# SELECTION MECHANISMS OF VISION:
# PERCEPTUAL INPUT VS. WORKING MEMORY MAINTENANCE

By

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Dissertation

Submitted to the Faculty of the

Graduate School of Vanderbilt University

In partial fulfillment of the requirements

For the degree of

DOCTOR OF PHILOSOPHY

In

PSYCHOLOGY

May 2013

Nashville, Tennessee

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# DEDICATION

To my husband, Jason:
For his remarkable patience, unwavering love, and for always believing in me.

and

To my Mom and Dad:
For instilling in me a love of learning and supporting me in all that I do.

and

To my son, Jordan:
For keeping me company during my late night writing sessions.

# ACKNOWLEDGEMENTS

This work would not have been possible without the members of my Dissertation Committee. Thank you for your feedback and guidance over the years. I am especially grateful to my advisor, Dr. Geoff Woodman, whose encouragement and support have shaped me into the researcher I am today.

I would also like to thank the members of my lab, both past and present. I cherish the many hours of insightful conversation and all the good memories. You have been like a second family to me.

Most importantly, I’d like to thank my family and friends. Thank you for pushing me to accomplish more than I ever dreamed possible.

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# Chapter I

## INTRODUCTION

Visual selection is a part of our everyday lives. While cooking, we must keep a recipe in mind while also attending to items on the stove. When shopping we try to remember how the previous shirt fit compared to the current one we are trying on. As we interact with our surrounding environment we must use selective attention[1] to perceive, identify, and maintain the most important representations (Posner & Boies, 1971). This experience requires our visual system to employ mechanisms that select relevant incoming information and subsequently retain it for short periods of time. Processes of perception and working memory maintenance require the use of selection to successfully focus on what is relevant. Currently, the literature is unclear as to whether or not visual selection is made up of one or two mechanisms. In other words, does our mind see the food on the stove while simultaneously going through the recipe? Or does it bounce back and forth between the two visual images?

The goal of my dissertation is to examine the role of visual selection within perception and working memory in order to determine whether a single mechanism oversees both processes. The remainder of this chapter will review the literature regarding models of working memory. The models provide a general explanation of perceptual input and maintenance, but studies have yet to distinguish which model's

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[1] I use the terms *visual selection* and *attention* in this dissertation to mean the ability to select particular information from a group. It refers to the filtering mechanism that blocks out distractors and attends to targets.

assumptions are accurate. In the following sections, I test contrasting predictions of the models of working memory. Finally, I compare selection mechanisms from different stages and examine the how different types of information are maintained.

## What is perceptual input?

To assess the relationship between perceptual input and working memory maintenance it is first necessary to understand each of these phenomena individually. Cognition can be broken down into two general categories: perceptual and post-perceptual. Early models in cognitive psychology have typically classified perception and memory as separate entities, with the first one feeding into the other (Atkinson & Shiffrin, 1968; Fodor, 1983). Perception is described as the input system that operates before iconic and sensory memory, and by some accounts it is automatic and effortless (Deutsch & Deutsch, 1963; Norman, 1968). Bottom-up processing can cause salient information to enter perception without any type of filtering. However, top-down selection of perceptual input allows for more efficient processing of the attended stimulus and increases a target item's chance of getting into working memory (Duncan, 1984; Duncan & Humphreys, 1989; Wolfe & Cave, 1989; Wolfe, Cave, & Franzel, 1989).

Mangun, Hillyard, & Luck (1993) measured attentional effects during a visuo-spatial task through the use of event-related potentials (ERPs). In their recordings, they found that an early-evoked positivity (P1) and negativity (N1) wave were amplified depending upon stimulus location. When participants were attending locations of the target stimulus, flashes in these spatial areas resulted in higher ERP amplitudes compared to the voltage measured from other non-attended locations. Moreover, these components were best measured over regions of the visual cortex suggesting that they are generated during early visual processing.

Consistent with this research is the neurophysiological data that shows the influence of spatial attention in area V4 and IT (inferior temporal) cortex (Moran & Desimone, 1985). In this study, monkeys were given special instructions regarding target and distractor information for the upcoming trial. When targets and distractors were competing for spatial representation, cells in these brain areas responded mainly to the target items. Thus, visual selection can be strategically deployed to bias perceptual input for higher priority stimuli.

### What is working memory maintenance?

In contrast to perceptual input, working memory processes are considered post-perceptual. Whereas perceptual input deals with stimuli that are available within the current environment, working memory handles stimuli that are no longer visible. Working memory refers to the temporary storage of information that can be manipulated. In addition to storage capabilities, working memory is believed to have a more active role in cognition (Baddeley & Hitch, 1974). According to Goldman-Rakic (1993; 1996), working memory tends to be more goal-driven in that something must be done with the information to reach an end result. The purpose of maintenance is to reactivate and manipulate items stored within memory by selecting the most important items (Baddeley & Logie, 1999; Cowan, 1999). Attentional selection is crucial for this system because working memory is extremely limited in capacity, on average holding only 3-4 items (Irwin & Andrews, 1996; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). Since working memory cannot hold and retain an unlimited number of items, maintenance acts as the selective mechanism of memory that attends to and rehearses only the relevant information.

One way to study maintenance has been to use electrophysiology. ERP studies have demonstrated an attentional selection mechanism used during a working memory task. For instance, when using cues during retention, Griffin and Nobre's (2003) ERP analyses revealed an evoked positive potential seen following retro-cues. Retro-cues are defined as a cue that follows the to-be-remembered stimuli and pre-cues are defined as occurring prior to stimuli. Whereas pre-cues can guide attention to the relevant item before the retention interval, trials with retro-cues must hold such information in working memory until a cue appears to orient attention to the correct location. Recently, Vogel and colleagues have measured a waveform known as the Contralateral Delay Activity (CDA) (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). In their experiments, participants were pre-cued to remember one hemifield of colored squares in order to successfully perform in a change-detection task. During the blank retention interval a negative-going voltage would arise. They found that the CDA reflected participants' ability to select the cued visual field and actively maintain the task-relevant information (Vogel & Machizawa, 2004). A study by Woodman and Vogel (2008) also offered evidence of visual selection during a working memory task. Subjects in their study had to remember either the color, shape, or a conjunction of the features of the stimuli presented. They hypothesized that participants would attend to only the task-relevant features and maintain just that information. Using the CDA as a measure of representations being held in working memory, Woodman and Vogel found that participants were able to selectively maintain only the features relevant to the task and ignore the task-irrelevant features. With CDA amplitude reflecting feature-selective storage, these results further support the claim that humans can purposely select and retain information needed for a memory task.

Neurophysiological studies also show that visual maintenance appears to be an active process that extends to various parts of the brain. Prefrontal brain regions used for visual processing also show sustained activity during maintenance (Chafee & Goldman-Rakic, 1998; Goldman-Rakic, 1993; Miller, Erickson, & Desimone, 1996). In fact, the prefrontal cortex is involved in selecting as well as maintaining task-relevant representations. Rainer (1998a) demonstrated how delay activity in this area conveyed information about the visual stimuli. In their study, they recorded from monkeys performing a delayed-matched-to-sample task- a working memory task that required the monkeys to temporarily maintain a stimulus then compare the test sample to the original sample. These recordings resulted in higher neural activity in the prefrontal cortex for target item locations than nontarget item locations suggesting that selection was occurring within maintenance. In addition, sustained activity during delay periods is also seen in other areas of the brain such as area IT and posterior parietal cortex (Chafee & Goldman-Rakic, 1998; Miller & Cohen, 2001). To conclude, both perception and working memory use visual selection to maximize performance.

## Two Models of Working Memory

There are two primary models of working memory, and both assert that we use attentional selection to determine what information enters and is subsequently stored in visual working memory. However, these two theories propose different mechanisms for the temporary maintenance of information. In a unitary model (Cowan, 1999; Crowder, 1982; Lovett, Reder, & Lebiere, 1999; Norman, 1968; Oberauer, 2002), attention and working memory are essentially the same. This crucial aspect of the model means that one mechanism selects perceptual inputs for preferential processing while simultaneously also maintaining representations stored in working memory. Under a multi-component model (Baddeley & Hitch, 1974; O'Reilly, Braver, & Cohen, 1999), representations are maintained in modality specific memory buffers by dedicated mechanisms that are distinct from other control processes - specifically, the mechanisms of selection that operate on perceptual inputs to the mind. Is the mechanism that selects attended inputs during perception the same one that maintains information in working memory, or is each cognitive system equipped with a selection mechanism of its own?

## The Unitary Model

The unitary model of working memory posits that information is stored in the mind by one memory system that is shared across all sensory modalities through which information is encoded (e.g., visual and auditory inputs). These types of models are further unitary in that attentional mechanisms are embedded within the representational structure of memory (Cowan, 1997; Crowder, 1982; Lovett, et al., 1999; Norman, 1968). Within the memory system, representations are organized hierarchically, with each level in the hierarchy governed by the activity level of a given representation. One description of this hierarchy, (Cowan, 1999; Oberauer, 2002), contains three levels: 1) the *focus of attention*, 2) *activated memories* that are not within the focus of attention, and 3) inactive *long-term memories*. A schematic representation of this hierarchy is shown in Figure 1. By this account, working memory representations are temporarily activated long-term memory representations that have been selected by attention to allow for processing of task-relevant information. The focus of attention not only reactivates long-term memory representations, but it also selects recently perceived inputs for storage in this memory system.

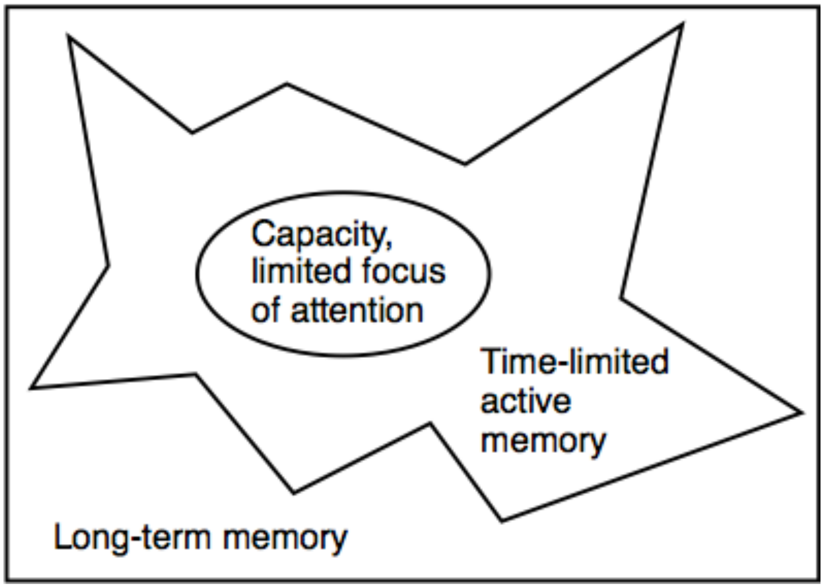

*Figure 1.* Illustration of the Unitary Model framework as suggested by Cowan (1998).

Here, I define a unitary model as one in which working memory and perceptual attention use the same mechanism. These models propose that a single mechanism explains evidence for capacity limits in human cognition (Cowan, 2000; Kane & Engle, 2002; Oberauer, 2002). Rather than having two separate selection mechanisms - one for encoding and one for storage - information that is relevant for the goals of the present task are processed by a single selection mechanism defined as the focus of attention. This selection mechanism is responsible for filtering perceptual inputs and maintaining information already stored in working memory. Maintenance in the unitary model simply means that selection is working to keep previously encoded representations in an active state to prevent decay. Supporters of unitary models suggest that maintaining information in visual working memory uses the same visual selection mechanism that operates during perception to preferentially process the most task relevant or otherwise salient information available from the environment (Barrouillet, Portrat, & Camos, 2011; Lovett, et al., 1999; Norman, 1968). Using one mechanism for perceptual selection and maintenance implies that such a selection mechanism must oscillate between these two functions. As a result, memory traces gradually fade when the selection mechanism is processing new sensory inputs. To prevent time-related decay, visual selection must return to these items to reactivate their representations. Essentially, unitary models argue that there is one central bottleneck responsible for both perceptual processing and temporary storage.

## The Multi-Component Model

While the unitary model argues for one central mechanism within one memory system, the multi-component model of working memory describes a temporary-memory system made up of a collection of memory stores and processing mechanisms. Rather than relying on one representational structure to both maintain information and perform a cognitive task, this theory suggests that there are many smaller components that contribute to the temporary storage of information (Baddeley & Logie, 1999; O'Reilly, et al., 1999). One such model was proposed by Baddeley and Hitch (1974) as a three-component working memory system and subsequently elaborated by Baddeley

(Baddeley, 1986; Baddeley & Logie, 1999). In their initial model, they assumed an attentional controller (the *central executive*) and two subsidiary systems; the *phonological loop* and the *visuospatial sketchpad* (see Figure 2). Supporters of a multi-component theory assert that each subsystem equipped with its own rehearsal mechanisms is actually a better representation for understanding the brain's architecture (O'Reilly, et al., 1999; Rumelhart & McClelland, 1986).

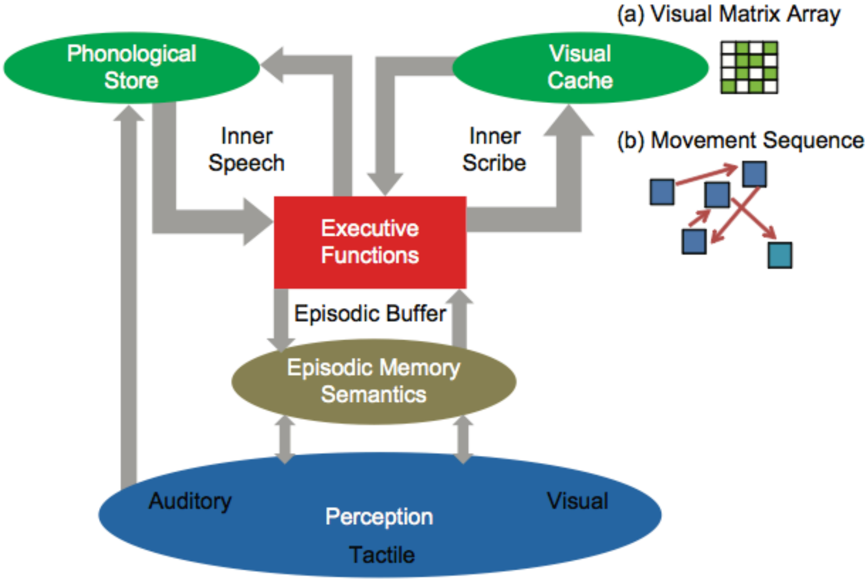

*Figure 2.* Multi-component working memory model as proposed by Baddeley, Hitch, and Logie. Adapted from Logie (2011).

