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# The relationship between visual working memory and attention: retention of precise colour information in the absence of effects on perceptual selection

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We examined the conditions under which a feature value in visual working memory (VWM) recruits visual attention to matching stimuli. Previous work has suggested that VWM supports two qualitatively different states of representation: an active state that interacts with perceptual selection and a passive (or accessory) state that does not. An alternative hypothesis is that VWM supports a single form of representation, with the precision of feature memory controlling whether or not the representation interacts with perceptual selection. The results of three experiments supported the dual-state hypothesis. We established conditions under which participants retained a relatively precise representation of a particular colour. If the colour was immediately task relevant, it reliably recruited attention to matching stimuli. However, if the colour was not immediately task relevant, it failed to interact with perceptual selection. Feature maintenance in VWM is not necessarily equivalent with feature-based attentional selection.

## 1. Introduction

Robust interactions exist between human systems of visual working memory (VWM) and visual attention. Visual attention influences encoding into VWM [1] and has been proposed to play a role in selective maintenance within VWM [2,3]. VWM content also biases attentional orienting towards matching objects in the visual field [4–6]. Given these close interactions—and the fact that both visual attention and VWM are inherently selective systems with limited capacity—several researchers have proposed that they are equivalent [7–12]. VWM may simply be visual attention oriented to the representations of previously visible stimuli [10–12].

Despite these claims, there is substantial evidence that visual attention and VWM are distinct systems that can be dissociated: it is possible to maintain one set of objects in VWM, while attending perceptually to different objects and locations. Rensink [9] argued that change blindness is caused by the fact that VWM is limited to currently attended objects, but several studies have demonstrated robust VWM retention even as visual attention is directed to a different set of objects [13]. Wheeler & Treisman [14] argued that feature binding in VWM requires sustained visual attention, but robust feature binding is observed under conditions that preclude sustained attention [15,16]. Finally, Griffin & Nobre [2] argued that selective maintenance of task-relevant objects in VWM depends on visual attention, but, again, robust prioritization is observed in the absence of sustained attention [17,18].

In this study, we examined the relationship between visual attention and VWM in the domain of attentional guidance to memory-matching stimuli. Several studies have indicated that this relationship is obligatory, with memory-matching stimuli recruiting attention automatically [6]. In this type of experiment, participants see a memory stimulus at the beginning of a trial, such as a colour patch, and maintain this information in VWM for a memory test. During the retention interval, they complete a visual search task that does or does not contain a

distractor with a task-irrelevant feature matching the remembered object. Despite the fact that a matching object is never the target, search is slower in the presence of a memory-matching distractor, indicating capture. Such results could be interpreted as demonstrating equivalence between VWM and feature-based attentional selection; feature-based attention may be nothing more than the maintenance of particular feature values in VWM. However, other studies have failed to observe capture by memory-matching stimuli [19,20], indicating that under some circumstances, VWM maintenance can be dissociated from feature-based perceptual selection.

To resolve the discrepancy among studies, Olivers *et al.* [21] proposed that there are two different states of representation in VWM with respect to perceptual selection: an *active* state that interacts with the sensory processing of visual stimuli and influences perceptual selection, serving as an attentional template; and an *accessory* state that does not involve direct sensory interaction and does not influence perceptual selection. This framework is consistent with theories of working memory that distinguish between items that are and are not within the 'current focus of attention' [8,22], where 'current focus of attention' refers to a state that is particularly accessible for use within and control over the current task.

Olivers *et al.* [21] cited two main studies as supporting the existence of an accessory state in VWM [19,23]. In these experiments, participants remembered two objects on each trial: (i) the target of an immediate search task and (ii) an item to be used later, either in a second search task or in a change-detection task. On some trials, the latter object appeared as a distractor in the initial search task, but its presence did not affect search times, suggesting that it was maintained in an accessory state that did not interact with perceptual selection. In a related method, Olivers *et al.* ([5], Experiment 6) had participants remember two colours at the beginning of a trial, followed by a retention-interval cue (sometimes termed a 'retro-cue') which indicated the item to be tested at the end of the trial. Thus, after the cue, participants no longer had an incentive to retain the uncued colour. Next, a search display was presented, which could contain a colour singleton distractor matching the cued colour, the uncued colour, or neither (i.e. a colour that was not part of the memory array). The cued colour reliably captured attention, but the uncued colour did not produce a search cost relative to a singleton colour that had never been part of the memory array. Again, only an item actively maintained as relevant to the immediate task interacted with perceptual selection.

