INFLUENCE OF TASK AND STRATEGY ON THE NEURAL AND BEHAVIORAL CORRELATES OF THE FOCUS OF ATTENTION

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ABSTRACT

Working memory (WM) is oft described as a mental workspace where information can be maintained and manipulated in the service of ongoing cognition. Theoretical accounts describe the focus of attention as a state within working memory where a limited number of items can be briefly maintained in a heightened status of awareness. Ongoing debate and conflicting empirical evidence surrounds the capacity and characteristics of the focus of attention. Substantial recency effects are reported in a group of WM studies, and these recency effects are interpreted as a marker of the focus of attention (e.g., Nee & Jonides, 2008; Oztekin, Davachi, & McElree, 2010). The present work considers whether these findings are specific to parameters of these particular studies or whether they generalize across a broader range of tasks.

An initial behavioral experiment tested performance across two tasks (judgment of recency and judgment of primacy), two information types (verbal and spatial), and two self-reported strategies (maintenance-based and retrieval-based). Central analyses averaged trials by the serial position of the correct item, and compared the accuracy and speed of retrieval of trials in different serial positions. Results showed evidence of both recency effects and primacy effects in all four types of task (verbal judgment of recency, verbal judgment of primacy, spatial judgment of recency, and spatial judgment of primacy). Moreover, a significant task by effect-type interaction showed that the size of recency and primacy effects shifted with the demands of the task (e.g., larger recency effects in judgment of recency than in judgment of primacy). Some similarities and some differences were found between verbal and spatial domains, while no differences were found across self-reported strategy.

A subsequent fMRI experiment examined the neural correlates of verbal judgment of recency and primacy. Again, behavioral results showed a task by effect-type interaction where
there was a larger recency effect in judgment of recency and a larger primacy effect in judgment of primacy. FMRI results showed no distinct correlates of a recency effect. In other words, contrasts comparing fMRI signal during retrieval of recency item trials and middle item trials did not reveal above threshold clusters of activation. In contrast, neural correlates of primacy were found in frontal lobe brain regions (BA 4, 6, 32) associated with active maintenance of information. Moreover, the precise neural correlates of primacy were task-specific. In sum, two experiments demonstrate that the behavioral and neural signatures of WM, specifically related to primacy and recency effects, are dependent on task-demands. Accounts of the architecture of WM should address these observations, which inform how competing claims are supported across studies of WM.
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CHAPTER 1

INTRODUCTION

Working memory (WM) is a central construct in cognitive neuroscience because it plays a critical role in a broad range of cognitive capabilities. Multiple accounts of WM describe this construct as a mental workspace where a limited amount of information can be stored and manipulated (Barrouillet, Bernardin, & Camos, 2004; Cowan, 2001; Oberauer, 2002). This mental workspace utilizes several component processes such as the focus of attention, short-term storage, retrieval from long-term memory, phonological rehearsal, and interference buffering. During testing of WM, these component processes may be differentially indexed depending on the details of the assessment task. If so, performance could differ according to the method used to test WM, and, across testing methodologies, conclusions about the characteristics of WM could vary. In an effort to inform ongoing debates in the WM literature, the present work compares WM performance across changes in testing methodologies.

Working memory is taxed frequently during daily life, and an extensive individual differences literature establishes the role of WM in cognition. WM performance correlates with performance on a wide array of tasks, and WM capacity is predictive of performance on measures of fluid intelligence (Engle, Tuholski, Laughlin, & Conway, 1999), reading comprehension (Daneman & Carpenter, 1980), language acquisition (Baddeley, 2003), nonverbal problem solving (Logie, Gilhooly, & Wynn, 1994), and verbal and spatial reasoning (Kane et al., 2004). A meta-analysis of 10 published studies and over 3,100 subjects estimates that WM capacity accounts for over half of the variance in fluid intelligence in healthy, young adults (Kane, Hambrick, & Conway, 2005). Moreover, fluid intelligence and WM are linked, through both structural and functional evidence, to a network of regions in the frontal and
parietal lobes including areas of the left parietal lobe and bilateral prefrontal cortexes (Burgess, Gray, Conway, & Braver, 2011; Colom, Jung, & Haier, 2007; Gray, Chabris, & Braver, 2003; Jung & Haier, 2007).

As a central psychological construct investigations of WM are of clear importance to an overall theoretical account of the human mind. Also, knowledge of the structure and function of WM can be usefully applied toward development of educational tools and clinical interventions aimed at optimizing the use of WM or expanding the size of WM capacity. Yet, some very basic questions about the architecture and capacity of WM are still consistently contested between theoretical models.

