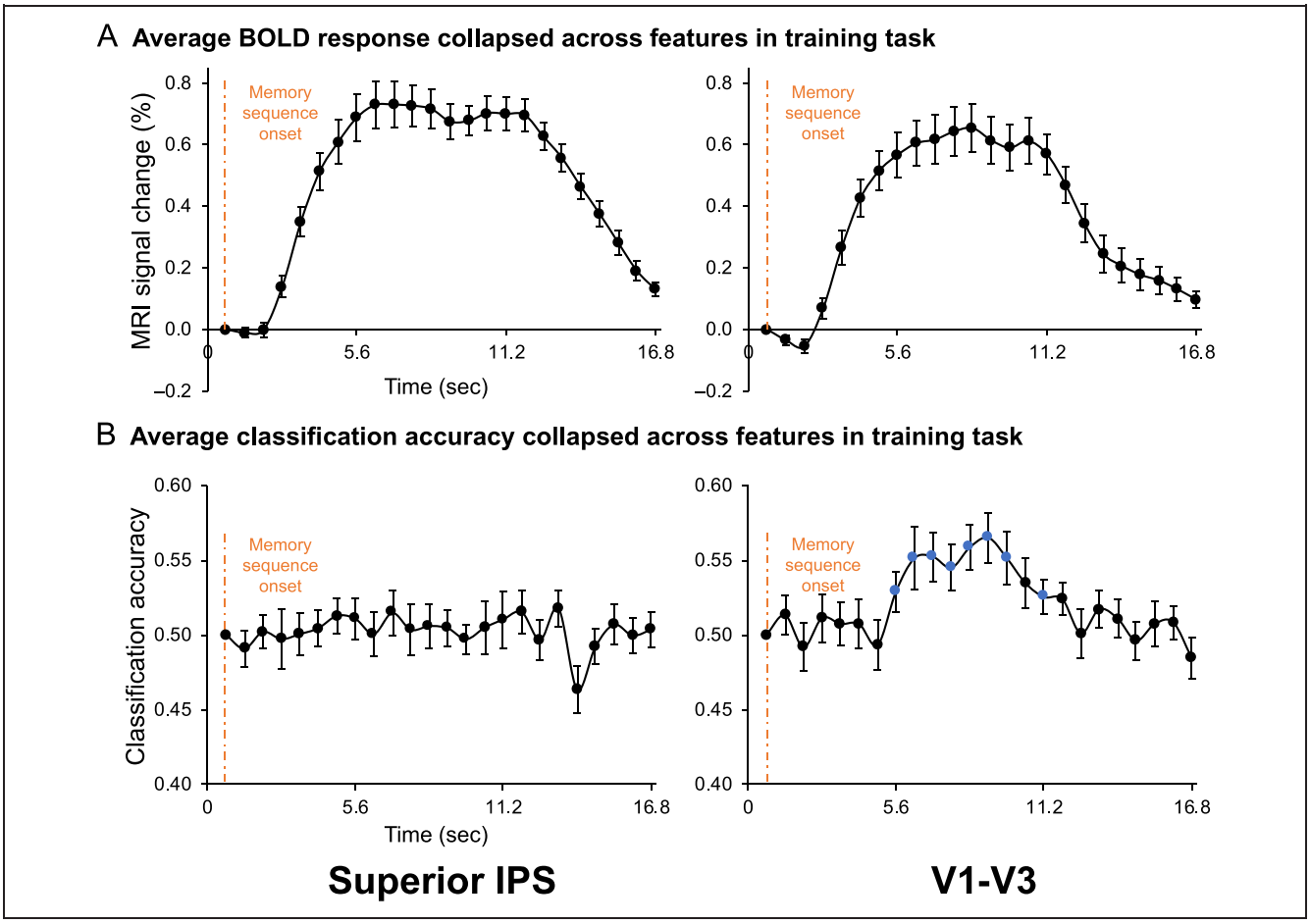


Figure A4. (A) fMRI BOLD response and (B) classification accuracy collapsed across features in the training task. Gray shaded region marks the time window for extracting the training data in MVPA analysis. Blue dots indicate the above-chance decoding. Error bars denote ±1 *SEM*.