However, there is a clear alternative to the explanation of these results in terms of qualitatively different states of VWM. The strength of the interaction between a VWM representation and perceptual selection may be governed, instead, by the informational content of the representation and its overlap with perceptual processing. Specifically, VWM representations that interact with perceptual selection may specify a particular feature value with more precision than those that do not, producing a better match between the remembered feature and the features of a similar object in the perceptual display. In the studies cited as supporting the dual-state account, participants may have established a more precise VWM representation for an object known to be immediately task-relevant. Because these studies did not directly compare memory for objects that did and did not interact with selection, they cannot speak to this possibility.

Such an account is more parsimonious than an account in terms of multiple, qualitatively distinct VWM states.

In this study, we tested the relative precision of VWM representations that do and do not interact with perceptual selection. We adapted the retention-interval cueing method used by Olivers *et al.* [5]. Experiment 1 was designed to confirm that uncued colours, deprioritized for retention, do not recruit attention to matching stimuli. In addition, we confirmed that cued colours, prioritized for retention, do recruit attention to matching stimuli. In Experiments 2 and 3, we probed the precision of memory for prioritized and deprioritized colours using a continuous recall technique [24].

## 2. Experiment 1

It is well established that task-relevant objects in VWM reliably recruit attention to matching stimuli [5,6]. In Experiment 1, we sought to confirm that an object feature deprioritized for retention in VWM no longer interacts with perceptual selection [5]. The primary task was colour change detection (figure 1a). Participants saw a memory array of two colour squares at the beginning of the trial, followed by a retention-interval cue that was valid on 80% of trials (indicating the to-be-tested item) and invalid on 20% of trials. The inclusion of invalid trials allowed us to test memory for the uncued colour. At the end of the trial, one test probe colour (same or changed) was displayed at the location of a memory array item.

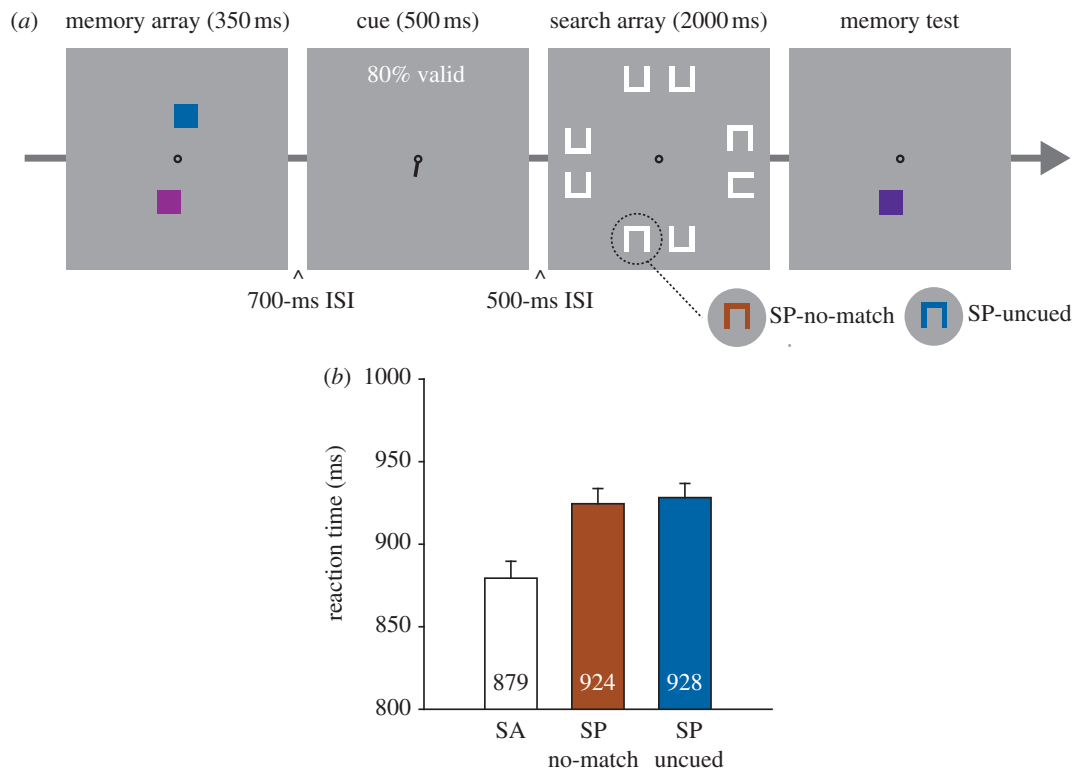
The secondary task was visual search. After the retention-interval cue, a search array was presented with an orientation-defined target. To examine the interaction between object features in VWM and perceptual selection, the primary manipulation involved the presence of a colour singleton distractor and the match between that singleton and the colours in the change-detection task. In the *singleton absent* (SA) condition, there was no singleton; all boxes were white. There were two *singleton present* (SP) conditions. In the *SP-uncued* condition, the colour singleton matched the uncued colour from the memory set. In the *SP-no-match* condition, the colour singleton did not match either of the colours from the memory set. If deprioritized objects no longer interact with perceptual selection, a singleton that matches the uncued colour should generate a capture effect no larger than the capture effect generated by a singleton colour that was not part of the memory array.

