

FLEXIBILITY IN WORKING MEMORY
GUIDANCE OF ATTENTION

Nancy B. Carlisle

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Approved:

Dr. Geoffrey Woodman

Dr. Adriane Seiffert

Dr. Gordon Logan

Dr. Megan Saylor

DEDICATION

To my husband, Mike:
I wouldn't have made it through without your help and support.
It's been fun to share the graduate school journey with you.

and

To my Mom and Dad:
Thank you for always encouraging my academic pursuits.

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LIST OF ABBREVIATIONS/NOMENCLATURE

Goal-related attentional template: The top-down attentional biases set for a search for a specific goal.

Guidance: Working memory guidance of attention.

CHAPTER 1

Introduction

To function normally in daily life, we must be able to attend to the most important visual information that is available. Control of attention is especially important given the multitude of objects in a typical setting. For instance, when walking to a coffee shop, we are confronted with thousands of objects. Our attention focuses on those that are surprising and salient, such as a stopped police car with flashing lights, and those that are relevant for the task at hand, such as a walk sign. Sometimes the salient stimuli are those that are most important, like a car ignoring a red light and speeding toward us, but often the visual information that is most relevant for the task at hand is not the most salient information in the scene. To complete our daily tasks, it is therefore important that we are able to control our attention.

The distinction between attention that is captured by salient stimuli in the visual field and attention that is directed by top-down control has been apparent in theoretical depictions of attention for more than 100 years. William James (1890) understood that our attention was influenced by two competing forces, external stimuli and internal control settings. James stated: “When... sensorial attention is at its height, it is impossible to tell how much of the percept comes from without and how much from within; but ... the *preparation* we make for it always partly consists of the creation of an imaginary duplicate of the object in the mind, which shall stand ready to receive the outward impression” (p. 439). He goes on to say “The image in mind *is* the attention; the *preperception*... is half the perception of the looked-for

thing” (p. 442). Surprisingly, James not only indicates that we prepare for a specific stimulus by activating its representation in memory, but also suggests that perception is a combination of this top-down activation of an object’s representation and the bottom-up activation from the visual field. The theories of attention since James have also maintained the idea that attention is a combination of the inherent salience of visual objects and the viewer’s internal control settings (Broadbent, 1957; Deutsch & Deutsch, 1963; Norman, 1968; Duncan & Humphreys, 1989; Bundesen, 1990; Wolfe, 1994; Cowan, 1995; Desimone & Duncan, 1995; Logan, 2002; Bundesen, Habekost & Kyllingsbaek, 2005).

Attentional control has been important across the past 50 years in many of the major lines of attention research. In dichotic listening tasks, a major question centers on which stage of processing attentional control affects (Treisman, 1969; Deutsch & Deutsch, 1963). In studies of attention as a binding mechanism, a major question is whether attentional control is necessary for all types of target identification or whether some stimuli can be identified preattentively (Treisman & Gelade, 1980). In studies of target-distractor similarity, there are clear limitations in the effectiveness of top-down attentional control based on bottom-up stimulus differences (Duncan & Humphreys, 1989). In studies of attentional cuing, the main goal is to contrast shifting spatial attention based on an endogenous top-down attentional control signal with shifting spatial attention based on exogenous cues (Posner, 1980). Finally, in studies of the attentional blink, the limitations of top-down control of attentional processing are demonstrated when multiple stimuli are presented quickly in time (Chun & Potter, 1995). These lines of research all rest on the assumption that we can control our attention, and, in a sense, examine the boundary conditions of attentional control. In spite of the consistent theoretical and empirical

importance of attentional control, the mechanisms behind this fundamental part of visual life have remained poorly understood. What is the nature of the internal representation used to guide attention?

One reason for the lack of empirical examinations of the mechanisms of attentional control is that most theories do not make specific claims about how top-down control is implemented. However, in 1995, Desimone and Duncan made a strong statement about the implementation of attentional control: working memory representations create top-down attentional biases. Once an item is in working memory, additional top-down control is not needed to create a biasing signal. This proposal is intriguing for its simplicity, but it has not been consistently supported by empirical tests of the influence of working memory on attention (see Olivers, Peters, Houtkamp, & Roelfsema, in press, for a review). Researchers have been unable to find a single methodological difference that can reconcile the discrepant results, and the range of findings suggests a flexible relationship between the contents of working memory and visual attention.

In this dissertation, I will describe multiple related lines of research focused on using new paradigms to better understand the relationship between working memory and top-down attentional control. As a whole, this work will help clarify the influence of working memory on attention and inform future theories about the mechanisms of top-down attentional control.

Background

Control of attention is important for successfully navigating our daily lives, and understanding the coordination of working memory and attention is a promising avenue for advancing our knowledge of attentional control. However, the current literature on working memory guidance of attention has become deeply rooted in a debate regarding whether working memory representations create an automatic influence on attention. This perseveration has limited forward progress in our understanding of the influence of working memory on attention. Most importantly, the literature does not distinguish between the following two important questions based on the predictions of biased competition. Do working memory representations create an automatic attentional bias? Is any automatic attentional bias from working memory the equivalent of attentional biases generated during goal-dependent search? The latter question is important for our understanding of the mechanism relating working memory and attention, but has frequently been overlooked in the literature.

To understand the current state of the literature on the influence of working memory on visual attention, three pieces of information need to be examined. To begin, it is necessary to explore the theoretical basis of the claim that working memory representations bias attention. Next, it is important to clarify the outcome of empirical research assessing the influence of working memory on attention. Finally, it is beneficial to examine the previous attempts to reconcile conflicting findings in the literature. Each of these pieces of information will be addressed in turn in the following sections.

Theoretical basis of working memory in attentional control

Many theories of attention propose that an internal template is used to direct attention to task-relevant items (Duncan & Humphreys, 1989; Bundesen, 1990; Desimone & Duncan, 1995). However, the only theory that defines a mechanism linking working memory templates and attention is the biased competition theory of attention (Desimone & Duncan, 1995). In biased competition, objects in the visual field compete for access to the limited capacity receptive fields of cells at multiple stages of processing throughout the visual system. Bottom-up biases increase the likelihood that salient items will be attended due to a competitive bias for local inhomogeneities in the visual field. These bottom-up biases are pervasive, and without another source of biasing our attention would be directed to the most salient item in the visual field. To ensure that we are able to control our attention, the biased competition theory also proposes top-down biases that increase the likelihood that task-relevant items will be attended.

The biased competition theory combines two findings from single-unit recordings in monkeys to explain how these top-down biases are created. Chelazzi, et al (1993) recorded from neurons in inferior temporal cortex (IT), an area that contains cells responsive to complex forms, when monkeys performed a delayed-match-to-sample task. In this task, the monkeys were presented with a cue and then later had to saccade to a cue-matching item instead of another item in the cell's receptive field. When the cue elicited a strong response from the cell, they found a sustained increase in firing rate during the delay period between the cue and the search stimuli. The biased competition theory proposes that this increased firing rate during the delay period is the neural basis of the attentional template for an object.

Moreover, because sustained activity is also found during the retention interval of a working memory task, they claim that this sustained activity is the outcome of an item being maintained in working memory and may reflect the coordination of prefrontal cortex and IT cortex. As Desimone and Duncan state “attentional templates for objects and their features may derive from the mechanisms underlying working memory” (p. 212, 1995). More generally, this proposal means that attentional templates are working memory representations, and are instantiated in the brain through sustained activations in cells selective for memory-matching information. Thus, biased competition generalizes findings from single-unit studies in monkeys to all search tasks. Biased competition proposes the mechanism of top-down influence derives from working memory guiding visual attention (henceforth, I will use the term *guidance* as shorthand for the top-down bias of working memory on attention).

The guidance mechanism in biased competition theory suggests an intimate linkage between the working memory system and attentional control. This idea of working memory creating attentional control has taken root in the literature (Awh & Jonides, 2001; Olivers, 2008; Soto, Hodsoll, Rotshtein & Humphreys, 2008), as a simple mechanistic explanation for what appears to be a complicated process. However, this elegantly simple mechanism for exerting top-down control comes with a cost; it does not allow flexibility in how working memory influences attention. This creates four important consequences for this explanation of top-down attentional control. First, since guidance is the only mechanism through which top-down control is exerted, this biasing signal should be sufficient to ensure that memory-matching items are frequently selected during search. Second, since this top-down biasing signal is present before the search array is presented and influences competition for attention,

guidance should influence the first stages of selective processing. Thus, evidence of a competitive advantage for memory-matching items should be present during the earliest portions of search. Third, while this mechanism suggests an obligatory relationship between covert attention and working memory representations, it does not necessitate that an early shift of covert attention will always lead to a later effect in overt attention. This means that measures of covert attention will be more sensitive than measures of overt attention in assessing guidance. Fourth, a goal of attending to memory-matching items is not necessary to create the bias, and therefore guidance should be involuntary. This means that guidance should be present when the goal of the task is to attend to the memory-matching items *and when the goal is to attend to another item*. Moreover, any representation in working memory should create an attentional bias that is the equivalent of a goal-related attentional template. Overall, the biased competition framework suggests that working memory representations create an involuntary bias for covert attention to be guided toward memory-matching items early in selective processing of information in the visual field.

Although biased competition suggests that the control parameters necessary for search are a fundamental consequence of holding information in working memory, many other theories of attention and working memory suggest that control parameters are separate from the simple storage mechanisms of memory. Atkinson and Shiffrin (1968), Baddeley and Logie (1999), and Bundesen & Habekost (2007) all propose separate executive processes that help to determine what will enter and be maintained in memory. Thus, in biased competition the distinction between storage and one ‘working’ aspect of memory is blurred.

The obligatory link between working memory and attention may limit the usefulness of biased competition theory. An alternate model that contains many of the mechanisms that

make biased competition strong, without the limitation of inflexibility, is Bundesen's Theory of Visual Attention (TVA, 1990). Like biased competition, TVA proposes competition for representation is the underlying mechanism of attention. In TVA the competitive process is related to the categorization of an item. The outcome of competition is that an object is simultaneously categorized, entered into working memory, and is attended. Like biased competition, the competition in TVA is influenced by bottom-up and top-down factors. In TVA, bottom-up factors come from sensory evidence. The sensory evidence depends on the match between an item and a category of stimuli. A good match will have strong sensory evidence, and a poor match will have weak sensory evidence. An object with higher salience provides stronger sensory evidence of a category match. Whether a specific object is selected is also dependent on its own competitive advantage compared to the other items in the visual field. Without any top-down control, TVA proposes that the object with the strongest sensory evidence will be attended. TVA also describes two additional forms of biasing from top-down control: a bias for categorizing the objects in the visual field along a specific dimension (pigeonholing), and attentional weights for specific features (filtering). Adjusting the bias and attentional weights can create a competitive advantage for task-relevant items, which can supersede the salience of other items in the visual field.

TVA proposes that items in working memory can be used as templates. In this case, the biases and attentional weights will be adjusted to select memory-matching items in the visual field. Although TVA is consonant with biased competition in describing working memory as the location of templates, the link between working memory and attentional control is more adaptable in TVA. Bundesen states that the top-down control parameters in TVA can be "manipulated freely to optimize performance in the experimental task" (p. 526,

1990). TVA states that working memory representations may be used to generate top-down control, but explicitly states that they need not do so in all situations (NTVA, Bundesen, Habekost, & Kyllingsbaek, 2005).

The contrasting statements in biased competition and TVA about whether working memory must influence attention is, at the core, a differing prediction about the mechanism of top down attentional control (Figure 1). Whereas biased competition suggests that executive control can only exert an influence before information is in working memory, TVA suggests that executive control mediates the influence between working memory and attention. Therefore, any assessments of whether working memory generates a consistent, involuntary attentional bias are essentially contrasting the predictions of biased competition and the predictions of TVA.

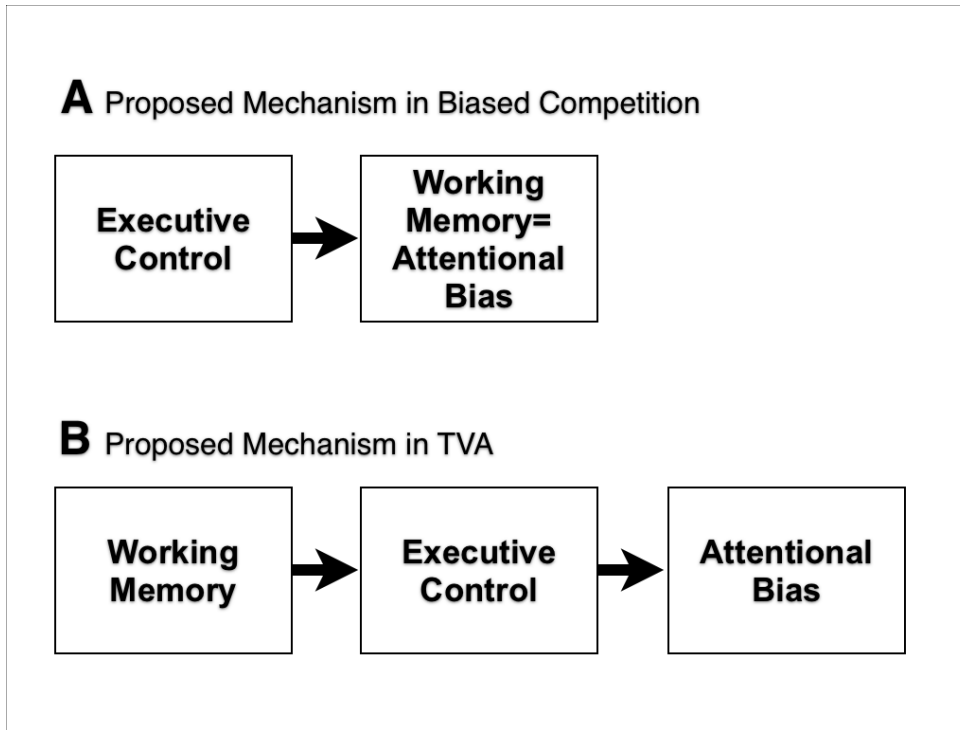


Figure 1. Simplified Diagrams of the Generation of Attentional Biases. Arrows reflect optional relationships between the cognitive processes. A) Biased competition (Desimone & Duncan, 1995). B) TVA (Bundesen, 1990).

Empirical studies of the influence of working memory on attentional control

The specific link between working memory and attention proposed by the biased competition theory has been tested in a number of empirical studies. The majority of these studies have used behavioral measures to assess whether items that match the contents of working memory show a competitive advantage over other items in the visual field.

Some studies have assessed guidance by determining whether a working memory item will be attended when there is no task, or when attending to the memory-matching item is compatible with the goals of the current task. In these studies, participants performed a working memory task, and were presented with multiple items during the delay interval, one of which could match the contents of working memory. These studies have consistently shown that working memory representations are attended more frequently than other

representations (Downing, 2000; Experiment 1-2, Soto, Heinke, Humphreys & Blanco, 2005; Soto, Humphreys, Heinke, 2006a; Soto, Humphreys, & Rotshtein, 2007; Huang & Pashler, 2007). However, these studies do not lead to the conclusion that the influence of working memory representations on attention is involuntary, because the results would be equally compatible with an alternative interpretation that individuals are directing their attention to memory-matches voluntarily. One reason to direct attention to memory-matching items during search would be to serve as an aid in the concurrent task of maintaining the memory representation (Woodman & Luck, 2007).

Many other studies have made a stronger test of the involuntary influence of working memory on attention by measuring whether memory-matching items will be attended, even though they are not beneficial for (or distract from) the current task. Using this stronger test of the influence of working memory on attention, many have still found that items matching representations in working memory are selectively attended (Experiment 4, Soto, Heinke, Humphreys, & Blanco, 2005; Olivers, Meijer, & Theeuwes, 2006; Soto & Humphreys, 2007; Soto & Humphreys, 2008; Experiment 1, Olivers, 2009). Some of these studies find longer reaction times when a memory-matching distractor is present in a search array, which is in line with the conclusion that the memory-matching item was attended. Others measure eye-movements and found memory-matching distractors are fixated, i.e. overly attended, more than other distractors. Because evidence has suggested that memory-matching items were selected even though attending to them did not match the goals of the current task, a recent review paper has concluded “working memory exerts an involuntary influence on visual attention” (p. 344; Soto, Hodsoll, Rotshtein, & Humphreys, 2008). This same review paper went on to suggest that “guidance of selection from working memory occurs automatically,

even when it is detrimental to task performance” (p. 342). These findings are compatible with the strong linkage between working memory and attention proposed by the biased competition theory.

In contrast, other studies have failed to find evidence that working memory representations guide visual selection using similar behavioral methods (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Woodman & Luck, 2007). Some of these studies have even shown speeding of search for another target when working memory distractors are present in the array, suggesting that the items can be actively avoided. These findings are certainly at odds with the claims of automatic and involuntary guidance of attention to memory-matching items. Instead, they are more consistent with the selective usage of working memory to guide attention as proposed by TVA (Bundesen, Habekost & Kyllingsbaek, 2005). The studies that fail to find evidence of working memory guiding attention conclude that all working memory representations do not create a top-down attentional bias. These conclusions suggest that biased competition’s explanation of top-down biases may be incorrect.

Attempts to reconcile conflicting findings

There are numerous proposed explanations for failures to show automatic guidance, and they are not mutually exclusive. Some of these explanations have been clearly elaborated, while others have been minor points in discussion sections. In the following section, I will provide a conceptualization of each proposal.

Some explanations are consistent with an unaltered version of biased competition, suggesting specific aspects of experimental designs may explain failures to find guidance.

According to these proposals, failures could be due to weak memory representations that do not provide a strong top-down bias (Soto, Hodsoll, Rotshtein, & Humphreys, 2008), weak bottom-up signals that are insufficient to activate a match between the external stimuli and the top-down biases (Olivers, 2009), or dependent measures that are insensitive to subtle changes in the earliest shifts of covert attention created by the memory representations (Carlisle & Woodman, in press). However, none of these explanations can account for suggestions in the literature that memory-matching stimuli may sometimes be suppressed (Woodman & Luck, 2007; Downing & Dodds, 2004).

Another set of proposals suggests that biased competition is missing a component. None of these proposals are inconsistent with the fundamental mechanism of biased competition, where attention is conceptualized as a competition between objects for neural representation. Instead, they suggest additional mechanisms that should be added to the fundamental biased competition mechanism to account for the inconsistent findings in the literature. The first additional mechanism would be a gating mechanism between working memory and bias, dependent on additional cognitive load (Soto & Humphreys, 2008). When load is low, automatic guidance occurs, but when load is high, no top-down signals are created. This suggests that we are only able to exert top-down control when there is not additional working-memory load (less than 3 object representations in Soto & Humphreys, 2008). A second proposal suggests a prioritization within working memory, where only a single working memory representation can create a top-down control signal (Olivers, 2009). This proposal does not explain what determines which item will get this prioritized status. The third proposal suggests that executive control can reduce the influence of automatic biasing signals, but with a delay (Han & Kim, 2009). The final proposal suggests that the

influence of working memory representations on attention is mediated by goals (Woodman and Luck, 2007).

This final proposal will be highlighted in the current work because it parallels the theoretical prediction of TVA and contrasts with the proposal of biased competition. A flexible relationship between working memory and attention is also compatible with the conclusions in empirical papers by Downing & Dodds (2004) and Houtkamp & Roelfsema (2006), which state that the items in working memory can be used flexibly. According to the *flexible guidance* proposal, working memory representations only create a top-down biasing signal if they are compatible with the current task. Although an instruction not to attend to memory-matching items failed to eliminate guidance in one study (Olivers, 2009), the proposal that guidance is flexible has received support from two other studies. Woodman and Luck (2007) showed that a guidance effect was only observed when the search target could be the memory-matching item. In addition, increasing the likelihood that a memory-matching item is a search target increased RT benefits when it was a search target and RT costs when it appeared as a distractor (Carlisle & Woodman, in press-a).

One ERP study has also supported flexibility, suggesting that attention may be actively shifted away from memory-matching items when they are task-irrelevant. An ERP study from Sawaki and Luck (2010) showed suppression of memory-matching distractors, finding that they elicited a component related to distractor suppression, the Pd. Evidence of suppression of memory-matching items can also be found in reaction time effects that show faster responses when memory-matching items are present as distractors, suggesting they may be actively avoided (Downing & Dodds, 2004; Woodman and Luck, 2007). These

findings suggest that working memory representations may be used to create attentional enhancement or suppression based on what is most beneficial for the task at hand.

Flexible use of memory representations to influence attention is incompatible with the generalization of the single-unit recordings studies linking working memory and attentional templates from biased competition, but it is compatible with another single unit recording study. When monkeys are looking for a change in a grating stimulus, responses of individual cells in V4 to the same amount of change are larger in a block where the majority of trials involved a difficult discrimination than in blocks where the majority of trials were an easy discrimination (Boudreau, Williford, & Maunsell, 2006). This flexibility in the way cells in V4 respond based on task difficulty suggests that the monkeys strategically choose how to distribute attention. A recent review of neuroscience findings related to top-down control suggests that templates may be maintained in the prefrontal cortex, and then create biases in inferotemporal cortex (Miller & D'Esposito, 2005). So, while it seems true that attentional templates can influence activity in areas such as IT and V4, the relationship between working memory and attentional templates may be flexible.

Although the flexible goal-dependent account of the previous findings has explanatory power and empirical support, it lacks predictive power. How can one be certain when participant's goals are to attend to the memory-matching item? Why was guidance found in some of the previous studies where the memory-match was always a distractor while other studies failed to find evidence of guidance? Additional support is needed before the flexible guidance account can be accepted.

