

How visual working memory contents influence priming of visual attention

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Abstract Recent evidence shows that when the contents of visual working memory overlap with targets and distractors in a pop-out search task, intertrial priming is inhibited (Kristjánsson, Sævarsson & Driver, *Psychon Bull Rev* 20(3):514–521, 2013, Experiment 2, *Psychonomic Bulletin and Review*). This may reflect an interesting interaction between implicit short-term memory—thought to underlie intertrial priming—and explicit visual working memory. Evidence from a non-pop-out search task suggests that it may specifically be holding *distractors* in visual working memory that disrupts intertrial priming (Cunningham & Egeth, *Psychol Sci* 27(4):476–485, 2016, Experiment 2, *Psychological Science*). We examined whether the inhibition of priming depends on whether feature values in visual working memory overlap with targets or distractors in the pop-out search, and we found that the inhibition of priming resulted from holding distractors in visual working memory. These results are consistent with separate mechanisms of target and distractor effects in intertrial priming, and support the notion that the impact of implicit short-term memory and explicit visual working memory can interact when each provides conflicting attentional signals.

Introduction

The phenomenon of *priming of pop-out* (PoP) has been known in the literature for over 20 years, and highlights the importance of intertrial effects on visual search. Although pop-out visual search is typically considered an automatic process, repetition of target color or location across trials can speed visual search even when the target pops out (Maljkovic & Nakayama, 1994). Response time benefits of feature-based PoP can depend both on repetition of targets and repetition of distractors (Kristjánsson & Driver, 2005, 2008; Kristjánsson & Jóhannesson, 2014; Lamy, Antebi, Aviani & Carmel, 2008; Maljkovic & Nakayama, 1994; Wang, Kristjánsson, & Nakayama, 2005), and both an increase in neural response to repeated targets and a suppression of neural responses to repeated distractors have been found in FEF (Bichot & Schall, 2002). While the mechanisms underlying PoP have consistently been associated with an implicit short-term memory for preceding target and distractor features, recent evidence suggests that explicit visual working memory may also influence PoP (Kristjánsson et al., 2013, Experiment 2). Our aim is to investigate the influence of explicit visual working memory on PoP.

The intertrial effects of PoP are assumed to change how attention is deployed. Although PoP is often measured using response times, intertrial priming is thought to be related to attentional rather than response-related processing. Consistent with this, priming has also been seen to occur in tasks measuring accuracy rather than speed (Ágeirsson, Kristjánsson, & Bundesen, 2015; Lamy, Yashar, & Ruderman, 2010; Sigurdardottir, Kristjánsson, & Driver, 2008). PoP search tasks are designed to dissociate the target-defining feature (singleton color) and the response property (often which side of a diamond is

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missing). Neural evidence supports the idea that the reaction time shifts are associated with altered attentional processing. The N2pc ERP component, a neural index of covert attentional deployments, emerged over 50 ms earlier for repeated targets and distractors than when target and distractors colors swapped across trials (Eimer, Kiss, & Cheung, 2011). fMRI measures of PoP in humans suggest that there is overlap between areas involved in top-down attentional control and PoP (Brinkhuis, Kristjánsson, & Brascamp, 2016; Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007; Rorden, Kristjánsson, Pirog-Revell, & Saevarsson, 2011).

The mechanism underlying this shift in attentional processing based on trial history is widely accepted to be an implicit short-term memory for the features from previous trials, which may influence attentional weights (Ásgeirsson, Bundesen, & Kristjánsson, 2014, 2015). Explicit knowledge of features does not seem to influence PoP. Providing participants with a consistent sequence of shifts between which target features will be presented and having participants subvocally rehearse the known target color for the upcoming trial does not alter PoP (Maljkovic & Nakayama, 1994, Experiment 4). While participants can explicitly remember the feature and location for only one preceding trial, at least five previous trials influence PoP (Maljkovic & Nakayama, 1994), showing how explicit and implicit memory for the search array features can be separated functionally. Moreover, filling visual working memory (VWM) with unrelated colored items does not prevent PoP (Lee, Mozer, & Vecera, 2009) providing additional support for the claim that PoP does not rely on explicit memory resources. These data together suggest that PoP is based on an implicit short-term memory that is functionally distinct from explicit short-term memory (Kristjánsson & Campana, 2010).