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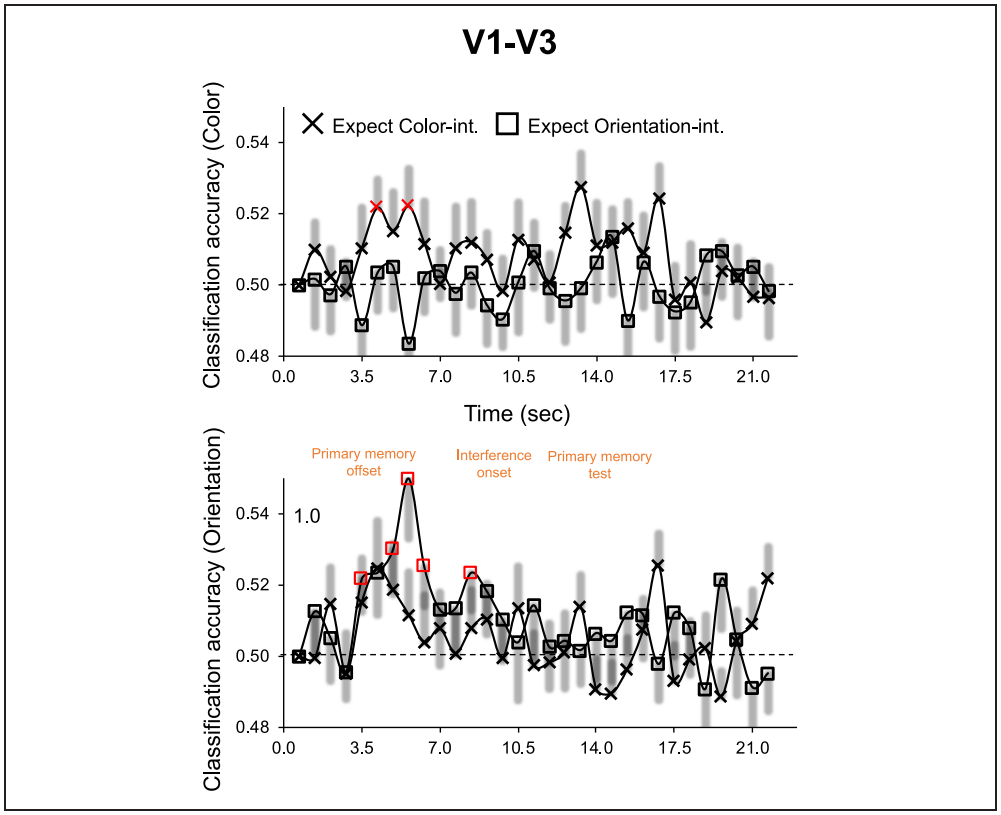


Figure A5. Decoding accuracy over time for the two different features, color (top) and orientation (bottom). Red markers indicate a significant difference relative to chance level uncorrected. Error bars denote ±1 *SEM*.

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Data Availability Statement

The raw data and procedure for all experiments are available upon request.

Author Contributions

Benchi Wang: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Visualization; Writing—original draft; Writing—review & editing. Chris Olivers: Conceptualization; Funding acquisition; Project administration; Supervision; Visualization; Writing—original draft; Writing—review & editing. Tomas Knapen: Data curation; Formal Analysis; Methodology; Resources; Software; Visualization; Writing—original draft; Writing—review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Note

1. We performed the same analyses on normalized data (see Methods section). This yielded the same pattern of results: In V1–V3, when observers anticipated color interference, decoding accuracy for color was above chance, $t(15) = 2.58$, $p = .021$, whereas we observed no such above-chance decoding

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for orientation, $t(15) = 0.21$, $p = .84$. Conversely, when observers anticipated orientation interference, decoding accuracy for orientation was above chance, $t(15) = 2.35$, $p = .033$, but not for color, $t(15) = 1.34$, $p = .20$. The same analysis on superior IPS again yielded no above-chance decoding of feature information, regardless of which type of interference was anticipated, all ps $> .08$.

REFERENCES

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839. https://doi.org/10.1038/nrn1201, PubMed: 14523382

Bae, G.-Y., & Luck, S. J. (2019). What happens to an individual visual working memory representation when it is interrupted? *British Journal of Psychology*, *110*, 268–287. https://doi.org/10.1111/bjop.12339, PubMed: 30069870

Bettencourt, K. C., & Xu, Y. (2016). Decoding the content of visual short-term memory under distraction in occipital and parietal areas. *Nature Neuroscience*, *19*, 150–157. https://doi.org/10.1038/nn.4174, PubMed: 26595654

Boettcher, S. E. P., van Ede, F., & Nobre, A. C. (2020). Functional biases in attentional templates from associative memory. *Journal of Vision*, *20*, 7. https://doi.org/10.1167/jov.20.13.7, PubMed: 33296459

Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J.-D. (2018). Cortical specialization for attended versus unattended working memory. *Nature Neuroscience*, *4*, 494–496. https://doi.org/10.1038/s41593-018-0094-4, PubMed: 29507410

Clapp, W. C., & Gazzaley, A. (2012). Distinct mechanisms for the impact of distraction and interruption on working memory in aging. *Neurobiology of Aging*, *33*, 134–148. https://doi.org/10.1016/j.neurobiolaging.2010.01.012, PubMed: 20144492