### (a) Participants

Eighteen University of Iowa undergraduates participated for course credit. All reported normal or corrected-to-normal vision.

### (b) Stimuli

Stimuli were presented on a grey background with a central, black fixation ring (0.3° diameter). Colour memory squares (1.48° × 1.48°) appeared at two locations evenly spaced around a virtual circle with a radius of 2.84°. The two memory colours were selected from an HSV, circular colour space. The hue value varied from 1° to 360°, with brightness and saturation values fixed at 70%. On each trial, four evenly spaced colours were chosen with a random initial offset within the colour wheel. Then, each colour value was jittered randomly within a range of -20° to +20° from the original colour. These four jittered colours constituted the set from which the trial stimuli were chosen. The two memory colours



**Figure 1.** (a) Sequence of events in a trial of Experiment 1. (b) Visual search reaction time results as a function of singleton condition for Experiment 1. Error bars in all figures are condition-specific, within-subject 95% CIs [25].

were chosen randomly from the set. On SP-uncued trials, the singleton colour was the same as the uncued memory colour. On SP-no-match trials, the singleton colour was randomly chosen from the remaining two colours in the set. To ensure that the singletons were sufficiently dissimilar from the cued colour in the SP-uncued and SP-no-match conditions, the singleton colour selection was constrained to colours at least  $130^\circ$  from the cued colour. The cue was a line ( $0.09^\circ$  width,  $0.5^\circ$  length) that extended from the central fixation ring towards one of the memory square locations, randomly selected. On 'changed' trials, the test colour differed by  $\pm 30^\circ$  in colour space (randomly chosen) from the memory colour appearing at that location.

The eight search stimuli were squares ( $0.85^\circ \times 0.85^\circ$ ) with a gap on one side. Distractors had the gap on the top or bottom, and the target had the gap on the left or right. Each search element was centred  $3.6^\circ$  from the centre of the screen and organized into four pairs. If a colour singleton was present, it was always a distractor. Target position, singleton position, target type and distractor type were randomly selected on each trial.

### (c) Apparatus

Stimuli were displayed at a viewing distance of 80 cm on a 17-inch CRT monitor (100-Hz refresh rate) with a resolution of  $800 \times 600$  pixels. Responses were collected by a serial button box. The experiment was controlled by E-PRIME software.

### (d) Procedure

Throughout each trial, participants repeated aloud a 4-digit sequence (randomly generated on each trial) to suppress verbal encoding of the memory stimuli. The participants pressed a pacing button to begin each trial, followed by a

500 ms delay. The memory array was presented for 350 ms, followed by a 700 ms interstimulus interval (ISI), the cue display for 500 ms, a 500 ms ISI, the search display for 2000 ms and finally the test display. Participants responded during the presentation of the search display to indicate target gap location (left/right). Then, they responded to the test display to indicate 'same' or 'changed'.

Participants completed 18 practice trials followed by two blocks of 150 experimental trials each. In each block, the trials were divided evenly among the three singleton conditions. In each condition, 80% of trials were valid and 20% invalid. Same versus changed was randomly determined on each trial. Trials from the various conditions were randomly intermixed.