Surprisingly, Kristjánsson, Saevarsson and Driver (2013) recently found that when the colors of targets and distractors presented during a pop-out search task were maintained in VWM, PoP was greatly reduced, while also replicating the finding from Lee et al. (2009) that holding *unrelated* items in VWM did not eliminate PoP. Therefore, it seems that items in VWM can influence PoP, but only when the features overlap between VWM and the pop-out search task. Why might the relationship between the contents of VWM and the implicit short-term memory that guides PoP depend on whether objects maintained in VWM overlap with the stimuli presented in the search task? For a possible explanation, we turn to work on the relationship between VWM and attentional deployments.

Recent investigations into the impact of holding a representation in VWM on subsequent attentional deployments have suggested that attention often selects items that match the contents of VWM (for a review see Soto,

Hodsoll, Rotshtein, & Humphreys, 2008 or Olivers, Peters, Houtkamp, & Roelfsema, 2011). This attentional guidance effect is particularly strong if attention guidance towards memory matches does not interfere with the current task (Downing, 2000; Huang & Pashler, 2007), and can be diminished or absent depending on the relationship between attending to a memory match and current task goals (Arita, Carlisle, & Woodman, 2012; Carlisle & Woodman, 2011a, 2011b; Downing & Dodds, 2004; Kiyonaga, Egner, & Soto, 2012). This suggests that VWM contents might direct attention toward memory matches but only if there is a benefit (or no cost) to attending to memory matches. Applying this concept to the PoP results suggests that it might matter whether the contents of VWM contained *distractor* color features which would conflict with the attentional goals of the pop-out search task.

Two findings suggest that this might be the case. First, Maljkovic and Nakayama (1994) showed that explicit rehearsal of the color of the upcoming *target* did not disrupt PoP (note, however, that the information maintained was verbal and not visual). This suggests, as has been seen in the attentional guidance literature, that maintaining information in VWM that is consistent with the search goals may guide attention toward the search target (Carlisle & Woodman, 2011a). Second, recently Cunningham and Egeth (2016) examined whether participants could learn to use a negative cue that indicated the color of half of the upcoming distractors in a non-pop-out search array. This was contrasted with performance in a neutral cue condition that did not provide any information about the colors of upcoming distractors. Over time, participants could learn to use the negative cue to ignore the known distractor color and improve performance. Most importantly for our discussion, they found an unexpected interaction between repetition of target color and cue condition. Target repetitions speeded search by 32 ms when participants were given a neutral cue, which would be a typical intertrial target repetition benefit. In contrast, target repetitions *slowed* search by about 50 ms if participants were given a negative cue. This suggests that holding information about a *distractor* in VWM (as would be necessary for the successful utilization of the negative cue) disrupts typical intertrial effects.

We designed our study to directly examine how the contents of VWM influence intertrial priming. Although there is some suggestive evidence that maintaining distractor-matching features in VWM may disrupt implicit intertrial effects while maintaining target-matching information may not, there has been no direct test of this hypothesis. In this study, we examine the relationship between the contents of VWM and PoP by manipulating whether the contents of VWM match targets or distractors. If a conflict only arises between the explicit VWM system

and the implicit PoP memory when the goals of the two tasks diverge, we would expect to see normal PoP when VWM contains target matching features, but disrupted PoP when VWM contains distractor-matching features. More broadly, this study addresses an important question about when we should expect an interaction between implicit and explicit memory systems.

Methods

Observers

16 observers (10 female) aged 23–33 volunteered for the study. Informed consent was obtained from all individual participants in the study. All had normal or corrected to normal vision.

Equipment

The experimental displays were programmed in C, and presented on a 75 Hz CRT display controlled by a 400 GHz G4 Macintosh computer.