According to the multi-component model, the central executive controls what information is fed into the subsidiary working memory stores from perceptual processing mechanisms and from long-term memory, however, once the information is represented in a subsidiary working memory store the rehearsal of that information is a self-contained process. For example, the phonological loop specializes in maintaining verbal and auditory information.  This verbal subsidiary subsystem is composed of a passive memory buffer (the phonological store) and an active rehearsal mechanism (the articulatory loop, called *inner speech* in Figure 2). The visual-spatial subsidiary store has been proposed to have a similar segregation of functions into passive storage and active rehearsal components.

The aspect of the multi-component model that is most relevant for this project and has been clearly specified is Baddeley and Logie's portrayal of the visual buffer's rehearsal component (Baddeley & Logie, 1999; Logie, 1995). The *inner scribe* is described as a spatial maintenance mechanism that serves to rehearse representations in the passive visual working memory buffer (known as the *visual cache*). Unlike the unitary model in which the focus of attention is controlled by the central executive and is responsible for activating and reactivating all representations, Baddeley's central executive appears to guide selection at the front end of cognitive processing (during the initial processing of perceptual inputs) leaving the subsystems to maintain information held in the storage buffers.

## Evidence for a Unitary Model

Although there has not been scientific consensus, some studies have provided data suggesting that the mechanism of spatial selection that operates during perception is the same selection mechanism that assists in the maintenance of representations of spatial locations in working memory. Awh and Jonides (2001) concluded that the same visual-spatial attention mechanisms are used during both perception and maintenance based on findings that visual-spatial attention is deployed to a location when subjects are asked to remember that location. A series of experiments showed that subjects' reaction times

(RTs) were faster when they had to detect a probe stimulus presented at remembered locations compared to other spatial locations (Awh, Jonides, & Reuter-Lorenz, 1998). These findings are consistent with the conclusion that attention was already focused on the to-be-remembered location when the probe stimulus was presented there, facilitating processing of the probe. Converging evidence for this conclusion was found using ERPs (Awh, Anllo-Vento, & Hillyard, 2000). Awh et al (2000) reported finding the same sensory-evoked components during both an attention task and memory task. Moreover, modulations for both conditions were similar in topography and latency. The proponents of unitary models argue these finding demonstrate that when the task-relevant representations are spatial in nature (i.e., locations); the visual selection mechanism engages in both perceptual encoding and maintenance.

Researchers have also made attempts to explain the unitary model in terms of short-term and long-term memory brain structures. This research tends to take a Hebbian view of memory processing (Hebb, 1949). In his dual-trace theory, Hebb asserted that short-term and long-term memory was defined by the nature of neural activity underlying the different types of representations. Short-term memory was reflected by reverberatory activity within a cell-assembly, a functional group of neurons. After-effects of a sensory image create this cellular reverberation. If an assembly of neurons is activated enough times, the associated cells essentially “learn” to help each other by lowering synaptic resistance. The assumption was that structural changes among neurons lead to lasting long-term memories (potentiation). Hebb explains that reverberatory activity, the neural equivalent of a short-term memory trace, is unstable and susceptible to interruptions, such as decay and interference, paralleling behavioral research. The reverberatory activity described in Hebb's theory is viewed as the neural equivalent of maintenance in short-term memory. The structural change that takes place among the cellular assemblies signifies that long-term memory learning has taken place. Based on this view, rehearsal activity in short-term memory can influence long-term memory representations, however, this process is one that requires multiple iterations of reverberatory activity.

Supporting this theory, regions associated with long-term memory have been found to be active both during working memory and perceptual processing (Khader, Burke, Bien, Ranganath, & Rösler, 2005; Ranganath, 2006; Ranganath, Cohen, & Brozinsky, 2005). Studies of patients with damage to the medial temporal lobe (MTL), have found conflicting data regarding working memory deficits from these participants. While long-term memory impairment is consistently observed, impairment on short-term retention is variable. In their review of these studies, (Ranganath & Blumenfeld, 2005) concluded that the type of information being maintained is fundamental to determine whether or not maintenance mechanisms could access long-term memory and that short-term storage was not always separable from long-term storage.

## Evidence for a Multi-component Model

A unitary model excels at accounting for findings from experiments suggesting that attention is used to aid the maintenance of information in memory, like those of Awh and colleagues (Awh, et al., 2000; Awh & Jonides, 1998; Awh & Jonides, 2001), however, it has difficulty explaining other experimental evidence. The unitary model is vague in its description of how different types of memories (i.e., verbal, visual, spatial, etc.) employ selection. Instead, it encompasses all forms of memory into one unit. The multi-component model asserts a number of subsystems for the various memories. For example, findings from dual-task experiments suggest that working memory representations of spatial locations might be stored in a different manner than representations of object features (Awh, et al., 1998; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006; Smyth & Pelky, 1992; Smyth & Scholey, 1994; Tresch, Sinnamon, & Seamon, 1993; Woodman & Luck, 2004), which is arguably inconsistent with the idea of a singular perception and maintenance selection unit. Tasks, such as the Brooks matrix task where participants must remember an item based on its spatial location, performed concurrently with the storage of verbal information result in minimal interference, whereas storing visual-spatial information is greatly interfered with by a concurrent visual-spatial task (Logie & Marchetti, 1991; Morris, 1987). By suggesting a model of working memory in which there are multiple, modality specific storage buffers and rehearsal mechanisms, the multi-component model can easily explain the discrepancies observed in visual-spatial tasks.

Given the findings of these studies, it might be possible that perceptual selection and object maintenance obey different rules than those of spatial working memory – so rather than fully indicating that perception and maintenance are handled by different mechanisms, these results at least suggest that different kinds of information may be processed by separate mechanisms. Additionally, the model also explains the wide range of cognitive impairments seen in lesion studies (D'Esposito & Postle, 1999, 2000). Patients with lesions in prefrontal cortex have difficulty performing a memory task when there are distractors present during retention. Just as the theory explains the purpose of specific memory modalities, it can also explain the split between executive functions and storage buffers. As seen with lesion patients, working memory storage and central executive work independently of one another. Patients are successful in the memory task until the central executive is needed to eliminate interference. Together, these behavioral and lesion studies provide strong support for the various systems described by the multi-component theory.

## A Shared Function or Two Separate Mechanisms?

The unitary and multi-component models have many similarities. Both acknowledge the existence of selective attention or perceptual enhancement of task-relevant stimuli. Both largely agree about the external factors of interference and memory degradation and their subsequent results on the accuracy of memory. The primary difference between the two models is their explanation of attentional mechanisms and the relationship between perceptual selection and subsequent storage in working memory. Other studies have attempted to provide solid evidence in favor of one model or the other, but have yet to distinguish which model is correct. Our limited working memory capacities force us to be selective during the encoding of perceptual information into working memory and to be additionally selective in what information is maintained in working memory, particularly as task demands change and new information about task relevance of items arrives. Therefore, it is important to understand the way in which these cognitive mechanisms interact because they play a crucial role in how we process everyday visual information.

The following chapters will discuss research aimed at understanding whether these two separate processes rely on a shared mechanism or if they are capable of functioning independently. In Chapters II and III, ERP techniques are used to record the time-course of each of these cognitive events. Each chapter focuses on ERP components that have historically represented either perceptual input or working memory maintenance. Chapter IV takes a different approach and uses eye-tracking techniques to determine if there is an overlap in selection mechanisms used during maintenance.

The general discussions section in Chapter V consolidates the findings from all of these chapters and reviews how the new data can be incorporated into the current literature. Here, I will synthesize the results of all three experiments into a cohesive framework for understanding relationship between the processing of perceptual selection and maintenance and, hopefully, suggest an answer to the underlying question: are perceptual input and maintenance controlled by the same selection component or are they separately regulated?

# Chapter II

# EXPERIMENT 1: DOES PERCEPTUAL SELECTION OCCUR DURING MAINTENANCE?

In this chapter, I investigated if mechanisms that are linked to perceptual selection tasks are elicited during memory maintenance. We can all think of a time when we had to attend to new, incoming stimuli while concurrently retaining some other important information. For instance, as you are walking in the supermarket, you may notice a light bulb go out in the corner of your eye. As you quickly perceive the sudden flash, you must still remember the items from your grocery list. In this section, I will present evidence showing that indices of perceptual selection occur while other representations are being retained in visual working memory.

## ERP Indices of Perceptual Selection

We know that selection of relevant information can occur at any time during visual processing. However, the timing of neural activity prior to 100-ms following stimuli onset is assumed to be perceptual and anything following 300-ms is deemed higher cognition. Object maintenance, for instance, is considered to be post-perceptual and as such, a part of working memory. Although cognition is often separated into perceptual and post-perceptual, there is not a clear delineation between these two processes in the context of attention and working memory. Given that visual selection must navigate within the realm of both perception and post-perception, it is better to think of cognition as a continuous process (Pashler, 1998). The question at hand is whether or not selective attention of perceptual input can occur simultaneously with working memory maintenance - the active rehearsal of stored information

The first and earliest visual ERP waves appear to act as markers of selection during perceptual input processing. These sensory components, known as the P1and N1, begin approximately 100-200 ms after the onset of stimuli. The time-course of these waves suggests that they arise from the primary visual cortex and reflect the locus of attention during perception. Both components exhibit larger amplitude voltage deflections when a target stimulus is presented in an attended space even when passively viewed (Luck, 1995; Luck, Heinze, Mangun, & Hillyard, 1990). This evidence is interpreted as indicating that perceptual selection mechanisms serve to increase the efficacy of perception at the earliest stages of visual processing (Luck, et al., 1990). The P1 and the N1 are best observed at the onset of stimuli (i.e., perceptual input), however, these components appear to indicate when perceptual attention is present at the stimulus location versus absent. Amplitudes for the components are modulated by the location of visual selection, with target-attended locations resulting in bigger amplitudes than non-target locations. Similar effects are observed when a probe stimulus is presented at the location of a target item during visual search (Luck, Fan, & Hillyard, 1993). Thus, P1 and N1 modulations appear to be general indicators of the deployment of perceptual selection to an object or a location in space.

To better understand the relationship between spatial attention and working memory some researchers have examined the shared neural regions of visual processing. Several fMRI studies have shown enhanced activity in the extrastriate cortex for sensory information during active memory maintenance (Awh et al., 1999; Corbetta, Kincade, &

Shulman, 2002; LaBar, Gitelman, Parrish, & Mesulam, 1999). Corbetta et al. (2002) demonstrated that the allocation of spatial attention remained throughout a prolonged maintenance delay. Spatial attention, which is selective towards memorized locations to bias perceptual processing, may also interact with rehearsal mechanisms in spatial working memory. To test this hypothesis, Awh and colleagues used a probe task and found that modulations of the early P1 and N1 components of subjects' ERP waveforms were similar in both perception and memory tasks (Awh, et al., 2000; Awh, Dhaliwal, Christensen, & Matsukura, 2001; Awh & Jonides, 2001).

The literature clearly shows that modulations in sensory-evoked components are produced during perception while engaging in visual search (Luck, 1995; Luck & Hillyard, 1990, 1994), yet it remains unclear whether these effects occur during working memory maintenance. For this reason, it is important to test if perceptual probes elicit attentional effects while the maintenance of other information is underway. In the current experiment, I reasoned that by using spatially defined perceptual probes, P1N1 modulations would be elicited at the locations of objects that people are remembering if the unitary model's description of attention and working memory is correct. Under that model, the sensory-evoked amplitudes for perceptual inputs would be expected regardless of ongoing maintenance activity. If perceptual selection uses the same mechanism as working memory maintenance, then the appearance of a probe at an attended location would inherently cause the mechanism to process both the new stimulus while also maintaining the relevant memory items. In other words, P1N1 attentional effects will be observed for probes that appear in a task-relevant location. In contrast, the multi-component model, which proposes that perceptual selection and maintenance are two distinct mechanisms would hypothesize that the P1N1 should not show differences in amplitude when elicited by probes presented at the location of objects people are remembering because perceptual selection and working memory selection use separate mechanisms.

### Enhancement vs. Suppression

Another potential purpose of spatial attention is that it can also suppress distractor information in addition to enhancing target information (Luck, 1995; Luck & Hillyard, 1994). Findings from ERP studies reveal that the P1 and N1 components may act as markers of spatial attention at a location even prior to the appearance of a salient probe (Jha, 2002; Luck, Woodman, & Vogel, 2000; Mangun & Hillyard, 1987, 1990a, 1990b, 1991). Although the P1 and N1 act as complimentary waveforms, the effects of each can be observed in the absence of the other (Luck, 1995). Traditionally, suppression effects are related to ipsilateral P1 and enhancement effects to contralateral N1. In a spatial cuing experiment, Luck and Hillyard (1995) reported that N1 amplitude was larger for a probe presented at target location compared to target-absent trials. P1 amplitude, however, was higher for probes in nontarget locations on target-absent trials compared to target-present trials. Subsequently, no enhancement was found for target locations on target-present trials. Based on these findings, the authors suggested that the N1 activity reflects attentional enhancement of target information while the P1 peak indexes attentional suppression of distractor information. Again, these reported differences are generally seen within a visual search or a dot-probe task, but not necessarily during a retention period. If spatial attention for perceptual input is present during active maintenance, it may also be possible to observe functional differences between the two sensory components. To further explore this idea, the current experiment is designed so that perceptual probes appear at both task-relevant (to-be-remembered) locations and task-irrelevant (to-be-forgotten) locations. Probes may also appear in neutral locations to act as a control. Though the initial aim is to measure perceptual selection amidst maintenance processing, additional analyses of the ERP data may expose previously unknown characteristics of these early components. Together, these findings can lean us towards one theory's conceptualization of visual selection and may also provide crucial information regarding the ability of the attentional mechanism to suppress task-irrelevant stimuli.