For example, the fundamental question of whether working memory and long-term memory are contained in different memory stores remains a topic of debate (Jonides et al., 2008; Nee & Jonides, 2008). At present, there is empirical support for both multistore and unitary store models of memory. Multistore models depict WM as a temporary workspace that is separate from long-term memory (Baddeley & Hitch, 1974; Moscovitch, 1992) while unitary store models suggest that all information resides in, and must be retrieved from, a single memory system regardless of the duration over which it is to be maintained (Crowder, 1993; Nairne, 2002; Sederberg, Howard, & Kahana, 2008). In unitary store models, WM and long-term memory are not viewed as separated systems, but rather, WM is conceived as an activated subset of the information in a single memory store (Cowan, 1999; Jonides, et al., 2008; McElree, 2006; Oberauer, 2002). So, although these models assume one memory store, they also assume that information in memory can exist in multiple memory states that differ in their level of accessibility to an individual. A matter of debate within this class of models, and a central focus in the present work, is the differentiation of alternative states within “WM”. Recent accounts
converge on the assumption of a “focus of attention” as the most immediate state of WM where a certain number of items can be maintained in a heightened state of awareness without a need for retrieval from longer-term memory states (Cowan, 1999; McElree, 2006; Oberauer, 2002). Accounts differ in their delineation of the focus of attention, short-term memory, and activated long-term memory as separate states and also in their assumptions about the capacity of the focus of attention (Figure 1).

The primary goal of the present work is not to empirically test any single theoretical account of the structure of human memory, but instead, to consider why evidence may at different times appear to support conflicting accounts. How is it that some evidence supports the notion of a roughly 4-item focus of attention (Cowan, 2001) while other evidence supports a single-item focus of attention (McElree, 2006)? A possible answer, which is pursued in the present work, is that specific aspects of different memory tasks influence the neural and behavioral signatures of WM as well as the measured properties of the focus of attention.

A variety of memory tasks are used to assess the focus of attention, and these tasks vary on several important dimensions such as the type of information presented (e.g., letters, spatial locations), the type of retrieval that is demanded (e.g., recognition, a judgment about the order of items), and the individual subject-strategies that they encourage (e.g., phonological rehearsal or reliance on familiarity). If these factors influence WM performance, the use of different memory tasks might yield different conclusions about the structure and qualities of WM. For example, one task might require several items to reside in a heightened state of activation (i.e., the focus of attention), while optimal performance in another task may be achieved with only a single item in this heightened state.
The possibility that task-demand and strategy influence the measurement of the focus of attention is pursued here through experimental manipulations conducted within a methodological approach that has become prevalent in the recent literature. The relevant group of prior studies have compared retrieval of items presented in different serial positions in a list (Nee & Jonides, 2008, 2011; Oztekin, Davachi, & McElree, 2010; Oztekin, McElree, Staresina, & Davachi, 2009; Talmi, Grady, Goshen-Gottstein, & Moscovitch, 2005). Differences in the characteristics of retrieval of different items are hypothesized to reflect differences in the memory or attentional state of the items (McElree, 2006). Multiple studies converge to demonstrate distinct neural characteristics and faster reaction times during retrieval of the final item of a list compared to other items (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010; Oztekin, et al., 2009). This retrieval advantage is often interpreted as evidence for a single item focus of attention (see Oztekin et al., 2010).

While this evidence is compelling, I have serious concerns about the extent to which these results may be influenced by task-demands and strategies. Specifically, three conclusions drawn from this prior work warrant further scrutiny: 1) that the large retrieval advantage for the final position (i.e., the recency effect) is observable across different types of memory tasks and strategies and not an artifact of task construction and experimental constraints, 2) that this retrieval advantage is in fact indicative of the focus of attention, and 3) that recency effects are observed without consideration of primacy effects (retrieval advantages for the earliest item(s)). While primacy effects are often present in examinations of WM, they are not integrated into models of the structure of WM. These three statements are carefully examined through parallel behavioral and neuroimaging experiments that test performance as a function of serial position across different WM tasks and subject strategies.
Three Competing Accounts of WM

WM is certainly an evolving construct (see D'Esposito, 2007), yet it is generally agreed upon as a cognitive system where a limited amount of information can be maintained and manipulated. Over the last several decades, a variety of theories have been advanced in the attempt to describe the structure and capacity of WM (Jonides, et al., 2008; Miyake & Shah, 1999). Importantly, the theoretical landscape of WM includes a large number of theories and support for these theories with a very wide range of research methodologies (behavioral, neuroimaging, lesion studies, computer modeling). The complex and expansive theoretical landscape itself is a key motivation for the present work, which aims to inform how competing accounts can be supported through empirical evidence.