In summary, understanding how attention is controlled is theoretically important because top-down control is an important factor in accounts of attentional deployment. The

control of attention is also practically relevant because it is a critical aspect of our daily lives. Without top-down attentional control, we would have difficulty performing goal-directed actions and would be easily distracted from our current tasks. In this work, I describe specific hypotheses regarding the flexibility of guidance aimed at gaining a better understanding of how top-down control is implemented. Understanding how this top-down control is generated is important for evaluating theories of attention, and providing strong empirical evidence will help to constrain future theories of attention. In addition, I hope that this work will help move the literature past the debate of automaticity and allow progress toward a more complete understanding of top-down attentional control.

Goals

1. To contrast neural evidence of selection of memory-matching objects when task-irrelevant and task-relevant.

While the biased competition account suggests that items matching working memory representations will be selected regardless of whether they are relevant for the current task, the flexible guidance account suggests that memory-matching items should only be selected if they are task-relevant. Previous behavioral work has led to support for each of these conflicting proposals. The lack of clear evidence could be due to the insensitivity of behavioral measures to early covert attentional effects. To assess the contrasting proposals of biased competition and flexible guidance, I have used a neural measure of attentional selection, the N2pc component of observers' event-related potentials (ERPs). Note that these data are currently in press (Carlisle & Woodman, in press).

2. To measure suppression or enhancement of memory-matching objects.

The flexible guidance account suggests that memory-matching items can be enhanced or suppressed based on their relevance for the current task. To assess this proposal, it is necessary to use accurate measurements of enhancement and suppression to contrast the attentional processing of memory-matching items with the processing of targets and distractors. There have been suggestions of suppression from behavioral findings (Downing & Dodds, 2004; Woodman & Luck, 2007) and an ERP study (Sawaki & Luck, 2010). On the other hand, there have also been suggestions of enhancement from behavioral studies (e.g. Soto, Hodsoll, Rotshtein & Humphreys, 2005; Olivers, Meijer, & Theeuwes, 2006) and

one ERP study (Kumar, Soto, & Humphreys, 2009). Therefore, before strong conclusions about the enhancement or suppression of memory-matching items are made, a more detailed contrast between the enhancement and suppression of memory-matching items, search targets, and distractors is needed. The P1 and N1 components have proved useful for detailed attentional comparisons (Luck, Fan, & Hillyard, 1993), and are used in the following work to contrast the attentional modulation of memory-matching items, goal-related search targets, and distractors.

3. To apply an alternate theoretical framework to guidance.

The flexible guidance account proposes that differing participant goals across previous studies can explain the different results found. When guidance was shown, individual participant's goals included attending to the memory-matching items. When individual participants did not show guidance, it was because they did not have a goal of attending to the item. This reasoning can certainly explain all the previous results, but it does not explain why participants would sometimes have a goal of attending to the memory-matching item even though it was never the search target. Before the debate about automaticity of guidance can be laid to rest, it will be important to find a general framework that can be used to explain all the findings in the previous literature.

Although the previous studies of working memory guidance of attention have used the same basic paradigm to assess guidance, there has been little attention to the specific stimulus parameters of targets and distractors. In addition, conclusions about whether attention is directed to memory-matching items have been muddled with conclusions about whether attentional biases from working memory representations are the equivalent of a goal-

related attentional template. The application of the TVA framework to the design of guidance tests allows for a more controlled comparison than has previously been used because TVA makes clear predictions about what bottom-up stimulus factors should be controlled to ensure they do not interact with measurements of top-down control. To directly test whether any item in working memory creates an attentional bias that is the equivalent of a goal-related attentional template, it is critical to make a controlled comparison between a task-relevant and task-irrelevant working memory item. I have applied the TVA framework within an eye tracking study to assess the prediction from biased competition that a task-irrelevant working memory representation creates the same attentional biases as a goal-related attentional template.

CHAPTER 2

ELECTROPHYSIOLOGICAL MEASURES OF SELECTION OF TASK-IRRELEVANT STIMULI MATCHING WORKING MEMORY REPRESENTATIONS

In daily life, we regularly perform visual search for specific items that we need for our current task in cluttered scenes. It is of significant theoretical importance to determine how we guide our limited-capacity processing mechanisms to these task-relevant objects. Several theories of attention propose that our top-down control over search is dependent on holding a template representation of the object we wish to find in working memory (Bundesen, 1990; Bundesen, Habekost, & Kyllingsbaek, 2005; Desimone & Duncan, 1995; Duncan, 1996; Duncan & Humphreys, 1989). The theory of biased competition makes the clearest statement about how working memory templates influence visual attention (Desimone & Duncan, 1995). It proposes that the act of holding a representation in working memory leads to increased activity of the cells in the visual system that code for the features of the template. This increased activity creates a bias for neurons to represent template-matching items during the pervasive competition for access to the limited-capacity processing mechanisms of the brain (e.g., the receptive field of a neuron, representation in working memory, response selection, etc.). This elegant mechanism of top-down attentional control is dependent only on the template representation being in working memory. In the present study, we directly tested the hypothesis that maintaining a representation in visual

working memory is sufficient for covert attention to be directed toward similar items in complex scenes.

Although the attentional template proposal from biased competition (Desimone & Duncan, 1995) is intriguing for its simplicity, previous studies of the influence of working memory representations on visual attention that measured overt behavior have yielded mixed results. A simple explanation for the variability of the findings based on behavioral evidence may be due to the nature of the evidence itself. It is possible that working memory representations consistently produce an attentional bias, but that behavioral measures are not sensitive enough to detect early deployments of attention to memory-matching items. Overt behavior measures the output of all cognitive processing. Although theories propose that attentional templates in working memory will influence mechanisms of perceptual attention, it is possible that the variability of processing time consumed during stages other than perception (e.g., response selection) result in behavioral measures that do not reliably show the early and automatic effects that working memory representations exert upon attentional selection. Consistent with this hypothesis, Han & Kim (2009) have proposed that attention is directed to memory-matching items early in perceptual processing of multi-element arrays, but that a relatively late onset of cognitive control can wash out this involuntary effect during search tasks with sufficiently long RTs. Similarly, measures of overt attentional selection (i.e., eye movements) may not be a consistent measure of the deployment of covert attention. Although shifts of covert attention appear to precede overt eye movements (Kowler, Anderson, Doshier, & Blaser, 1995), covert attentional orienting need not be followed by an overt shift of gaze (Posner, 1988). Therefore, it is critical to directly measure deployments of covert attention if we wish to know how working memory representations influence the

focusing of perceptual attention. Fortunately, ERPs can provide such measures and, thus, provide critical information about the nature of the interactions between working memory representations and attention.

An alternative to the hypothesis that behavioral measures are simply imprecise is that additional executive-control mechanisms mediate the influence of representations in working memory on mechanisms of perceptual attention. This hypothesis is supported by theoretical proposals (Bundesen et al., 2005) and by evidence from a number of empirical studies (Downing & Dodds, 2004; Peters, Goebel, & Roelfsema, 2009; Woodman & Luck, 2007). However, it is contrary to the proposal that the representation of an item in working memory is sufficient to create an involuntary bias to similar environmental inputs (Soto, Hodsoll, Rotshtein, & Humphreys, 2008). One finding from Woodman and Luck (2007) suggests that a goal to attend to memory-matching items may be necessary for perceptual attention to be influenced by working memory. The study showed when participants knew that memory-matching items in the search array would never be the target of search, there was no significant influence of the presence of memory-matching items on RTs. However, when participants knew that the memory-matching items would be the search target on some trials, attention was then directed to the memory-matching items. These findings suggest that a *goal* of attending to memory-matching items might mediate the relationship between working memory and perceptual attention.

If executive control is necessary for a working memory representation to direct attention to a matching perceptual input, then we expect different patterns of findings across studies with different task demands. These different patterns should be present in studies that directly measure of early shifts of covert attention. Findings from two ERP studies show

different patterns, supporting the idea that more direct measures also show flexibility in the use of working memory representations. Kumar, Soto, and Humphreys (2009) reported that memory-matching distractors elicited a contralateral negativity (i.e., the N2pc component) during an efficiently performed visual search task. This supports the proposal that covert attention is deployed to distractors that match a working memory representation because the N2pc is believed to index the deployment of covert perceptual attention (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994b; Woodman & Luck, 2003b). In contrast, Peters, Goebel, and Roelfsema (2009) had observers detect targets in serially presented streams of objects. They found that distractors that matched a memory representation elicited a P3b that was indistinguishable from that elicited by the other distractors, but different from the P3b elicited by targets. This latter study contradicts the former in suggesting that memory-matching items are not selected by perceptual attention mechanisms like task-relevant targets are. These opposing patterns of findings could be explained by the hypothesis that different cognitive control settings were operative in these different task contexts. However, many methodological differences exist between the two studies precluding direct comparisons. One of our present goals was to determine whether working memory representations influence ERP measures of early covert attention in different ways depending on task demands while controlling other experimental variables.

In the present study, we used the N2pc component to directly measure where attention was covertly deployed during visual search while an object representation was maintained in working memory for a concurrent change-detection task. The N2pc component provides an index of selection by a covert perceptual attention mechanism that operates prior to awareness and working memory encoding (i.e., early in the course of visual

processing, see Woodman & Luck, 2003a). Due to the lateralized nature of the N2pc, it can be used to measure where attention is focused throughout an extended process of visual search as attention is shifted between multiple objects, including nontargets (Woodman & Luck, 1999, 2003b). If working memory representations consistently and involuntarily bias perceptual attention to select matching items early in the course of processing complex scenes (i.e., automatic attentional capture by memory-matching items), then we should find that memory-matching items elicit an early N2pc regardless of whether attending to memory-matching items is consistent with task demands. We tested this prediction in Experiments 1-3 in which the memory-matching item was never the search target. In contrast, the executive control hypothesis predicts we should only find evidence of memory-matching items eliciting an N2pc when attending to these items is consistent with the goals of the task. We tested this prediction in Experiment 4, where we examined whether the influence of working memory representations on attention occurs when the participant's goal is to report a feature of the memory-matching input. Contrasting these two predictions will help clarify our understanding of how working memory influences attention, what properties an attentional control mechanism should possess, and which existing theories of attention can account for the findings.

Experiment 1

In Experiment 1, we recorded ERPs from participants while they performed a visual search task during the retention interval of a change-detection task. Figure 2 shows an example of the Landolt-square stimuli and procedure for these two concurrently performed

tasks. To test the potency of the guidance of attention by working memory representations, the memory item on each trial never shared features with the search target and participants were made aware of this during the instructions (e.g., Downing & Dodds, 2004; Folk, Remington, & Johnston, 1992; Woodman & Luck, 2007). Our design provided three trial types based on the items in the search array. On *memory-match absent* trials, no memory-matching distractor was in the search array. On *memory-match opposite* trials, a memory-matching distractor was in the opposite visual hemifield as the search target. On *memory-match same* trials, a memory-matching distractor was in the same visual hemifield as the search target.

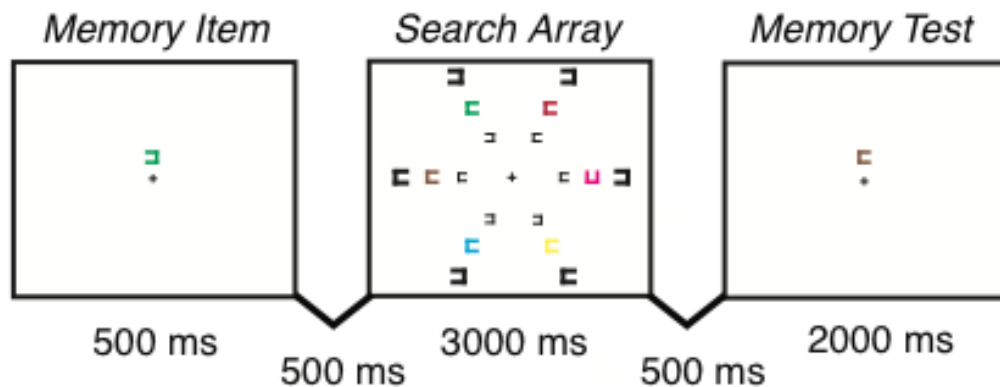


Figure 2. Example of the stimuli and sequence of events in Experiment 1. The search array shown is an example of a memory-match opposite hemifield array in which the green memory-matching item is in the upper, left part of the array and the magenta target is to the right of fixation. This illustrates the general trial structure used in all the experiments.

During search tasks performed while an item is maintained in working memory for another task (e.g., change detection), the search target template and the other working memory representation may compete for attention (Downing & Dodds, 2004). To create a situation in which we were most likely to see an effect of the memory-matching item during visual search, we used a shape-defined target and a color-defined memory-matching

distractor. This was done for two reasons. First, most of the previous studies of the N2pc component using visual search tasks have defined the task-relevant item based on color and the use of such stimuli results in a large and early N2pc to the color-defined target (e.g., a $\sim 1.0 \mu\text{V}$ effect beginning about 175 ms poststimulus; Luck, in press). Second, previous behavioral research has shown that it is easier to orient attention to items based on their color (using highly distinguishable colors) than even moderately complex shapes (e.g., Duncan & Humphreys, 1989; Olivers & Humphreys, 2002; Wolfe, 1998a). If the search target and memory representation are competing for control of attention, then our stimuli and experimental design should help the color maintained in working memory for the change-detection task win the competition for attentional guidance over the actual search target defined by the feature of gap location on the Landolt-square stimuli. Thus, we stacked the deck in favor of observing an influence of the memory-matching items on covert perceptual attention.

Our paradigm allows for two complementary measures of early covert attention during search using the N2pc. First, we can measure an N2pc to the memory-matching item. Second, we can determine how the presence of the memory-matching item influences the N2pc to the search target by comparing memory-match absent trials with trials in which the memory match was in the same or opposite hemifield. We predicted that if memory-matching items automatically guide covert attention and previous failures to see evidence of guidance were due to imprecise measures of early covert attention, then the N2pc would index attentional deployments to memory-matching distractors. The strong prediction based on the proposals that memory-matching items automatically capture attention (Han & Kim, 2009; Soto et al., 2005; Soto et al., 2008), is that when the memory-matching item is present

in the search array it will elicit the first N2pc activity following array onset. Figure 3 illustrates the pattern of N2pc activity predicted if memory-matching items capture attention (see also Kumar et al., 2009). The hemisphere contralateral to the memory-matching item should become more negative than the ipsilateral hemisphere at approximately 175 ms poststimulus regardless of the location of the search target in the array. When the memory-matching distractor is in the same hemifield as the search target, we expect to see the N2pc to these items summate, because attention will be immediately and consistently summoned to this hemifield, unlike trials when the memory match is absent and attention is first inadvertently shifted into hemifield that does not contain the target on a subset of trials. A more moderate automatic capture prediction would be that the memory-matching item captures attention on a subset of trials. This would result in a reduced N2pc amplitude to the search target on memory-match opposite hemifield trials and increased N2pc amplitude on memory-match same hemifield trials relative to memory match absent trials.

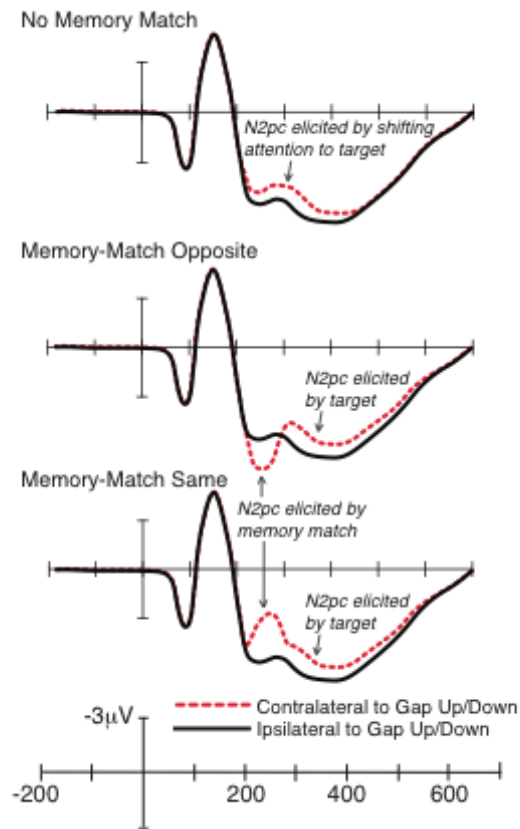


Figure 3. Hypothetical predictions of the pattern of N2pc activity based on the idea that attention will be captured by the memory-matching item.

The competing hypothesis is that task goals determine whether a given memory representation will be used to guide attention (Bundesen et al., 2005; Downing & Dodds, 2004; Logan & Gordon, 2001; Woodman & Luck, 2007). If this hypothesis is correct, then memory-matching distractors should not elicit an N2pc during the search task in Experiment 1, because participants know that memory-matching items are not the target and attending to them is inconsistent with the goals of the search task. This would mean that the N2pc elicited by the search target would be unaffected by the presence or location of the memory-matching item.

Methods

Participants. 10 participants were paid \$10 per hour of participation. All reported normal or corrected-to-normal vision, and provided informed consent before participation. The Vanderbilt University Institutional Review Board approved all procedures. Three participants were replaced due to excessive artifacts (i.e., artifacts on more than 30% of the trials with correct search and memory performance).

Stimuli and Apparatus. Participants were seated approximately 114 cm from a computer screen and responded using a gamepad (Logitech Precision, Switzerland). All stimuli were presented on a light gray background (33.1 cd/m^2). A black fixation cross (0.13° line length, 0.03° line thickness, 0.84 cd/m^2) was presented at the center of the screen throughout each trial. Memory and search stimuli were drawn from 7 highly distinguishable colors (red, $x = .616$ $y = .337$, 13.9 cd/m^2 ; green, $x = .284$ $y = .959$, 44.1 cd/m^2 ; blue, $x = .146$ $y = .720$, 6.42 cd/m^2 ; yellow, $x = .407$ $y = .504$, 54.3 cd/m^2 ; magenta, $x = .295$ $y = .153$, 19.3 cd/m^2 ; white, $x = .290$ $y = .313$, 57.2 cd/m^2 ; sienna, $x = .432$ $y = .405$, 16.1 cd/m^2). Memory stimuli were colored Landolt squares ($0.33^\circ \times 0.33^\circ$, 0.07° line thickness, gap size 0.20°) centered 0.49° above the fixation cross. Six possible search targets were colored Landolt squares ($0.33^\circ \times 0.33^\circ$, 0.07° line thickness, with a gap size of 0.20°) presented equidistant on an imaginary circle, centered 2.61° from fixation. Two rings of black Landolt squares (0.84 cd/m^2) were presented as distractors and scaled according to the cortical magnification factor with eccentricity (inner ring stimuli: $0.20^\circ \times 0.20^\circ$, 0.03° line width, 0.11° gap width, 1.57° from fixation; outer ring stimuli: $0.46^\circ \times 0.46^\circ$, 0.10 line width, 0.28° gap width, 3.65° from fixation, see Woodman & Luck, 2003b). Articulatory suppression stimuli were presented on an instructional screen at the beginning of each set of 30 trials ('1 2 3 4'; '6 7 8

9'; 'a b c d'; or 'w x y z'; each digit or letter was approximately $0.40^\circ \times 0.40^\circ$ and was drawn in black, 0.84 cd/m^2).

Procedure. The timing and stimulus sequence is illustrated in Figure 2. Each trial began with the presentation of the fixation point for 800-1200 ms (randomly jittered with a square distribution). Next, the memory item was displayed for 500 ms followed by a 500 ms period where only the fixation point was visible. Next, the search array was presented for 3000 ms. After the search array offset, a fixation point was presented for 500 ms followed by the memory test which was presented for 2000 ms. After the memory test, a blank screen was presented for 1400-1800 ms (randomly jittered with a square distribution) before the next trial began. It is important to note that these timing parameters have been shown to elicit consistent RT effects of 30 ms or larger due to the presence of memory-matching distractors (Dombrowe, Oliver, & Donk, 2010).

The search target was the one Landolt square in each array with a gap on the top or bottom while distractors had a gap on the right or the left. Half of the search arrays contained no memory-matching distractor. The other half of the trials contained a memory-matching distractor presented at a random location in relation to the target. This memory-matching distractor matched the memory item on color. Analyses were performed to determine if the presence of distractors with an exact memory match (i.e., color and shape) led to effects that differed from those of color-only memory matches. In this and the following experiments, no difference was found between exact and color-only memory matches in the N2pc analyses (all $ps > .15$). Thus, we collapsed across these trials in the analyses reported. This led to three search array types: memory match absent, memory match same hemifield, and memory match opposite hemifield. The memory test item could

be the same as the memory item (half of all trials) or the gap could move to the opposite side (quarter of all trials) or the color could change (quarter of all trials). All of these types of trials were randomly interleaved within each block of trials during the experiment.

Participants made a speeded response to report whether the target had a gap on the top or the bottom. They used the thumb on their left hand to press either the up or down directional button on the gamepad indicating the target gap location. Participants responded whether the memory test was the same or different as the memory item by pressing one of two buttons with the thumb on their right hand in an unspeeded manner.