## Method

### *Participants*

Fifteen volunteers between the ages of 18 and 35 were recruited from the Vanderbilt University community. Each participant provided informed consent and was monetarily compensated. All reported having normal or corrected-to-normal vision and no colorblindness. One participant was unable to complete the task and another participant's data was excluded due to eye movement artifacts. This resulted in a total of thirteen participants.

### *Stimuli*

The stimuli consisted of simple colored squares presented against a gray (155, 155, 155) background. Each square was approximately 0.8° of visual field with only six squares presented each trial. The color of each representation was randomly selected from a set of nine colors: red (255, 0, 0), green (0, 255, 0), blue (0, 0, 255), yellow (255, 255, 0), black (0, 0, 0), magenta (255, 0, 255), cyan (0, 255, 255), purple (100, 0, 200), and orange (255, 100, 0). Probe squares were slightly larger than the memory items (1°) and were presented in white (255, 255, 255). Throughout each trial, a fixation cross (a black plus sign) was present at the center of the screen. Locations for the stimuli were centered on a predefined annulus and were presented about 1° apart. Memory items appeared only in the top left or bottom right corners of the screen. The cue stimuli were the words "left" and "right" (sans serif font, approximately 1° X 2.4°) presented at the center of the monitor above the fixation point. An example trial is illustrated in Figure 3.

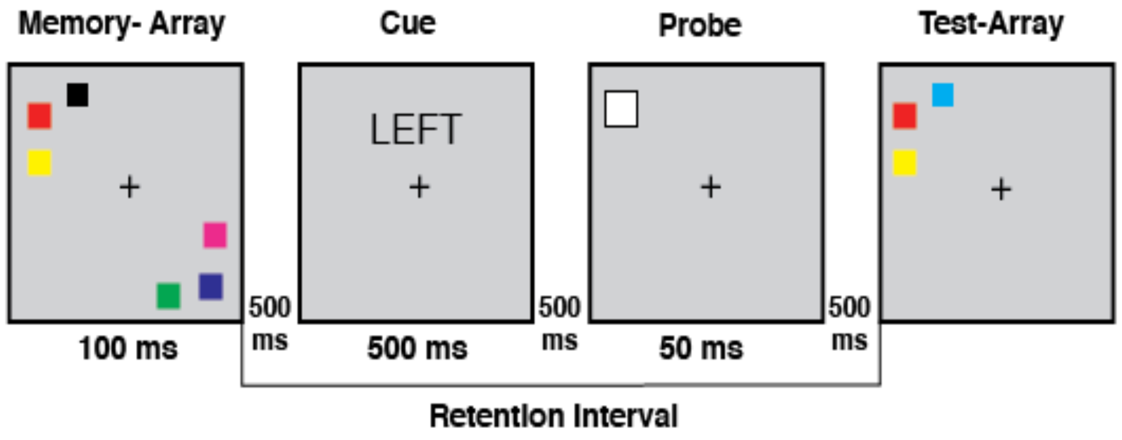

*Figure 3.* Stimuli used in Experiment 1. Probes could appear in one of the four quadrants. In this example, the probe is presented in a target location.

*Procedure*

Participants engaged in a simple memory change-detection task. Memory arrays consisted of six squares: three in the upper left quadrant and three in the lower right quadrant of the screen presented for 100-ms. After a 500-ms blank interval, a brief 500-

ms cue appeared instructing participants to remember either the left or right side squares. 500-ms after the cue, a perceptual probe appeared for 50-ms during retention. The probe could appear in one of three locations: 1) in one of the to-be-remembered locations (*target* probe), 2) in one of the to-be-forgotten locations (*nontarget* probe), or 3) in a quadrant where no items were presented (*neutral* probe). Neutral probes were randomized between the non-item quadrants (upper right and lower left). Probes occurred during the maintenance period when subjects were expected to be focusing on the relevant visual hemifield for test. Probed types were intermixed. After the probe, another blank interval occurred for 500-ms followed by the test array where participants responded “same” or “different” by pushing a button.

### *ERP Recording and Analysis*

Electroencephalograph (EEG) activity 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), and two nonstandard sites, OL and OR. The electrooculogram (EOG) was recorded by one electrode placed 1 cm lateral to each of the external canthi to measure horizontal eye movements and one electrode below the left eye to measure vertical eye movements and blinks. The right mastoid served as the online reference for the active electrodes. Signals were re-referenced offline to the average of the left and right mastoids (Nunez, 1981). To amplify the EEG and EOG, an SA Instrumentation amplifier with a gain of 20,000 and a bandpass of 0.01-100 Hz was implemented. Amplified signals were digitized at 250 Hz by a PC-compatible computer and averaged offline.

Incorrect response trials and trials including ocular or myogenic artifacts were eliminated from the averages. To reject ocular artifacts, a two-step procedure described in Woodman & Luck (2003) was used. ERP data of participants who successfully refrained from making detectable eye movements and had above-chance accuracy were included in the analyses. Prior to averaging, parameters were assessed that led to the removal of trials with large eye movements. This included looking at the averaged data collected from the horizontal EOG (HEOG) waveforms to reject any subject with marked residual eye movement. If a participant had greater than 25% of individual trials rejected or systematic movement HEOG voltage deflections greater than 3.2 (this corresponds to an ocular deviation of ± 0.1° (Nunez, 1981)) his/her data was removed.

## Results and Discussion

### *Behavioral Results*

Overall change-detection accuracy was 79.8%. Accuracy was similar across all probe types (79.8% for targets, 79.6% for nontargets, and 80% for neutral) meaning that the perceptual probes did not interfere with performance in the working memory task. A within-subjects ANOVA revealed that these means did not differ statistically as evidenced by a nonsignificant main effect of probe type, $F(2,24) = 0.16$, $p = 0.85$.

### *ERP Results*

Figure 4 shows the ERPs recorded during the retention interval following a perceptual probe. Separate waveforms are shown for contralateral and ipsilateral electrode sites relative to the probe location. Difference waves are plotted in Figure 4B to better illustrate the contralateral and ipsilateral effects of the components. As expected, the probes elicited the P1N1 sensory components in all trial types. The critical result is the amplitude differences observed following each probe type. Specifically, the unitary model predicts that perceptual attention should be deployed to the locations of the target probes in service of maintaining the object representations initially presented at these locations. This would result in an enhanced contralateral N1 at target locations relative to nontarget or neutral probes.  This pattern is precisely what is shown in the left panel of Figure 4 relative to the middle and right panels. It also predicts that attention should suppress the nontarget locations relative to the target and neutral probes.  This prediction was confirmed by a larger amplitude ipsilateral P1 in the middle panel compared to the left and the right panels of Figure 4. If perceptual attention and visual working memory maintenance were entirely separate mechanisms, as I predicted based on the multicomponent model, then all of the probes should have elicited similar ERPs. This prediction was falsified.

To verify the statistical significance of this pattern of results, I first ran an ANOVA focused on the P1 component to test the competing predictions of the two models. I ran a within-subject ANOVA with the factors of probe type (target, nontarget, neutral), hemifield (left versus right), contralaterality (ipsilateral versus contralateral to the cued items), and electrode (PO3/4, P3/4, O1/2, OL/R, T5/6). The analysis window

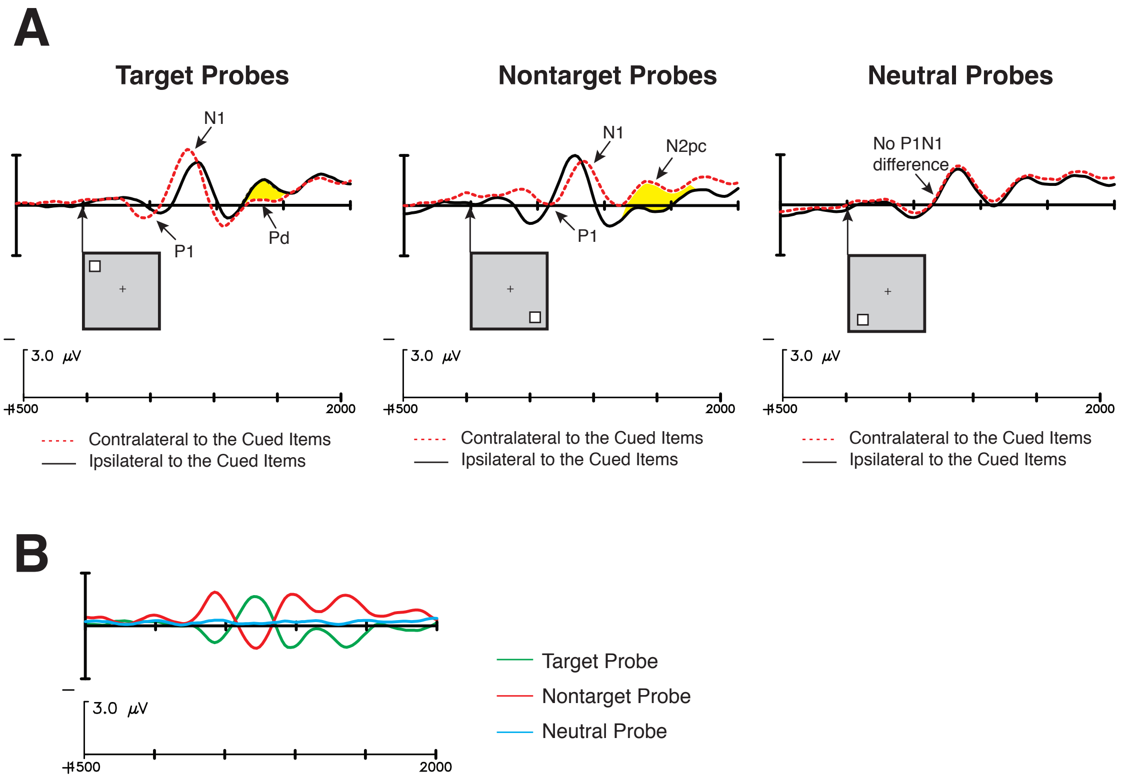

*Figure 4.* ERP results time-locked to 100-ms prior to the onset of the perceptual probe. In this example, participants were remembering the items in the upper-left quadrant. A: The waveforms from electrodes P3/4 relative to the cued items. The sensory-evoked P1N1 components are labeled with arrows. The yellow region shows the significant post-perceptual components. B: The difference waves (contralateral – ipsilateral) for each of the probe types.

measured the voltage between 50-ms to 125-ms post cue onset. This ANOVA yielded a significant main effect of Contralaterality, $F(1,12) = 6.86$, $p < 0.05$ driven by larger ipsilateral P1s. This ANOVA also yielded a significant interaction of Probe Type X Contralaterality, $F(2,24) = 10.19$, $p < 0.01$, due nontarget probes eliciting a larger ipsilateral P1 relative to the other probes (see Figure 4A). These results reflect the amplitude differences seen between ipsilateral and contralateral measures of the P1 component for the nontarget probe compared to the neutral probe. It also provides evidence of suppression at the onset of a distractor item. Other effects from the ANOVA include significant interactions of Probe X Hemifield X Contralaterality, $F(2,24) = 3.82$, $p < 0.05$, due to the ipsilateral P1 being larger in the left visual hemisphere, and also an interaction of Hemifield X Contralaterality X Electrode, $F(4,48) = 3.58$, $p < 0.05$ caused by larger P1 amplitudes at electrodes PO3/4, P3/4, and T5/6.

To test if ipsilateral P1 was an indicator of distractor suppression, I ran an ANOVA for each probe type with the factors of Hemifield, Contralaterality, and Electrode. As predicted by the unitary model, nontarget probes yielded a significant main effect of Contralaterality, $F(1,12) = 21.92$, $p < 0.01$, due to larger ipsilateral P1s following this probe type.  Nontarget probes also resulted in an interaction of Contralaterality and Electrode, $F(1,12) = 2.88$, $p < 0.05$, due to larger ipsilateral voltages at electrodes in the posterior region. Target probes had an interaction of Hemifield X Contralaterality, $F(1,12) = 18.14$, $p < 0.01$ due to larger P1 amplitudes in the left visual field. Finally, neutral probes also displayed some amount of distractor suppression. There was a main effect of Contralaterality, $F(1,12) = 4.9$, $p < 0.05$, caused by larger ipsilateral P1s following these probes. Neutral probes also yielded a significant interaction of Hemifield X Contralaterality X Electrode, $F(1,12) = 6.86$, $p < 0.05$, due to larger ipsilateral P1s at electrodes OL/R and T5/6.

I also ran a pairwise comparison for target probes versus neutral probes and nontarget probes versus neutral probes focusing on the P1 time window. The target and neutral analysis yielded a significant interaction of Probe Type X Contralaterality, $F(1,12) = 7.41$, $p < 0.05$, due to the neutral probes larger ipsilateral P1 indicating that neutral probes were suppressed. Other interactions include Hemifield X Contralateraility, $F(1,12) = 11.28$, $p < 0.01$, due to larger ipsilateral P1s in the left visual hemifield, Probe

Type X Contralaterality X Hemifield, $F(1,12) = 8.63$, $p < 0.05$, due to neutral probes eliciting a larger ipsilateral P1 in the left hemifield, and Contralaterality X Hemifield X Electrode, $F(4,48) = 4.21$, $p < 0.01$, due to ipsilateral P1s larger voltage in the left hemifield at electrodes O1/2, OL/R, and T5/6. The analysis between neutral and nontarget probes further supported the distractor suppression theory since it yielded a significant main effect of Contralaterality, $F(1,12) = 20.19$, $p < 0.01$, due to both probes eliciting a larger ipsilateral P1 component compared to contralateral P1. An interaction of Probe type X Contralaterality, $F(1,12) = 7.9$, $p < 0.05$, was found due to nontarget probes producing a much larger ipsilateral P1 amplitude than neutral probes. There was also an interaction of Contralaterality X Electrode, $F(1,12) = 6.86$, $p < 0.05$, due to ipsilateral P1 being larger at electrodes OL/R and T5/6.