Procedure and stimuli

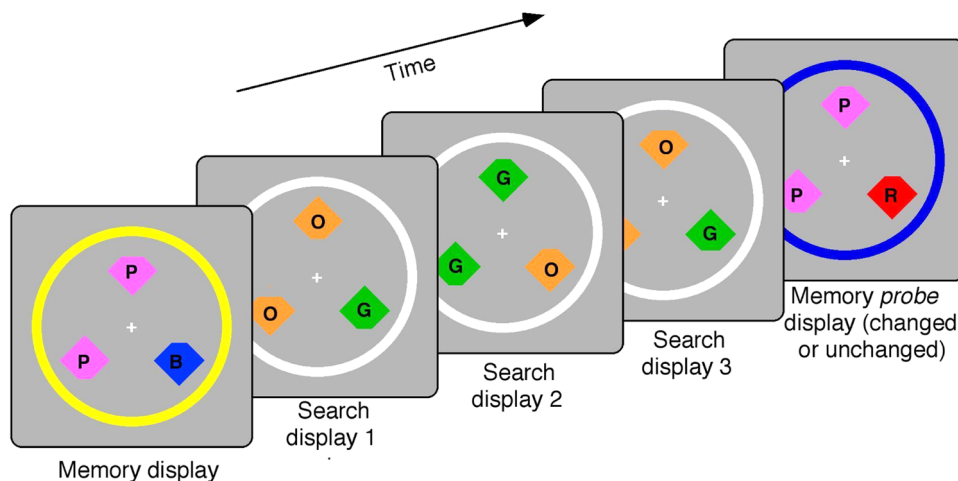
In the *memory + search* condition, observers had to perform a visual search task between the encoding and probe test of visual memory task (see Fig. 1). All search and memory screens contained three diamonds (2.4 by 2.4°), a singleton of one color and two of another color [chosen from red (41 cdm^{-2}), green (56 cdm^{-2}), blue (37 cdm^{-2}), purple (39 cdm^{-2}), yellow (98 cdm^{-2}), or orange (62 cdm^{-2})] presented on a mid-gray (49 cdm^{-2}) background. A task-denoting annulus and fixation cross appeared 800–1400 ms before each array. For a particular set of trials, observers first saw the annulus denoting the memory

display (blue or yellow ring, counterbalanced across observers; thickness 1.1°) and observers memorized the colors and locations of the three diamonds. Next, the searches were presented. On searches (denoted by a white, 101 cdm^{-2} annulus), the observers searched for the odd-one-out diamond and judged whether there was a cutoff at the top or bottom (see Fig. 1). After 1–6 searches (determined randomly), the memory probe was displayed. The annulus color denoting a memory probe (blue or yellow, the converse color of the annulus denoting the items to be memorized) appeared and they pressed a key, indicating whether the display had changed or not. We refer to this sequence of memory display, searches (1–6, randomly determined), and memory probe, as a single trial.

The relationship between the targets and the memory items was of critical importance to our analysis. For each search, the color of the target could match, or be unrelated to the colors held in memory (*target color in VWM*). Similarly, the color of the distractor could match information held in memory or not (*distractor color in VWM*). Manipulating each of these factors independently led to 4 possible trial types with regard to VWM (*VWM-neither*, *VWM-target*, *VWM-distractor*, and *VWM-both*). Across search trials, we could also have a repetition of the target color or a new target color (*target color repetition*). Similarly, the color of the distractors could match the previous search trial or be a new color (*distractor color repetition*). This led to four possible trial types combining these two search repetition factors (*no repetition*, *target repetition*, *distractor repetition*, *both repeat*).

As a control, we also included a *passive memory* condition which contained the same stimulus presentation as the search + memory condition; however, participants only passively viewed the memory screens and were not required to respond. This condition was included to measure whether the dual-task nature of the memory + search condition alone would disrupt the normal PoP effects.