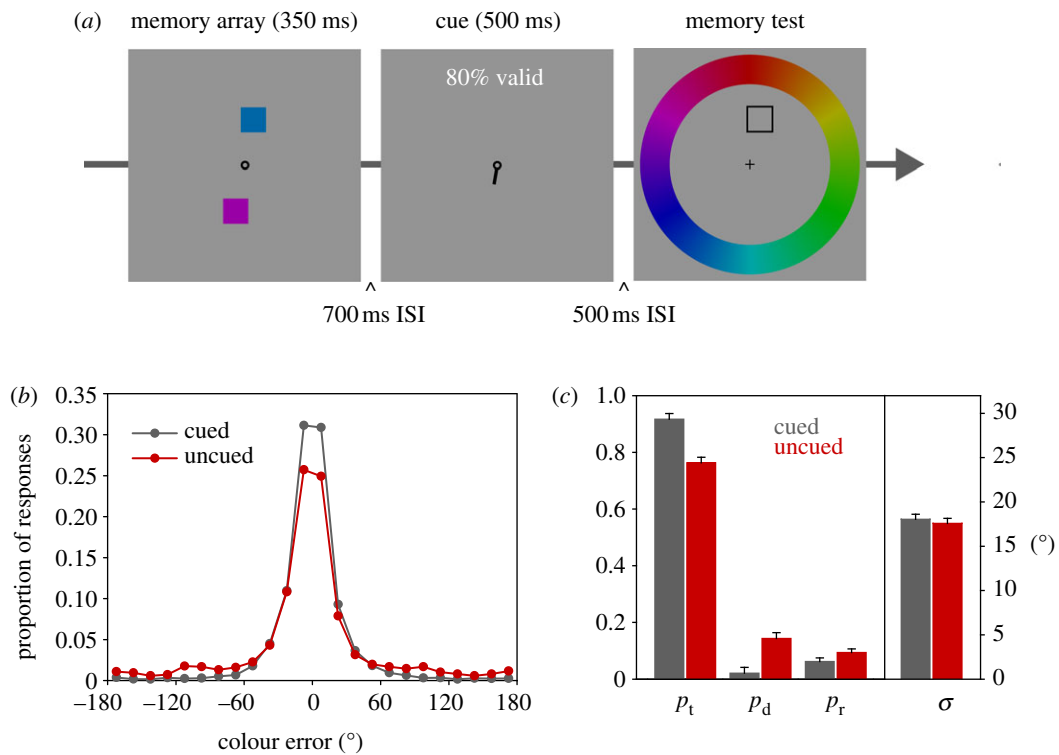
## (e) Results

### (i) Memory task

Mean change-detection accuracy was reliably higher in the valid-cue condition (71.7%) than in the invalid-cue condition (63.6%),  $t_{17} = 4.00$ ,  $p < 0.001$ . Thus, we can be confident that participants prioritized the cued colour for retention. Note, however, that memory performance in the invalid-cue condition was significantly higher than chance level of 50%,  $t_{17} = 6.30$ ,  $p < 0.001$ . On at least some trials, participants retained information from the uncued object despite the relatively low probability that it would be tested.

### (ii) Search task

Participants responded to the search display during the 2000 ms that it was visible on 98.2% of trials. Mean target discrimination accuracy was high (98.5%) and did not vary as a function of singleton condition (SA = 98.6%, SP-no-match = 98.8%, SP-uncued = 98.0%).



**Figure 2.** (a) Sequence of events in a trial of Experiment 2. (b) Histograms of colour recall error for cued and uncued colours. Mixture modelling parameter estimates for the probability of probed object (target) report ( $p_t$ ), probability of unprobed object (distractor) report ( $p_d$ ), probability of random guess ( $p_r$ ) and standard deviation of the target-report distribution ( $\sigma$ ).

Mean correct response time (RT; excluding responses of more than 2000 ms) is reported in figure 1*b*. First, there was a capture effect attributable to the presence of a colour singleton, even when the singleton was not part of the memory array [26]: search RT was reliably higher in the SP-no-match condition than in the SA condition,  $t_{17} = 3.14$ ,  $p < 0.01$ . Second, the capture effect was no greater for a deprioritized colour than for a colour that had never been part of the memory set: there was no RT difference between the SP-uncued and SP-no-match conditions,  $t_{17} = 0.32$ ,  $p = 0.76$ .

Experiment 1 confirmed that when an object is deprioritized for retention in VWM, its features have no observable effect on perceptual selection [5]. This might occur for several reasons: (i) information from the deprioritized object was no longer present in VWM on many trials [27], (ii) the representation of the deprioritized object became imprecise, limiting its ability to interact with perceptual selection or (iii) information from the deprioritized object was retained reliably (perhaps with considerable precision) but in a state that did not interact with perceptual selection [21]. Above-chance change detection for uncued objects in Experiment 1 demonstrated some degree of retention, but this result cannot tell us about the precision of the information or the proportion of trials on which it was retained.<sup>1</sup>

### 3. Experiment 2

To tease apart these possibilities, in Experiment 2, we used a continuous colour recall procedure [24] within the cued-VWM paradigm (figure 2*a*). The events in a trial were identical to those in Experiment 1 through the ISI following the cue. At this point, a colour wheel was displayed, surrounding the stimulus locations, and one colour memory location was probed by a box. Participants marked the location on the

colour wheel corresponding to the remembered value of the colour at the probed location. The response data were modelled as a mixture of distributions corresponding to trials on which the probed object was and was not retained, which allowed us to estimate, for cued and uncued objects, the probability that a colour was retained in VWM and the precision of the colour memory representation.

#### (a) Participants

Twenty-two new University of Iowa undergraduates participated for course credit. All reported normal or corrected-to-normal vision.

#### (b) Stimuli and procedure

After the 500 ms ISI following the cue (i.e. at the same point in the trial that the search array appeared in Experiment 1), an HSV colour wheel annulus was displayed (inner and outer radii 5.12° and 6.94°). Colour wheel orientation was selected randomly on each trial. In addition, one of the two memory square locations was marked by a black box (probe). On 80% of trials, this was the cued colour location (valid trials) and on 20% the uncued colour location (invalid trials). A plus-sign cursor was presented at the centre. The participant moved the cursor with a mouse and clicked on the colour wheel location corresponding to the remembered value of the probed colour.