Next I ran ANOVA with the factors of probe type, hemifield, contralaterality, and electrode focusing on the N1 component. The analysis window was for the 125-ms to 200-ms post cue onset. There was a significant main effect of Contralaterality, $F(1,12) = 5.18$, $p < 0.05$, due to a large contralateral N1 component arising from all probe types. The analysis also yielded a significant interaction of Hemifield X Contralaterality, $F(1,12) = 7.46$, $p < 0.05$, due to larger negativity in the left visual hemifield and Hemifield X Contralaterality X Electrode, $F(4,48) = 4.7$, $p < 0.05$, driven by the negativity in the left visual field at electrodes P3/4, OL/R, and T5/6.

To test if contralateral N1 was an indicator of target enhancement, I ran an ANOVA for each probe type with the factors of Hemifield, Contralaterality, and Electrode. Contrary to the enhancement hypothesis, there was not a significant main effect of contralaterality for target probes, $F(1,12) = 1.48$, $p = 0.25$. However, target probes did produce an interaction of Hemifield X Contralaterality, $F(1,12) = 8.11$, $p < 0.05$, due to more negative voltages in the left hemifield, as well as an interaction of Contralaterality X Electrode, $F(4,48) = 6.07$, $p < 0.01$, due to the contralateral N1 being stronger at electrodes P3/4, OL/R, and T5/6. For neutral probes there was a marginal main effect of Contralaterality, $F(1,12) = 4.78$, $p = 0.049$. This effect can be attributed to larger contralateral N1 following this probe type. There was also a significant interaction of Hemifield X Contralaterality X Electrode, $F(1,12) = 4.91$, $p < 0.01$, due to the contralateral N1 being larger in the left hemifield at electrodes OL/R and T5/6. Nontarget probes yielded no significant effects or interactions.

As a follow-up, I ran pairwise comparisons for neutral probes versus target probes and neutral probes versus nontarget probes again focusing on the N1 component time window. The first comparison resulted in a main effect of Contralaterality, $F(1,12) = 7.61$, $p < 0.05$, due to larger contralateral N1s compared to ipsilateral N1s therefore suggesting that these probe types led to an N1 attentional enhancement. This analysis also yielded interactions of Probe Type X Hemifield X Contralaterality, $F(1,12) = 5.63$, $p < 0.05$, caused by larger N1 amplitudes following target probes in the left visual hemifield, Contralaterality X Electrode, $F(4,48) = 6.69$, $p < 0.01$, due to contralateral N1 being larger at electrodes OL/R and T5/6, and Hemifield X Contralaterality X Electrode, $F(4,48) = 3.67$, $p < 0.05$, due to left hemifield having larger contralateral N1s at electrodes OL/R and T5/6. Interestingly, the comparison between neutral probes and nontarget probes yielded no significant effects or interactions. These results and the ones above suggest that the contralateral N1, a marker of target enhancement, was not produced during the perception of nontarget probes.

Finally, I performed post-hoc analyses to examine the time-course of attention shortly after perceptual processing. The 300-ms window used to capture the early-sensory components may have also picked up on post-perceptual selection. For these analyses, I narrowed the time window down to 1800-ms to 1900-ms (150ms-250-ms postprobe) to isolate the N2pc or Pd components. This ANOVA resulted in a significant main effect of Probe Type, $F(1,12) = 6.17$, $p < 0.01$ due to differences following target and nontarget probes and Contralaterality, $F(1,12) = 5.59$, $p < 0.05$, due to contralateral and ipsilateral differences post cues (see Figure 4A). There were also significant interactions of Probe X Contralaterality, $F(1,12) = 22.83$, $p < 0.01$, due to there being a more positive voltage following target probes and a more negative voltage following nontarget probes. Other effects include an interaction of Hemifield X Contralaterality, $F(1,12) = 9.0$, $p < 0.05$, due to contralaterality in the left hemifield. In a follow-up analysis, I found a significant main effect of Contralaterality for both the target probe, $F(1,12) = 6.36$, $p < 0.05$, driven by a larger positive component and the nontarget probe, $F(1,12) = 44.08$, $p < 0.01$, driven by a large negative component. No effect was found following a neutral probe. Again, negativity and positivity voltages drove differences in amplitudes for these cue types. As highlighted in Figure 4A, the processing of target probes led to a more positive waveform following the P1N1. The time-course of this component is consistent with that of the Pd, an ERP component that is believed to be a measure of attentional suppression (Sawaki & Luck, 2011, 2012). Conversely, after a nontarget probe, a negative voltage known as the N2pc arises following the P1N1. The presence of the Pd and N2pc components suggests that there is an attentional shift that occurs shortly after processing the perceptual probes.

## General Discussion

In this chapter, I found that perceptual selection for probes could be measured during the maintenance of other stimuli representations. The results of this experiment appear to support the assertion of unitary models that a singular selection mechanism used to guide perceptual input can be observed during concurrent maintenance. Though visual selection was temporarily drawn away to detect new stimuli, we know that rehearsal of the memory array was not entirely destroyed. The behavioral performance for the change-detection task demonstrates that processing the probes was quick and not notably detrimental to the items in retention.

It is important to also note that indices of selection did not occur for all probe types. Biased selection was only observed for probes that appeared in spatial locations relevant to maintenance, either target locations or nontarget locations. In addition, I found evidence of attentional redeployment following these types of probes. After a target probe appeared, perceptual selection enhanced the initial representations as seen with the P1N1 amplitudes. However, because the perceptual probe was irrelevant for the memory task itself, this enhancement is soon followed by a Pd component. The Pd component generally arises after attention has been involuntarily captured and must then work to suppress the distracting information in order to reorient (Sawaki & Luck, 2011, 2012). Conversely, on trials with a nontarget probe, perceptual selection occurs for this probe (as marked by the P1N1), but then we see attention reoriented to the target hemifield. In this case, the neural measure of the attentional shift is characterized by the N2pc (Eimer, 1996; Woodman & Luck, 1999; Woodman & Luck, 2003). The presence of these post-perceptual components is further evidence that visual selection not only detected the probes during maintenance, but that it also biased the processing of locations of stored information both before and after perceptual input.

## Conclusion of Chapter II

The experiment presented in this chapter utilized a technique designed to isolate attentional activity during a working memory task. Introducing a perceptual probe while also rehearsing earlier representations created a situation where a singular selection mechanism would have to abandon the retained objects to attend to the incoming stimulus. Enhanced processing for probes at remembered locations indicates that perceptual selection did occur during maintenance. The results provided here show evidence of this solitary mechanism and provide support for the unitary model of working memory.

# Chapter III

# EXPERIMENT 2: DOES PERCEPTUAL PROCESSING MODULATE CONCURRENT MAINTENANCE?

In the previous chapter, I presented research suggesting that perceptual input selection intrudes on simultaneous maintenance processing. When visual selection is used to bias perception for incoming stimuli, this mechanism is inherently pulled away from other tasks it may be overseeing. In a real world example, you can imagine seeing and reacting to a stoplight while driving to your friend's house. To complete this task, you must perceive, process, and respond to the stoplight while simultaneously keeping the street name in mind in addition to the speed limit, the position of other vehicles, etc. Although this switch may be brief and virtually unnoticed, it is clear from the electrophysiological data that the retention or rehearsal of stored representations is temporarily interrupted. In this chapter, I present research examining the extent to which perceptual selection disruption impacts concurrent working memory maintenance.

## ERP Indices of Working Memory Maintenance

Orienting attention prior to stimulus presentation can facilitate perception and encoding processes (Posner, 1980). Similarly, shifting attention to prior locations in working memory can also result in the protection and continued rehearsal of retained items (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Matsukura, Luck, & Vecera, 2007). According to unitary models, the focus of attention actively selects perceptual input and also maintains information in the memory store. Conversely, in the multi-component theory, the inner scribe is the visual equivalent of the phonological loop. This subsystem is capable of rehearsing stored representations without direct input from the central executive, and can do so even while other systems attend to new stimuli. If visual selection is a single mechanism as suggested by unitary working memory models, it is responsible for both perception and maintenance processing. However, if there are two separate visual selection mechanisms, as suggested by multi-component models, then perceptual selection is not needed for rehearsal once an object has been encoded into working memory.

One way to distinguish between these models is to examine the underlying physiological indicators of object maintenance. Using an electrophysiological component known as the CDA (Contralateral Delay Activity), researchers have found neural correlates of maintenance show that subjects are able to manipulate and select items which are being held in working memory. The CDA is a negative-going voltage that is observed over the posterior parietal and occipital parts of the brain (Eimer & Kiss, 2010) (Vogel & Machizawa, 2004). Of the many ERP components being studied, the CDA is one that appears to strictly represent cognitive processing during memory-retention intervals. It gradually rises after the offset of to-be-remembered stimuli and asymptotes once the participant reaches their maximum working memory capacity. The component is spatial in nature, in that the contralateral hemifield of the to-be-remembered stimuli is more negative in amplitude than the ipsilateral hemifield. Nevertheless, the magnitude of the waveform reflects the number of object representations currently being held in working memory (Ikkai, McCollough, & Vogel, 2010; Vogel & Machizawa, 2004;

Vogel, et al., 2005). As set size increases, the CDA amplitude also increases, asymptoting once it reaches memory capacity.

Given that maintenance has a limited capacity for the number of objects that can be stored (due to working memory constraints) we can assume that the CDA would be influenced if a task required selecting more items from a visual array. Essentially, participants are more likely to reach maximum capacity when the array set size increases. Research suggests that when given instructional cues, subjects are able refocus maintenance mechanisms to improve their working memory performance (Averbach & Coriel, 1961; Griffin & Nobre, 2003; Sperling, 1960; Williams & Woodman, 2012; Woodman, Vecera, & Luck, 2003). Williams and Woodman (2012) found that subjects were able to select the task-relevant representations from working memory following post-cues. Post-cues are presented during the retention interval of a memory task and convey to participants which hemifield will be tested. In the study, either a to-be-remembered cue or a to-be-forgotten cue would be presented to guide participants' maintenance selection. The presence of the CDA during the retention intervals suggested that while participants initially tried to maintain stimuli from both hemifields, they were able to reorient to the relevant representations until test (with minimal interference from the cue itself). This data provides strong evidence in favor of a working memory maintenance mechanism that is able to selectively maintain the most relevant information even after encoding has occurred. Unlike perception, which uses selection to navigate among currently seen stimuli, maintenance mechanisms appear to work even after the representations are removed from the environment.

In Chapter II, perceptual indices of selection were observed during maintenance in a working memory task. The sensory-evoked components not only appeared while maintenance activity was ongoing, but they also showed evidence of perceptual selection. As seen in the previous experiment, spatial selection helped to guide perceptual input for the new stimuli. What is currently ambiguous about these findings is whether or not spatial attention was used for maintenance throughout the entire delay period. The unitary and multi-component models would each have competing predictions. A unitary model would reason that visual selection must have temporarily ceased object maintenance to process the incoming perceptual items because spatial attention can either focus on perceptual input or maintenance activity, but cannot do both at once. The multi-component model would explain that selection mechanisms of maintenance continued uninterrupted by perceptual selection utilizing the buffers in working memory which have their own mechanisms of selection and can work independently of the central executive allowing both systems to work in parallel.

The purpose of the current experiment is to test mechanisms of selection during a dual-task paradigm. In the previous task, participants were not instructed to make a response to the perceptual probes. Within the present experiment, I again included a condition where participants were instructed to ignore the perceptual probes. Doing so allowed me to have a controlled baseline measure of the effect of the probes when they were irrelevant to the task. In a separate condition, participants were instructed to remember colored squares and also respond to (or ignore) perceptual probes that appeared during the retention interval based upon the probe type. Earlier studies investigating dual-task interference have found that working memory maintenance can avoid interference when the secondary search task uses the same stimulus each trial (Logan, 1979; Woodman & Luck, 2009; Woodman, Vogel, & Luck, 2001). However, when participants must search for a different target item, working memory performance suffers (Woodman, Luck, & Schall, 2007). One explanation of these findings is that target templates for the search task are stored in working memory along with the retained items (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). When that target changes from trial to trial, working memory must update the template to complete the task. Unless there were two selection mechanisms, the focus of attention would have to move back and forth among the items in memory, working to either maintain the memory representations or select the target template for search. In the case where the search target remains the same, the assumption is that the template representation is gradually moved from working memory into long-term memory (Carlisle, Arita, Pardo, & Woodman, 2011; Woodman & Chun, 2006). The research on this memory handover is currently being pursued, but for the purposes of this study, the role of a unitary visual selection mechanism remains the same even in long-term memory (Cowan, 2008). By this account, the focus of attention would still have to maneuver between activated representations and long-term memory representations to successfully perform the dual-task.

Since Chapter II demonstrated that perceptual selection is likely to occur for target stimuli, I wanted to push the limits of selection by manipulating the amount of information to be processed. By varying the set size of the memory array up to the bounds of capacity, we should be able to measure any decrement caused by perceptual interruption to the objects being retained. Rather than focusing on the perceptually evoked ERP components as I did in the previous experiment, I will instead concentrate on the maintenance component, the CDA. Here, the crucial manipulation is whether or not the CDA will be disrupted to attend to the secondary task probe. A unitary model hypothesis would predict that visual selection will be pulled away from object maintenance to attend to perceptual probes and the CDA will not only be interrupted, but it will also diminish in amplitude. Moreover, as set size increases, the dual-task demands will result in the selection mechanisms having to drop an item or two perceive and respond to the target probes. The loss of an object to accommodate perceptual selection should therefore be reflected by a decreased CDA amplitude. In contrast, a multi-component model would predict an ongoing CDA regardless of the perceptual probe's appearance. By this account, central executive functions that work to attend to the probe should not have to enter the subsystem buffers and thereby interrupt maintenance. The number of items being held in memory will modulate the CDA, however, the secondary perceptual task should not replace any of the items from the memory array.