Each participant was instructed to maintain fixation during each trial and blink during the inter-trial interval. Participants were informed that a memory-matching item might appear in the search array, but that it would never be the search target. Participants performed 8 practice trials before the experimental trials began and completed 960 experimental trials in 4 blocks with 15-second breaks every 30 trials. During breaks, a countdown was shown on the screen along with an instructional sentence and new articulatory suppression stimuli. Articulatory suppression stimuli were to be repeated silently to prevent the muscle noise due to articulation from interfering with the ERP recordings but to prevent the recoding of the visual stimuli into verbal working memory (Baddeley, 1986). The experimenter asked participants to report the articulatory suppression stimuli after the practice block, and during a subset of the breaks to ensure compliance. After each block, participants were allowed to take a self-paced break.

ERP Recording and Analysis. We recorded the electroencephalogram (EEG) from tin electrodes embedded in an elastic cap (Electro-Cap International, Eaton, OH). The caps contained a subset of the International 10/20 System sites (Fz, Cz, Pz, F3, F4, C3, C4, P3, P4,

PO3, PO4, T3, T4, T5, T6, O1, and O2) in addition to two non-standard sites (OL, placed halfway between O1 and T5; OR, placed halfway between O2 and T6). These electrodes were referenced online to the right mastoid, and re-referenced offline to the average of the right and left mastoids (Nunez, 1981). We recorded the horizontal electrooculogram (EOG) from two electrodes placed approximately 1 cm from the external canthus of each eye. An electrode placed approximately 3 cm below the left eye, referenced to the right mastoid, measured vertical EOG. Signals were amplified using a SA Instrumentation amplifier with a gain of 20,000 and a bandpass of 0.01-100 Hz. The amplified signals were digitized by a PC-compatible computer at a rate of 250 Hz and averaged offline. All trials with incorrect search or memory responses were excluded from the averages. We rejected individual trials with eye movements, blinks, muscle noise, or channel blocking prior to averaging the signal (an average of 14% of trials per subject). In addition, participants who had more than 30% of correct-performance trials rejected due to these artifacts were replaced.

The N2pc was measured across the posterior electrode sites (O1/2, OL/R, and T5/6) contralateral versus ipsilateral to the target location for each type of visual search array (memory-match absent, memory-match opposite, and memory-match same hemifield). Specifically, we measured mean amplitude from 200-400 ms post-search-array onset and entered these ERP data into an ANOVA with the within-subjects factors of array type (memory-match absent, memory-match opposite, versus memory-match same), contralaterality (ipsilateral versus contralateral relative to the target), hemisphere (left versus right), and electrode (O1/2, OL/R, versus T5/6). The mean reported target elicited N2pc voltages are calculated by subtracting the ipsilateral from the contralateral activity measured during the 200-400 ms window at electrodes OL/R (Woodman & Luck, 2003b). To further

test for effects due to the presence of the memory-matching item, we performed a separate analysis of the waveforms averaged relative to the location of the memory-matching item in the search arrays, collapsed across target location. We entered the waveforms relative to the memory match into an ANOVA with the within-subjects factors of hemifield (left versus right), contralaterality (ipsilateral versus contralateral to the memory-matching item), and electrode (O1/2, OL/R, versus T5/6). For these analyses, we used a time window of 200-300 ms based on previous studies of the N2pc (Luck, in press; Luck & Hillyard, 1994a, 1994b) and what would be expected if the first shift of attention were to the color-defined memory matching item (Woodman & Luck, 1999, 2003b). In addition to this 200-300 ms window used to measure the predicted N2pc, we also used a measurement time window from 300-400 ms post-search-array onset due to the presence of a lateralized positivity relative to these memory-matching items during this period. The mean voltages reported for this positivity are measured across the three posterior pairs of electrodes by subtracting the ipsilateral from the contralateral waveforms with respect to the memory match. All p-values from the ANOVAs were corrected as necessary with the Greenhouse-Geisser correction for violations of sphericity (Jennings & Wood, 1976).

Results

Behavior. Visual search accuracy was near ceiling whether the memory-matching item was present or not (99.5% correct and 99.6% correct, respectively $t(9) = 1.59; p > .14$). Participants were slower to respond when the memory-matching item was present ($M = 948$ ms) than when there was no memory-matching item in the search array ($M = 910$ ms; $t(9) = 3.57, p < .01$) on trials with correct search and memory performance. Memory accuracy was

similar whether the memory item was present ($M = 90.8\%$ correct) or absent from the search array ($M = 91.7\%$ correct; $t(9) = 1.19, p > .26$). It is interesting to note that this pattern of RTs is identical to that previously interpreted as evidence for the capture of attention by memory-matching items (i.e., the early, involuntary orienting of attention to memory-matching inputs).

ERP. Figure 4A shows the N2pc elicited by the search target. Across the three types of trials (i.e., memory-match absent, memory-match opposite, memory-match same hemifield), the N2pc related to focusing covert attention on the search target was essentially unchanged (contralateral minus ipsilateral to the target using electrodes OL/R from 200-400 ms post-search-array onset; memory-match absent, $M = -0.36 \mu\text{V}$; memory-match opposite, $M = -0.38 \mu\text{V}$; memory-match same, $M = -0.33 \mu\text{V}$). Our statistical analyses supported these observations. We found a significant N2pc to the search target evidenced by a main effect of contralaterality from 200-400 ms poststimulus ($F(1,9) = 11.9, MSE = 0.84, p < .01$) and an interaction of contralaterality and electrode ($F(2,18) = 4.3, MSE = 0.08, p < .05$) due to the N2pc being larger at T5/6 and OL/R than at O1/2 ($M = -0.43 \mu\text{V}, M = -0.36 \mu\text{V},$ and $M = -0.22 \mu\text{V}$, respectively). An automatic influence of memory match on the deployment of covert attention would be expressed by an interaction of array type X contralaterality, however, this interaction was not significant ($F(2,18) = 0.19, MSE = 0.45, p = .83$). No other effects or interactions were significant.

In Figure 4B we show that no early negativity was observable contralateral to the memory-matching item. Indeed, the waveforms actually show a trend in the opposite direction later in the time window. Specifically, the presence of the memory-matching distractor lead to a positivity, most evident approximately 375 post-search-array onset,

contralateral to the visual hemifield containing this critical distractor. Consistent with this observation, the effect of contralaterality relative to the memory-matching item from 200-300 ms poststimulus was not significant ($F(1,9) = 0.39, MSE = 0.25, p = .55$) nor were there higher-level interactions involving this factor. Moreover, the analysis of the positivity contralateral to the memory match using the 300-400 ms window yielded a significant effect of contralaterality ($F(1,9) = 5.29, MSE = 0.33, p < .05$). We also found a significant interaction of contralaterality X hemifield ($F(1,9) = 5.12, MSE = .43, p < .05$) due to the N2pc being larger when the memory-matching item was in the left hemifield. No other effects or interactions were significant.

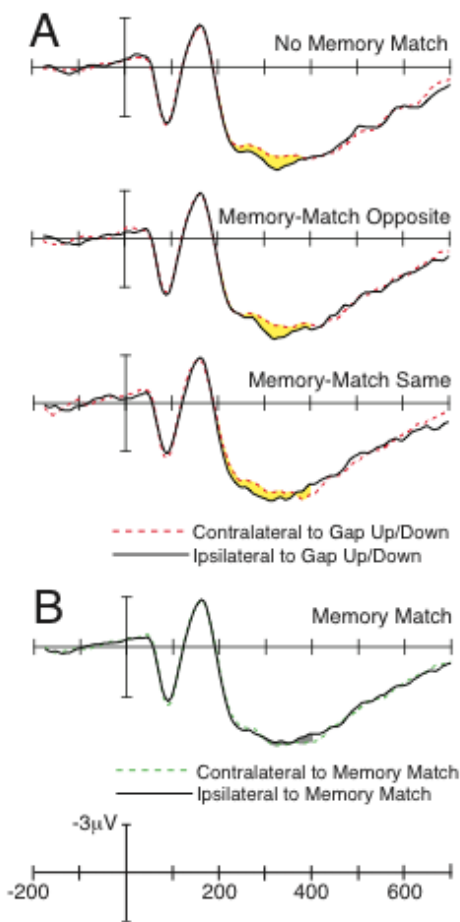


Figure 4. The ERP results of Experiment 1 time-locked to the search array onset. A) The waveforms from electrodes OL/R relative to the search target across the three trial types, the yellow shaded regions show where significant N2pc activity was measured. B) The waveforms from OL/R relative to the memory-matching item. The gray shaded region indicates the measurement window relative to the memory-matching item.

Discussion

We found that the search targets elicited a robust N2pc that was unmodulated by the presence or location of the memory-matching distractor. The only lateralized effect elicited by the memory-matching distractors was a relatively late contralateral positivity. This observation is consistent with two possible mechanistic explanations. First, it is possible that

the focus of attention actively avoids the memory-matching items, increasing the amplitude of the target-elicited N2pc into the opposite hemifield. Alternatively, this pattern of lateralized activity might be due to the active suppression of the memory-matching items in the search arrays. Recent work suggests that active distractor suppression elicits a *distractor positivity*, or Pd (Hickey, Di Lollo, & McDonald, 2009). These findings and both of the mechanistic explanations are contrary to the predictions of the hypothesis that memory-matching items attract attention to themselves early in the process of visual search (e.g., compare Figures 2 and 3). If this hypothesis had been supported, then we should have first observed an N2pc elicited by the memory-matching item and only later an N2pc to the target. It is striking that the ERP results show that attentional capture by memory-matching items did not occur although the simultaneously measured RTs were slower on trials with memory-matching items than trials without. This finding confirms an assumption that we made in motivating the present study. Specifically, behavioral RTs alone do not provide a precise enough measure to infer that an RT effect is due to the earliest deployments of attention and not subsequent processes.

As described above, our search stimuli were designed so that the color-defined memory-matching item would be easy to orient attention toward, while the search target (defined by the location of the gap on the Landolt squares) would require scrutiny within the focus of attention (Wolfe, 1998b; Woodman & Luck, 1999, 2003b). Our observation of a smaller amplitude and longer latency N2pc to the search target compared to previous N2pc studies (Luck, in press; Luck & Hillyard, 1990, 1994b) is consistent with this logic and supports the idea that the point in time when attention was focused on the search target varied

from trial-to-trial. However, this shift of attention to the target was essentially uninfluenced by the presence of the memory-matching items.

Experiment 2

In Experiment 1, we found that the search targets, but not the memory-matching items, elicited an N2pc. If the search target and memory item were competing to control attention, then it is possible that our N2pc findings may have been due to the search target being too easy to discriminate in Experiment 1. In Experiment 2, we tested this hypothesis by reducing the discriminability of the search target. This entailed making the gap size of the Landolt squares smaller than those used in Experiment 1, a manipulation known to decrease the efficiency of visual search (e.g., Woodman, Vogel, & Luck, 2001). If we failed to find that attention was captured by memory-matching distractors in Experiment 1 due to attentional guidance of the search target overpowering the capture of attention by the memory-matching item, then in Experiment 2 we should see a modulation of the N2pc elicited by the difficult to discriminate targets based on the location of the conspicuous memory-matching items in the search array.

Methods

All methods were the same as Experiment 1, except as follows.

Participants. A new group of 10 participants was recruited and two participants were replaced due to artifacts on more than 30% of trials with correct search and memory performance.

Stimuli. As shown in Figure 5A, the gap size of the Landolt-square stimuli was reduced to one third of the size of the gaps in Experiment 1. Stimuli at the six potential target locations were identical to Experiment 1 except the gaps were 0.07° wide. The gaps in the two rings of black Landolt-c distractors were similarly scaled (inner ring stimuli: 0.20° X 0.20°, 0.03° line width, 0.03° gap width; outer ring stimuli: 0.46° X 0.46°, 0.10° line width, 0.10° gap width).

Analyses. Across participants, an average of 15% of trials with correct search and memory responses were removed due to ocular or other EEG artifacts.

Results

Behavior. Mean accuracy of visual search responses was 96.2% correct when the memory-matching item was present and 96.6% correct when absent ($t(9) = 2.46, p < .05$). On trials with correct search and memory performance, participants were slower to respond when the memory-matching distractor was in the array ($M = 1124$ ms) than when the memory-matching item was absent ($M = 1093$ ms; $t(9) = 2.70, p < .05$). These search RTs were slower than those from Experiment 1 ($t(18) = 2.22, p < .05$), demonstrating the effectiveness of our difficulty manipulation between Experiment 1 and 2. Memory task performance did not significantly differ based on whether a memory-matching item was present ($M = 82.9%$) versus absent from the array ($M = 84.9%$, $t(9) = 2.06; p = .07$).

ERP. Figure 5B shows the ERP waveforms relative to the search targets in Experiment 2. Just as in Experiment 1, we reliably measured an N2pc contralateral to the hemifield containing the search target that was first apparent just after 200 ms poststimulus and continued until approximately 400 ms poststimulus onset. Most importantly, the

presence of the memory-matching item in the array had little influence on this N2pc to the search target (memory-match absent, $M = -0.31 \mu\text{V}$; memory-match same, $M = -0.25 \mu\text{V}$; memory-match opposite, $M = -0.71 \mu\text{V}$). Note that the N2pc elicited by the targets tended to be larger when the target was *opposite* the memory match compared to when it was in the same hemifield. This is the reverse of what we expect from memory-matching items that are capturing attention. The statistical analyses supported these observations. We found a significant N2pc to the search target evidenced by a significant effect of contralaterality ($F(1,9) = 14.7$, $MSE = 0.83$, $p < .01$) due to more negative waveforms contralateral to the search target. We also found an interaction of contralaterality X electrode ($F(2,18) = 6.9$, $MSE = 0.10$, $p < .01$) due to the N2pc being larger at T5/6 and OL/R than at O1/2 ($M = -0.49 \mu\text{V}$, $M = -0.43 \mu\text{V}$, and $M = -0.19 \mu\text{V}$, respectively). Contralaterality did not interact with array type ($F(2,18) = 2.6$, $MSE = 0.62$, $p = .10$), because the N2pc elicited by the search target was not significantly influenced by the presence or location of the memory match. We did find a higher order interaction of array type X hemifield x electrode ($F(4,36) = 2.9$, $MSE = 0.04$, $p = .05$). No other effects or interactions were significant.

Figure 5C shows the lateralized effects relative to the location of the memory-matching item. These waveforms show that the presence of the memory-matching item in a hemifield did not elicit an early N2pc, but instead had the opposite effect later in the processing of the search array (i.e., $M = 0.61 \mu\text{V}$ contralateral minus ipsilateral relative to the memory match from 300-400 ms poststimulus). As in Experiment 1, the absence of an early N2pc elicited by the memory-matching item resulted in the effect of contralaterality not being significant in the ANOVA using the ERP data from 200-300 ms relative to the memory-matching distractor ($F(1,9) = 0.10$, $MSE = 0.24$, $p = .75$). We also found an

interaction of hemifield and electrode ($F(2,18) = 4.19, MSE = 2.22, p < .05$). However, the positivity in the 300-400 ms time window created a significant effect of contralaterality ($F(1,9) = 8.57, MSE = 1.01, p < .05$). We also found an interaction of contralaterality X electrode ($F(2, 18) = 4.61, MSE = 0.06, p < .05$) due to the positivity being larger at T5/6 and OL/R than at O1/2 ($M = 0.66 \mu V, M = 0.61 \mu V, \text{ and } M = 0.34 \mu V$, respectively).

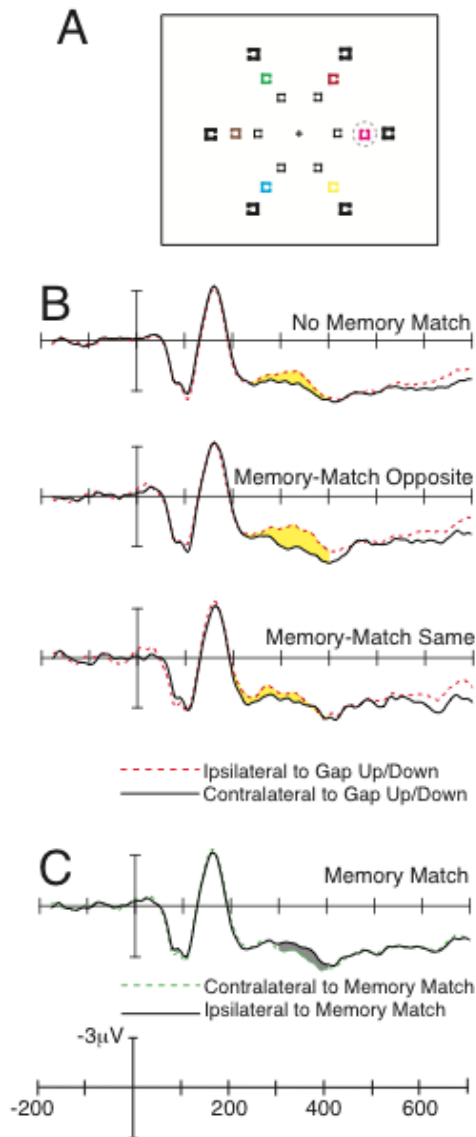


Figure 5. The stimuli and ERP results of Experiment 2. A) Example of the search arrays with the target indicated by the dashed circle (not visible to participants). B) ERPs elicited by the search targets from electrodes OL/R. C) The ERPs relative to the memory-matching items using the same shading scheme was in Figure 3.

Discussion

In Experiment 2, we replicated the finding that the memory-matching items did not capture covert attention during visual search as indexed by the N2pc. Contrary to such

predictions, we again found that the memory-matching items elicited a contralateral positivity from 300-400 ms poststimulus. This again suggests that the focus of attention actively avoids the hemifield containing the memory-matching item or that this item is actively suppressed, eliciting a positivity. RTs were longer in Experiment 2 than Experiment 1, indicating that our manipulation of decreasing the size of the gap did make the search task more difficult. However, this increase in the difficulty of target discrimination did not reveal evidence for early and automatic shifts of attention to the memory-matching distractors.

Experiment 3

In Experiments 1 and 2, we observed a significant N2pc elicited by the search targets but did not find that the working memory representations resulted in the deployment of covert attention to memory-matching items. Previous research has shown that the amplitude of the N2pc increases when distractors appear near attended items (Luck et al., 1997) and adding additional items to a search array will decrease the distance between an attended item and the nearest distractor by increasing spatial crowding (Cohen & Ivry, 1991). It is possible that in Experiment 1 and 2, attention was directed to the memory-matching item, but no significant N2pc was generated during the shifts of attention to the memory-matching item because we presented search arrays with too few distractors. That is, the absence of nearby distractors in Experiments 1 and 2 may have minimized the amplitude of any N2pc that was present but not of sufficient amplitude to be detectable (e.g., see Woodman & Luck, 2003b). Thus, in Experiment 3 we increased the number of distractors by 450% to provide an

aggressive test of the explanation that the memory-matching items in Experiments 1 and 2 were eliciting undetectably small N2pc.

Methods

All methods were the same as Experiment 1, except as follows.

Participants. A new group of 10 participants was recruited from the same pool used in the previous experiments. Two participants were replaced due to excessive artifacts (i.e., more than 30% of trials with correct search and memory performance).

Stimuli. Figure 6A shows that we increased the number of black distractors in the search arrays of Experiment 3 to 54, compared to the 12 black distractors Experiment 1 and 2 (compare Figure 2, 4A, and 6A). Specifically, we increased the number of distractors in the inner and outer ring from 6 to 12 and we added black distractors between the potential search targets in the middle ring. We also added two more rings of distractors, one between the inner and middle ring ($0.26^\circ \times 0.26^\circ$, 0.05° line width, 0.16° gap width, 2.09° from fixation) and one between the middle and outer ring ($0.39^\circ \times 0.39^\circ$, 0.08 line width, 0.23° gap width, 3.13° from fixation).

Analyses. An average of 14% of trials with correct search and memory responses were excluded from the analyses due to eye movements, blinks, and other EEG artifacts.

Results

Behavior. Participants were slower to respond when the memory-matching distractor was in the array ($M = 993$ ms) than when it was absent ($M = 958$ ms; $t(9) = -3.71$, $p < .01$), although search accuracy did not differ between these trial types (98.9% versus 99.1%

correct, respectively, $t(9) = 1.57, p > .15$). These RTs were not significantly slower than those of Experiment 1 ($p = .50$) and were faster than those in Experiment 2 using the difficult to discriminate target shapes ($t(18) = 2.28, p < .05$). Memory task accuracy was 89.1% correct when a memory-matching item was in the array and 89.6% correct when absent ($t(9) = 0.67, p = .51$).

ERP. Figure 6B shows the ERP waveforms relative to the search targets in Experiment 3. Replicating a now familiar pattern, we observed that the search targets elicited an N2pc, but the memory-matching distractor did not modulate the target-elicited N2pc in the manner expected if such memory matches were capturing covert attention. Specifically, the amplitude of the target-elicited N2pc on memory match absent ($M = -0.23 \mu\text{V}$), memory match same hemifield ($M = -0.17 \mu\text{V}$), and memory match opposite hemifield ($M = -0.35 \mu\text{V}$) trials were similar (using the 200-400 ms measurement window). Any potential modulation of the lateralized activity was again in the direction opposite to what would be expected if attention were being deployed to the memory-matching items (i.e., there was a late, increased positivity contralateral to the memory match). Consistent with these observations, the ANOVA of the ERP data related to the search target yielded a significant effect of contralaterality ($F(1,9) = 23.0, MSE = 0.21, p < .01$), but not an interaction of contralaterality X array type ($F(2,18) = 0.91, MSE = 0.22, p = .42$). We also found an interaction of array type X electrode ($F(4,36) = 3.5, MSE = 0.06, p < .05$). No other effects or interactions were significant.