#### (c) Results

The colour recall data were fitted with a probabilistic mixture model to estimate the proportion of trials on which the probed colour was retained and the precision of the memory representation. Error on each trial was assumed to come from three possible sources: Gaussian variability in

memory for the probed object, Gaussian variability in memory for the unprobed object (on trials when the participant reported the wrong object) and uniform variability for random guesses (for details of the model, see electronic supplementary materials and [28]). The relative frequency of responses from the target (i.e. probed) distribution ( $p_t$ ), from the distractor (i.e. unprobed) distribution ( $p_d$ ), and from the uniform distribution of random guesses ( $p_r$ ), as well as the variability of the colour estimates from the target distribution ( $\sigma$ ), were estimated separately for each participant and condition. An initial analysis indicated that several participants had very high rates of distractor responses in the invalid condition: they consistently reported the value of the cued colour rather than the value of the uncued colour. This may have reflected binding errors or failure to attend to the memory probe. Because of the difficulty of interpreting memory performance on these trials, we eliminated three participants from the main analysis with  $p_d > 0.5$  on invalid trials.

The distributions of colour memory error around the target value are illustrated in figure 2*b*, and the estimated parameter values are reported in figure 2*c*. Probability of colour retention ( $p_t$ ) was reliably higher in the cued condition (0.92) than in the uncued condition (0.76),  $t_{18} = 5.49$ ,  $p < 0.001$ . Strikingly, the precision of the memory representation when the probed colour was retained did not differ between the cued ( $\sigma = 18.0^\circ$ ) and uncued ( $\sigma = 17.6^\circ$ ) conditions,  $t_{18} = 0.56$ ,  $p = 0.58$ .<sup>2</sup> Thus, the effect of cueing on change detection in Experiment 1 was likely to have been caused by a difference in the probability of colour retention rather than by a difference in memory precision.

In Experiment 1, 500 ms after the cue to selectively retain one of the items in memory, a deprioritized colour had no effect on perceptual selection above that attributable to any colour singleton. However, when participants were probed to report the deprioritized colour at the same point in Experiment 2, they could do so relatively accurately. Probability of report from the target distribution dropped only modestly for uncued versus cued objects, and there was no difference in the precision of the memory representation in the cued and uncued conditions. Thus, it appears that relatively precise colour information can be retained in a form that does not necessarily interact with perceptual selection, consistent with the claim that there are multiple states of object representation in VWM [21].

## 4. Experiment 3

In Experiment 3, we added the search task back into the paradigm, combining the search task manipulations from Experiment 1 with the recall test from Experiment 2. Specifically, the method was the same as in Experiment 1 (figure 1*a*), except that the memory test was continuous recall, as in Experiment 2, rather than change detection. Delaying the memory report until after search has the disadvantage of probing memory well after the point at which capture was assessed, potentially underestimating memory precision. However, the advantage of the design is that it enabled us to measure, on a trial-by-trial basis, the accuracy of the memory representation of the uncued colour. We could then assess capture by the uncued colour in an analysis limited to those trials in which a relatively accurate representation of that colour was known to have been retained.

### (a) Participants

Thirty-two new University of Iowa undergraduates participated for course credit. All reported normal or corrected-to-normal vision.

### (b) Stimuli and procedure

The sequence of events on a trial was the same as in Experiment 1, except for the memory test (continuous recall rather than change detection).