## Method

### *Participants*

Ten volunteers between the ages of 18 and 35 were recruited from the Vanderbilt University community. Each participant provided informed consent and was monetarily compensated for each session. All reported having normal or corrected-to-normal vision and no colorblindness. Two participants were unable to return for the second part of the experiment and two participants' data was excluded due to eye movement artifacts. This resulted in a total of 6 participants.

*Stimuli*

The stimuli consisted of simple colored squares presented against a gray (155, 155, 155) background. Each square was approximately 0.8° of field of vision and there between 2 – 8 squares each trial. The color of each representation was randomly selected from a set of nine colors: red (255, 0, 0), green (0, 255, 0), blue (0, 0, 255), yellow (255, 255, 0), black (0, 0, 0), magenta (255, 0, 255), cyan (0, 255, 255), purple (100, 0, 200), and orange (255, 100, 0) without replacement. Throughout each trial, a fixation cross (a black plus sign) was present at the center of the screen. Perceptual probes were defined as a change in color of the fixation cross to either a light blue (75, 200, 255) or dark yellow (225, 200, 75). Locations for the stimuli were centered on a predefined annulus and were presented about 1° apart. Memory representations appeared on the left and right side of fixation, with equal number of squares being presented in each hemifield. The cue stimuli were the words "left" and "right" (sans serif font, approximately 1° X 2.4°) presented at the center of the monitor above the fixation point. An example trial is illustrated in Figure 5.

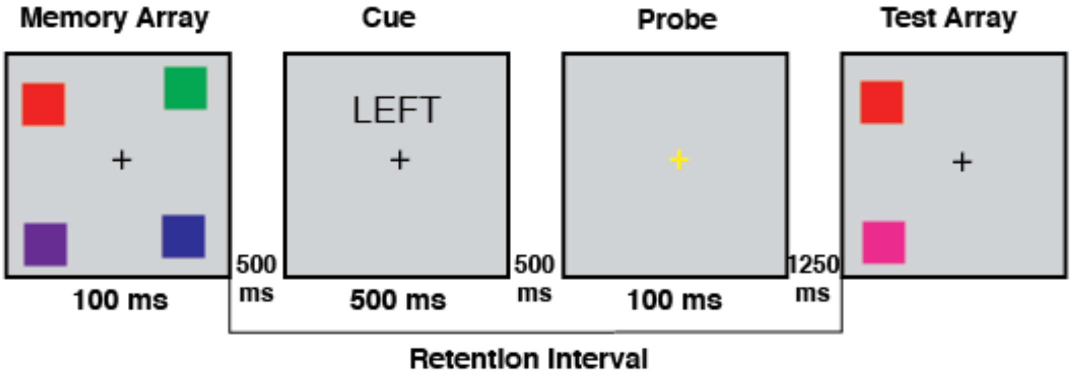

*Figure 5.* Stimuli used in Experiment 2. Probes would appear during both the passive viewing and active viewing condition.

### *Procedure*

This experiment was run as a two-part study. All participants took part in both conditions. The first was the *passive viewing* condition during which perceptual probes would occur during the retention interval, but observers were unaware of their purpose and were instructed to ignore them. The second session was the *active viewing* condition in which participants were instructed to respond to certain probes as a part of a secondary task. At the start of each trial, a memory array appeared with two, four, or eight colored squares (equally distributed in each hemifield). The array was presented for 100-ms during which participants were expected to remember all the colors on the screen. After a short delay of 500-ms, a directed-remembering cue appeared for 500-ms indicating which subset of squares was task-relevant for the test. The cue was the word “left” or “right” and appeared directly above the fixation cross. Next there was a prolonged retention interval. During this time the fixation-probe could flash. This was the secondary perceptual task. On the probe trials, the central cross could change from black to yellow or light blue for 100-ms at some point during the 2850-ms retention interval (post-cue). Participants were instructed to respond if the probe changed to the target color. If the probe flashed to the target color, observers were to press a button to indicate that they saw the probe. On nontarget probe trials, the cross would change color, however, participants were to refrain from responding. Similarly, participants were instructed not to respond if the cross remained black. Probes made up two-third of the trials with target and nontarget colors counterbalanced across subjects. At the end of the retention interval, a test array of one, two, or four items was shown and participants responded “same” or “different” to determine a color change.

*ERP Recording and Analysis*

The same criteria as described in Chapter II were also used for this experiment.

## Results and Discussion

*Behavioral Results*

Overall accuracy for the memory task was slightly better in the passive viewing condition than in the active viewing condition, 83.1% versus 81.1%. As set size increased, accuracy decreased for both conditions. In the passive condition, accuracies were 97.5%, 86.2%, and 65.7% for set size 2, 4, and 8, respectively. Similar accuracies were found within the active condition, 96.9%, 83.6%, and 62.6%. I conducted a within-subjects ANOVA with factors of Condition, Probe Type, and Set Size that yielded significant main effects of Condition, $F(1,5) = 7.39$, $p = 0.04$ due to higher accuracy in the passive condition, and Set Size, $F(2,10) = 110.70$, $p < 0.01$ due to higher accuracy at lower set sizes. Planned comparisons revealed a significant interaction, $F(1,5) = 41.27$, $p < 0.01$, due to higher accuracy at set size 4 in the passive condition compared to the active condition. No other effects were found.

Mean RT in the passive condition was 733-ms. As set size increased from 2 to 8 items, RTs increased, 597-ms, 739-ms, 863-ms, respectively. Mean RT in the active condition was 654-ms. Similar to the passive condition, as set size increased, RTs also increased, 570-ms, 660-ms, and 731-ms. An ANOVA with the factors of Condition and Set Size revealed a main effect of Condition, $F(1,5) = 7.03$, $p < 0.05$, due to RTs being significantly faster in the active condition, and a main effect of Set Size, $F(2,10) = 25.14$, $p < 0.01$, due to RTs increasing as set size increased.

Overall accuracy for the probe task was 96.6%. Probe accuracy in set size 2 was 96.9%, 96.8% at set size 4, and 96.3% at set size 8. The difference between accuracy in set size 4 and 8 was significant, $F(2,10) = 12.27$, $p < 0.05$. Mean probe RT was 530-ms. As set size increased from 2 to 8, RTs also increased; 523-ms, 530-ms, and 538-ms. However, this difference was not significant (*p's* > 0.05).

In summary, the behavioral data are consistent with the predictions of the unitary model, since memory performance was decreased in the active condition due to perceptual probes.

### *ERP Results*

Recall that the unitary model predicts that probes should interfere with concurrent maintenance since a single selection mechanism would have to cease rehearsal in order to attend to incoming stimuli. That means that the CDA should be disrupted at the appearance of a perceptual probe. The multi-component model, however, posits that central executive functions can process perceptual input without having to enter the memory buffers. This model would therefore predict that the CDA would continue uninterrupted despite the onset of a probe. As shown in Figure 6, the waveforms separated by passive and active condition, set size, and probe type appear to be consistent with the unitary model. These ERPs are time-locked to the onset of the memory cue, 600-ms into the trial. The most critical portions of the waveforms occur directly before and after the dual-task probe. I found that although there was not a significant measure of the CDA, there was a disruption in the form a P3 component following the processing of a perceptual probe.

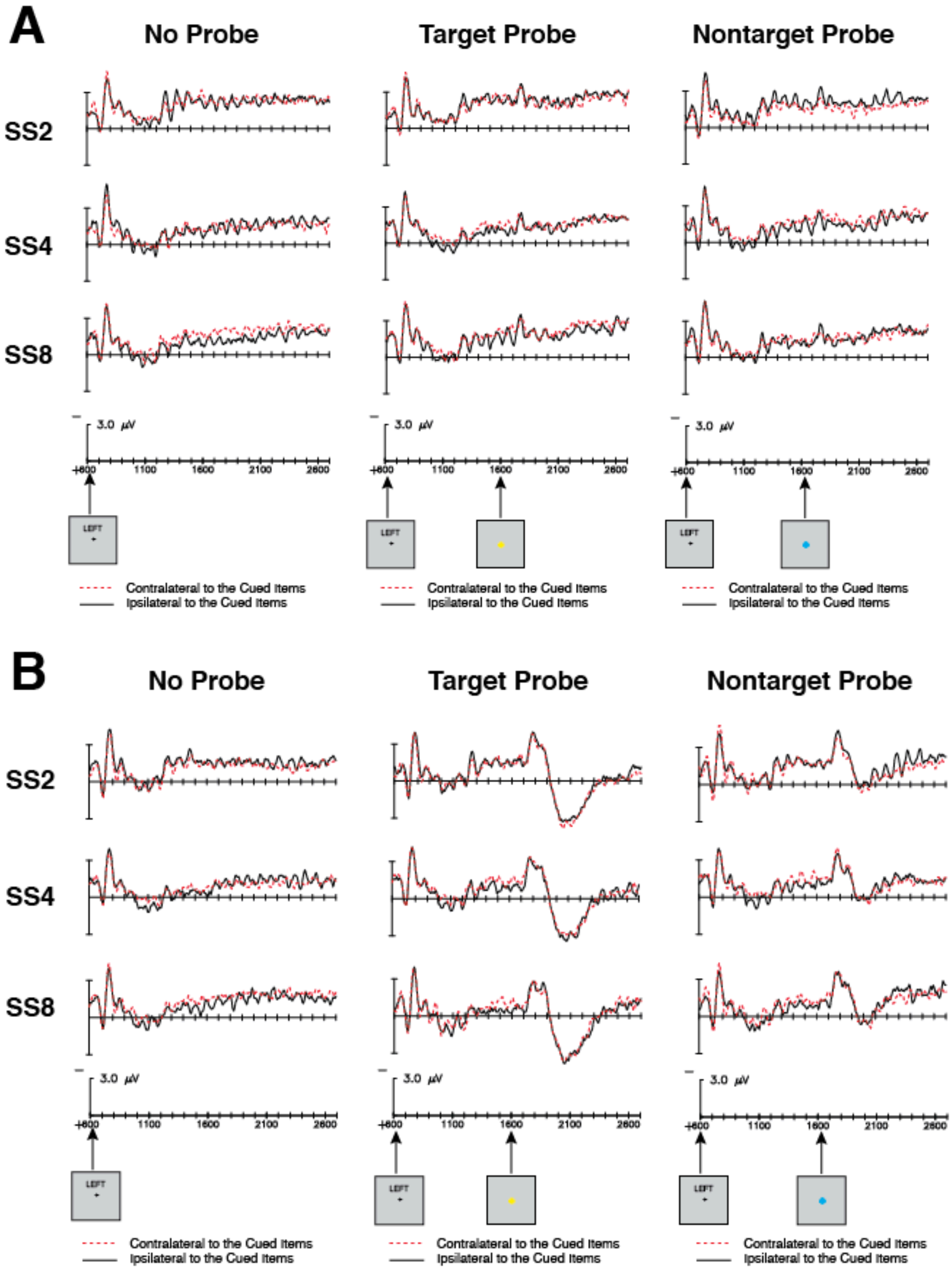

*Figure 6.* ERP results time-locked to the onset of the memory cue. In this example, participants were remembering the items in the left hemifield, target probes were yellow, and nontarget probes were blue. Waveforms are plotted from electrodes T5/6 relative to the cued items. A: The passive viewing condition. B: The active viewing condition.

To measure if the CDA was statistically significant for the passive viewing and active viewing condition, I analyzed two time windows - the 1,000-ms before the probe and the 1,000-ms following the probe. The unitary model predicts that the CDA should differ significantly between these two time windows in the active viewing condition. I ran an omnibus ANOVA for each condition with the factors of time window, set size, probe type, hemifield, contralaterality, and electrode. The passive condition did not have any significant main effects of the time windows. There was, however, a main effect of Electrode, $F(4,20) = 6.74$, $p < 0.05$, due to larger voltages at parietal electrodes. The ANOVA also yielded interactions of Set Size X Contralaterality, $F(2,10) = 6.78$, $p < 0.05$, due to larger CDA measures in one of the set sizes, Contralaterality X Electrode, $F(4,20) = 4.9$, $p < 0.01$, due to contralateral differences at electrodes T3/4, Set Size X Probe Type X Hemifield, $F(4,20) = 5.10$, $p < 0.01$, due to perceptual probes in one of the set sizes creating voltage differences in the right hemifield, and Time Window X Probe X Hemifield X Contralaterality, $F(2,10) = 6.35$, $p < 0.05$, due to the second time window following perceptual probes creating slight CDAs within the right hemifield.

I also ran the ANOVA with the same factors as above for active condition. I found several interactions which supported the unitary model's prediction: Time window X Contralaterality, $F(1,5) = 24.87$, $p < 0.01$, due to larger measures of the CDA in the window prior to the perceptual probes, and Time window X Set size, $F(2,10) = 4.39$, $p < 0.05$, due to the disruptive effects of the probes at larger set sizes. Together, these results suggest that perceptual probes 1) disrupted maintenance activity that was happening prior to the secondary task, and 2) interfered with the number of items that was original being retained. The ANOVA also produced other interactions; Time Window X Probe, $F(2,10)$

= 8.51, $p < 0.01$, due to the differences in the periods before and after the onset of the probes, Probe X Hemifield, $F(2,10) = 8.83$, $p < 0.01$, due to perceptual probes eliciting stronger voltages in the right hemifield, Time window X Electrode, $F(4,20) = 6.75$, $p < 0.01$, due to the second time window having a larger positivity at parietal electrodes, and Time window X Probe X Electrodes, $F(8,40) = 6.24$, $p < 0.01$, due to task-relevant probes eliciting P3s at parietal electrodes.

Next, I ran a within-subjects ANOVA for each time window with the factors of Condition, Set Size, Probe Type, Hemifield, Contralaterality, and Electrode Site. For the epoch between 1,000-ms prior to the cue there was an interaction of Set Size X Contralaterality, $F(2,10) = 12.10$, $p < 0.01$. No other significant effects were found within this analysis.