Fig. 1 The experimental displays. Each display contained a singleton diamond among distractor diamonds of another of the six colors. A memory display was denoted by the color of the annulus (*blue* or *yellow*, counterbalanced across observers). Within each trial, one to six searches followed, before the probe display appeared (denoted by the opposite color to the memory-display color). See methods for further details



Observers performed two blocks of 100 search + memory trials and two blocks of 100 trials for the passive memory trials.

Results

Visual search

To examine whether VWM only conflicts with PoP when distractors are being maintained in VWM, we examined the RTs for each combination of memory factors and search repetition factors in the memory + search condition (Fig. 2 top panel). Broadly, we found that repetitions of search target color and search distractor color led to PoP effects when the contents of VWM did not overlap with the colors in the search array (VWM-neither) and when the contents of VWM overlap with the target colors in the search array (VWM-target). However, when the contents of VWM matched the distractor in the search array (VWM-distractor) or contained both a match to the distractor and a match to the target in the search array (VWM-both), PoP

was severely disrupted. The dependence of PoP on whether a distractor match is held in VWM is easiest to see when looking at the priming effects (repetition RT—no repetition RT) for the different memory conditions (Fig. 2 bottom panel).

The main effects and interactions of memory condition and repetition were addressed with a two (target color in VWM) by two (distractor color in VWM) by two (target color repetition) by two (distractor color repetition) repeated-measures ANOVA on the memory + search condition. There was a significant effect of repeating target color ($F(1, 15) = 37.16$; $p < 0.001$; partial $\eta^2 = 0.71$) and repeating distractor color ($F(1, 15) = 17.65$; $p = 0.001$; partial $\eta^2 = 0.54$), indicating that the data overall showed evidence of PoP, from both target and distractor set repetition. There were significant main effects of memorizing both the color of the target ($F(1, 15) = 7.37$; $p = 0.016$; partial $\eta^2 = 0.33$) and of the distractors ($F(1, 15) = 45.65$; $p < 0.001$; partial $\eta^2 = 0.75$) upon search performance. These main effects are best understood in relation to the interactions described below.