Figure 6C shows that the memory-matching item did not elicit an early N2pc. The analysis of the waveforms relative to the memory match from 200-300 ms did not result in a significant effect of contralaterality ($F(1,9) = 0.54; MSE = 0.15; p = .48$) or interactions

involving this factor. The contralateral positivity relative to the memory-matching item measured from 300-400 ms, led to a significant effect of contralaterality in the ANOVA ($F(1,9) = 26.5, MSE = 0.10, p < .001$). The interaction of contralaterality X electrode ($F(2,18) = 5.46, MSE = 0.02, p < .05$) was because this positivity was largest at OL/R ($M = 0.36 \mu\text{V}$) and T5/6 ($M = 0.36 \mu\text{V}$) followed by O1/2 ($M = 0.18 \mu\text{V}$).

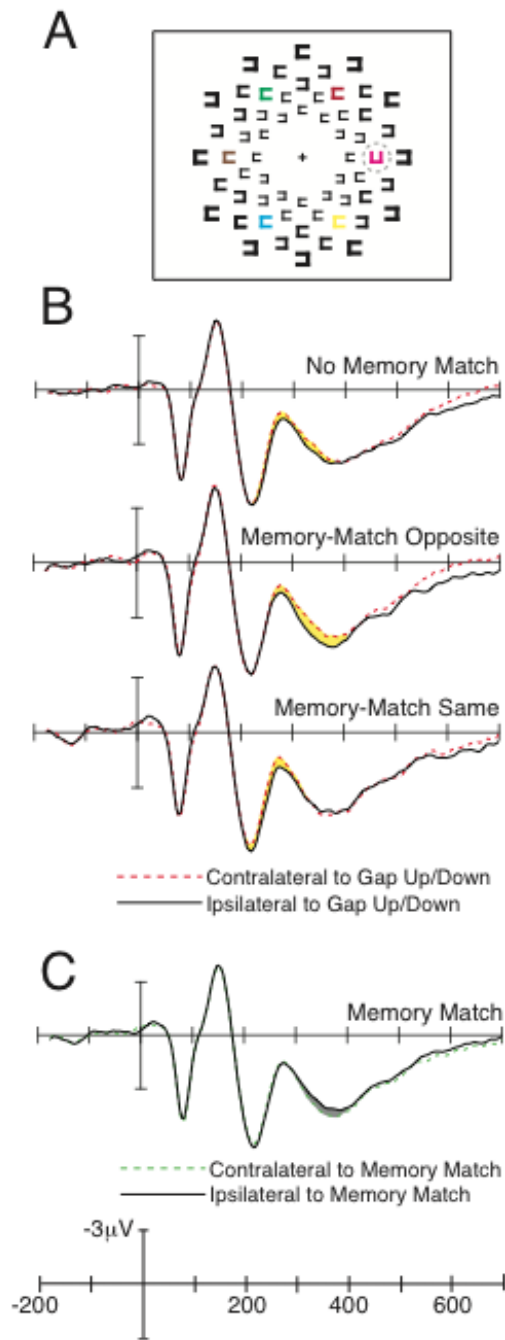


Figure 6. The stimuli and ERP results of Experiment 3. A) Example of the search arrays. B) ERPs elicited by the search targets from electrodes OL/R. C) The ERPs elicited by the memory-matching items, using the same shading scheme was in Figure 3.

Discussion

In Experiment 3, we replicated the pattern of results from Experiments 1 and 2 using denser search arrays. These findings rule out one possible explanation for the findings of Experiment 1 and 2-- that we used search arrays with too low a density to observe a memory-matching N2pc. The search arrays in Experiment 3 had 450% more distractors than Experiment 1 and 2 but the same pattern of results was found. Thus far, we have seen no evidence that covert attention, as measured by the N2pc, is directed to memory-matching items. To the contrary, the findings are consistent with observers avoiding shifting attention to these known non-target items, perhaps due to active suppression of these items. The hypothesized early and automatic capture of attention by memory-matching items predicts that the N2pc should have indexed a shift of attention to the memory-matching item prior to orienting attention to the visual search target. We have not observed this pattern of results regardless of the difficulty of perceiving the target-defining feature or the number of distractors present in the visual search arrays.

Although the findings from Experiments 1-3 are inconsistent with the hypothesis that visual working memory representations cause matching perceptual inputs to capture attention, they could be accounted for by the idea that covert attention is deployed to items when doing so is consistent with the goals of the tasks at hand (Downing & Dodds, 2004; Peters et al., 2008; Woodman & Luck, 2007). In Experiments 1-3, it was consistent with the goal of the search task (i.e., find the search target as fast as possible) to avoid shifting attention to the memory-matching items that were known to not be the target. The ERPs we observed were consistent with such a goal. However, a simpler alternative explanation is that

observers simply could not shift attention to memory-matching items early in the course of visual search given the stimuli we used. We next addressed these competing explanations.

Experiment 4

In Experiments 1-3, if we would have observed early deployments of covert attention to the memory-matching items (i.e., an N2pc), then they would have been involuntary by definition, because attending to the memory-matching item was contrary to the goal of the search task (Jonides, 1981). The absence of an N2pc to memory-matching items in Experiments 1-3 is inconsistent with the proposal that “working memory exerts and involuntary influence on visual attention” (p. 344; Soto, Hodsoll, Rothstein & Humphreys, 2008). In contrast, other researchers have proposed that it is necessary for the participant to have a goal of attending to the memory-matching item for working memory representations to guide attention (Downing & Dodds, 2004; Peters et al., 2008; Woodman & Luck, 2007). Consistent with this proposal from the empirical literature, the Neural Theory of Visual Attention (NTVA, Bundesen et al., 2005) posits that templates are held in working memory, but an additional process must trigger a biasing signal before a working memory representation can guide attention. One could interpret this additional process as an executive function that determines which of multiple available templates in short or long-term memory should be used to direct attention. To assess whether early deployments of covert attention to memory-matching items are determined by voluntary control, we altered the participants’ search task while using the same stimuli and memory task used in Experiment 3.

In Experiment 4, participants were required to report the gap location of the memory-matching item, thus, making the memory-matching item task relevant. If the influence of working memory on early deployments of covert attention is goal dependent, then we should find early attentional deployments are directed to the memory-matching items in Experiment 4. This would be evidenced by an early N2pc to the memory-matching item. Alternatively, our previous failures to observe attentional deployments to memory-matching items could have been due to a specific aspect of our experimental design. Recently, Olivers (2009) has suggested that certain stimuli may not be capable of generating a guidance effect. Specifically, this paper proposed that Landolt-squares may produce *stimulus energy* that is too low for memory-matching items to capture attention. In other words, weak bottom-up signals from certain types of search items do not strongly engage the memory representation and, thus, it is difficult for attention to select such items. This explanation would also hold for stimuli other than Landolt-squares that have weak bottom-up signals that match memory. If our failures to find early deployments of attention to memory-matching items can be explained by the low stimulus energy of our particular stimuli, then we should once again find no early N2pc to the memory-matching item. Attention would only be directed to the task-relevant memory-matching item later in the search process. Thus, the design of Experiment 4 serves to distinguish between these competing explanations of our previous findings in this study.

Methods

All methods were the same as those of Experiment 3, except as follows.

Participants. A new group of 10 volunteers was recruited from the same pool. One participant was replaced due to ocular and EEG artifacts on more than 30% of trials with correct search and memory performance.

Stimuli and Apparatus. Figure 7A shows an example of the search arrays that were identical to those in Experiment 3 except that the memory-matching item was task relevant (i.e., see the dashed circle indicating the target). Correct search responses were defined by the location of the gap on the item that matched the color of the memory item. Responses were made using the directional buttons on the gamepad with the left arrow indicating a gap to the left and the right arrow indicating a gap to the right. Both buttons were pressed with the left-hand thumb of the participants.

Procedure. Participants were instructed to attend to the item that matched the color of the item in memory and report the direction of the gap location on this search item. They were instructed that an object with a gap up or down would appear in the search array, but that this item would never be the search target. As in Experiments 1-3, participants had to remember both the color and gap direction of the memory item and reported a change or no change when viewing the memory test with a right-hand button press at the end of each trial.

Analyses. Across participants, an average of 11% of trials with correct search and memory responses were excluded from the analyses due to eye movements and other EEG artifacts.

Results

Behavior. Mean change-detection accuracy was 90.8% correct. The search responses for discriminating the gap location of the memory-matching item resulted in a mean RT of 652 ms and accuracy of 98.9% correct.

ERP. The ERP waveforms recorded during the search task are shown in Figure 7B and 7C. The waveforms show that the N2pc elicited by the memory-matching items from 200-300 ms was large in amplitude (i.e., $M = -1.41 \mu\text{V}$ at OL/R) and onset early (i.e., approximately 175 ms poststimulus). The polarity of this N2pc flipped when the hemispheres were defined relative to hemifield containing the search element with a gap up or down (see Figure 7B). This is the pattern that is expected if the element with the gap up or down had little or no influence on the early N2pc elicited by the memory-matching item ($M = -0.08 \mu\text{V}$, see also below).

To confirm our observations, we subjected the ERP data relative to the memory-matching item from 200-300 ms after search-array presentation to an ANOVA with the within subjects factors of hemifield (left versus right), contralaterality (ipsilateral or contralateral to memory-match), and electrode (O1/2, OL/R, versus T5/6). In contrast to the findings from Experiments 1-3, when participants were instructed to report the gap location of the memory-matching color, the contralaterality factor relative to the memory-matching item was significant, ($F(1,9) = 12.7$, $MSE = 2.88$, $p < .01$), as was the main effect of electrode ($F(2,18) = 27.57$, $MSE = 4.28$, $p < .0001$). We also found significant interactions of contralaterality X electrode ($F(2,18) = 4.3$, $MSE = 0.20$, $p < .05$) due to the N2pc being larger at OL/R and T5/6 than O1/2 ($M = -1.41 \mu\text{V}$, $M = -1.09 \mu\text{V}$, and $M = -0.89 \mu\text{V}$,

respectively), and hemifield X contralaterality X electrode ($F(2,18) = 3.7$, $MSE = 0.05$, $p < .05$).

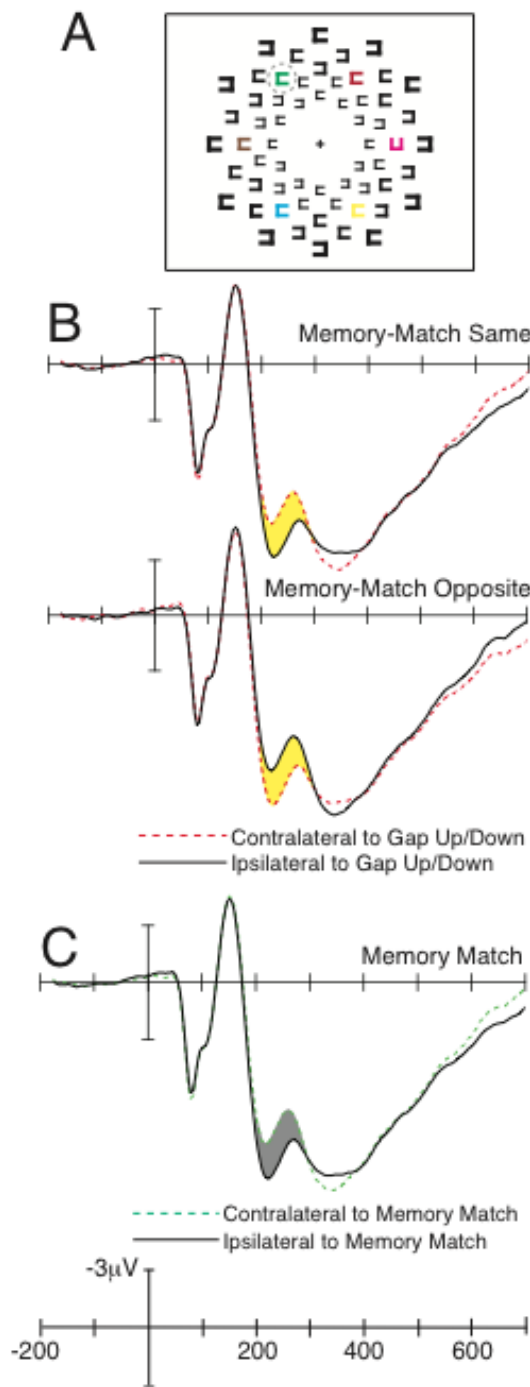


Figure 7. The stimuli and ERP results of Experiment 4. A) Example of the search arrays. B) The ERPs from electrodes OL/R relative to the search item with a gap up or down. C) The ERPs relative to the task-relevant, memory-matching items. The significant N2pc activity is shaded using the same scheme as in Figure 3.

Discussion

When the goal of the search task required that the memory-matching item be processed, we found clear evidence that covert attention was deployed to these items early in course of analyzing the search arrays. This indicates that the specific stimuli we used throughout this study did not prevent attention from being directed to the memory-matching items early in the attention-demanding search process. This allows us to rule out a ‘low stimulus energy’ account of the findings from Experiments 1-3 (Olivers, 2009). These findings support the competing hypothesis that the influence of working memory on attention is goal dependent (e.g., Woodman & Luck, 2007) as opposed to involuntary (Soto et al., 2008).

Chapter 2 Discussion

The findings from Experiments 1-3 consistently showed that the targets of the visual search tasks elicited an N2pc, a sensitive measure of the deployment of covert perceptual attention (Luck, in press; Woodman & Luck, 2003a, 2003b). However, we found no evidence of deployments of covert attention to memory-matching items, either early or late in the process of analyzing the search arrays. Instead, we found a consistent pattern in the waveforms suggesting that the focus of attention either actively avoided the memory-matching items or these items were actively suppressed from 300-400 ms after search onset. That is, the memory-matching items may have elicited a distractor positivity (i.e., Pd) due to their active suppression, or increased the amplitude of the N2pc due to attention mechanisms

avoiding the memory-matching distractor. However, both of these interpretations are in direct opposition to the proposal that memory-matching items capture attention.

When the goal of the search task involved attending to memory-matching items in Experiment 4, we found an early and large amplitude N2pc elicited by these objects. This latter finding supports proposals that attention is not deployed to memory-matching inputs unless it is part of a task goal (Bundesen et al., 2005; Woodman & Luck, 2007). These findings demonstrate that memory-matching items in our visual field do not consistently and involuntarily capture covert attention. Instead, our findings suggest that early covert attention is deployed to items that are relevant for the goal of the task at hand.

The crux of the debate regarding how working memory representations interact with attention is that working-memory representations cause an early and involuntary orienting of attention to memory-matching items (Soto et al., 2005; Soto et al., 2008). How can we be certain that memory-matching items do not capture attention before the N2pc is elicited? This explanation is unlikely for the following reasons. First, previous studies showed that the N2pc measures the first shifts of attention during demanding search tasks using the same type of stimuli used in the present study (Woodman & Luck, 1999, 2003b). Second, masking experiments have shown that the N2pc can measure the deployment of perceptual attention to targets that are presented so briefly that subjects are not aware that they were shown (Woodman & Luck, 2003a). Thus, it is extremely unlikely that shifts of attention were occurring that we were unable to measure.

In this study, we observed a striking contrast between the pattern of behavioral findings and the ERP effects. The RTs were significantly longer when a memory-matching item was present in the search display than when it was absent in Experiments 1, 2, and 3.

These are the type of findings typically interpreted as evidence that memory-matching items automatically capture attention, slowing the deployment of attention to the actual search target. However, the N2pc measured in Experiments 1-3 showed that covert attention was not directed to the memory-matching distractors early (or at all) during the attention-demanding search process.

How do we reconcile these seemingly contradictory findings from the behavioral and ERP measures? Our ERP findings support the explanation that participants may have avoided attending to the memory-matching items in Experiments 1-3, perhaps via active suppression. If so, this may have slowed search RTs when the search target happened to be near the memory-matching item relative to when the memory match was at a distant location or absent from the array. To assess the likelihood of this explanation of the RT effects, we combined the search RTs from Experiments 1-3 based on the distance between the memory-matching item and the search target. RTs were slowest when the memory-matching distractor appeared next to the search target ($M = 1034$ ms) faster when the memory match and target were separated by one additional colored distractor ($M = 1016$ ms) and faster still when the memory-matching item was opposite the search target ($M = 1008$ ms). We entered these RTs into an ANOVA with the between subjects factor of experiment (Experiment 1, 2, and 3) and the within-subjects factor of distance (one, two, and three spatial locations removed from the target). We found a significant effect of distance ($F(2,54) = 4.913$, $MSE = 0.001$, $p < .05$), a marginal effect of experiment ($F(2,27) = 3.34$, $MSE = 0.07$, $p = .05$), and no interaction of these factors. This slowing of RT based on the proximity of the memory-matching item to the target, taken together with the ERPs indicating that memory-matching items were actively avoided or suppressed, support the conclusion that the elevated RTs

when the memory-matching distractors were present was due to the suppression of the memory-matching items spreading to the search target. Our converging evidence from the RTs and ERPs emphasize the caution necessary in relying upon a behavioral effect to infer the operation of attentional mechanisms early in the course of processing.

The hypothesis drawn from the elegant proposal of the theory of biased competition (Desimone & Duncan, 1995), that the maintenance of an object representation in visual working memory is sufficient to bias perceptual attention to select similar objects, appears to be incomplete. The present findings show that attention is only driven to select items matching those in working memory if it is task relevant to do so. We propose that an additional process should be added to the theory of biased competition in which goal-dependent executive control is an intermediate step between working memory representations and the biasing of visual attention. The result of such an addition will draw biased competition closer to NTVA (Bundesen et al., 2005), a theoretical cousin that has the flexibility to account for the findings of this study.

The present results and the previous studies of the influence of working memory on attention (Downing, 2000; Han & Kim, 2009; Huang & Pashler, 2007; Olivers, 2009; Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005; Soto & Humphreys, 2006; Soto & Humphreys, 2007; Soto & Humphreys, 2008; Soto, Humphreys, & Heinke, 2006a, 2006b) cannot be explained by a simple mechanism creating an involuntary attentional bias based on just any working memory representation. An account that emphasizes a goal-dependent interaction between working memory and attention is necessary to explain the sum of the findings. If goals influence whether working memory representations guide attention toward or away from memory-matching inputs, then

differences across studies may be seen as evidence of the flexibility of the control mechanism. We propose that the influence of working memory on attention may be described as a form of conditional, goal-dependent automaticity (Bargh, 1989), in which working memory representations guide attention only when one's goals are consistent with attending to memory-matching items.

CHAPTER 3

ELECTROPHYSIOLOGICAL MEASURES OF THE ENHANCEMENT AND SUPPRESSION OF STIMULI MATCHING WORKING MEMORY REPRESENTATIONS

Numerous theories of visual attention suggest that information about the goal of the current search is held in working memory as an attentional template. Biased competition theory (Desimone & Duncan, 1995) predicts a direct relationship between the sustained neural activity created from a working memory representation and attentional biases, suggesting that attention will be biased toward items in the visual field that match the contents of working memory. However, tests of the influence of working memory on attention suggest that the relationship between working memory and attention may be more flexible (Woodman & Luck, 2007; Carlisle & Woodman, 2011). While some studies show evidence that working memory representations are used to guide attention, there is growing evidence that working memory representations do not always create an attentional bias.

The diversity of findings suggests that the relationship between working memory and attention may be more flexible than suggested by biased competition. There is accumulating evidence that the relationship between working memory and attention may be dependent on the current task goals. For instance, in one study attention was preferentially directed to the memory-matching items in the visual field only when the information in working memory is relevant for the current task (Woodman & Luck, 2007). This data suggests an off or on

relationship between the contents of working memory and attention, where working memory representations need not be used to guide attention toward memory-matching items, but may be used to do so when the contents of working memory are important for the search task.

One more extreme prediction of a flexible relationship between working memory representations and visual attention would include being able to set separate attentional biases for different representations in working memory. The ability to preferentially enhance certain memory-matching stimuli may be important for the effective control of attention. For instance, if you were looking for one set of keys in your friend's house, and your friend told you 'I'm pretty sure they have a blue keychain but they might have a pink keychain', would you be able to flexibly prioritize your attention to blue key chains through stronger attentional enhancement? One study hints that such flexibility is possible. In Carlisle and Woodman (2011), as the importance of memory information for a search task increased, the benefits of having a memory-match as the search target and the costs of having a memory-match as a distractor also increased. A demonstration that we can create different attentional biases for relevant memory matches and irrelevant working memory matches, including evidence that we can suppress task-irrelevant information, would suggest that top-down control can be closely tailored to fit the current situation.

The literature assessing the influence of working memory on attention has produced behavioral and electrophysiological evidence that working memory matching items can be suppressed. Reaction time measures provided the first evidence that working memory matches could be suppressed when they were consistently task-irrelevant. Two behavioral studies suggest that task-irrelevant memory-matching items can be avoided during search (Downing & Dodds, 2004; Woodman & Luck, 2007). These studies found faster reaction

times when memory-matching items were present in the array, which would be consistent with participants only searching through non-memory-matching items when the memory-match is present, effectively reducing the set size by one item.

More recently, two studies have found electrophysiological evidence that the representations in working memory may be suppressed. These electrophysiological measures provide stronger evidence of suppression, because they involve a more direct measurement of the proposed neural mechanism of attentional suppression. Reaction time measures necessarily require the inference that something is suppressed. These studies measured a lateralized ERP component called the distractor positivity (Pd), which is suggested to be a measure of distractor suppression (Hickey, Di Lollo, & McDonald, 2008). Both studies found that memory-matching items that are consistently task-irrelevant elicited a Pd, suggesting that they were actively suppressed (Experiments 1-3 above; Sawaki & Luck, 2010). While this evidence provides support for the proposal that task-irrelevant working memory representations can be suppressed, the Pd has a relatively short history and has not been widely tested.