In the analysis for 1,000-ms after the cue, the behavioral difference between the passive and viewing conditions was also seen at the ERP level as there was a main effect of Condition, $F(1,5) = 47.67$, $p < 0.01$, due to decreased performance in the active condition. However, unlike the behavioral data, there was also a significant main effect of Probe Type, $F(2,10) = 4.74$, $p < 0.05$, due to a large positivity known as the P3 following target and nontarget probes, and an interaction of Condition X Probe, $F(2,10) = 6.20$, $p < 0.05$ due to the P3 following target and nontarget probes in the active condition (see Figure 6B). The presence of a P3 component indicates that detection of the perceptual probe required a separate comparison process that temporarily interrupted maintenance. Several other interactions were seen within this time-window: Set Size X Contralaterality, $F(2,10) = 7.86$ $p < 0.01$, due to larger contralateral differences at set size 8; Probe X Hemifield, $F(2,10) = 8.95$, $p < 0.01$, due to perceptual probes creating a large

P3 in the right hemifield; Condition X Electrode, $F(4,20) = 6.60$, $p < 0.01$, due to the active condition creating larger positive waveforms at electrodes PO3/4 and P3/4; Probe X Electrode, $F(8,40) = 3.75$, $p < 0.01$, due to target and nontarget probes creating a large P3 at posterior electrodes; Hemifield X Electrode, $F(4,80) = 5.68$, $p < 0.05$, due to the right hemifield driving larger P3s at posterior electrodes; Condition X Probe X Electrode, $F(8,40) = 3.06$, $p < 0.01$, due to perceptual probes creating a large P3 in the active condition at electrodes PO3/4 and P3/4; and Condition X Set Size X Hemifield X Contralaterality, $F(2,10) = 4.67$, $p < 0.05$, due to a larger CDA at set size 8 in the right hemifield.

Next, I performed a series of planned comparisons to further analyze the data for Condition information. The initial analysis focused on the first time window for just the passive viewing condition. I found a large CDA at set size 8, Set Size X Contralaterality, $F(2,10) = 2.03$, $p < 0.05$. The second time window revealed the same interaction, Set Size X Contralaterality, $F(2,10) = 6.49$, $p < 0.05$. These ANOVA's also revealed several effects driven by hemifield or electrode location; in the first time window there was a main effect of Electrode, $F(4,20) = 4.38$, $p < 0.05$, due to larger voltages at parietal electrodes, as well as significant interactions for Contralaterality X Electrode, $F(4,20) = 5.23$, $p < 0.01$, due to a larger CDA at electrode T5/6. Other interactions included, Set Size X Probe X Hemifield, $F(4,20) = 3.02$, $p < 0.05$, due to a large positivity in the right visual hemifield, and Set Size X Probe X Electrode, $F(16,80) = 2.33$, $p < 0.01$, due to larger voltages at PO3/4 and P3/4. The significant effects of probe are difficult to interpret, however, since the probes were yet seen during this time window. Interestingly, these were the same significant effects yielded by the ANOVA for the second time window in this condition. There was also a main effect of Electrode, $F(4,20) = 6.52$, $p < 0.01$, due to larger voltages at parietal electrodes; along with several interactions: Contralaterality X Electrode, $F(4,20) = 4.18$, $p < 0.05$, due to the ipsilateral differences at electrodes PO3/4 and P3/4; Set Size X Probe X Hemifield, $F(4,20) = 6.01$, $p < 0.01$, due to perceptual probes at set size 8 creating larger P3s in the right hemifield; and Set Size X Probe X Electrode, $F(16,80) = 1.84$, $p < 0.05$, due the perceptual probes at set size 8 being larger at parietal electrodes. The similar findings for the time before and after the probes suggest that participants in the passive viewing condition were able to successfully ignore their appearance.

I performed the same analyses with data from the active viewing condition. The first time window yielded no significant effects. Analyses from the second time window, following the dual-task probe, found a main effect of Probe, $F(2,10) = 5.18$, $p < 0.05$, due to the P3 component being larger on target and nontarget trials. Again, other effects found include a main effect of Electrode, $F(4,20) = 7.91$, $p < 0.01$, due to parietal electrodes measuring a larger positivity, and also significant interactions of Probe X Hemifield, $F(2,10) = 7.74$, $p < 0.01$, due to perceptual probes being larger in the right hemifield, Probe X Electrode, $F(8,40) = 3.53$, $p < 0.01$ due to perceptual probes creating larger P3s at electrodes PO3/4 and P3/4, Hemifield X Electrode, $F(4,20) = 4.15$, $p < 0.05$, due to the differences in the parietal electrodes in the right hemifield, and Set Size X Hemifield X Contralaterality, $F(2,10) = 4.28$, $p < 0.05$, due to set size 8 producing a CDA in the right hemisphere of the visual field;

Lastly, I conducted analyses examining the set size data in the active viewing condition. Set Sizes 2 and 4 reported no statistically significant findings for the time window before the probe ($p$'s $> 0.05$). Set Size 8, however, yielded a significant interaction of Hemifield X Contralaterlity, $F(1,5) = 16.02$, $p < 0.05$ for the pre-probe time window due to CDA measures in the right hemifield. For the 1,000-ms after the probe, all set sizes had a main effect of Probe, $F(2,10) = 6.11$, $p < 0.05$, $F(2,10) = 7.09$, $p < 0.05$, $F(2,10) = 4.19$, $p < 0.05$, for 2, 4, and 8, respectively, due to the occurrence of a P3 component. As expected, responding to the task-relevant probes made a difference when compared to no probe trials. The P3 following task-relevant probes was consistently larger at electrodes P3/4 and PO3/4 for set size 2. This resulted in a main effect of Electrode, $F(4,20) = 7.48$, $p < 0.01$ and Probe X Electrode, $F(8,40) = 5.60$, $p < 0.01$. There was also an interaction of Hemifield X Electrode, $F(4,20) = 4.09$, $p < 0.05$, due to parietal electrodes in the right hemifield. Set size 4 yielded a significant main effect of Electrode, $F(4,20) = 7.30$, $p < 0.01$, due to parietal electrodes, and interactions of Probe X Hemifield, $F(2,10) = 4.36$, $p < 0.05$, due to perceptual probes in the right hemifield, and Probe X Electrode, $F(8,40) = 8.24$, $p < 0.01$, due to perceptual probes at electrodes PO3/4 and P3/4. Finally, set size 8 resulted in a main effect of Electrode, $F(4,20) = 5.71$, $p < 0.01$, again due to larger voltages at parietal electrodes.

As illustrated in Figure 6, contralateral differences were not consistently observed throughout the task. Post-hoc analyses revealed an interaction of Contralaterality X Electrode for Set Size 8 following the probe, $F(4,20) = 3.50$, $p < 0.05$. It is possible that the CDA was not produced by the lower set sizes of 2 and 4, whereas in set size 8, participants had to remember 4 items thereby pushing the limits of their memory capacities. To assess if working memory capacity and probe task interference were related (Fukuda & Vogel, 2009), I conducted a median split using participants' accuracy at set size 8 in the passive viewing condition. This analysis assigned three participants to a high capacity group (with an average accuracy of 69.9%) and three participants to a low capacity group (61.5%). However, I did not find a significant main effect of Capacity, $F(1,4) = 4.91$, $p = 0.07$ or an interaction of Capacity X Contralaterality for either the first time window, $F(1,4) = 9.42$, $p = 0.61$, or the second time window, $F(1,4) = 2.06$, $p = 0.19$.

The difficulty of the task may explain the decreased memory maintenance activity. What was observed was the extent to which the probes impacted memory when a response was needed compared to when they were passively observed. Following a dual-task probe there is a large P3 waveform. Although the P3 arises after a nontarget probe, the amplitude is much larger following a target probe (see Figure 6B). This explains the significant main effects of probe seen within each set size. Some researchers have argued that the P3 is related to updating the contents of working memory (Beteleva & Sinitsyn, 2008; Donchin & Coles, 1988; Hyun, Woodman, Vogel, Hollingworth, & Luck, 2009). Thus, after responding to the task-relevant probes participants then returned to the representations being maintained to update that information following the lag.

## General Discussion

This chapter, like the previous one, found that perceptual selection for probes could be measured during maintenance but only when the probe is task-relevant. Although active maintenance was not electrophysiologically observed by eliciting the CDA it is clear that maintenance for the memory array still occurred because participants' accuracies were above chance. The findings of this experiment support the idea that perceptual selection is intrusive to working memory maintenance. In the passive viewing condition, participants experienced the same perceptual probes that were later seen in the active condition, however, the electrophysiological data shows no evidence of the probes interfering with visual rehearsal. When the probes become relevant for the secondary task, they encroach on working memory maintenance by forcing participants to update the contents after making a response. Furthermore, updating is especially prevalent on trials where participants must maintain objects and also make a response to the probe. On trials with a nontarget probe, the working memory is updated but not nearly as much as with a target probe.

The results found here are most aligned with a unitary model of working memory. In this dual-task paradigm, the focus of attention must select both the items of the memory array and the incoming perceptual probe. When a target probe appears, the focus of attention temporarily leaves the rehearsed items in activated memory; essentially, the items are passively stored while the selection mechanism processes the perceptual input. The return of attention to maintenance may be reflected by the onset of the P3 component. Smaller P3 amplitudes following nontarget probes may imply that maintenance was ceased just long enough for selection mechanisms to interpret the probe as irrelevant before returning its full attention to the retained items.

Additionally, the lower accuracy for the active viewing condition observed in the behavioral data suggests a disruption effect of attending to the probe. This most closely conforms to the expectations of the unitary model because it suggests that the information in working memory deteriorates more when attention is shifted from maintenance to perceptual selection. The multi-component model may also be able to explain these results if it could be shown that processing the probe requires moving it into the working memory buffer. This argument could be contradicted, however, if it were shown that rather than being fed into the visual subsystem, probe analysis was done at the long-term memory level, completely bypassing working memory.

## Conclusion of Chapter III

This chapter attempted to use ERPs as a method of measuring maintenance processing in a dual-task paradigm. By doing so, I aimed to determine whether or not perceptual selection of target and nontarget probes created significant interference with concurrent memory rehearsal. Unfortunately, the established measure of maintenance (the CDA) was not observed in this experiment. Although it is clear that participants were successful at retaining the memory items for a short period, the lack of a CDA makes it difficult to conclude that simultaneous perceptual processing directly impacted maintenance. The results do, however, show evidence of a strategic selection mechanism. Rather than interrupting rehearsal to attend to all new, incoming information, we see that the processing of perceptual probes only occurred in instances where the probe required cognitive discrimination. These findings, along with those of Chapter II, lend support to a unitary model that is equipped with a selection mechanism capable of performing top-down control when necessary.

Future studies could be designed to better elicit the CDA by using set sizes that require selective maintenance. Additionally, future research could utilize probe conditions which readily process into long-term memory, as shown in Carlisle et al (2011). Incorporating these controls could help to draw out a CDA if one were forthcoming, and would help to better evaluate the precise interplay between mechanisms (or lack thereof) shown in the results of this experiment.

## Chapter IV

## EXPERIMENT 3: DO OBJECT AND LOCATION REPRESENTATIONS SHARE THE SAME MAINTENANCE MECHANISM?

The next chapter will take a closer look at the proposed spatial rehearsal mechanism and examine if it has the ability to maintain both location and object information. Chapters II and III explored the role of spatial selection on visual representations. In both experiments, memory arrays consisted of only colored squares. In Chapter II, I found that perceptual selection was observed when specific locations were probed during retention. However, Chapter III demonstrated that working memory maintenance occurs even when electrophysiological markers are not measured. The previous experiments have shown mixed evidence regarding whether or not spatial attention supports non-spatial representations. Spatial representations are generally defined by location(s) or movement sequences in visual space while non-spatial representations refer to information such as objects and/or an object's features (i.e., color and shape). Both experiments also suggest that the visual selection mechanism has an inherent spatial characteristic. In this chapter, I will determine if spatial attention deployed for object maintenance is similar to that used to maintain spatial location.

### Object versus Spatial Maintenance

Behavioral dual-task paradigms show evidence that working memory mechanisms can be separated by specializing in either object information or spatial information (Baddeley & Lieberman, 1980; Baddeley & Logie, 1999; Logie, 1995; Logie &

Marchetti, 1991). In these studies, participants were required to remember a sequence of movements or spaces in a matrix while concurrently performing a physical spatial task (finger tapping or moving their arms in a directed pattern). They have found that additional movement in the secondary task led to accuracy impairment in the spatial memory task. However, when participants were remembering object features rather than spatial locations, performance in the memory task remained intact. To account for this discrepancy, Logie (Baddeley & Logie, 1999; Logie, 1995) argued that object representations are stored in a visual cache while spatial components rely on the inner scribe for rehearsal. The inner scribe is described as a spatial rehearsal mechanism that maintains spatial information (location or movements) by retracing those original representations. Meanwhile, object information is stored in a visual cache. How these representations are maintained over time is unclear. Although the dissociation between object and spatial information is generally accepted, the nature of the selection mechanisms used to activate and maintain them is still under debate.

One neuroanatomical hypothesis suggests that object and spatial working memory functions are segregated in dorsal and ventral pathways, much like in perception (Goldman-Rakic, 1996; Jonides & Smith, 1997; Ungerleider, Courtney, & Haxby, 1998). During their study of the cerebral cortex of macaque monkeys, Ungerleider and Mishkin (1982) found that lesions of the parietal cortex impaired performance on a spatial task, leaving the ability to recognize other features of task-relevant objects unimpaired. Lesions in the temporal cortex impaired performance on an object discrimination task but left spatial memory unimpaired. They proposed that there were two visual streams. The dorsal-ventral hypothesis states that visual processing is split into the dorsal stream, which is responsible for “where” information and the ventral stream, which is responsible for “what” information (Goldman-Rakic, 1995; Goodale & Milner, 1992).