Clapp, W. C., Rubens, M. T., & Gazzaley, A. (2010). Mechanisms of working memory disruption by external interference. *Cerebral Cortex*, *20*, 859–872. https://doi.org/10.1093/cercor/bhp150, PubMed: 19648173

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*, 87–114. https://doi.org/10.1017/S0140525X01003922, PubMed: 11515286

de Vries, I. E. J., van Driel, J., Karacaoglu, M., & Olivers, C. N. L. (2018). Priority switches in visual working memory are supported by frontal delta and posterior alpha interactions. *Cerebral Cortex*, *28*, 4090–4104. https://doi.org/10.1093/cercor/bhy223, PubMed: 30215669

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. (1999). Working memory, short-term memory, and general fluid intelligence: A latent-variable approach. *Journal of Experimental Psychology: General*, *128*, 309–331. https://doi.org/10.1037/0096-3445.128.3.309, PubMed: 10513398

Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., et al. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, *16*, 111–116. https://doi.org/10.1038/s41592-018-0235-4, PubMed: 30532080

Feldmann-Wüstefeld, T., & Vogel, E. K. (2019). Neural evidence for the contribution of active suppression during working memory filtering. *Cerebral Cortex*, *29*, 529–543. https://doi.org/10.1093/cercor/bhx336, PubMed: 29365078

Fougnie, D., Asplund, C. L., & Marois, R. (2010). What are the units of storage in visual working memory? *Journal of Vision*, *10*, 27. https://doi.org/10.1167/10.12.27, PubMed: 21047759

Fougnie, D., & Marois, R. (2009). Attentive tracking disrupts feature binding in visual working memory. *Visual Cognition*, *17*, 48–66. https://doi.org/10.1080/13506280802281337, PubMed: 19609460

Gao, J. S., Huth, A. G., Lescroart, M. D., & Gallant, J. L. (2015). Pycortex: An interactive surface visualizer for fMRI. *Frontiers in Neuroinformatics*, *9*, 23. https://doi.org/10.3389/fninf.2015.00023, PubMed: 26483666

Geng, J. J., & Witkowski, P. (2019). Template-to-distractor distinctiveness regulates visual search efficiency. *Current Opinion in Psychology*, *29*, 119–125. https://doi.org/10.1016/j.copsyc.2019.01.003, PubMed: 30743200

Gresch, D., Boettcher, S. E. P., van Ede, F., & Nobre, A. C. (2021). Shielding working-memory representations from temporally predictable external interference. *Cognition*, *217*, 104915. https://doi.org/10.1016/j.cognition.2021.104915, PubMed: 34600356

Hakim, N., Feldmann-Wüstefeld, T., Awh, E., & Vogel, E. K. (2021). Controlling the flow of distracting information in working memory. *Cerebral Cortex*, *31*, 3323–3337. https://doi.org/10.1093/cercor/bhab013, PubMed: 33675357

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*, 632–635. https://doi.org/10.1038/nature07832, PubMed: 19225460

Hollingworth, A., & Maxcey-Richard, A. M. (2013). Selective maintenance in visual working memory does not require sustained visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *39*, 1047–1058. https://doi.org/10.1037/a0030238, PubMed: 23067118

Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, *8*, 679–685. https://doi.org/10.1038/nn1444, PubMed: 15852014

Lee, J., & Geng, J. J. (2020). Flexible weighting of target features based on distractor context. *Attention, Perception, & Psychophysics*, *82*, 739–751. https://doi.org/10.3758/s13414-019-01910-5, PubMed: 31741317

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2011). Neural evidence for a distinction between short-term memory and the focus of attention. *Journal of Cognitive Neuroscience*, *24*, 61–79. https://doi.org/10.1162/jocn_a_00140, PubMed: 21955164

Mallett, R., & Lewis-Peacock, J. A. (2019). Working memory prioritization impacts neural recovery from distraction. *Cortex*, *121*, 225–238. https://doi.org/10.1016/j.cortex.2019.08.019, PubMed: 31629945

McNab, F., & Klingberg, T. (2008). Prefrontal cortex and basal ganglia control access to working memory. *Nature Neuroscience*, *11*, 103–107. https://doi.org/10.1038/nn2024, PubMed: 18066057

Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience*, *16*, 5154–5167. https://doi.org/10.1523/JNEUROSCI.16-16-05154.1996, PubMed: 8756444

Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, *15*, 327–334. https://doi.org/10.1016/j.tics.2011.05.004, PubMed: 21665518