Although there has been evidence from the Pd that memory-matching items that are consistently task-irrelevant may be suppressed, additional ERP components may be able to provide richer information about the flexible use of information in working memory than the Pd. The P1 and N1 are two early sensory components that are present after the onset of a visual stimulus. ERP researchers initially referred to these waveforms as *exogenous* components because they can be elicited by any visual stimuli, whether they are relevant or task irrelevant, or even during passive viewing (Rugg & Coles, 1995). However, further work demonstrated the amplitude of the P1 and N1 components scale with the allocation of

spatial attention, such that larger P1 and N1 components are elicited by the same stimulus at an attended location than an unattended location (Hillyard, Vogel, & Luck, 1998). The spatial attention enhancements of the P1 and N1 are strongest contralateral to the probed location and have been demonstrated to occur earlier than any attentional enhancements due to feature processing (Hillyard & Munte, 1984; Anllo-Vento & Hillyard, 1996).

Although both the P1 and N1 show increased amplitude at attended locations, each component is thought to index a separate mechanism of attention. This distinction was revealed during a spatial cuing task (Luck, Hillyard, Mouloua, Woldorff, Clark, & Hawkins, 1994). By comparing the responses to probes presented at valid, neutral, and invalidly cued locations, it was possible to assess whether the P1 and N1 reflected enhancement or suppression. Neutral cues should lead to neither enhancement nor suppression, and provided a comparison point for measurements of valid and invalid cues. Validly cued locations should be enhanced when compared to neutral locations, and invalidly cued locations should be suppressed compared to neutral locations. As illustrated in Figure 8, Luck and colleagues (1994) found that the P1 was larger for validly cued locations and neutral locations than invalidly cued locations, suggesting that this component reflects the suppression of distractors. In contrast, the N1 was larger at validly cued locations than neutral or invalidly cued locations, suggesting that this component reflects enhancement of a subset of the available information that is thought to be task relevant. Thus, the P1 component appears to measure attentional suppression of irrelevant information and the N1 represents enhancement of relevant information.

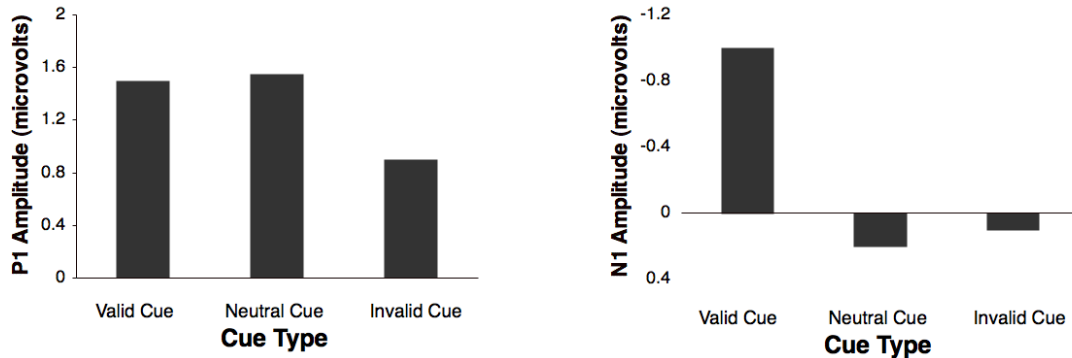


Figure 8. Amplitude changes in P1 and N1 in response to spatial cues, data taken from Luck, Fan, & Hillyard (1993). A) P1 responses indicate suppression of stimuli after an invalid cue. B) N1 responses indicate enhancement of stimuli presented after a valid cue.

Attentional enhancement effects of the N1 component can be seen in anterior and posterior electrode sites, but the different locations have different latencies. The anterior N1 is found at approximately 95 ms post-stimulus onset (Luck, Fan, & Hillyard, 1993), and has been associated with the motor preparation to a target stimulus, because no attentional enhancement was found in a choice-counting task where no motor response is required after each stimulus (Vogel & Luck, 2000). The posterior N1 is found later, at approximately 135 ms (Luck, Fan, & Hillyard, 1993) and has been shown to be modulated by the need to discriminate a stimulus (Hillyard, Vogel, & Luck, 1998; Vogel & Luck, 2000), because the amplitude of the N1 is smaller during simple detection tasks relative to choice reaction time

tasks. In spite of the different latencies and different processes that appear to boost the anterior and posterior N1, modulation in most attentional studies has been found in both components (Hopfinger, Luck, & Hillyard, 2004) and both are valid measures of target enhancement.

Attentional effects measured using the P1 and N1 have been extended beyond spatial attention tasks through the use of task-irrelevant probes (Luck, Fan, & Hillyard, 1993). Sensory responses to probes can be determined at multiple locations and multiple time points during an attentional task. Probes presented at attended locations will show the typical amplitude increase due to the allocation of spatial attention to target stimuli, presumably because other types of attentional tasks such as visual search also rely on the mechanisms of spatial attention (Mangun & Hillyard, 1995). Because task-irrelevant probes require no explicit response from participants, they can be used to expose the differential responses from P1 suppression and N1 enhancement mechanisms without strongly influencing how participants perform an attentional task. The P1 attentional effects have been most frequently reported at electrodes contralateral to the probed location. The N1 attentional effects have been most frequently reported at electrodes ipsilateral to the probed location, although the effects are often present bilaterally. This task-irrelevant probe technique was first used to assess feature-based attention early and late in search (Luck, Fan, & Hillyard, 1993), and has subsequently been used to assess attentional allocation during multiple object tracking (Drew, McCollough, Horowitz, & Vogel, 2009), and individual differences in the allocation of attention to targets and distractors (Fukuda & Vogel, 2009).

Application of the task-irrelevant probe technique during a visual search task that contains memory-matching distractors holds the possibility of providing a rich picture of the

relative enhancement and suppression of task-irrelevant memory-matching information. By placing task-irrelevant probes on targets, memory-matching distractors, and other distractors it will be possible to contrast the relative enhancement and suppression for each object type. In this design, there is no equivalent to the neutral probe condition in the original Luck, Fan, & Hillyard (1993) study. Probes presented at the target location should be enhanced, and probes presented at a distractor location should be suppressed. The target enhancement should be shown as an increased amplitude N1 response to target probes than distractor probes. The distractor suppression should be shown as a decreased P1 response to distractor probes than target probes. Comparing the probe responses on the memory-matching distractors against the probe responses on the target and distractor should allow for a thorough examination of the attentional processing of task-irrelevant working memory-matching items.

Two extreme predictions are possible. If there is a flexible relationship between working memory and attention, probes on the task-irrelevant memory-matching items will elicit P1 and N1 responses that are indistinguishable from the probes on other distractors. The other extreme option comes from the proposal that any item in working memory is the equivalent of a goal-relevant attentional template. In this case, probe responses on memory-matching distractors will be indistinguishable from probes presented on the search target. However, it is also possible that probe responses to memory-matching distractors will be intermediate between these two extreme predictions.

The P1 will be treated as a measure of suppression. If the P1 probe responses on memory-matching distractor are of equivalent amplitude as the P1 responses to probes on a distractor, we would assume that the memory-matching item is being suppressed like any

other distractor. If the memory-matching distractor is found to be suppressed like any other distractor, we would expect to find no evidence of enhancement within the N1 components. In contrast, if the memory-matching distractor is not treated as another distractor, the P1 response to the memory-matching item probes will be similar to the target probes. Remember that attended stimuli and neutral stimuli elicit similar P1 responses (Luck & colleagues, 1994). Therefore, similar P1 responses to search target and memory-matching items could be found either because the memory match is treated like a target or because the response to the probe on a memory-match is similar to a neutral stimulus. In this situation, assessing the N1 responses will further clarify how the memory-matching item is processed.

If the memory-matching distractor is not suppressed, we can next look for enhancement of memory-matching distractors using the N1 components. If the memory-matching distractor is treated as a neutral stimulus, it could escape suppression, but not be enhanced like targets. If this is the case, the N1 amplitude to probes on memory-matching distractors will be smaller than probes on search targets. In contrast, if the memory-matching distractor is the equivalent of a goal-relevant attentional template, probes on memory-matching distractors should elicit an enhanced N1 that will be the same as the N1 responses to probes on search targets.

Methods

Participants. 36 participants were recruited through the Vanderbilt online participant scheduling service, SONA. Participants gave informed consent and were compensated for their time at a rate of \$10/ hour. Three participants were unable to maintain fixation while performing accurately on the task and were asked to leave. An additional 7 participants were excluded due to eye movements or other artifacts on more than 25% of trials, or due to residual HEOG activity greater than 3.2 μV after artifact rejection. This left 24 participants in the experiment.

Stimuli. An example trial is presented in Figure 9. Memory and search items were selected from a set of 7 colors (red, $x = .570$ $y = .333$, 13.9 cd/m^2 ; green, $x = .283$ $y = .601$, 26.9 cd/m^2 ; blue, $x = .159$ $y = .095$, 7.8 cd/m^2 ; yellow, $x = .408$ $y = .506$, 46.6 cd/m^2 ; magenta, $x = .373$ $y = .233$, 17.2 cd/m^2 ; orange, $x = .471$ $y = .457$, 27.8 cd/m^2 ; purple, $x = .245$ $y = .126$, 9.3 cd/m^2). Each trial began with a light gray fixation cross ($0.2^\circ \times 0.2^\circ$; 43.5 cd/m^2) presented for 600-1000 ms on a dark gray background (13.7 cd/m^2). Next, a single circle was presented as a memory cue ($0.5^\circ \times 0.5^\circ$; 0.1° line width, surrounding the fixation cross) for 500 ms, followed by a fixation cross for 500 ms. Then, the search array was presented until 200 ms after response, or until 1800 ms if no response was given. The search array contained 6 colored items as possible search targets ($0.5^\circ \times 0.5^\circ$; 0.1° line width, presented on an imaginary circle, each centered 2.5° from fixation). Probe stimuli ($1.3^\circ \times 1.3^\circ$, 49.5 cd/m^2) were presented 250 ms after search array onset, and remained on the screen for 50 ms. The probe surrounded one of the possible search targets, but did not obscure the item. In addition, each array contained 12 distractor circles (inner ring: $0.3^\circ \times 0.3^\circ$, presented on an imaginary circle 1.5° from fixation; outer ring: $0.7^\circ \times 0.7^\circ$, presented on an imaginary

circle 3.5° from fixation). These distractor circles were included to ensure that an N2pc would be elicited by selection of the target (Luck, Girelli, McDermott, & Ford, 1997). Finally, a single circle was presented as a memory test (0.5° x 0.5°; 0.1° line width, surrounding the fixation cross) until response, or for 2000 ms if no response was made.

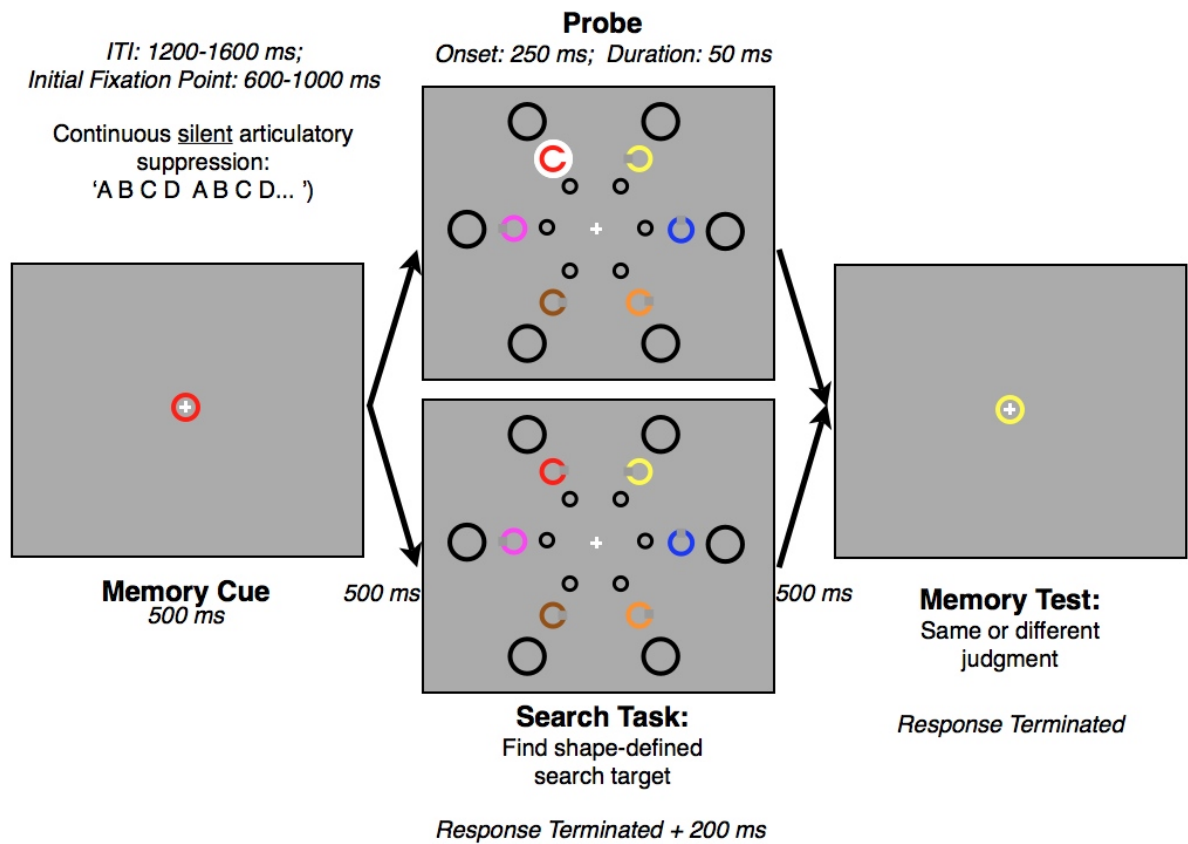


Figure 9. Stimulus sequence in Experiment 5. Trials with probes are indicated by the trial sequence following the top arrows, and no probe trials are indicated by the trials sequence following the bottom arrows. Probes were presented on 75% of trials, The 25% of trials with no probe were used to subtract out visually-evoked responses to the search array.

Procedure. Participants held a color in memory while performing a search task for a shape-defined target. Participants looked for the item with a gap at the top or bottom, while distractors contained gaps opening to the left or right. All search arrays contained Landolt-C

stimuli: a memory-color-matching distractor, a shape-defined search target, and 4 colored distractors (Figure 9). In addition, there were two rings of distractors that are not potential search targets. On 75% of trials, a single probe was presented 250 ms after search array onset to assess attention. These probes were equally likely to occur at the location of the target, the memory-matching item, or a distractor. The remaining trials were no-probe trials, and were used to isolate the response to the probe from the response to the search array, as described below. Participants had to report the location of the gap on the search target. They were instructed that the memory-matching item would never be the search target, and were told to do their best to ignore the probe. At the end of each trial, memory was tested.

Participants performed a practice block of 15 trials, and were allowed to repeat the practice block if they had not mastered the task. Participants completed 5 blocks of 240 trials, with a self-timed break after each block. Short 15-second breaks after every 30 trials contained the presentation of new articulatory suppression stimuli (selected from ABCD, WXYZ, 1234, or 6789). Articulatory suppression compliance was also tested during a subset of breaks. The experimental session lasted approximately 3 hours, including electrode set-up.

ERP Recording and Analysis. The electroencephalogram (EEG) was recorded from tin electrodes held on the scalp by an elastic cap (Electrocap International, Eaton, OH). A subset of the International 10/20 System sites were used (Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, PO3, PO4, T3, T4, T5, T6, O1, and O2) in addition to nonstandard sites OL (halfway between O1 and T5) and OR (halfway between O2 and T6). The right mastoid electrode served as the online reference for these active electrode sites, and the signals were re-referenced offline to the average of the left and right mastoids (Nunez, 1981). The

electrooculogram (EOG) was recorded by placing electrodes 1-2 cm lateral to the external canthi to measure horizontal eye movements and by placing an electrode beneath the left eye, referenced to the right mastoid, to measure vertical eye movements and blinks. An SA Instrumentation amplifier with a gain of 20,000 amplified signals and a bandpass of 0.01-100 Hz, digitized at 250 Hz by a PC-compatible computer, and averaged offline.

Trials accompanied by ocular or myogenic artifacts were excluded from the averages. A two-step procedure for ocular artifact rejection that has been described previously was used (Woodman & Luck, 2003b). Individuals with frequent eye movements were rejected prior to averaging, and averaged horizontal EOG (HEOG) waveforms were used to reject any subjects with significant unrejected eye movements. This procedure required replacing 7 participants due to excessive eye movements (either greater than 25% of individual trials rejected or any residual systematic eye movement that resulted in voltage deflections greater than 3.2 μV , corresponding to an ocular deviation of $\pm 0.1^\circ$). The remaining participants had a rejection average of 8.2% of trials per participant (with a single participant maximum of 17.8%)

The N2pc to the search array target was measured as the difference between electrode sites contralateral and ipsilateral to the target location. On the basis of the N2pc experiments with similar search stimuli presented in Experiments 1-3, and confirmed by visual inspection of the data, analysis focused on the period 200-400 ms after the onset of the search array. Analyses of variance (ANOVAs) were used for all statistical tests, and p-values were adjusted when appropriate with the Greenhouse-Geisser epsilon correction for non-sphericity (Jennings & Wood, 1976). Data was first entered into an ANOVA with the following

within-subjects factors: contralaterality with respect to the search target location (ipsilateral versus contralateral), and electrode site (OL/R, versus T5/6).

To isolate the visually evoked responses to the probe, ERP responses to the no-probe trials were subtracted from the responses to the probe trials. For probes on memory-matching distractors and distractors, this subtraction was performed separately for trials where the probe was in the same hemifield as the search target and trials where the probe was in the opposite hemifield as the search target. This ensured that the N2pc response due to attention to the target (as illustrated in Experiments 1-3) would be removed during the subtraction procedures. To assess the validity of this subtraction procedure, I looked for early differences between probed objects from 0-50 ms after probe onset. Differences between conditions in this early time window would indicate that the subtraction procedure failed to remove all search-related responses. Early differences between probed objects were found for the ipsilateral waveforms ($F(2,46) = 4.21$; $MSE = 0.14$; $p < .05$). No early differences were shown for the contralateral waveforms ($p = .64$). Therefore, all analyses of probe response were restricted to the contralateral waveforms.

The visually evoked responses to the probes were measured contralateral to the location of the probe (Luck and colleagues, 1994). The P1 was measured from 60-125 ms after probe onset at electrodes OL/R and T5/6. The anterior N1 was measured from 100-200 ms after probe onset at electrodes F3/4 and C3/4. The posterior N1 was measured from 125-250 ms after probe onset at electrodes OL/R and T5/6. Statistical analyses of the probes were conducted using 3 x 2 ANOVA comparisons of probed object (search target, distractor, and memory-matching distractor) and electrode (P1 and posterior N1, OL/R and T5/6; anterior N1, F3/4 and C3/4).

Results

Behavioral Results

Accuracy was high on both the search (96.8% accurate; additional 2.8% trials without response) and memory tasks (92.6% accurate; additional 0.4% trials without response).

Mean response time for the search task was 848 ms.

ERP Results

Search Array Analysis. I began by the assessing the N2pc during the search task, to ensure that we were able to determine that attention was directed to the target (Figure 10). I found a contralateral negativity to the shape-defined search target that extended from 200-400 ms after the presentation of the search array (contralateral- ipsilateral $M = -0.26 \mu\text{V}$). Confirming this observation, the ANOVA of the voltages from the N2pc time window showed a significant effect of contralaterality ($F(1,23) = 11.27$; $MSE = 0.15$; $p < .01$). The analysis also showed a main effect of electrode ($F(1,23) = 6.36$; $MSE = 2.62$; $p < .05$) and an interaction of contralaterality x electrode ($F(1,23) = 6.62$; $MSE = 0.02$; $p < .05$).

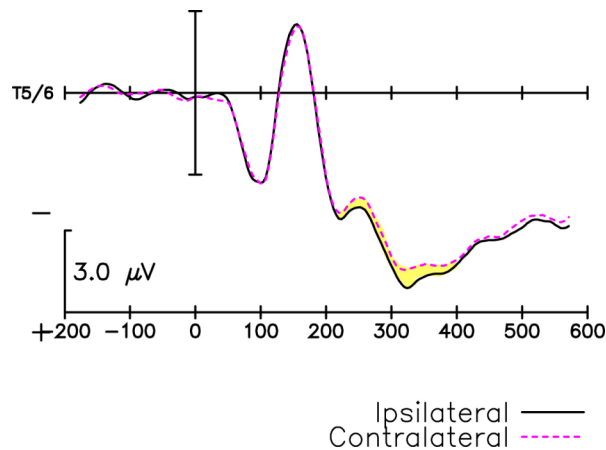


Figure 10. Visually evoked-responses to the search array at electrodes T5/6. N2pc measurement window is highlighted in yellow.

The effects of contralaterality suggest that the target was selected between 200 and 400 ms after the onset of the search array. The long duration of the N2pc suggests that attention was sometimes directed to the target before the probe was presented (250 ms after search onset). This raises the concern that the effect of the probe might be different for trials where the target was selected early and trials where the target was selected later. Therefore, in addition to the basic analyses on the electrophysiological response to the probed object, I also conducted analyses contrasting the electrophysiological response to the probed object for trials in which reaction times were fast and trials in which reaction times were slow, based on a median split of reaction times.