A divergence between spatial and object working memory maintenance is also observed within the frontal cortex (Wilson, O' Scalaidhe, & Goldman-Rakic, 1993). The prefrontal cortex is involved in selecting and maintaining task-relevant representations. (Rainer, Asaad, & Miller, 1998b) demonstrated how delayed neural activity in this area conveyed information about the visual stimuli. Their data implied that the prefrontal cortex is structurally designed to maintain spatial and object visual information as two separate components while at the same time allowing for some regional overlap (Courtney, Ungerleider, Keil, & Haxby, 1996). Spatial working memory cells have been located in the dorsolateral prefrontal cortex (DLPFC) and in the right premotor cortex. Both the parietal and prefrontal cortices have been identified as regions necessary to maintain spatial locations (Chafee & Goldman-Rakic, 1998). The ventral stream also shares the DLPFC when processing object information (Rainer, et al., 1998a). However, unlike spatial working memory, which uses the DLPFC for rehearsal, the ventral stream may be used for object storage (argued to be the visual cache) (Wilson et al., 1993). Object memory cells have also been located within the ventral prefrontal cortex (Courtney & Ungerleider, 1997; D'Esposito et al., 1998). Based on the findings from these neurological studies, it would appear that working memory maintenance is not isolated to one area of the brain. Instead, this type of cognitive processing occurs in a distributed network of neural regions that ranges from early visual cortex all the way up to the prefrontal cortex.

The multi-component model splits the spatial and object-based mechanisms of visual working memory, so it is able to account for existing evidence suggesting that storing spatial representations differs qualitatively from storing object representations. Data from patient studies also supports this hypothesis of a split visual stream. In their study, Farah and colleagues (Farah, Hammond, Levine, & Calvanio, 1988) studied a patient with brain damage to the ventral stream (including the inferotemporal cortex). The patient in this study displayed impaired performance during object memory tasks but had normal performance on spatial working memory tasks. This type of dissociation among patient studies further supports the findings from dual-task behavioral studies looking at object and spatial working memory differences.

## Eye Movements and Spatial Attention

Previous studies have shown that eye movements (saccades) are typically considered overt and quantifiable measures of attentional shifts (Posner, 1980). The use of saccades to navigate our surroundings has been consistently measured with complex scenes and in long-term memory (Henderson & Hollingworth, 2003; Hollingworth & Henderson, 2002; Richardson & Spivey, 2000; Spivey & Geng, 2001). Spivey and Geng (2001) found that observers spontaneously moved their eyes to spatial locations that held information relevant to the memory task. In their experiment, participants listened to stories with descriptions of directions. During retention, saccades were recorded moving to locations of the visual field that corresponded with the directional information form the story. This same pattern was also observed when participants were instructed to maintain semantic and imagery information (Richardson & Spivey, 2000).

Recent research has also shown that observers make saccades to blank locations during retention intervals of working memory tasks even though the stimuli is no longer present. These eye movements and re-fixations are argued to represent the rehearsal and refreshing of object information held in working memory (Brockmole & Irwin, 2005; Williams, Pouget, Boucher, & Woodman, in press; Zelinsky, Loschky, & Dickinson, 2011). Williams et al (in press) found that object representations in visual working memory rely on spatial selection for successful maintenance over time. In a series of eye-tracking experiments, they observed that participants intentionally moved their eyes during the retention intervals of a change-detection task to the prior locations of remembered items when not required to fixate throughout each trial. The freedom to make such eye movements resulted in superior change-detection performance relative to conditions where fixation was required during each trial. Moreover, when observers fixated on the locations of specific items during the retention interval, they were more accurate at detecting a change of those items than if they had not been fixated. By measuring the overt deployment of attention during visual working memory maintenance, we found that spatial selection of an object's location increased the fidelity of that representation. Though this study showed enhanced working memory performance following eye movements in maintenance, other studies suggest that certain eye movements may actually interfere with previously stored representations, especially if those representations are spatial in nature. In these studies, irrelevant eye movements were detrimental to memory for spatial representations (Baddeley, 1986; Postle, et al., 2006; Smyth, 1996; Smyth & Scholey, 1994). One explanation of these findings is that irrelevant eye movements create unnecessary spatial information that interferes with the maintenance of spatial representations. When eye movements are strategically made to previous object locations, the selection of these locations appears to benefit the maintenance of objects.

The current experiment aims to test if the overt spatial selection mechanism (saccades) observed during object maintenance is also implemented the same way when maintaining spatial representations. To examine this hypothesis, participants engaged in a working memory task. Participants were free to move their eyes voluntarily during the blank retention interval. I wanted to determine if the same benefit that was seen in Williams et al (in press) for object information would also be observed for spatial location information.

Based on the literature above, I expected one of three possible outcomes. The first two predictions come out of the multi-component model in that differences between memory features are expected given the distinction of the different visual mechanisms. In other words, participants would make more eye movements for one condition than the other. If participants make significantly less saccades in the location condition, it is potentially to avoid conflicting spatial rehearsal mechanisms with concurrently stored spatial representations. Instead we would observe a greater benefit for color information if the inner scribe were more important for object memory (consistent with Williams et al). The second possibility is that more eye movements are made for memory for locations. This would also make sense given the direct mapping between overt spatial selection and memory for locations. The third prediction is that participants would make the same number of eye movements in both conditions. This outcome is expected under a unitary model since it does not fractionize visual working memory into separate subsystems. Under the unified premise, saccades to object location would boost working memory performance when maintaining both spatial and object information. Unlike previous studies, participants in the current task were not directed to engage in a secondary task during retention, so any saccades made during maintenance were presumably to help with memory for the primary change-detection task.

## Method

### *Participants*

Thirty volunteers between the ages of 18 and 30 were recruited from the Vanderbilt University community. Participants were compensated monetarily or with course credit. Each provided informed consent and reported having normal or corrected-to-normal vision and no colorblindness. Two participants were unable to complete both conditions of the task and one participant's data was excluded due a number of unrecorded responses. This resulted in a total of 27 participants.

### *Stimuli*

The stimuli consisted of solid colored squares (each 0.8° X 0.8° of field of vision) presented on a gray background (155, 155, 155) and centered approximately 7.5° from fixation (a black plus sign, 0.3° X 0.3°) with a minimum inter-item spacing of 3.5°. Stimuli were randomly placed along the virtual annuli surrounding the center fixation. In the *color* condition, the color of each square was randomly selected with replacement from a set of 7 colors using: red (255, 0, 0), green (0, 255, 0), blue (0, 0, 255), yellow (255, 255, 0), black (0, 0, 0), magenta (255, 0, 255), and cyan (0, 255, 255). In the *location* condition, only black squares were used in the memory array. The position of each square was randomly selected from a set of 12 locations. On each trial, 1, 3, or 6 squares were presented in the memory and test arrays. The articulatory-suppression stimuli were two black numbers (1° X 0.5°) randomly selected from digits 1 to 9, without replacement centered, 1° above fixation. An example trial is illustrated in Figure 7.

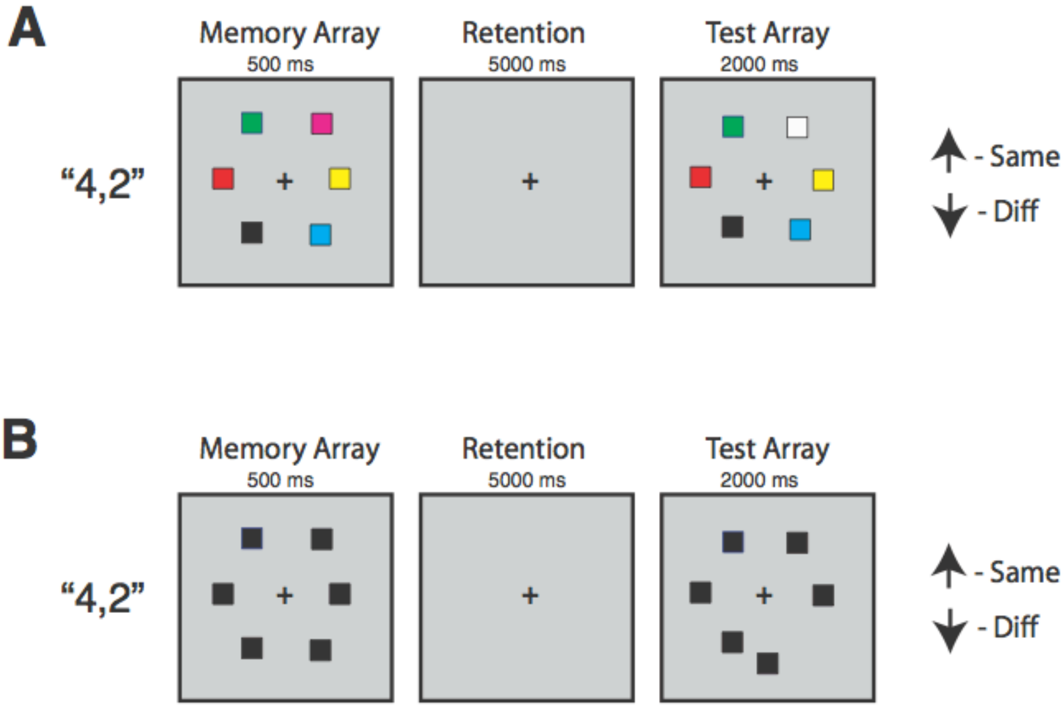

*Figure 7.* Stimuli used in Experiment 3. A: An example trial from the color condition B: An example trial from the location condition.

*Procedure*

Prior to starting the experiment, participants were fitted with head-mounted eye-tracking cameras and given the instructions for the condition they would perform during that session. Participants engaged in a change-detection task where they were instructed to remember the colors of squares or the location of squares. Once the eye-tracking cameras were calibrated and drift correction performed, each trial began with the articulatory-suppression task (repeating approximately 3-4 numbers per second) as soon as the numbers appeared. The memory task began with an array consisting of 1, 3, or 6 squares presented for 500-ms followed by a 5,000-ms blank retention interval; then finally a 2,000-ms test array. At test, participants indicated whether or not they saw a change in the array (depending on the condition either a new color square or a differently located square). Half of the trials remained the same, half contained a change. Conditions were counterbalanced across participants with all participants performing in each condition. Participants made all responses using two keys on the directional pad of a computer keyboard. The up arrow indicated “same” and the down arrow indicated “different”.

### *Eye-tracking Recording*

Eye movements were measured using an EyeLink II infrared eye tracker (SR Research; Ontario, Canada) with eye position sampled at a rate of 250 Hz.  We used a velocity criterion algorithm to automatically detect saccades (35°/sec) created by SR Research to be used with the EyeLink II tracker.

## **Results and Discussion**

Change-detection accuracy for the two conditions is shown in Figure 8. Overall participants performed better in the location condition (89.3%) than in the color condition (83.8%). Participants also had 20% higher accuracy at set size 6 in the location condition compared to the color condition. In sum, these results appear to support the multi-component model since performance is better in the location condition than the color condition suggesting that there is a benefit of using eye movements as a rehearsal mechanism for spatial information.

A 2 x 3 within-subjects ANOVA yielded a significant main effect of condition, $F(1,26) = 22.13$, $p < 0.01$, due to higher accuracy in the location condition, a significant main effect of set size, $F(1,26) = 82.88$, $p < 0.01$, due to differences at set size 6, and a significant interaction of these factors, $F(2,52) = 57.19$, $p < 0.01$, due to lowered performance at set size 6 in the color condition (see Figure 8B). Memory performance in the color condition decreased as set size increased ($F(1,26) = 9.16$, $p < 0.01$ from set size 1 to 3 and $F(1,26) = 103.97$, $p < 0.01$ from set size 3 to 6). In the location condition, accuracy decreased as set size increased from 1 to 3 ($F(1,26) = 7.53$, $p < 0.05$) but not from 3 to 6, $F(1,26) = 1.94$, $p = 0.18$. Mean reaction time for the color condition was 991.9-ms and 960.14-ms in the location condition. The differences in these times were not statistically significant, $F(1,26) = 1.46$, $p = 0.23$.

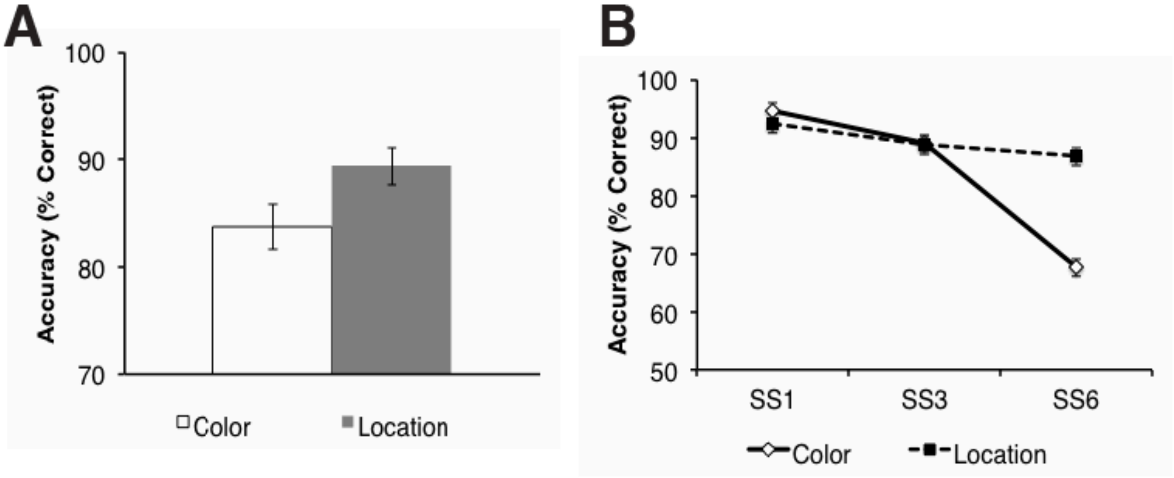

*Figure 8.* Change-detection performance for Experiment 3. A: Mean accuracies for each condition. B: Mean accuracies as a function of condition and set size. Error bars show 95% within-subjects confidence intervals.

For the eye-tracking data, I only focused on saccades made during the 5,000-ms retention interval. Table 1 shows the different measures obtained from this period. Objects were defined as the 2° window around locations of previously presented stimulus. Unspecified locations were areas of the screen outside of the 2° object window; this could include the fixation cross, spaces between objects, and saccades made outside of the computer monitor. As predicted by the unitary model, the total number of saccades did not significantly differ between the two conditions, $F(1,26) = 0.0006$, $p = 0.98$. However, in line with the multi-component model, participants made more saccades to previous item locations when they were remembering spatial information (37.4%) than when they were remembering color information (33.4%), $F(1,26) = 6.29$, $p < 0.05$.