Before delving into specific theories, brief attention to terminology is useful. Use of the terms WM and short-term memory vary substantially in the literature. At times the terms are used interchangeably, and at other times short-term memory is considered memory storage only, while WM also encompasses manipulation or processing of information. The literature that motivates the present work adopts the term WM as a broad term for short-term memory applied to cognitive tasks, and here, I use the term WM in this inclusive fashion.

Three specific accounts of WM are detailed here, McElree’s single item focus of attention (McElree, 2006; McElree & Dosher, 1989, 1993), Cowan’s multiple item focus of attention (Cowan, 1995, 1999, 2001), and Oberauer’s three level model of memory (Oberauer, 2002; Oberauer & Lange, 2009). These accounts were selected because they make specific predictions about the structure and capacity of differing memory states within WM. Moreover, in WM studies highlighting recency effects, these models have informed the specific interpretation of the findings (e.g., Oztekin, et al., 2009).
These three accounts vary on two important dimensions: the number of memory/attentional states involved in WM and the number of items that can be maintained in each state (particularly, within the focus of attention). Figure 1 depicts the architecture of memory as delineated by these three accounts.

Figure 1. Three Competing Accounts of the Structure of Working Memory.
FOA = Focus of Attention.

**McElree’s Single Item Focus of Attention.** Several models of WM envision it as a mental workspace where a few items remain in an active state. However, according to McElree (2006), rather than a flexible mental workspace, memory contains a single item focus of attention tied to the most recent item in a list. All items outside of this focus of attention are retrieved via common retrieval processes, and no distinction is drawn between longer and shorter term memories. Regarding the type of information held in the focus of attention, McElree’s work primarily concerns retention of verbal information, and a brief mention of spatial memory argues that verbal and spatial memory involve qualitatively different cognitive operations (McElree, 2006).
Evidence supporting McElree’s perspective comes from a variety of sources. First, in an item recognition task, recognition of items presented in the final serial position of a list is associated with faster reaction times than recognition of other items in the list (McElree & Dosher, 1989, 1993; Oztekin, et al., 2010). Faster reaction times for the item presented in the final serial position has been found in several other memory tasks, including judgment of recency task, paired associate recognition, n-back, and sentence processing (McElree, 2006). In order to examine recency effects on a neural level, McElree and colleagues conducted fMRI studies comparing the retrieval period of trials probing items different serial positions (Oztekin, et al., 2010; Oztekin, et al., 2009). Retrieval of the final item showed weaker activation in areas of the left hippocampus and left inferior frontal gyrus when compared with retrieval of items in other positions (Oztekin, et al., 2010; Oztekin, et al., 2009). As these two brain areas are associated with long-term memory retrieval (Golby et al., 2001; Hermann, Seidenberg, Wyler, & Davies, 1996; Schacter & Wagner, 1999), the authors interpreted their results as evidence that the final item in the memory task need not be retrieved from long-term memory. Instead, this item is said to inhabit the focus of attention.

Support for a single item focus of attention is also obtained using a speed accuracy tradeoff procedure, which involves measurement of retrieval speed through consideration of both reaction times and strength of the memory trace (Dosher, 1979; Reed, 1973; Wickelgren, 1977). In this procedure, subjects are presented with an item recognition trial and cued by a tone to respond at varying intervals following the onset of the retrieval probe (e.g., 100–3000 ms after onset) (e.g., McElree & Dosher, 1993). This approach allows characterization of the probability of accurate retrieval, the time the information first becomes available, and the time it takes for responses to increase from chance to asymptotic accuracy. Results with an item recognition task
demonstrate that the final item shows a distinct pattern, and all earlier items are indistinguishable (i.e., best fit by identical parameters) (McElree & Dosher, 1989). McElree (2006) concludes from these experiments that the final item resides in a focus of attention, and all other items are retrieved via the same mechanisms that underlie retrieval from long-term memory (McElree, 2006).

**Cowan’s Multiple Item Focus of Attention.** According to Cowan, (1995, 1999, 2001) “working memory refers to cognitive processes that retain information in an unusually accessible state suitable for carrying out any task with a mental component” (Cowan, 1999, p 62). In Cowan’s model, the architecture of WM includes an activated subset of long-term memory and a subset of this activated information that is presently in conscious awareness, termed the focus of attention. Here, information enters and is maintained in the focus of attention through automatic processes (e.g., a noticeable event like a loud conversation) or through a deliberate controlled process (e.g., choosing to keep attention on the present task goal). Information is made available (or sustained) as a heightened subset of long-term memory through activation in the focus of attention and/or processes such as phonological rehearsal or visualization of memory items.