### (c) Results

#### (i) Memory task

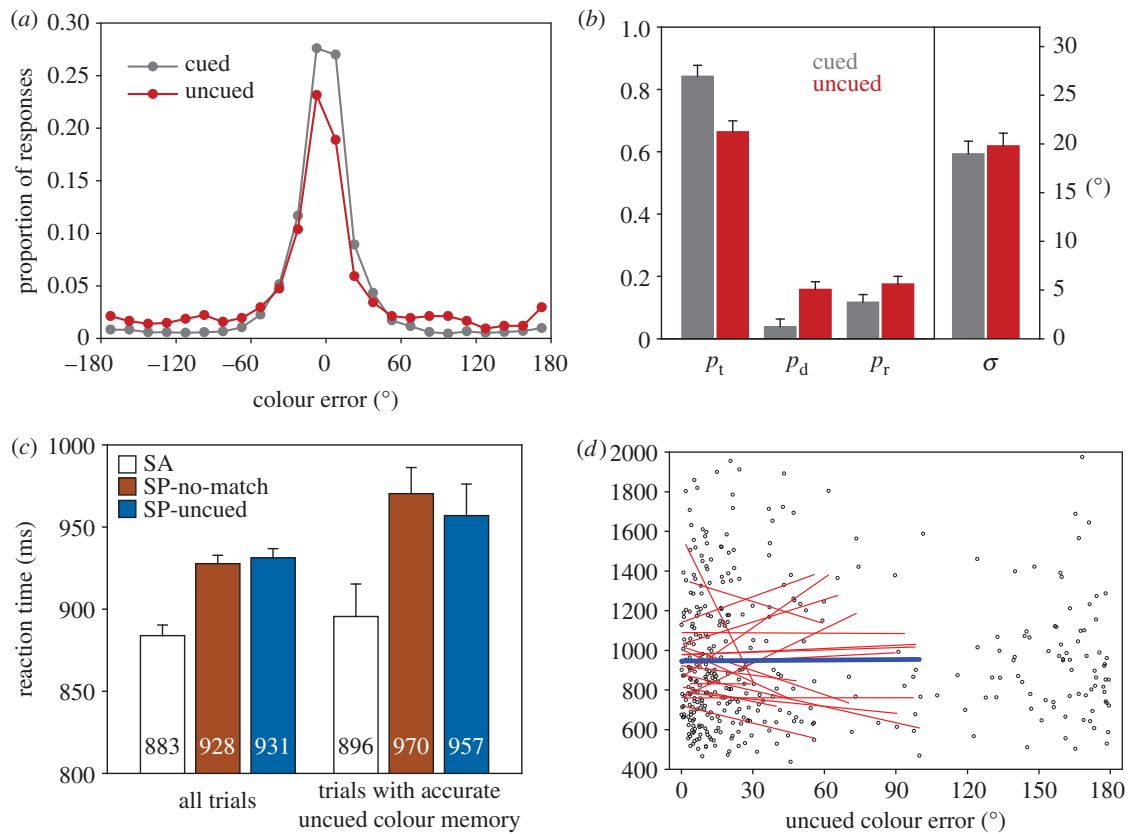
We fit the recall data with the same model as in Experiment 2. Twelve participants had  $p_d > 0.5$  in the invalid condition, potentially reflecting an increase in position-memory confusion given the spatial demands of the search task. For the remaining 20 participants, the distributions of colour error around the target value are illustrated in figure 3*a*, and the estimated parameter values are reported in figure 3*b*. The results replicated the main findings of Experiment 2. Probability of colour retention ( $p_t$ ) was reliably higher in the cued condition (0.84) than in the uncued condition (0.67),  $t_{19} = 3.87$ ,  $p = 0.001$ . However, the precision of the memory representation when the probed colour was retained did not differ between the cued ( $\sigma = 19.0^\circ$ ) and uncued ( $\sigma = 19.8^\circ$ ) conditions,  $t_{19} = 0.57$ ,  $p = 0.64$ . Note that overall lower probability of retention relative to Experiment 2 was likely to have been due to the delay and to the perceptual demands introduced by the search task.

#### (ii) Search task

Participants responded to the search display during the 2000 ms that it was visible on 98.4% of trials. Mean target discrimination accuracy was 98.9%. There was an effect of singleton condition on search accuracy,  $F_{2,62} = 3.82$ ,  $p = 0.03$ , with slightly lower accuracy in the SP-no-match condition (98.4%) than in the SP-uncued (99.0%) and SA (99.2%) conditions. Though statistically reliable, the absolute differences between conditions were minimal.

We first examined search RT across the entire dataset. The results replicated Experiment 1 (figure 3*c*). First, there was a reliable capture effect attributable to having any colour singleton in the display: search RT was reliably higher in the SP-no-match condition than in the SA condition,  $t_{31} = 5.25$ ,  $p < 0.001$ . Second, the uncued colour did not capture attention relative to a colour that was never part of the memory array: there was no RT difference between the SP-no-match and SP-uncued conditions,  $t_{31} = 0.51$ ,  $p = 0.61$ .

Next, we conditionalized the RT analysis on the accuracy of memory performance at the end of the trial. The participants excluded from the mixture model analysis were also excluded here. For the remaining 20 participants, we limited the analysis to invalid trials on which the reported colour value was within two standard deviations of the uncued colour (i.e. within  $38.4^\circ$  in colour space). Thus, we included only those trials on which we could be confident that the participant retained a fairly accurate representation of the uncued object colour. Participants averaged 12 observations in each of the three cells of the analysis. The results replicated the main analysis (figure 3*c*). There was a reliable difference between the SP-no-match condition and the SA condition,



**Figure 3.** (a) Histograms of colour recall error for cued and uncued colours in Experiment 3. (b) Mixture modelling parameter estimates. (c) Visual search reaction time results as a function of singleton condition, for all trials and for trials with a relatively accurate report of the uncued colour value. (d) Individual-trial scatter plot of visual search reaction time on SP-uncued trials as a function of memory accuracy for the uncued colour, with individual participant regression lines (red) and the omnibus regression line (blue).