**Table 1**

*Eye-tracking metrics measured during the 5,000-ms retention interval of Experiment 3.*

| | Average Number of Total Saccades | Average Number of Saccades to Object Locations | Average Number of Saccades to Unspecified Locations |
|---|---|---|---|
| Color | 546.22 (±209.3) | 182.41 (±91.37) | 363.81 (±132.77) |
| Location | 544.66 (±200.33) | 203.85 (±95.71) | 340.81 (±122.45) |

*Note*. Values in enclosed in parentheses represent 95% confidence intervals of the mean.

## General Discussion

The findings of the current experiment suggest that spatial attention can be strategically deployed to maintain spatial representations. Across both conditions, participants made approximately the same number of saccades during the blank retention interval. We know from previous studies that free eye movements result in better change-detection performance compared to forced fixation (Williams, et al., in press). However, the use of eye movements appears to be more effective depending on the type of information being held in memory. Using overt attention to re-fixate item locations appears to be an implicit strategy used by observers, with this guidance of attention being most beneficial for remembering spatial representations. Unlike other studies, which have found interference from eye movements during a spatial memory task, this experiment reveals that when spatial attention is purposely directed to task-relevant locations, working memory maintenance is actually aided. Moreover, eye movements appear to provide a greater advantage for location memory even beyond normal capacity limits. As set size increased from 1 to 3 and from 3 to 6 in the color condition, participants' memory performance significantly decreased, whereas in the location condition, the decrement from set size 3 to 6 was non-significant.

Theoretically, the idea of a spatial selection mechanism used to maintain both object and spatial information fits within the conceptual framework of both models. In a unitary model, a single selection mechanism is proposed to activate items held within memory. Cowan describes the focus of attention as having the ability to work within all domains of memory. Overt attention, or in this case, eye movements, help to index spatial and object representations held within activated memory (Cowan, 2008). Another interpretation of these findings would be provided by the multi-component's theory of separate buffers and separate rehearsal mechanisms. Although Logie's (1995) description of the inner scribe indicates that it is responsible for retracing spatial representations, it is possible that visual working memory shares this mechanism across visual buffers. Object representations are held in a visual cache, which is purportedly a passive storage system. One way to explain how we actively maintain object features is to assume that spatial attention is also used to rehearse these representations. While location information receives the benefit of reactivation via tracing, object representations may receive enhancement by boosting the maintenance activity of neurons that have coded for both the location and color information of the item.

## Conclusion of Chapter IV

In summary, this chapter used eye movements as a measure of spatial attention to determine if maintenance mechanisms differed based on the type of information being rehearsed. Previous studies measuring spatial attention during a working memory task have typically found interference from distracting physical movements as well as task-irrelevant saccades. Here there is evidence to suggest that spatial attention, when purposely directed to relevant spatial locations, can be used as a maintenance tool for both object and location information. The role of spatial attention as a shared resource can also be reconciled within both of the primary models of working memory. These results provide empirical evidence to support the theoretical implication of a multi-purpose maintenance mechanism.

Chapter V

# GENERAL DISCUSSION

## Summary of Results

The goal of this dissertation was to examine the interaction between the mechanism of visual selection in perception and maintenance within working memory. Chapter I discussed the importance of using attentional selection in both of these cognitive processes. This section also described the two dominant models of working memory, focusing on the differences in the conceptualization of how visual selection and working memory maintenance interact. To address the question of whether selection was a singular mechanism or multiple mechanisms, I conducted three experiments. The experiment presented in Chapter II found that probes during a retention interval elicited perceptual indices of selection. The results of my experiment in Chapter III further demonstrated that the selection and processing of perceptual probes during retention impacted the concurrent maintenance of objects within working memory. Finally, Chapter IV's experiment examined the role of maintenance selection with regard to representation characteristics. The current chapter will summarize the importance between the experiments and attempt to synthesize the findings in order to deepen our understanding of perceptual and working memory selection.

In Chapter II, ERPs were used to determine the timing of perceptual selection within working memory maintenance. Participants were instructed to remember colored squares for a short period of time. During the retention interval, task-irrelevant white squares would sometimes appear in task-relevant locations. The critical finding from this design was that even though the probes were task-irrelevant their appearance interfered with attentional selection. In other words, if a participant was attending to a spatially relevant location when a probe appeared, the perceptual input from the probe led to a series of cognitive events to adapt. First, there was enhanced processing for the probe (since attention was already focused at its location prior to the probe's appearance) followed by immediate suppression. The suppression following target-located probes suggests that participants attempted to rid their minds of the new information since selecting the probe would not benefit performance in the memory task, and further suggests that the new information made maintenance of the task-relevant information more difficult. When probes appeared in a nontarget location, the opposite pattern of waveforms was observed. There was decreased amplitude in selective components suggesting that attention was not initially present in that location. Finally, there was a distinct shift in attention back to the task-relevant hemifield. This activity is consistent with the proposal of a singular selection mechanism. The focus of attention, as described by unitary models, is responsible for processing perceptual input as well as maintaining representations in the memory store. In this experiment, the focus of attention would already be centered on the location of the previously presented items, thus, the appearance of a new stimulus in that location would cause the selection mechanism to enhance its processing. When neutral probes occurred, the focus of attention was able to process the input, but enhancement of that information was not needed. If there were separate selection mechanisms for perception and maintenance, as suggested by the multi-component model, perceptual selection of the irrelevant probes should have displayed the same electrophysiological activity across all probes. A maintenance mechanism would be focused on rehearsing the squares being stored in working memory while the perceptual mechanism would have been free to attend to any new stimulus equally, regardless of location. The fact that shifts of attention are also observed following the intrusion when probes were displayed in task-irrelevant locations reveals that attention must move back and forth between perceptual selection and maintenance.

The experiment presented in Chapter III also used ERPs in an attempt to measure maintenance activity during a dual-task paradigm. Participants were instructed to remember colored squares for a change-detection task, in addition to responding to target probes in a secondary perception task. Unfortunately, the expected marker of working memory maintenance was not observed during the experiment. Despite the lack of a CDA, the findings from this experiment still provided evidence in favor of a unitary selection mechanism. Under a unitary model, attentional selection would be required to temporarily stop maintaining the memory array items in order to perceive the probe. Arguably, after multiple trials, the probe eventually became a long-term memory representation. If this were the case, the focus of attention would still have to cease maintenance to access the secondary task instructions within long-term memory. In both situations, the focus of attention would eventually return to the encoded items to continue maintenance. This experiment also found that the secondary task of responding to the probe elicited the P3, an ERP component reflective of working memory updating. The observed P3 marks the return of the selection mechanism to the stored items either from perceptual selection of the probe or from the probe's long-term memory template. Under a multi-component theory, the central executive would oversee the secondary perceptual task, leaving the visual buffers free to maintain the items from the memory array. Since the probes should not need to be stored in a working memory subsystem, there would not be a need for maintenance to stop with a subsequent P3 component indicating updating following the probes appearance. Together, Chapter II and III provide strong evidence for a solitary selection mechanism which processes both perceptual selection and maintenance selection in visual tasks.

Chapter IV, the final experiment, took a closer look at the maintenance mechanism of working memory. There are many types of representations which can be encoded and stored in memory. The differences in these representations can determine how they are processed and also maintained. Using eye-tracking devices to measure overt attention, this experiment revealed similar maintenance strategies for object and spatial information. Elaborating on previous research (Williams, et al., in press) which found that eye movements aids the maintenance of objects in working memory, here I found that location information also benefits from strategic and task-relevant saccades. Importantly, eye movements were actually more valuable for the rehearsal of spatial locations than object features. These results, depending on their interpretation, could fit into both working memory models. Within a unitary model, one mechanism would be used to maintain both object and location representations. This would explain the similar number of eye movements seen in both the color condition and the location condition. In terms of the multi-component model, the eye movements observed fit the theoretical description of the inner scribe. The inner scribe acts as the rehearsal mechanism for spatial information in working memory; it maintains location information by retracing the target representations. Although the model does not explicitly state it, these findings suggest that the inner scribe may also assist in rehearsing object information held within the visual cache. A deficit of the multi-component theory is that it fails to explain *how* color information is rehearsed. While eye movements do not necessarily recreate the original color percept, they do reactivate the representations' locations which may in turn create sustained neural activity for those objects even if the explicit rehearsal mechanism is specific to spatial information.

## Redeeming the Multi-Component Model

Although the results found in this dissertation primarily support a unitary model of working memory, completely discarding the multi-component theory would be premature. The defining characteristic of the multi-component theory is that it asserts that working memory contains multiple mechanisms specific to each subsystem. These mechanisms, specifically the inner speech and inner scribe, work independently of central executive functions. This conceptualization of the memory system implies that each level can function in parallel without interference with one another. Essentially, the central executive can interact with perceptual input without needing to concurrently manage maintenance in the visual cache or phonological store. The findings of this study suggest otherwise. Rather than observing the pure processing of perceptual selection and maintenance, I found that attentional mechanisms vacillate between the two cognitive demands. Thus, selection of perceptual stimuli and maintenance of encoded information are serially processed. To fit a multi-component theory to these findings we must rethink the independence of the subsystems and the central executive. If we accept that the central executive has the ability to override concurrent rehearsal activity then this would explain the intrusion seen when perceptual probes are introduced. Visual maintenance may still occur in the visuo-spatial sketchpad, however, when information enters the working memory system, the central executive interrupts all ongoing processes to attend to the new input despite these processes potentially occurring within different subsystems.

An alternative explanation for these findings is that the experimental techniques used here are incapable of accurately measuring these rapid and overlapping cognitive processes in the way that is needed. While electrophysiology provides very fine temporal resolution allowing for cognition to be measured in milliseconds, it does not account for spatial properties. Perception and working memory are two processes with substantial overlap, and in this study I have tried to isolate the different mechanisms. A major assumption I have made is that specific ERPs, such as the P1N1 and CDA, are strict indices of specific processes. I have labeled P1N1 as a marker of perception and CDA as a measure of maintenance without accounting for the possibility that these components are not as process pure as the literature suggests. If selection for perceptual input and maintained items occurs within close neural proximity to one another, this activity could very well be picked up by the combined electrophysiology. In other words, the CDA could also include some amount of perceptual processing. If the applied techniques were not precise enough to separate out two types of visual attention, the results of my experiments in Chapters II and III are not necessarily incongruous with a multi-component view of separate mechanisms.

## Modifying the Models

The empirical evidence provided by this dissertation makes it clear that visual selection is more complicated than is described by either of the two models. The findings suggest that the current models are incomplete and need to be updated. Unitary models must consider the consequences of relying on one mechanism to perform two tasks. A singular attentional mechanism is bound to encounter instances when selection becomes overwhelmed or reaches maximum capacity. As such, it would then fail to perform both perceptual selection and maintenance efficiently. Furthermore, this model fails to account for differences in the type of information entering the memory system. One way that unified theorists have attempted to remedy this dual-processing problem is to introduce the idea of a multi-faceted selection mechanism. Originating from verbal studies of working memory, Cowan (1988) proposed that maintenance was made up of two types of components: covert rehearsal and an attentional refreshing mechanism. Since then, several researchers have applied this understanding to explain why some visual working memory tasks require attention while some do not (Barrouillet, Bernardin, & Camos, 2004; Portrat, Barrouillet, & Camos, 2008; Ricker & Cowan, 2010). However, the exact purpose of an attentional refresher versus a covert rehearsal mechanism is still not understood.

Conversely, for a multi-component theory to account for the present results, further explanation of how memory systems communicate is needed. If executive functions and subsystem mechanisms do not work in parallel with another, then what happens when two processes must co-occur? As was seen in these experiments, selection from the executive may have dominated the subsystem’s maintenance. While performance for the task remained mostly intact, one must wonder what would happen if rehearsal for the representations were of utmost importance. One issue that theorists of the multi-component model have tried to tackle over the years is whether or not the central executive has storage capabilities separate from the subsystem buffers (Baddeley, 1986; Baddeley & Hitch, 1974; Baddeley & Logie, 1999). If executive processes do demand storage in working memory, then would this process take place in a general workplace or within the subsystem buffers? Most recently, Baddeley and colleagues have addressed this question by assigning the episodic buffer as the locale for central executive storage (Baddeley, 2011; Repovs & Baddeley, 2006). The use of the episodic buffer for executive storage would allow the central executive to continue working independently of the buffer systems, however, this addition is particularly controversial given the findings from Chapter III. If central executive process relied on subsystem storage to engage in the perceptual task, then the multi-component model would be better equipped to explain the interruption that is observed following a perceptual probe.

## Implications

From a theoretical standpoint, the current study advances our academic understanding of attentional selection and working memory maintenance. However, understanding these cognitive mechanisms also have for real-world implications. The cognitive mechanisms discussed here play a crucial role in how we process everyday visual information.  If visual selection behaves differently at the various stages of visual working memory, or for different types of visual information, this could explain some of the limitations and deficits we see between individuals and in patients (Barch et al., 2001;

Driesen et al., 2008; Sobel, Gerrie, Poole, & Kane, 2007; Vogel & Machizawa, 2004; Vogel, et al., 2005). If the multi-component theory is correct, problems or deficiencies in perceptual selection may require different approaches than those in maintenance, both in measuring or diagnosing issues and in attempting to treat such issues. Rather than assuming an all-encompassing working memory deficit, we could more reliably narrow down which phase or subsystem of processing is producing the shortfall, and isolate efforts to the appropriate mechanism. If the unitary model is accurate, then there may not be mechanical differences in addressing issues with perceptual selection and maintenance, however understanding the unitary nature of the mechanism may assist in developing ways to address these issues. A more detailed understanding of the interplay between (or within) mechanisms could also lead to a better understanding of the neurophysiological underpinnings of these mechanisms. The neural mechanisms of one system make up just a small part of the larger network; by taking the time to explore each piece at its most basic level, we can hope to eventually understand more areas of the brain and essentially the mind as a whole.

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