Probe Evoked-Response Analysis. I examined modulations in the sensory evoked components related to the presentation of the task-irrelevant probe to assess enhancement and suppression of the various object types. The P1 component shown in Figure 11, a measure of distractor suppression, was numerically larger in response to probes on memory-matching distractors ($M = 0.86 \mu\text{V}$) and targets ($M = 0.79 \mu\text{V}$) than distractors ($M = 0.62 \mu\text{V}$). The specific pattern of results was different for each electrode (see Table 1).

A 3 x 2 ANOVA with the factors of probed object (target, memory-matching distractor and distractor) and electrode (OL/R and T5/6) failed to show a significant main effect of probe type ($p = .11$). There was a main effect of electrode ($F(1,23) = 6.64$; $MSE = 0.20$; $p < .05$) due to larger P1 amplitude at electrodes OL/R than T5/6. There was also an interaction of probed object and electrode ($F(2,46) = 9.81$; $MSE = 0.02$; $p < .001$). Post-hoc analyses were conducted to determine the source of the interaction of probed object and electrode. Contrasts showed that the probe response to the target and memory-matching distractors did not differ at either electrode (OL/R: $p = .98$; T5/6: $p = .23$). The difference between probes on the memory-matching distractor versus other distractors was significant at electrodes OL/R ($t(23) = 2.44$, $p < .05$) and marginally significant at T5/6 ($t(23) = 2.03$, $p = .05$). The difference between probes on the targets and distractors was significant at electrodes OL/R ($t(23) = 2.30$, $p < .05$) but not significant at T5/6 ($t(23) = 0.54$, $p = .59$). Overall, the pattern of probe P1 responses to the memory-matching distractor was more similar to the responses to the search target than the other distractor items.

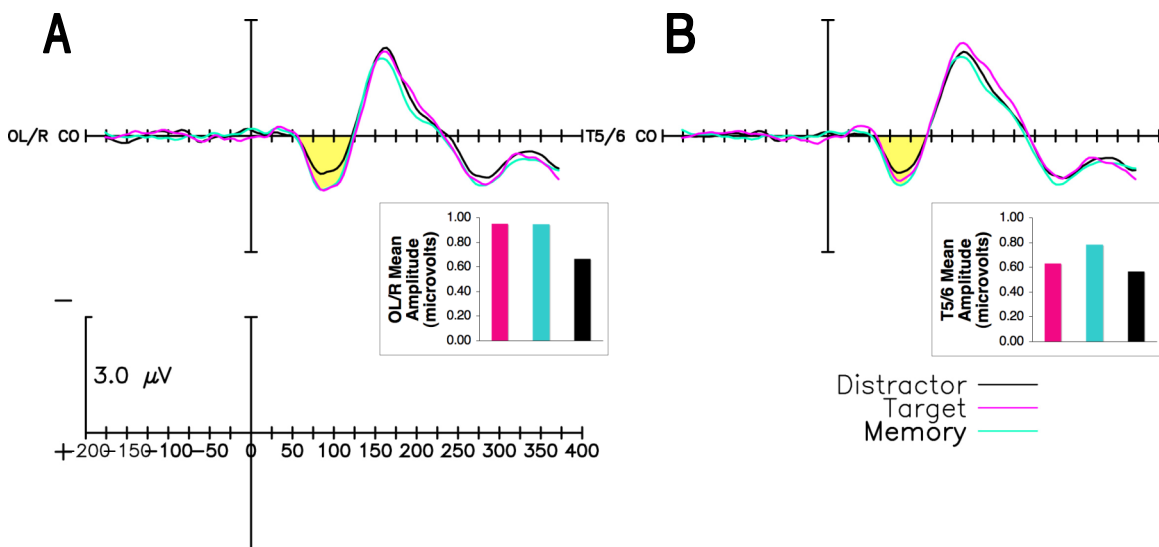


Figure 11. Visually evoked P1 responses to the task-irrelevant probe. P1 measurement window from 60-125 ms is highlighted in yellow. A) Responses at electrodes OL/R. B) Responses at electrodes T5/6.

Table 1

P1 Mean Amplitude (μV)

Object Type	<u>OL/R</u>	<u>T5/6</u>
Target	0.95	0.63
Memory	0.95	0.78
Distractor	0.66	0.57

Figure 12 shows that the posterior N1 component was numerically larger in response to probes on targets ($M = 1.18 \mu\text{V}$) followed by distractors ($M = 1.06 \mu\text{V}$) and memory-matching distractors ($M = 0.94 \mu\text{V}$). However, while both electrodes showed the same ordering of the response amplitudes for the three probed objects, the specific pattern of results differed by electrode (see Table 2).

A 3 x 2 ANOVA with the factors of probed object (target, memory-matching distractor and distractor) and electrode (OL/R and T5/6) did not find a main effect of probe type ($p = .15$). There was a main effect of electrode ($F(1,23) = 13.30$; $MSE = 0.21$; $p < .01$) due to larger N1 amplitude at electrodes T5/6 than OL/R. There was also a significant interaction of probed object and electrode ($F(2,46) = 9.75$; $MSE = 0.02$; $p < .01$). Post-hoc analyses were performed to further explore this interaction. At electrodes OL/R, the target probe response did not differ from the memory-matching distractor probe response ($p = .30$) or the distractor probe response ($p = .97$), but the probe responses to the distractor were marginally stronger than probe responses to the memory-matching distractor ($p = .08$). In

contrast, at electrodes T5/6 the target elicited a stronger probe response than the memory-matching distractor ($t(23) = 2.32, p < .05$) and a marginally stronger probe response than the distractor ($p = .08$), but the responses to probes on the memory-matching distractor and distractor did not differ ($p = .36$). The lack of a consistently larger posterior N1 probe response to targets than distractors converges with the results of the N2pc analysis to suggest that the target was frequently not selected by the time the probe was presented. As mentioned above, this possibility was examined more directly through a median split of trials based on response time.

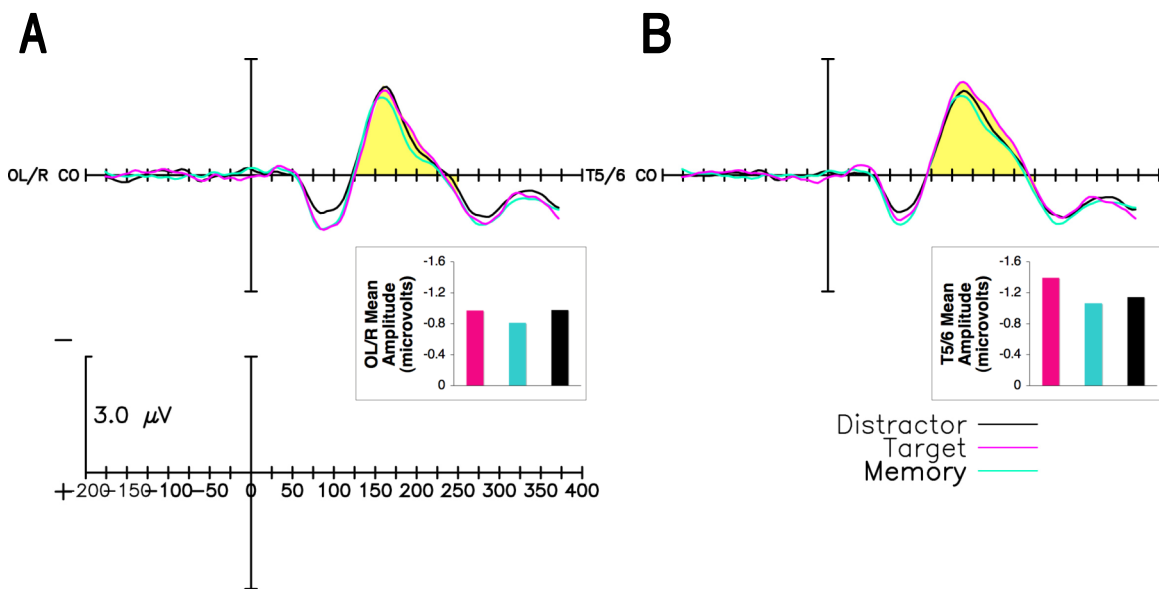


Figure 12. Visually evoked Posterior N1 responses to the task-irrelevant probe. Posterior N1 measurement window from 125-250 ms is highlighted in yellow. A) Responses at electrodes OL/R. B) Responses at electrodes T5/6.

Table 1

Posterior N1 Mean Amplitude (μV)

Object Type	<u>OL/R</u>	<u>T5/6</u>
Target	-0.97	-1.39
Memory	-0.81	-1.06
Distractor	-0.98	-1.15

Figure 13 shows that the anterior N1 component was largest for probes on the search targets ($M = -1.21 \mu\text{V}$) followed by probes on memory-matching distractors ($M = -0.83 \mu\text{V}$) and distractors ($M = -0.79 \mu\text{V}$). A 3 x 2 ANOVA with the factors of probed object (target, memory-matching distractor and distractor) and electrode (F3/4 and C3/4) showed a significant main effect of probed object ($F(2,46) = 5.34$; $MSE = 0.50$; $p < .01$) and a main effect of electrode ($F(1,23) = 7.46$; $MSE = 0.24$; $p < .05$) due to a larger anterior N1 amplitude at electrodes C3/4 than F3/4. There was no interaction of probed object and electrode ($p = .35$). Planned comparisons showed that the probes on targets elicited a larger response than probes on memory-matching distractors ($t(23) = 2.60$, $p < .05$) and distractors ($t(23) = 3.42$, $p < .01$).

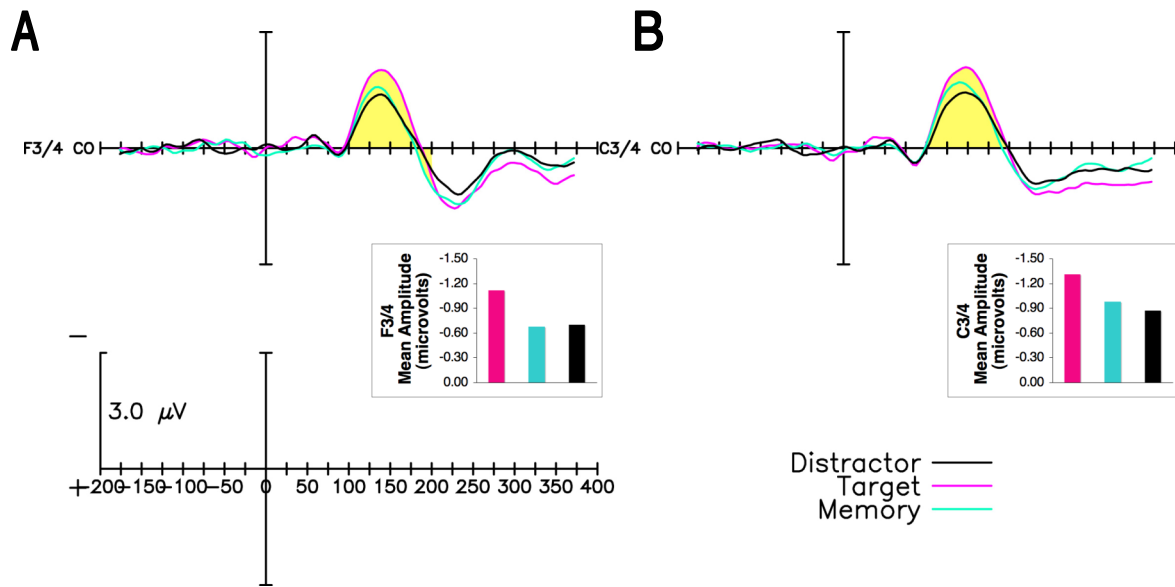


Figure 13. Visually evoked anterior N1 responses to the task-irrelevant probe. Anterior N1 measurement window from 100-200 ms is highlighted in yellow. A) Responses at electrodes F3/4. B) Responses at electrodes C3/4.

Median Split Probe Evoked-Response Analysis. Two findings suggested that that the probe might have been presented before the target was selected on a significant proportion of trials. First, the duration of the N2pc, an index of the deployment of attention to a target, extended well after the time the probe was presented. Second, there was no consistent difference between target and distractor probes in the posterior N1 component which is thought to provide an index of target discrimination and the allocation of attention (Vogel & Luck, 2000). Because attention-related differences in the P1 and N1 between probes on targets and distractors are thought to be due to the deployment of spatial attention to the target (Mangun & Hillyard, 1995), this raises the possibility that the previous probe analyses might be weakened by trials where the target had not yet been selected. This possibility motivated separate analyses contrasting trials in which the target was selected early versus late, indexed by a median split based on search reaction times. The median RT average

across participants was 785 ms and creating the fast and slow RT split resulted in mean RTs of 643 ms in the fast and 1054 ms in the slow half. Analyses of the evoked response were conducted with a 2 x 3 x 2 within-subjects ANOVA contrasting split half (fast trials and slow trials) with probed object (target, memory-matching distractor and distractor) and electrode (OL/R and T5/6 for P1 and posterior N1; F3/4 and C3/4 for anterior N1). If the time of target selection influences the attentional effects of probe response, then I expected to find stronger effects of the object probed object at 250 ms when reaction times were fast because the target is more likely to have been selected on these trials at the time of probe presentation.

Figure 14 shows the P1 component probe responses based on probed object did not show a clear difference in responses for fast and slow trials. The ANOVA showed a main effect of split half ($F(1,23) = 5.75$; $MSE = 1.96$; $p < .05$) due to a stronger evoked response for trials with fast responses than trials with slow responses. The analysis also revealed a main effect of electrode ($F(1,23) = 6.09$; $MSE = 0.42$; $p < .05$), an interaction of probed object and electrode ($F(2,46) = 9.18$; $MSE = 0.03$; $p < .001$) and a 3-way interaction of split half x probed object x electrode ($F(2,46) = 3.67$; $MSE = 0.02$; $p < .05$). All other main effects and interactions were not significant ($ps > .10$).

I followed up on the 3-way interaction of split half x probed object x electrode with separate analyses for the fast and slow halves. The 3-way interaction was driven by a non-significant interaction of probed object and electrode for the slow half ($p = .27$), while for the fast half, the interaction was significant ($F(2,46) = 10.72$; $MSE = 0.03$; $p < .001$). This was driven by a significant difference between electrodes for the target ($t(23) = 3.46$, $p < .01$) that was not present for probes on the memory or other distractor.

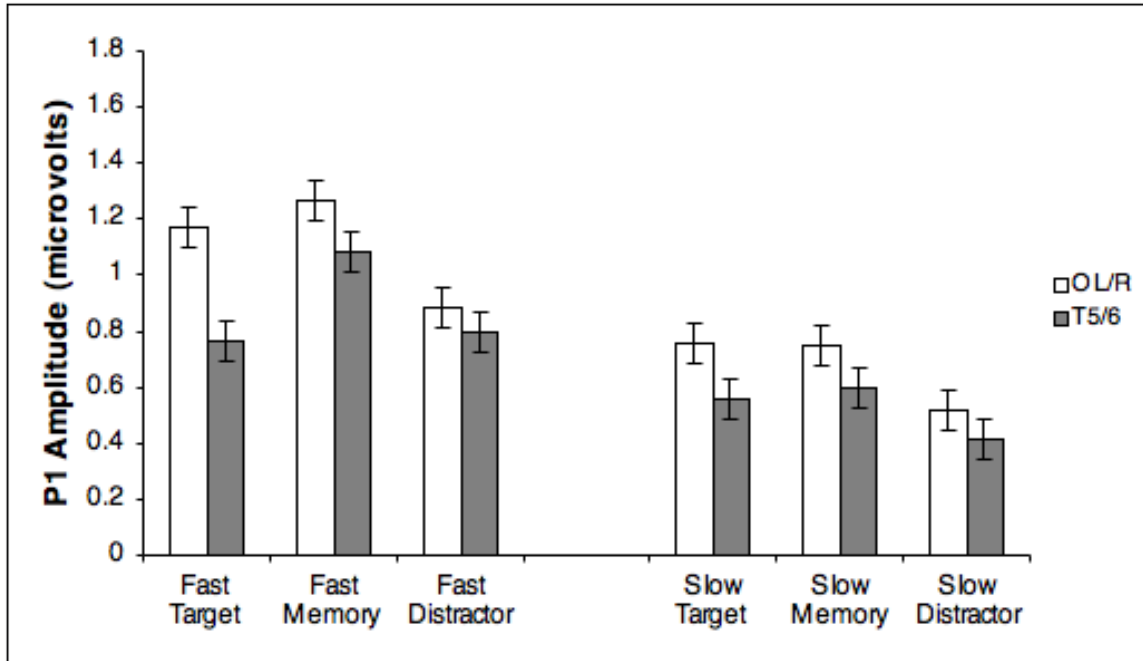


Figure 14. Mean P1 response amplitude to the probe. Error bars represent 95% within-subjects confidence intervals for the 3-way interaction of split half x probe x object.

In contrast to the P1 results, the posterior N1 results in Figure 15 show that probe object responses clearly exhibited a different pattern of results between the fast half, in which the target was more likely to be selected at the time of the probe, and the slow half. For the fast half, N1 probe amplitude in response to the target ($M = -1.35 \mu\text{V}$) was larger than the N1 probe response to the distractor ($M = 0.82 \mu\text{V}$) and the memory-matching distractor ($M = 0.57 \mu\text{V}$). In contrast, for the slow half, the N1 amplitude was similar for probes on all objects (target $M = -0.94 \mu\text{V}$; memory-matching distractor $M = -1.08 \mu\text{V}$; distractor $M = -1.12 \mu\text{V}$). The ANOVA showed a significant main effect of probed object ($F(2,46) = 3.68$; $MSE = 0.67$; $p < .05$) as well as the critical interaction of probed object and split half ($F(2,46) = 5.77$; $MSE = 0.95$; $p < .01$). The analyses also revealed a main effect of electrode ($F(1,23) = 13.96$; $MSE = 0.46$; $p < .01$) due to larger N1 amplitude at electrodes T5/6 than OL/R. There was an interaction of probed object and electrode ($F(2,46) = 8.59$; $MSE =$

0.04; $p < .01$) and a marginally significant 3-way interaction of split half x probed object x electrode ($p = .09$). All other main effects and interactions were not significant ($ps > .16$).

I followed-up on the interaction of split half and probed object for the posterior N1 by running separate 3 x 2 ANOVAs with the factors of probe type and electrode for the fast half and slow half data. For the fast half, there was a significant main effect of probed object ($F(1,23) = 7.25$; $MSE = 1.04$; $p < .01$), a main effect of electrode ($F(1,23) = 13.06$; $MSE = 0.26$; $p < .01$) and an interaction of probed object and electrode ($F(2,46) = 6.37$; $MSE = 0.05$; $p < .01$). Post-hoc analyses were performed to further explore this interaction. At electrodes OL/R, the target probe response was larger in amplitude than the memory-matching distractor probe response ($t(23) = 3.11$, $p < .01$). The probe response to the distractor was not different than the probe response to the target ($p = .11$) or memory-matching distractor ($p = .09$). In contrast, at electrodes T5/6 the target probes elicited a larger response than the memory-matching distractor probes ($t(23) = 3.96$, $p < .001$) and a larger response than the distractor probes ($t(23) = 2.98$, $p < .01$), but the responses to probes on the memory-matching distractor and distractor did not differ ($p = .41$).

For the posterior N1 responses on the slow half, there was no main effect of probed object ($p = .50$), but there was a main effect of electrode ($F(1,23) = 10.07$; $MSE = 0.30$; $p < .01$) due to a larger anterior N1 amplitude at electrodes T5/6 than OL/R. The interaction of probed object and electrode was significant ($F(2,46) = 5.40$; $MSE = 0.02$; $p < .01$) due to a larger difference between electrodes for the target probes ($t(23) = 3.77$, $p < .001$) than the memory-matching distractor probes ($t(23) = 2.39$, $p < .05$) or other distractor probes ($t(23) = 2.61$, $p < .05$).

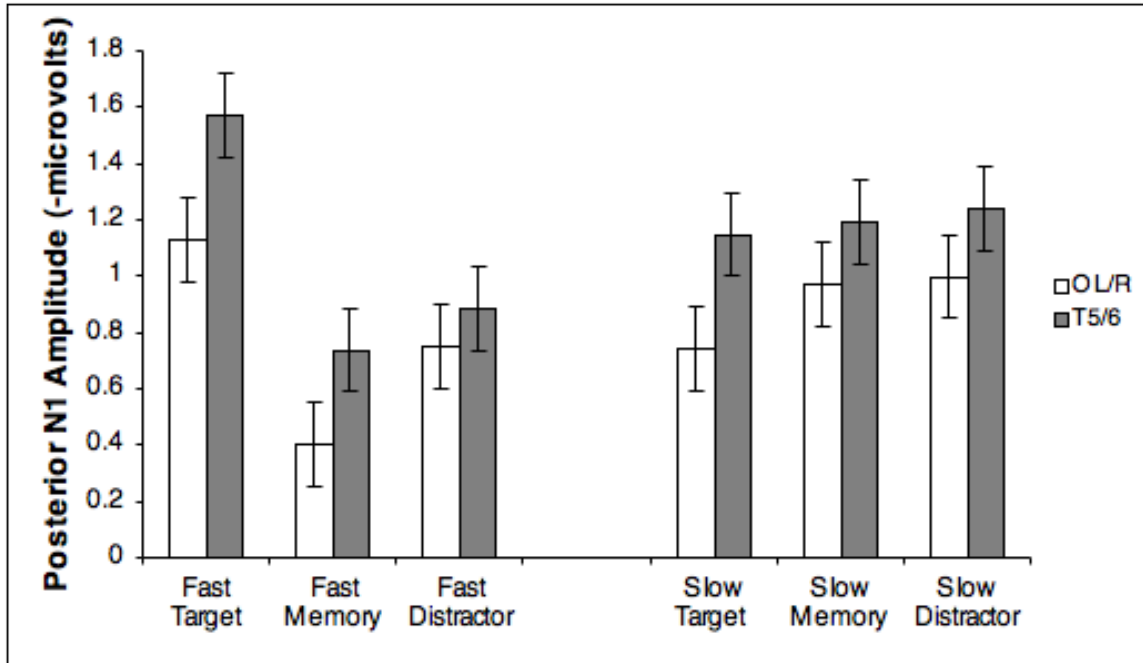


Figure 15. Mean posterior N1 response amplitude to the probe. Error bars as in Figure 14.