$t_{19} = 3.27$ ,  $p < 0.01$ , but no difference between the SP-no-match and SP-uncued conditions,  $t_{19} = 0.54$ ,  $p = 0.60$ .

As a converging analysis, for each of these 20 participants, we calculated the correlation between colour error and search RT for invalid trials in the SP-uncued condition. Each trial is plotted in figure 3d. If there were an obligatory attraction of attention towards objects that match, precisely, a feature value in VWM, trials with a precise representation of the uncued colour should have produced greater capture by that colour than trials with an imprecise representation: RT should have increased as colour error decreased. To ensure that the correlations were not influenced by trials in which the participants incorrectly reported the cued object colour (see concentration of responses with more than  $130^\circ$  error), we limited the analysis to trials on which colour error was less than  $100^\circ$ . This left an average of 15 observations per participant. Individual regression lines are plotted in red in figure 3d. Mean  $r$  was  $-0.029$ . Individual correlation coefficients were Fisher's Z transformed for comparison against the null hypothesis of no relationship. The mean correlation did not significantly differ from zero,  $t_{19} = 0.54$ ,  $p = 0.60$ . We also calculated the correlation across all 301 observations, collapsing across participants (blue regression line in figure 3d). There was no observable relationship between the two variables,  $r = 0.005$ ,  $t_{299} = 0.08$ ,  $p = 0.94$ .

In summary, when the analysis of potential capture by an uncued colour was limited to trials on which the colour was known to have been retained relatively accurately, there was still no evidence that the colour interacted with perceptual selection. In addition, there was no relationship between the precision of colour memory for deprioritized colours and the degree of capture. Thus, it appears that precise information is

often retained in VWM from deprioritized objects—information as precise as that retained from the cued object—but this information is maintained in a state that does not necessarily interact with perceptual selection.

## 5. General discussion

This study supports a distinction between two states of object representation in VWM. This raises the question of the nature of the difference between VWM representations that do and do not interact with perceptual selection. Olivers *et al.* [21] discussed the possibility that both types of representation rely on storage in prefrontal cortex but may be segregated according to their relevance for the immediate task. Only task-relevant objects are maintained in a manner that allows feedback to lower visual regions, biasing perceptual selection. A second possibility is that the two forms of representation differ in the extent to which they involve sustained activation of feature-specific neural populations in visual-sensory regions. Several studies have indicated that delay-period activity in V1 through inferotemporal cortex is correlated with VWM content [29–31], and VWM content interacts with the initial sensory processing of visual stimuli, increasing the salience of memory-matching objects and biasing attention towards them [4]. Items in VWM that do not interact with perceptual selection would not be accompanied by visual-sensory activation during maintenance, would not interact with the sensory processing of new stimuli, and thus would not bias perceptual selection. Of course, to account for the present results, the involvement of visual-sensory regions in VWM maintenance could not be a

key factor in the precision of those representations. In the absence of direct neural evidence, however, both possibilities are currently speculative.

Although our results are consistent with the dual-state hypothesis, other aspects of the Olivers *et al.* [21] framework are less strongly supported. Olivers *et al.* [21] claimed that only one object or feature at a time can be maintained in an active state that controls perceptual selection (see also [32]). However, recent evidence suggests that attention can be guided simultaneously by multiple feature values [33]. In this study, participants searched for a target defined by two colour values (e.g. the target could be red or blue among yellow and green distractors). They either searched the two colour groups sequentially (all the red items and then all the blue items) or simultaneously. In the sequential condition, there was a cost associated with switching from one colour template to the other. However, when participants searched simultaneously, they frequently shifted back and forth between colours, and there was no switch cost when doing so, suggesting that both colours were controlling attention simultaneously.

A second issue concerns how to characterize the difference between items in VWM that do and do not recruit attention to matching stimuli. Of course, the central, defining difference concerns the interaction with perceptual selection. However, Olivers *et al.* [21] extended this distinction, arguing that items that interact with perceptual selection are immediately relevant to a visual search task and comprise a search template, whereas items that do not interact with perceptual selection are not represented in the search template. This extension is limited by the fact that search-irrelevant items in VWM often interact with perceptual selection. For example, in the typical memory-based capture paradigm [5,6], colour is not a defining feature of the visual search target, yet a match to a colour actively maintained in VWM reliably captures attention. Olivers *et al.* [21] argued that in these cases, the target feature is constant across many trials, and the search template is offloaded to long-term memory [34]. In the absence of a task-relevant search template in VWM, other items in VWM are automatically ‘promoted’ to an active state and influence selection, acting as a template. Although possible, this resolution is speculative, and it complicates the basic concept of a search template: to accommodate the results of memory-based capture experiments, the definition of a search template must be modified to include items that are not relevant to the search task. We consider it preferable to claim, in a manner more closely tied to the observed results, that items actively maintained in VWM interact with perceptual selection, regardless of whether they do or do not comprise the current top-down attentional set for the guidance of visual search.