Peirce, J. W. (2007). PsychoPy—Psychophysics software in python. *Journal of Neuroscience Methods*, *162*, 8–13. https://doi.org/10.1016/j.jneumeth.2006.11.017, PubMed: 17254636

Postle, B. R., D'Esposito, M., & Corkin, S. (2005). Effects of verbal and nonverbal interference on spatial and object visual working memory. *Memory & Cognition*, *33*, 203–212. https://doi.org/10.3758/BF03195309, PubMed: 16028575

Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of sensory and mnemonic information in human visual cortex. *Nature Neuroscience*,

Downloaded from http://direct.mit.edu/jocn/article-pdf/34/7/1148/2028516/jocn_a_01853.pdf by VU Amsterdam user on 22 September 2022

22, 1336–1344. https://doi.org/10.1038/s41593-019-0428-x, PubMed: 31263205
Rerko, L., Souza, A. S., & Oberauer, K. (2014). Retro-cue benefits in working memory without sustained focal attention. *Memory & Cognition*, *42*, 712–728. https://doi.org/10.3758/s13421-013-0392-8, PubMed: 24442551
Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science*, *20*, 207–214. https://doi.org/10.1111/j.1467-9280.2009.02276.x, PubMed: 19170936
Seymour, K., Clifford, C. W. G., Logothetis, N. K., & Bartels, A. (2009). The coding of color, motion, and their conjunction in the human visual cortex. *Current Biology*, *19*, 177–183. https://doi.org/10.1016/j.cub.2008.12.050, PubMed: 19185496
Seymour, K., Clifford, C. W. G., Logothetis, N. K., & Bartels, A. (2010). Coding and binding of color and form in visual cortex. *Cerebral Cortex*, *20*, 1946–1954. https://doi.org/10.1093/cercor/bhp265, PubMed: 20019147
Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics*, *78*, 1839–1860. https://doi.org/10.3758/s13414-016-1108-5, PubMed: 27098647
Souza, A. S., Rerko, L., & Oberauer, K. (2016). Getting more from visual working memory: Retro-cues enhance retrieval and protect from visual interference. *Journal of Experimental Psychology: Human Perception and Performance*, *42*, 890–910. https://doi.org/10.1037/xhp0000192, PubMed: 26752731
Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*, 751–754. https://doi.org/10.1038/nature02466, PubMed: 15085133
van Es, D. M., Theeuwes, J., & Knapen, T. (2018). Spatial sampling in human visual cortex is modulated by both spatial and feature-based attention. *eLife*, *7*, e36928. https://doi.org/10.7554/eLife.36928, PubMed: 30526848
van Loon, A. M., Olmos-Solis, K., Fahrenfort, J. J., & Olivers, C. N. (2018). Current and future goals are represented in opposite patterns in object-selective cortex. *eLife*, *7*, e38677. https://doi.org/10.7554/eLife.38677, PubMed: 30394873
van Moorselaar, D., Foster, J. J., Sutterer, D. W., Theeuwes, J., Olivers, C. N. L., & Awh, E. (2017). Spatially selective alpha oscillations reveal moment-by-moment trade-offs between working memory and attention. *Journal of Cognitive Neuroscience*, *30*, 256–266. https://doi.org/10.1162/jocn_a_01198, PubMed: 29040014
van Moorselaar, D., Theeuwes, J., & Olivers, C. N. L. (2016). Learning changes the attentional status of prospective memories. *Psychonomic Bulletin & Review*, *23*, 1483–1490. https://doi.org/10.3758/s13423-016-1008-7, PubMed: 26892228
Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1436–1451. https://doi.org/10.1037/0096-1523.32.6.1436, PubMed: 17154783
Wang, B., Theeuwes, J., & Olivers, C. N. L. (2018). When shorter delays lead to worse memories: Task disruption makes visual working memory temporarily vulnerable to test interference. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *44*, 722–733. https://doi.org/10.1037/xlm0000468, PubMed: 29094991
Wang, B., Theeuwes, J., & Olivers, C. N. L. (2019). Momentary, offset-triggered dual-task interference in visual working memory. *Journal of Cognition*, *2*, 38. https://doi.org/10.5334/joc.84
Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*, 864–871. https://doi.org/10.1038/nn.4546, PubMed: 28414333
Xu, Y. (2018). Sensory cortex is nonessential in working memory storage. *Trends in Cognitive Sciences*, *22*, 192–193. https://doi.org/10.1016/j.tics.2017.12.008, PubMed: 29482822
Xu, Y. (2020). Revisit once more the sensory storage account of visual working memory. *Visual Cognition*, *28*, 433–446. https://doi.org/10.1080/13506285.2020.1818659, PubMed: 33841024
Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*, 91–95. https://doi.org/10.1038/nature04262, PubMed: 16382240

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