Figure 16 shows the anterior N1 responses based on probed object also differed for the fast half and the slow half. For the fast half, anterior N1 amplitude in response to the target probes ($M = -1.44 \mu\text{V}$) was much larger than the anterior N1 response to either distractor type (both $M = 0.57 \mu\text{V}$). In contrast, for the slow half the anterior N1 amplitude was similar for probes on all objects (target $M = -1.07 \mu\text{V}$; memory-matching distractor $M = -0.98 \mu\text{V}$; distractor $M = -0.94 \mu\text{V}$). The ANOVA showed a significant main effect of probed object ($F(2,46) = 6.27$; $MSE = 1.25$; $p < .01$) as well as the critical interaction of probed object and split half ($F(2,46) = 3.86$; $MSE = 1.19$; $p < .05$). The analyses also showed a significant interaction of split half and electrode ($F(1,23) = 4.68$; $MSE = 0.26$; $p < .05$) and a marginally significant main effect of electrode ($p = .06$). All other main effects and interactions were not significant ($ps > .40$).

To follow-up on the interaction of split half and probed object for the anterior N1, I computed separate 3 x 2 ANOVAs with the factors of probe type and electrode for the fast split half and slow split half data. For the fast half, there was a significant main effect of probed object ($F(1,23) = 8.04$; $MSE = 1.51$; $p < .01$), with no main effect of electrode ($p = .64$) or interaction of probed object and electrode ($p = .72$). For the slow half, there was no main effect of probed object ($p = .77$), but there was a main effect of electrode ($F(1,23) = 7.15$; $MSE = 0.46$; $p < .05$) due to a larger anterior N1 amplitude at electrodes C3/4 than F3/4. The interaction of probed object and electrode was not significant ($p = .16$).

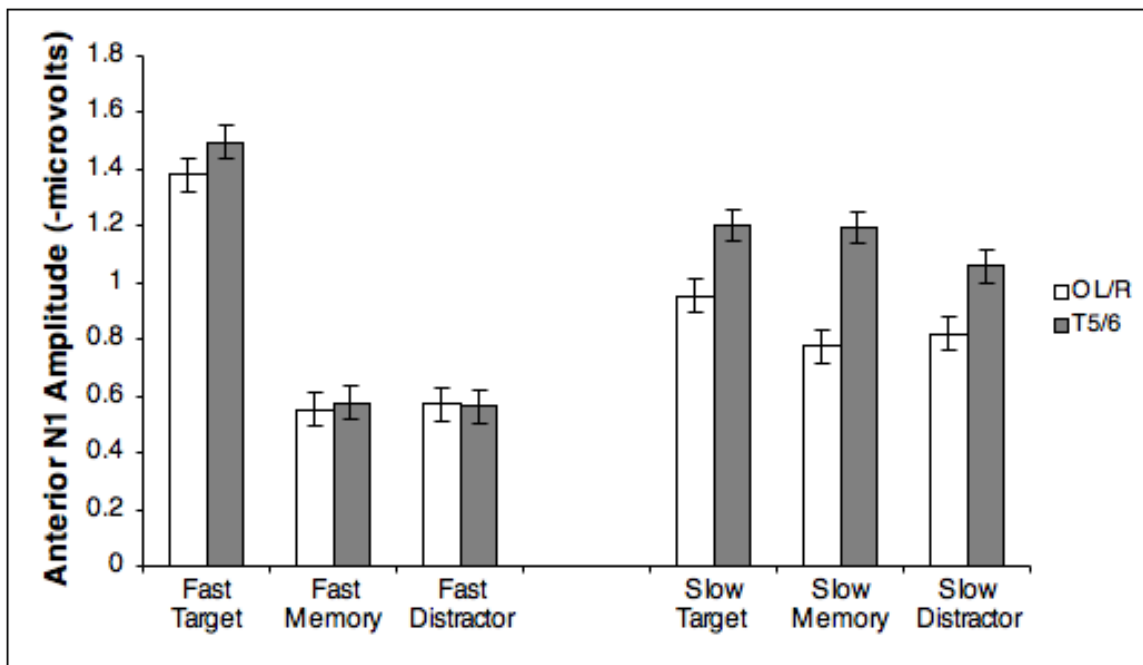


Figure 16. Mean anterior N1 response amplitude to the probe. Error bars as in Figure 14.

Chapter 3 Discussion

The goal of this experiment was to gain a richer understanding of how task-irrelevant memory-matching items are processed during a visual search task. The results of the P1

probe analyses, a measure of the suppression of distractors, demonstrated that the memory-matching distractors were not suppressed like the other distractors. The anterior and posterior N1 probe results showed that, for the half of trials with the fastest behavioral responses, the target showed an enhanced response while both the memory-matching distractor and other distractors elicited a smaller response. Both the anterior and posterior N1 results for probes that occurred on trials with slow behavioral responses showed little differentiation based on probed object. The N1 responses suggest that only the target is enhanced, and that the memory-matching distractor is treated like any other distractor. The differing pattern of results for the P1 and N1 measures confirms the generally accepted view in the literature that the two components index different mechanisms of attentional selection (Luck, et al., 1994).

The P1 data suggest that the memory-matching items are not suppressed like the average distractor in the search array. This finding was surprising given the previous electrophysiological evidence from the Pd component, an index of distractor suppression. Both the present Experiments 1-3 and Sawaki & Luck (2010) showed that task-irrelevant memory-matching items elicited a Pd. These findings suggest that the memory-matching items can be actively suppressed. One possible explanation for these incongruous findings is the timing of the measures. The Pd effect found in Experiments 1-3 in relation to a memory-matching distractor extended from 300-400 ms after the onset of the search array. In the current experiment, the probe was presented 250 ms after the onset of the search array and did not show memory-matching distractor suppression. It is possible that a task-irrelevant probe presented within the 300-400 ms time window would show memory-matching distractor suppression via the Pd, indicating that the memory-matching items were

suppressed. This would suggest that suppression of the memory-matching distractors occurs at a different time point than suppression of a typical distractor. In future work using the task-irrelevant probe technique, I plan to assess this possibility by presenting probes at different times.

Both the anterior and posterior N1 results for trials with fast responses showed an enhanced response only for targets. I found that the memory-matching distractor probe responses elicited ERP responses equivalent to the other distractors, suggesting that they were not subject to the enhancement of a goal-relevant search target. This finding is consistent with another electrophysiological finding from Peters, Goebel & Roelfsema (2009) using the P3 component to contrast responses to memory-matching distractors, targets, and other distractors. The posterior P3 is related to stimulus evaluation, and is elicited when a target is presented (Kutas, McCarthy, & Donchin, 1977). Peters, Goebel & Roelfsema (2009) reasoned that if memory-matching items created an automatic attentional template, then they would elicit a P3 response similar to targets. They found that the P3 responses to memory-matching distractors were indistinguishable from the responses to the other distractors, and concluded that the memory-matching distractors were not evaluated as another type of target.

There are two possible mechanisms for the differences between search targets and task-irrelevant memory matching items. First, it is possible that there is a single prioritized location in working memory that is used to create biases (Olivers, Peters, Houtkamp, & Roelfsema, in press). If there is a single prioritized representation in memory, I expect that on some trials the memory item might be placed in this prioritized location, consistent with the proposal in the literature that memory-matching items capture attention (Olivers, Meijer,

& Theeuwes, 2006). The P1 and N1 data can be used as a first attempt to examine this prediction. On some proportion of trials in which it took participants longer to identify the search target, the memory item may have gained access to this prioritized location. If the slowed trials were due to the memory-match being in the prioritized location in memory, we would expect the memory-match to be enhanced on slowed trials. However, when we look at the slow half of trials, we do not see any evidence that the memory-matching item was prioritized during these trials.

The second possibility, consistent with the results of Experiments 1-4, is that there are flexible attentional biases that can be scaled based on the relevance of items in working memory. This possibility is consistent with the clear difference between responses to targets and memory-matching distractors in the N1 components, and the lack of suppression of memory-matching items in the P1 component. Overall, the data are more consistent with a relative weighting of task-relevant and task-irrelevant memory-matching items than with a single prioritized storage location in memory (Olivers, Peters, Houtkamp, & Roelfsema, in press).

The current experiment utilized a technique that provided a richer picture of the attentional prioritization of a task-irrelevant working memory representation. Task-irrelevant memory-matching items seem to have a unique type of attentional processing. At 250 ms after search onset, memory-matching distractors are not suppressed like other distractors, but are also not enhanced like search targets. I am currently running follow-up studies to determine if this pattern holds at all time points, or whether the relative enhancement and suppression of the memory-matching items varies during the course of search.

CHAPTER 4

MEASURES OF OVERT ATTENTION TO TASK-RELEVANT AND TASK-IRRELEVANT MEMORY-MATCHING ITEMS

The biased competition theory of attention proposes that the contents of working memory create an automatic attentional bias, which is the equivalent of the attentional template used during tasks such as visual search. Empirical tests of the influence of working memory on attention have assessed the proposals of biased competition. These tests have often focused on one aspect of the proposed relationship between working memory and attention, namely that the contents of working memory create an automatic attentional bias. Many studies have not focused on the more direct prediction that the working memory generated attentional biases should be the equivalent of a goal-related attentional template.

Understanding whether working memory representations create an attentional bias that is equivalent to a goal-related attentional template is critical for determining the structure of top-down attentional control. Specifically, this distinction is critical for understanding where executive control exerts an influence in generating attentional biases (see Figure 1). If working memory representations create an attentional bias that is the equivalent of a goal-related attentional template, then executive control would only be able to exert an influence by determining what information gains entry into working memory. Once information is in working memory, executive control would no longer be able to exert an influence. Alternatively, if a goal-related attentional template creates an additional attentional bias beyond an item that is simply maintained in working memory without a goal, this suggests

that executive control exerts an influence after entry into working memory. In this case, executive control would mediate the relationship between working memory and attention.

Within the previous literature, there have not been direct tests that provide a comparison of the strength of attentional biases to a goal-irrelevant memory match and a goal-relevant memory match. Because previous studies were designed to assess the influence of goal-irrelevant memory-matches on attention, their designs prove inadequate for drawing a strong conclusion about relative attention biases on goal-irrelevant and goal-relevant working memory-matching items. The designs have failed to meet four specific criteria that are necessary for assessing relative attentional biases.

First, some studies have measured attention to the goal-irrelevant memory item when the goal-relevant search target remains the same across the study, in essence contrasting a goal-irrelevant item in working memory with a goal-relevant item in long-term memory (Soto, Heinke, Humphreys, & Blanco 2005; Woodman & Luck, 2007). Biased competition suggests that items in long-term memory can influence attention, but does not explain how such items with long-term learned biases would compete with items in working memory. These studies are inadequate because they do not compare attentional biases of a goal-relevant to a goal-irrelevant working memory representation. It is unclear whether a long-term or working memory representation would have a stronger top-down attentional bias. Furthermore, degraded representations would not generate the same top-down biases as a strong memory representation (Soto, Hodsoll, Rotshtein, & Humphreys, 2008) and it is unclear whether working memory or long-term memory would have a stronger representation. Therefore, these studies are also inadequate for assessing attention to goal-relevant and goal-irrelevant memory matches because they do not equate the strength of the

goal-irrelevant and goal-relevant memory representations. Third, some studies have measured attention to a very salient goal-irrelevant memory-matching item while in the presence of a less salient goal-relevant memory-matching item (Soto, Heinke, Humphreys, & Blanco, 2005; Woodman & Luck, 2007; Olivers, 2006). Because these studies are not ensuring that both goal-relevant and goal-irrelevant items have the same bottom-up biases, it is difficult to determine whether attention to the goal-relevant and goal-irrelevant items are driven by top-down biases or bottom-up stimulus differences.

Finally, some studies use measurements that do not directly quantify the frequency of attention to goal-relevant and goal-irrelevant memory-matching items. One measurement that has frequently been used is reaction time (Downing, 2000; Downing & Dodds, 2004; Olivers, 2006; Han & Kim, 2009). Although reaction times are well suited to assessing whether attention is directed to memory-matching items, no one has used reaction times to determine how frequently attention is directed to a goal-irrelevant memory-matching item. Eye tracking is another measurement of attention that has been used to assess attention to memory-matching items. One study directly compared attention to a goal-irrelevant and goal-relevant memory-matching item during search (Houtkamp & Roelfsema, 2006). This study measured the proportion of all fixations to the targets, distractors, and memory-matching distractors before a search response, creating a situation where other factors such as proximity (Najemnik & Geisler, 2004) or inhibition of return (Klein, 2000) may have masked an attentional advantage for goal-irrelevant memory-matches early in search. Therefore, the previous literature has not provided a strong test of the more direct proposal of biased competition, that working memory representations are the equivalent of a goal-related attentional template.

To assess whether goal-related items in working memory are prioritized by executive control, I have used an experimental design to meet the four specific criteria that have been lacking in the previous literature. First, both the goal-relevant and goal-irrelevant memory representations should be in working memory. Having both a goal-relevant and goal-irrelevant item in working memory allows for each item to compete for attention within a trial, so in my design one of two working memory representations was designated as important for the attentional task. Second, the two representations should both be strong representations at the time of search onset. To this end, I included catch trials to assess memory for the goal-relevant and goal-irrelevant item at the beginning of search. Third, the match between each memory representation and a perceptual representation should be equivalent. This is drawn from biased competition and TVA, which both predict that a perceptual item that is a better match to an internal template will be selected more frequently. I used two memory representations that are equally similar to their perceptual match during search, and used search items of equivalent salience across the study to ensure that there is no bottom-up bias to select one item. Fourth, the measurement should create a quantifiable approximation of the strength of the attentional biases to goal-relevant and goal-irrelevant working memory-matching items. Specifically, I measured the first fixations that fall on an object on each trial. Since participants began search with their eyes in the center of the screen, each item should have similar bottom-up salience. This creates a situation best suited to contrast the top-down attentional biases to each item.

The goal of meeting these four criteria was to establish a measure capable of determining if maintaining a representation in working memory is sufficient to create an attentional template for search, in which case the frequency of attending to a goal-relevant

memory match should be equivalent to the frequency of attending to a goal-irrelevant memory match. Alternatively, if executive control creates a prioritization after items enter working memory, then goal relevant memory matches should be attended more frequently than goal irrelevant memory matches.

Methods

Participants. 10 participants were recruited through the Vanderbilt online participant scheduling service, SONA. Participants gave informed consent and were compensated for their time at a rate of \$10/ hour.

Stimuli. An example trial is presented in Figure 17. Memory and search target colors were randomly selected for each trial from a set of 6 colors (red, $x = .634$ $y = .36$, 14.5 cd/m^2 ; green, $x = .286$ $y = .603$, 41.5 cd/m^2 ; blue, $x = .143$ $y = .068$, 11.7 cd/m^2 ; yellow, $x = .439$ $y = .486$, 84.3 cd/m^2 ; magenta, $x = .293$ $y = .150$, 37.5 cd/m^2 ; orange, $x = .569$ $y = .385$, 36.5 cd/m^2 ; purple, $x = .279$ $y = .147$, 4.8 cd/m^2). Each trial began with the presentation of two digits for articulatory suppression (randomly selected from the set of 0-9, $0.7^\circ \times 0.5^\circ$; 0.06 cd/m^2) presented for 1500 ms. Next, the memory and search cues were presented ($0.7^\circ \times 0.7^\circ$; 0.1° line width, 3.4° to the left and right of the black fixation cross; $0.3^\circ \times 0.3^\circ$; 0.06 cd/m^2), followed by the fixation cross only for 500 ms. Then, the search array was presented until response, with a maximum of 1800 ms. The search array contained 6 colored items ($0.7^\circ \times 0.7^\circ$, presented on an imaginary circle 6.9° from fixation). Half of the items in each array had a gap opening to the left, and the remainder had a gap opening to the right. Finally, a single circle was presented as a memory test ($0.7^\circ \times 0.7^\circ$; 1.0° above the fixation cross) until response, with a maximum presentation duration of 2000 ms.

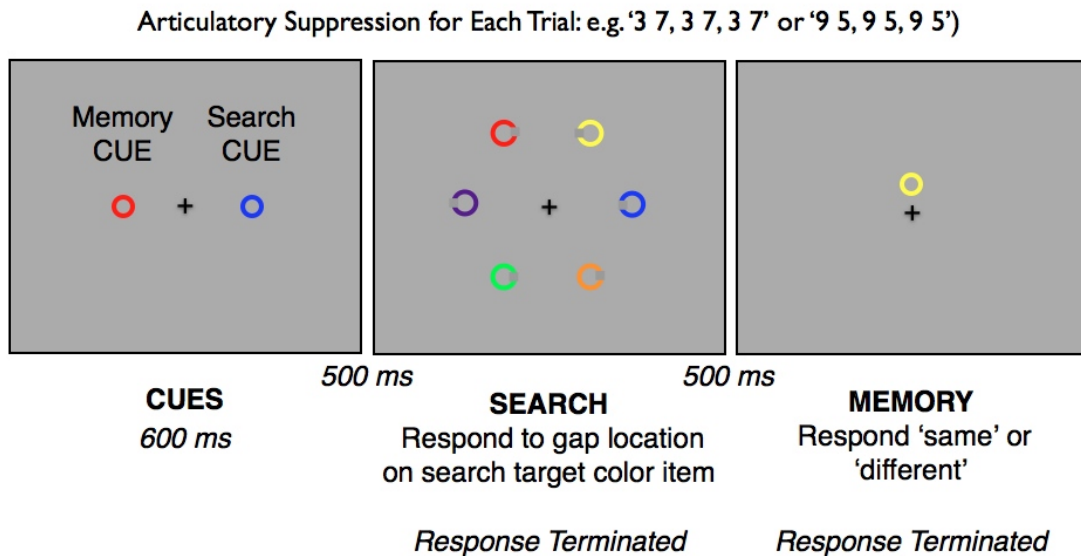


Figure 17. Stimulus sequence in Experiment 6. 'Memory Cue' and 'Search Cue' titles are for illustrative purposes and were not presented during the actual trials.

Procedure. Participants held a color in memory while performing a search task for a color-defined target on 75% of trials. On the other 25% of trials, participants performed a catch trial to assess memory for the search or memory color, with equal numbers of tests on each item type. Search trials and catch trials were randomly interleaved. New search and memory cues were presented on each trial, and the location of the search and memory cues (search left or search right) was counterbalanced across participants. Participants were instructed to keep their eyes on the fixation cross during the presentation of the cues to

ensure that the eyes would be at the center of the screen when the search task began. On search trials, participants looked for the item that matched the search cue color, and reported whether the search cue had a gap on the left or right by a button press using their right hand. Half of all trials had a target with a gap to the left, and the gap appeared on the right on the other half of trials. All search arrays contained Landolt-C stimuli: a memory-color-matching distractor, a search-color target, and 4 colored distractors (see Figure 17). At the end of each trial, memory was tested and participants pressed one of two buttons using their right hand to indicate whether the memory test was the same color as the memory cue or a different color. There was a color change on half of all trials. Like search trials, catch trials began with articulatory suppression and cue stimuli. Instead of being presented with a search array, participants were presented with a single item at the location of one of the two cues. They pressed one of two buttons with their right hand to indicate whether the test item was the same color as the cue that had previously been presented at that location. Participants were told to emphasize speed and accuracy on the search task and accuracy on the memory test.

Participants performed a practice block of 12 trials, and were allowed to repeat the practice block if they felt they had not mastered the task. Participants completed 8 blocks of 30 trials, with a self-timed break after each block. During each break, participants were shown a feedback screen with their speed and accuracy on the search task and accuracy on the memory test for the last block. An experimenter listened online for articulatory suppression compliance. The experimental session lasted approximately 1 hour.

Eye Movement Recording and analysis. Eye movements were measured with an EyeLink II head-mounted eye tracker (SR Research, Canada). The eyetracker measured the pupil (mean participant precision of 0.41° was measured during the validation of calibration)

while sampling at 250 Hz for data analysis offline. Participants performed a 9-point calibration sequence at the beginning of the experiment, and single point drift correction was calculated before each trial of the study. Additional recalibrations were performed as needed throughout the course of the experiment if the drift correction was frequently failing on the initial attempt.

Offline analyses focused on fixations of the search targets, memory-matching distractors and other distractors. I used a broad measure of fixations on an object to ensure that no fixations were missed. Any fixation that fell within 2.5° of an object was defined as being on that object. Any fixations that were not within 2.5° of an object were not analyzed. The primary analysis focused on the proportion of first fixations after the onset of the search array that fell on targets, memory-matching distractors, and other distractors.