The results of Experiments 2 and 3 inform our general understanding of top-down control over VWM representations. Despite the low probability of being tested, colour retention from uncued objects was surprisingly robust and precise. The probability of retention dropped only modestly for uncued versus cued objects, and when retained, the precision of the representation was equivalent in the two conditions. These results contrast, however, with a recent report by Williams *et al.* [27]. Using a method similar to that in Experiment 2 (retention-interval cueing followed by continuous colour recall), they found that deprioritized colours were retained on less than 10% of trials (compared with 76% of trials in Experiment 2), suggesting almost perfect purging of no-longer-relevant items from VWM.

There are two plausible explanations for the differing results. First, Williams *et al.* [27] probed the deprioritized colour on only 10% of trials (rather than 20% in this study), potentially providing participants with greater incentive to eliminate it from VWM. Second, Williams *et al.* [27] did not account for the possibility that on invalid-cue trials, participants may have reported the wrong colour, without necessarily having forgotten the deprioritized colour. In their method, the prioritized colour was probed on 90% of trials, and participants were not informed that invalid cues would be included in the experiment. Thus, participants may have developed a strategy of always reporting the cued colour and ignoring the memory probe. Indeed, such behaviour was observed in both Experiments 2 and 3 of this study, despite a larger proportion of invalid trials and despite clear instructions that the cue could be invalid. Because Williams *et al.* [27] did not include responses near the distractor value (i.e. the cued colour on invalid trials) as a component in their mixture model, these responses would have been attributed to the uniform distribution corresponding to random guesses [28], and thus a strategy of always reporting the cued colour may have gone undetected.

Finally, the lack of a difference in precision between cued and uncued colour representations in Experiments 2 and 3 is consistent with the claim that the loss of information from VWM occurs in an all-or-none fashion. Zhang & Luck [35] contrasted two modes of information loss from VWM: incremental reduction in the precision of representations (gradual decay) and the complete loss of information from an object (sudden death). In the context of mixture modelling and the continuous recall procedure, the former predicts that a manipulation resulting in the loss of information from VWM will increase variability within the target distribution ( $\sigma$ ), whereas the latter predicts a reduction in the probability of target recall ( $p_t$ ). Across a manipulation of retention interval, Zhang & Luck [35] observed a reduction in probability of target recall with no reduction in variability. The cueing method in this study is a converging means to manipulate information loss from VWM. Likewise, we observed a change in the probability of recall with no change in precision.

## 6. Summary and conclusions

The results provide support for the basic distinction between two states of object representation in VWM [21]: an active state that interacts with perceptual selection and a passive (or accessory) state that does not. In particular, maintaining a relatively precise representation of a feature value in VWM is not sufficient to bias attention towards matching stimuli. Colours that were deprioritized for retention in VWM were often maintained precisely, yet they did not capture attention relative to non-matching control colours. Thus, feature maintenance in VWM is not necessarily equivalent with feature-based attentional selection.

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## Endnotes

<sup>1</sup>Experiment 1 confirmed that deprioritized objects fail to interact with perceptual selection, but it did not confirm that task-relevant objects in VWM recruit attention to matching stimuli. Although this latter effect

is already well established in the literature, our search paradigm differed in several respects from the search tasks used in the previous studies. Thus, we ran a follow-up experiment ( $n = 24$ ) to ensure that our method would produce the standard effect of capture by task-relevant features in VWM (for details, see the electronic supplementary materials). The retention-interval cue was either valid or neutral. In the valid condition, the singleton could match either the cued colour (SP-cued) or uncued colour (SP-uncued). Singletons in the neutral condition (SP-neutral) matched one of the memory items, providing a baseline measure of capture when the singleton colour was neither prioritized nor deprioritized. Search RT was reliably higher in the SP-cued condition than in the SP-uncued condition, confirming that prioritized colours reliably recruit attention. We observed both costs and benefits of cueing. Search RT was reliably higher in the SP-cued

condition than in the SP-neutral condition. In addition, search RT was reliably lower in the SP-uncued condition than in the SP-neutral condition, consistent with the Experiment 1 observation that uncued objects fail to interact with perceptual selection.

<sup>2</sup>One possible limitation of this modelling approach is that the standard deviations of the target (probed) and distractor (unprobed) distributions were assumed to be equivalent, which could have influenced the estimate of standard deviation for the target distribution, particularly in the invalid condition, which had a substantial proportion of distractor-report trials. In follow-up analyses for Experiments 2 and 3, we eliminated trials with a response near the distractor value and re-estimated variability for the target distribution (see the electronic supplementary materials). The results were equivalent with the main analyses.

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