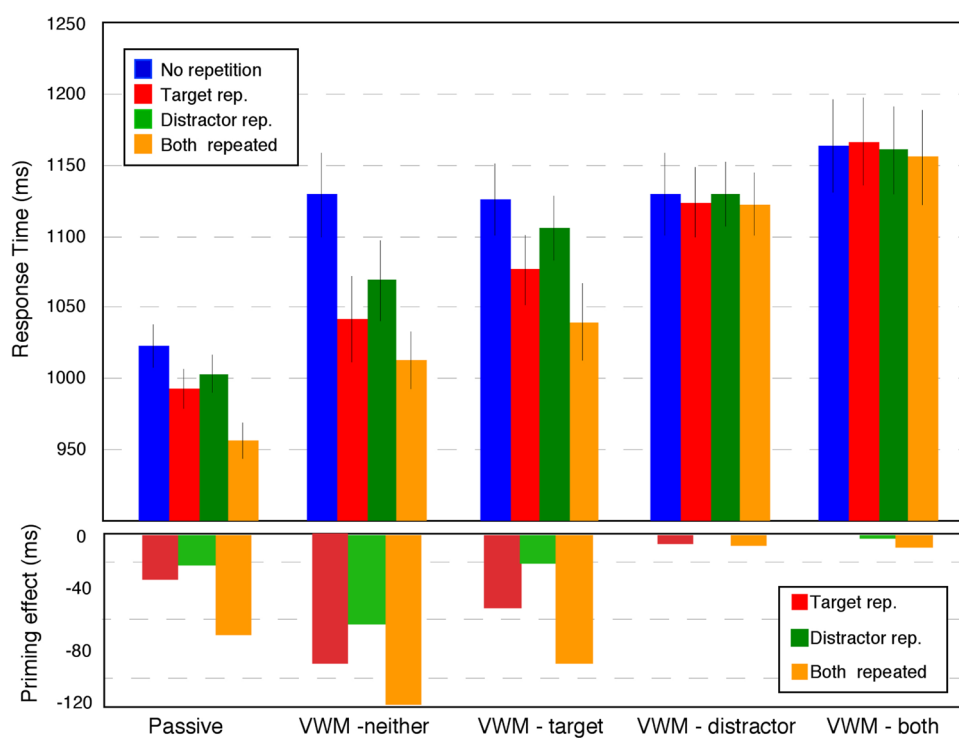


Fig. 2 Response times and priming effects as a function of working memory condition (on abscissa). The *leftmost* bundle (passive blocks) shows aggregated performance over the different conditions for the passive memory control blocks where no working memory task was performed. The other four bundles show performance from the memory + search condition as a function of VWM condition (shown on the abscissa; see “Methods” for a description of the conditions). For the *top graph*, blue denotes trials where neither target nor

distractor color repeated; red denotes that target color only repeated; green denotes that distractor color only repeated and yellow denotes that both colors repeated. The *lower panel* below shows the same results, but now highlighting the size of the priming effects from target repetition (red), distractor repetition (green) and when both colors repeated (yellow), relative to response times when neither color repeated

There were two significant interactions. First, an interaction of search distractor in memory and target repetition ($F(1, 15) = 11.99$; $p = 0.003$; partial $\eta^2 = 0.44$), reflecting that the target repetition effect was far smaller when distractors were memorized than when they were not. In addition, there was also a significant interaction of search distractor in VWM and distractor repetition ($F(1, 15) = 14.98$; $p = 0.002$; partial $\eta^2 = 0.5$). Importantly, there was no hint of any such interaction when target colors in the search were to be memorized (p values > 0.3). This result statistically confirms the pattern seen in the data presented in Fig. 2, and highlights that it is specifically holding information matching the *distractors* in VWM that disrupts PoP.

To assess whether including a dual task in the memory + search condition led to a significant alteration in the normal PoP effects, we contrasted the pattern of RTs in the VWM-neither condition with the passive memory condition. A three-way ANOVA with the factors dual task (passive memory versus VWM-neither search + memory trials), target repetition, and distractor repetition showed a main effect of task ($F(1, 15) = 13.76$; $p = 0.002$; partial $\eta^2 = 0.48$) indicating that the addition of the VWM task slowed RTs for the memory + search condition compared to the passive memory condition where no dual task was performed. In addition, we found main effects of target repetition ($F(1, 15) = 10.7$; $p = 0.005$; partial $\eta^2 = 0.42$) and distractor repetition ($F(1, 15) = 18.7$; $p < 0.001$; partial; $\eta^2 = 0.55$). The interaction between target and distractor repetition was significant ($F(1, 15) = 4.88$; $p = 0.043$; partial $\eta^2 = 0.25$), indicating a larger PoP effect when both target and distractors repeated, but this was independent of task (passive memory versus VWM-neither search + memory) which did not interact with either the target or the distractor repetition effect. This replicates the findings from Lee et al. (2009) and Kristjánsson et al. (2013) that merely having information in VWM does not disrupt PoP.

Working memory performance

Working memory performance was high as measured both with percent correct as well as with the A' measure (Donaldson, 1993; Grier, 1971; see Fig. 3)¹ where response strategies are taken into account, and did not differ across VWM condition ($p > 0.5$). This result is crucial since it shows that any differences in the priming pattern cannot be attributed to differential concentration or task interaction effects induced by our dual-task design. We also measured

¹ A' is derived from the more traditional d' but is more accurate for tasks of this sort and is more robust to lacks of false alarms. It is calculated as follows: $A' = 0.5 + \left[\frac{(H-FA)(1+H-FA)}{4H(1-FA)} \right]$.