In addition to the main analyses on the proportion of saccades to each object type, I also performed an analysis of saccade onset for the first saccades landing on an object after the onset of the search array. This analysis was conducted to assess whether it was likely that covert attention was directed to the memory-matching item before overt attention was directed to the search target. If covert attention was frequently directed to the memory-matching distractors before overt attention was directed to the search target, we would expect to see slower saccade onsets of eye movements on trials where the first fixation was on the target than trials where the first fixation was on the memory-matching distractor. This prediction was based on the evidence that covert attentional selection occurs prior to an eye movement to a location or object (e.g., Hoffman & Subramaniam, 1995), and can occur without subsequent overt selection. If people covertly shift attention to the memory-matching item before overtly shifting attention to the target, then this will slow saccadic

onset relative to when people shift covert attention to the memory match and make an eye movement to that item.

Results

Accuracy was high on the search task (97.5%) and memory task (90.7%). Accuracy on the catch trials was similar for tests of the memory cue (94.5%) and tests of the search cue (87.7%; $t(9) = 1.35, p = .21$). While overall catch trial accuracy was high, a one-sample t -test indicated that it was not at ceiling ($t(9) = 2.78, p < .05$). Reaction times on the catch trials were numerically slower for tests of the memory cue (945 ms) than for tests of the search cue (908 ms), but this difference was not significant ($t(9) = 0.98, p = .35$).

No eye movements were measured on 14.4% of trials, and on an additional 20.8% of trials with eye movements, the first fixation did not fall within 2.5° of an object. These trials were not included in analyses of first fixation location. Figure 18 shows the first fixations on an object most frequently fell on the search target (80.9% of trials), followed by the memory-matching distractor on 5.9% of trials, and the average non-memory-matching distractors on 3.3% of trials (13.3% of trials falling on any of the four distractors).

I entered the mean first fixations into a repeated-measures ANOVA to contrast the likelihood of attending to the target, the memory-matching distractor and the average non-memory-matching distractor, and there was a significant main effect of object type ($F(2,18) = 437.24; MSE = .004; p < .0001$). Follow-up comparisons showed that the search target was overtly attended more frequently with the first fixation than the memory-matching item (80.9% vs. 5.9%; $t(9) = 20.16; p < .0001$) and the memory-matching distractor was attended more frequently on the first fixation than the average non-memory-matching distractor (5.9%

vs. 3.3%; $t(9) = 3.80$; $p < .01$). However the memory-matching distractor was attended less frequently than all the non-memory-matching distractors combined (5.9% vs. 13.3%; $t(9) = 4.09$; $p < .01$).

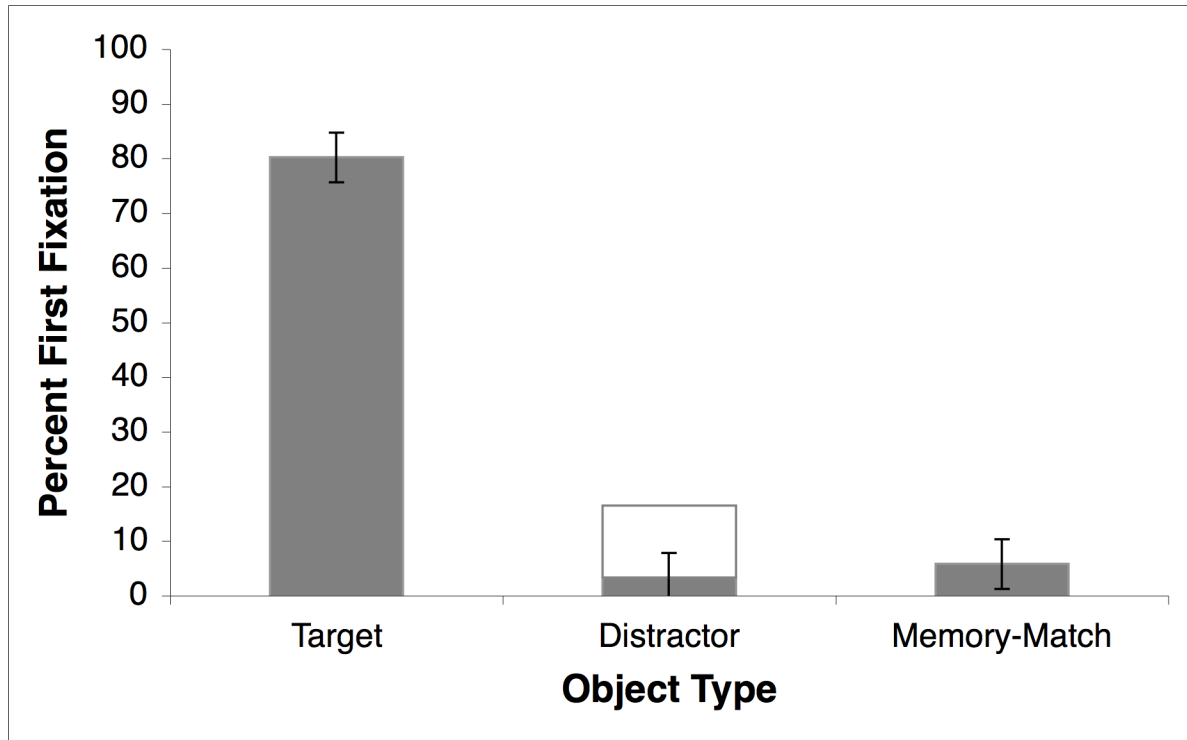


Figure 18. Means of the first fixations on each object type. Error bars represent the 95% within-subjects confidence intervals. The white bar represents the all fixations to any of the 4 distractors.

Next, I analyzed the saccade onsets towards search targets, memory-matching distractors and non-memory-matching distractors (one subject was not included in this analysis because the non-memory-matching distractor first fixations cell was empty). This analysis was conducted to determine if there is any evidence that covert attention was directed to the memory-matching distractor before overt attention was directed to the search target. Saccade onsets were similar regardless of whether the saccade was toward a target ($M = 348$ ms), a memory-matching distractor ($M = 375$ ms), or a non-memory-matching

distractor ($M = 345$ ms). A one-way ANOVA of saccade onsets for the three object types failed to show an influence of object type on saccade onset ($p = .63$).

Chapter 4 Discussion

This experiment was designed to assess whether goal-related items in working memory are prioritized by executive control. When two items were maintained in working memory, the stimuli that matched the task-relevant representation were attended via overt attention five times more frequently than the stimuli matching task-irrelevant working memory representations. This finding indicates a clear prioritization in attention for task-relevant working memory representations.

One explanation that has been proffered for different amounts of guidance is that the working memory representations themselves were degraded (Soto, Hodson, & Humphreys, 2008). This explanation would suggest that the prioritization of the task-relevant item would be achieved by weakening the task-irrelevant memory representation. However, memory accuracy on catch trials was equivalent for tests of search and memory stimuli. Therefore, the differential attention to task-relevant memory matches in this study cannot be explained by a degraded memory account. Because non-exact color matches (Olivers, Meijer, & Theeuwes, 2006) and verbal working memory loads (e.g. 'red square', Soto & Humphreys, 2008) can lead to working memory guidance of attention, it seems that both memory representations should would have a sufficiently high fidelity to influence attention if an automatic effect existed.

In spite of the clear prioritization of task-relevant information, stimuli matching the task-irrelevant working memory representations were attended more frequently during search than the distractors. Several other studies have shown that items in working memory are attended more frequently than distractors. Some of these studies have concluded from these effects that automatic attentional templates are generated from working memory representations (Soto, Heinke, Humphreys, & Blanco, 2005; Olivers, Meijer, & Theeuwes, 2006; Soto & Humphreys, 2007; Huang & Pashler, 2007; Soto, Hodsoll, Rotshtein, & Humphreys, 2008), consistent with the biased competition theory (Desimone & Duncan, 1995). Although the current data is consistent with these previous studies in showing that the task-irrelevant memory-matching items were attended more frequently than other distractors, it is not consistent with the conclusion that working memory representations automatically generate attentional templates. However, some of these previous studies used targets that were held constant across trials and such target representations are believed to be held in long-term memory (Carlisle, Arita, Pardo, & Woodman, in press; Logan, 1988).

The current findings add to the literature by directly comparing the frequency of attentional deployment to memory-matching items that are task relevant with those that are task irrelevant while controlling for the bottom-up salience of the two memory-matching items and the strength of the representations of each item in working memory. The finding that task-relevant working memory representations are attended more frequently suggests that there is prioritization of working memory representations that are task relevant. Moreover, this prioritization is not accomplished by enhancing the quality of the task-relevant working memory representation, as indicated by similar catch trial accuracy for search and memory items. This rules out an explanation of the results based on the task-

irrelevant item being a ‘degraded memory representation’ as proposed by Soto, Hodson, Rotshtein, & Humphreys (2008).

The evidence of goal-related prioritization is inconsistent with the mechanism proposed by biased competition theory, where executive control is only able to act at the entry point into working memory (see Figure 1). Instead, it is more consistent with an executive control mediated relationship between working memory and attention.

This study provides a new starting point from which to contrast the competitive strength of different memory representations. When memory strength and the match between internal representations and external stimuli are controlled, it is possible to gain a clear measure of the top-down control settings generated from task-relevant and task-irrelevant memory representations. In ongoing work, I am using this paradigm in computational modeling of top-down attentional control. In addition, I am extending beyond the basic prioritization effect demonstrated in this study to assess the influence of competition during search between task-relevant and task-irrelevant memory matches. Taken together, this continuing line of research will provide new insights into the flexibility of top-down attentional control.

CHAPTER 5

GENERAL DISCUSSION

Theories of visual attention suggest that internal representations, or target templates, are used to guide attention to task-relevant information in the visual field. Many of these theories do not provide a clear description of how these target templates are represented in the brain. However, the biased competition theory (Desimone & Duncan, 1995) proposes that target templates are working memory representations that create increased firing rates in cells that are selective for their features. This proposal leads to the prediction that executive control should only influence attention by influencing what is entered into working memory, and that items in working memory should have the same attentional influence as a goal-relevant item. In contrast, TVA (Bundesen, 1990) allows for an additional step of executive control between the contents of working memory and the creation of attentional templates. The experiments conducted in this dissertation were aimed at providing better measures of the influence of task-irrelevant working memory representations on visual attention.

In Experiments 1-4, I used the N2pc as an electrophysiological measure of selection to assess whether memory-matching items were attended. In Experiments 1-3 the memory-matching items were task-irrelevant and participants were informed that the memory-matching items would never be the search target. In this case, no evidence was shown for the selection of memory-matching items by covert attention. Instead, there was consistent evidence that the memory-matching items were actively avoided or suppressed from 300-400 ms after the search array onset. In Experiment 4, the memory-matching item was always the

target item, making attending to the memory-matching item task relevant. In this case, the memory-matching items were selected frequently, early in search. Taken together, this work suggests flexibility in the influence of working memory on attention based on task goals.

In Experiment 5, I used electrophysiological measures of attentional enhancement and suppression, the N1 and P1 components. Task-irrelevant probes were used to determine whether working memory-matching distractors are suppressed like other distractors or enhanced like a search target. Working memory-matching items were not suppressed like a distractor, but were not enhanced like a target. These findings suggest that task-irrelevant memory-matching items may have a weak automatic effect on attention. However, an automatic effect of attention is not the equivalent of what is typically described as an attentional template. These findings are inconsistent with the suggested mechanism of biased competition that storage in working memory is the attentional control signal. Instead, they suggest a flexibility that could be accounted for in the TVA framework.

In Experiment 6, I used eye tracking to measure of overt attention and contrast the probability of attending to memory-matching distractors with the probability of attending to targets or distractors. The results indicated that memory-matching items were not attended as frequently as search targets, but were attended more frequently than distractors. The prioritization of task-relevant working memory representations occurred even though both items had high-fidelity representations. Once again, the results show that stimuli matching task-irrelevant working memory representations may at best produce a weak effect on attention. These findings fail to support the simple relationship between working memory storage and attentional guidance suggested by biased competition (Desimone & Duncan, 1995).

In summary, the current results suggest that task-irrelevant memory-matching items may create a weak effect on attention (Experiment 6) or be suppressed (Experiments 1-3). However, when the representations being maintained in memory are relevant for the task at hand, attention can efficiently select (Experiment 4; search cue color Experiment 6) and enhance processing (Experiment 5) of memory-matching items presented in the visual field. These findings suggest that representations in memory are used flexibly based on current task demands.

Examining Executive Control

Where do these findings leave the biased competition theory (Desimone & Duncan, 1995)? While the idea that the mechanisms of working memory are attentional templates may be the most provocative aspect of the theory, it is not the core postulation. The main point of the biased competition model is that objects compete for representation within limited capacity receptive fields of cells, and the winner of this competition is attended. Top-down biasing is suggested to arise as an interaction of frontal areas and more posterior regions, such as IT. The lack of an executive component makes the theory incomplete, but it does not preclude the remainder of biased competition theory from being a strong explanation for the mechanism of attention.

Indeed, there has been support for the proposed interactions of frontal and posterior regions in attentional processing. The importance of prefrontal cortex in top-down control has been demonstrated in many findings. Prefrontal responses during a delay period in a

delay-match-to-sample task are unaffected by intervening stimuli in contrast to the responses in area IT which are disrupted by distracting stimuli (Miller, Erikson, & Desimone, 1996). This suggests that the source of biasing may be prefrontal, and the outcome seen in more posterior areas. Disrupting the signals from prefrontal cortex can prevent effective top-down modulation of single-cell responses in monkeys (Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999) and creates problems with orientation to targets especially when the target changes frequently (Rossi, Pessoa, Desimone, & Ungerleider, 2008). In humans, frontal lobe lesions can cause people to perseverate on a memory-matching distractor, although it does not increase the likelihood of attending to this distractor (Soto, Humphreys, & Heinke, 2006a). The prefrontal cortex is important in top-down control (Buschman & Miller, 2007; Corbetta & Shulman, 2002) and may hold the general rules for performing a task (Miller, 2000). Moreover, the PFC is widely connected to many other areas important for attention and reward, and is likely an important source of top-down control signals. Other areas, such as LIP and SC are better positioned to respond to both top-down and bottom-up signals, and might be the putative location of attentional priority maps (Baluch & Itti, 2011). These findings suggest that the general proposal of biased competition that frontal areas and more posterior areas interact to generate top-down control may be correct.

The current work demonstrates that the suggestion from biased competition that these interactions of frontal and more posterior regions are a natural part of the working memory mechanisms seems to be too simplistic. Working memory representations are not the equivalent of a goal-related attentional template. In spite of this clear distinction between working memory and attentional control, there are numerous results in the literature showing working memory representations influence attention (Soto, Hodsoll, Humphreys, & Blanco,

2005; Olivers, Meijer & Theeuwes, 2006; Huang & Pashler, 2009). What could be the mechanisms underlying these findings supporting guidance? Next, I will describe two possible explanations for the results.

First, it is possible that working memory representations create a weak, automatic effect on attention. This might be especially true if there are no intervening stimuli between the presentation of a memory cue and the presentation of an attentional target (Miller, Erikson, & Desimone, 1996), as was the case in the original data showing sustained activations during the delay period between a cue and search (Chelazzi, et al. 1993). What purpose could such weak influence serve? Recent work suggests that a mechanism such as this could be beneficial for eye movements. Frequently after a saccade, small corrective saccades need to be made until the desired saccade target is actually fixated. Hollingworth and Luck (2009) created a paradigm that shifted an array slightly during a saccade, necessitating corrective saccades. Their results showed that a memory-matching distractor introduced during the shift attracts more corrective saccades than another introduced item. A weak working memory guidance signal like this could create a frequent effect of a memory-matching distractor if the distractor was very salient, and the search target was very difficult to find. This has been the case in a number of studies supporting guidance. Sometimes with memory-matching distractors that are larger in size than the target (e.g. Soto, Hodsoll, Humphreys, & Blanco, 2005), sometimes they are a pop-out item (Olivers, Meijer, & Theeuwes, 2006). In addition, sometimes memory-matching distractors are a match based on color, while targets are defined by a difficult shape discrimination (Han & Kim, 2009). Since colors are faster mechanisms of selection than shape (Kim & Cave, 1995), these differences in the types of features defining task-relevant and task-irrelevant memory-matching items

could potentially create differences in the competitive advantage early in search. This early feature-based advantage could interact with a weak top-down signal and increase the probability of selection. Perhaps unsurprisingly, this interaction would predict stronger effects of memory-matching distractors which are more salient. The TVA framework suggests that such interactions of stimulus factors and weak top-down factors may be very important for determining which item will win the competition for attention.

The second explanation is that the small attentional effects from working memory representations are due to infrequent failures to adjust attentional control settings. In the typical guidance paradigm, participants have to switch quickly between updating the memory task set when the memory cue is presented, instantiating the search task set to perform search, and finally reinstantiating the memory task set to perform the memory test. Infrequent failures to switch task set would not be uncommon in such a demanding task, and are analogous to residual switch costs described in the task switching literature. Switching a task will lead to longer reaction times than performing the same task again, an effect called a switch cost (Logan, 2003). If participants are given a sufficiently long time between performing the first task and performing the second task, much of the switch cost can be ameliorated. However, even with very long durations between two tasks, some residual switch cost remains.

De Jong (2000) explains residual switch cost as a Failure to Engage (FTE) in the new task. He suggests that while individuals have control of when to switch task sets, and can choose to begin switching sets before stimuli are presented, on some proportion of trials they fail to do so. He supports his claim with the finding that stressing speed on the second task (making switching quickly important) can reduce residual switch costs, and with the finding

that shorter durations between the two tasks create more failures to engage. Analogous findings have been seen in the guidance literature. Carlisle, Boucher, & Woodman (2009) showed that when speed on search was not stressed, more guidance was shown. In addition, shorter differences in the timing between stimuli have been shown to create more guidance (Han & Kim, 2009; Dombrowe, Oliver, & Donk, 2009).

De Jong (2000) also suggests that keeping both task sets partially active could be a strategic choice, as a way to reduce switch time in demanding situations. This logic could also apply to the guidance literature because the working memory task set will need to be reinstated after search is complete. Keeping a weak task set for a working memory item could benefit speed in memory response (De Jong, 2000) or prevent inhibition of working memory representations as distractors (e.g. negative priming, Tipper, 1985), leading to later benefits on memory performance. This could also explain why studies that place no penalty on attending to memory-matches (Downing, 2000; Experiments 1-3 Soto, Heinke, Humphreys, & Blanco, 2005; Huang & Pashler, 2007) find guidance, because in this case there is no need to switch task sets.

Future work will be needed to clearly distinguish between a weak automatic effect and failures to - or strategic choices not to - change task set. Both are possible explanations for the findings. What is clear, based on either explanation, is that a flexible executive component is necessary to create a goal-related attentional template. What would this executive component be like?

Tasks may be described in terms of their executive components as well as subordinate processes (Logan, 2003). One useful model that contains the flexibility necessary to describe the various findings in the guidance literature is TVA (Bundesen, 1990). TVA allows for

optimization of control parameters for the current task, but does not explain how the top down parameters of bias and pertinence are set. ECTVA (Logan & Gordon, 2001) extends TVA to dual-task situations, using TVA as a subordinate process and adding parameters for the time to switch between task sets and to partially flush evidence accumulation. These parameters will be important for modeling the guidance literature because task sets need to be changed twice during each trial. However, to explain the flexibility demonstrated in the guidance literature, it will be important to add another parameter that determines the top-down weighting of items maintained in memory based on the relevance for the task at hand. This weighting parameter could interact with ECTVA in order to determine what task sets should be instantiated.

This weighting parameter should be able to draw information from working memory or long-term memory (Carlisle, Arita, Pardo, & Woodman, in press) based on what is currently relevant. When an item in memory is not important for the current task, it should be able to set very low weights (Experiment 6) or suppress incoming information that matches the contents of working memory (Experiments 1-3). Low weights might be set in order to aid in maintainance of the memory item (Woodman & Luck, 2007) or to ensure that typical distractor suppression does not disrupt a memory representation. In contrast, when a memory representation is relevant for a task it should be able to set various weights based on the likelihood of the information in memory being relevant for the attentional task (Carlisle & Woodman, 2011), with stronger weights being set when the items in memory are better predictors of search targets. Adding an additional parameter to ECTVA which allows for flexible weightings of task sets based on the current task demands would be a useful tool for working to explain the various results in the literature. Differences in stimulus salience, the

relevance of memory for search, templates being maintained in working or long-term memory, and instructions may help to explain differing results. Incorporating all of this information into a single framework that can provide estimates of the likelihood of attending to various items could serve to provide a clear explanation for the disparate findings in the literature. While this additional component would only be a “customized executive” (Kieras, Meyer, Ballas, & Lauber, 2000) capable of explaining executive control within a specific realm, it will take some of the burden from the ‘homunculus’.

In summary, the current work makes it clear that working memory representations are not the equivalent of a goal-related attentional template, challenging a prediction of the biased competition theory that has gained popularity in the literature (Soto, Hodsoll, Rotshtein, & Humphreys, 2008). More importantly, this data is inconsistent with any account of attention that does not include an executive control process mediating working memory storage and top-down attentional control. The current work provides new evidence about the mechanisms underlying top-down attentional control, and suggests attentional control is a flexible process, capable of being optimized for the task at hand. TVA (Bundesen, 1990) may provide a model that is capable of representing the flexibility of top-down attentional control. This type of control would allow us to prioritize looking for speeding cars as we cross the road, while still maintaining our goal of finding coffee in working memory. This flexibility is advantageous for humans existing in a complex visual environment with frequently changing behavioral goals.

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