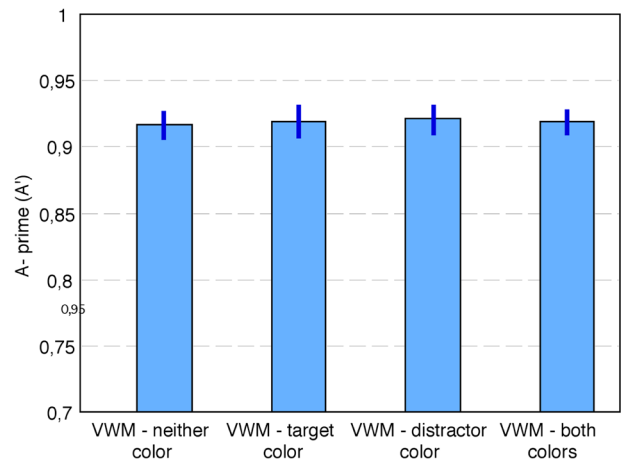


Fig. 3 Working memory performance (measured with A') for the different working memory conditions in the *active* condition

whether there was any effect upon memory response times from the different conditions, finding no difference by VWM condition ($p > 0.15$).

Discussion

Our results are consistent with previous results showing that merely holding information in VWM does not disrupt PoP (Lee et al., 2009) while holding information in VWM that overlaps with the search stimuli interferes with PoP (Kristjánsson et al., 2013). But importantly, the pattern of interference is more nuanced than this implies. It depends on whether the information held in VWM is consistent with where attention should be directed during visual search. Holding a color in VWM that matches a search distractor leads to a significant reduction in PoP effects, while no significant reduction in PoP was found when information matching the search target was held in VWM. In other words, the disrupting effect of VWM content on PoP is mainly explained by maintaining distractor colors in VWM.

Findings from both the literature on VWM guidance and priming are broadly consistent with this differential impact of task relevance of VWM representations. The influence of VWM on attention during search is modulated by the task relevance of that VWM representation, with working memory leading to default attentional biases (Downing, 2000; Huang & Pashler, 2007) which become stronger with increased task relevance of a VWM representation (Carlisle & Woodman, 2011a, 2013), or may decrease if an attentional task and the contents of working memory are in conflict (Arita et al., 2012; Carlisle & Woodman, 2011b; Kiyonaga et al., 2012; Woodman & Luck, 2007). Kruijnen, Brascamp, Kristjánsson and Meeter (2015) have recently proposed that the intertrial priming mechanisms reflect

sustained activity or excitability of the target feature from the previous trial (see also Ásgeirsson, Kristjánsson, & Bundesen 2014; Ásgeirsson & Kristjánsson, 2011). This is similar to the proposed operation of mechanisms involving sustained working memory activations proposed to account for top-down working memory guidance of attention in the biased competition theory of attention (Desimone & Duncan, 1995).

Although both target priming and distractor priming contribute to repetition effects in singleton search, the two processes have been shown to be independent (Wang, Kristjánsson, & Nakayama, 2005; Kristjánsson & Driver, 2005, 2008; Lamy et al., 2008). Together with the current findings, these results argue for separate mechanisms of target and distractor effects in intertrial priming. In the current task, the VWM colors must be maintained for subsequent recall. When the contents of VWM match the current search target, there is little conflict between VWM and priming. The default influence of VWM and priming both leads to selection of the search target. In contrast, when distractor colors must remain active for later recall, this may inhibit the natural mechanism of inhibition of distractors (Bichot & Schall, 2002). In addition, sustained activations from priming of the target and from maintenance of distractor colors in VWM might lead to conflicting guidance signals. This may lead participants to avoid the use of these ambiguous activations to guide attention, since they do not consistently aid search performance.

Although previous evidence suggests that the implicit memory mechanism subserving PoP is immune to influences from explicit VWM (Maljkovic & Nakayama, 1994; Lee et al., 2009), our findings suggest how these two memory systems can interact, and highlight how target and distractor effects in intertrial priming are based on separate mechanisms. Moreover, the current results support the notion that VWM content has differential impact based on task relevance in line with evidence on working memory guidance of attention (Arita et al., 2012; Carlisle & Woodman, 2011a, 2011b, 2013; Kiyonaga et al., 2012; Woodman & Luck, 2007). Importantly, our results show that the implicit and explicit memory systems may interact or inhibit each other during attentional processing if they provide conflicting signals.

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Compliance with ethical standards

Statement of human rights All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and

with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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