The focus of attention described in this model can accommodate 4 +/- 1 items. Cowan (2001) notes that this approximately 4 item limit has been proposed in other models of attention and memory, and for a variety of information types (Broadbent, 1971; Halford, Wilson, & Phillips, 1998; Henderson, 1972; Schneider & Detweiler, 1987). For example, Luck & Vogel (1997) presented subjects with arrays containing a number of colored squares ranging from 1 to 12 squares. Each array was presented for 100 ms each, and after a 900 ms delay, subjects were shown another array and asked whether this array was the same or different. Arrays of 1-3 squares produced near perfect accuracy, there was a decline in performance for arrays of 4
squares, and an even larger decrement for arrays of 5 or more squares. This discontinuity in performance for arrays exceeding 4 squares is interpreted as a marker of the capacity of the focus of attention. Very similar results were yielded using the same procedure and more complex stimuli (i.e., configurations of colored bars) (Luck & Vogel, 1997).

Support for a 4 +/- 1 item focus of attention is also demonstrated using verbal memoranda. Cowan (2001) compiled evidence from 17 studies where subjects were given variants of an immediate serial recall task with monosyllabic words and rehearsal of these items was limited by articulacy suppression (e.g., repeating “the the the” at different stages of the task). Sixteen of the 17 studies provided estimates of capacity limits that were between 3 and 5 items (see Cowan, 2001).

Cowan’s notion of the focus of attention can accommodate items of more than one type at the same instance. For example, a 4 +/- 1 item capacity has been demonstrated in arrays that include both colored squares and spoken digits (Saults & Cowan, 2007). Moreover, a recent imaging study presented subjects with 4 colored squares, 4 spoken digits, or 2 colored squares and 2 spoken digits (Cowan et al., 2011). Over two different experiments, activation in an area of the parietal lobe near the left intraparietal sulcus (BA 40) was found to increase with the memory load of the task. Importantly, activation increased with the number of items regardless of the type of information (verbal, spatial, or a combination). Other recent imaging experiments show overlapping neural activation patterns for retention of verbal and spatial memoranda (Chein, Moore, & Conway, 2011; Majerus et al., 2010). Cowan and others (2011), interpret this imaging evidence as support for a multiple item focus of attention that can accommodate at least two domains of information.
**Oberauer’s Three Level Model.** Oberauer’s model of WM describes three distinct cognitive states: an activated subset of long-term memory, a state of direct access to short-term memory, and a single item focus of attention (Oberauer, 2002; Oberauer & Lange, 2009; Oberauer & Suss, 2000). Like McElree, Oberauer (2002) postulates a single item focus of attention tied to the most recent item in a memory task (e.g., McElree 2006). Oberauer’s model also proposes a multiple item state of short-term memory, which has similar traits to the focus of attention described by Cowan (2001). Only items in short-term memory can enter the focus of attention. According to Oberauer (2002), the capacity of WM as a whole is limited by at least two factors, overwriting between item representations that share features in short-term memory and from the difficulty of selecting a single item from short-term memory to inhabit the focus of attention.

This model is supported through behavioral studies with a WM memory paradigm involving updating and manipulation of items (Oberauer, 2002). Here, subjects remembered a group of numbers in different locations on a grid. For 9 total trials, one value in the grid was updated by performing a mathematic operation (e.g., add 3) and the result of the operation was remembered. Following 9 such cycles of math problems, subjects were asked to recall the final values in the grid (i.e., the product after all 9 math operations). In this procedure, some items were updated and others were not. Oberauer found that correctly updated digits were retrieved significantly faster than others words, and argued that the updated numbers were in a heightened state (short-term memory) while the others numbers were in a less active state (i.e., activated long-term memory). Results also showed a “switch cost”—faster performance when two trials in a row updated the same item than when the second trial required updating of a different item. This switch cost has been interpreted as indicative of the focus of attention, and experiments
probing this switch cost demonstrate an advantage for a single item, or a single chunk of items (Oberauer & Bialkova, 2009).

Two fMRI studies test Oberauer’s three level predictions of the structure of WM (Nee & Jonides, 2011; Oztekin, et al., 2010). Both studies administered verbal item recognition tasks, and compared aspects of recognition of items in different serial positions. Oztekin and others (2010) reported differing activation patterns between retrieval of the most recent item and all other items but not a dissociation in hippocampal activity between items in the outer two levels of Oberauer’s model (but see Cowan, 2011). In contrast, Nee & Jonides (2011) found evidence for this three-tiered model, by demonstrating distinct neural patterns for retrieval of items each of the three levels. These two studies and their implications will be considered in greater detail below.

In sum, at present all three models are supported with empirical evidence. Due to the accumulation of evidence supporting competing claims, and differences in interpretation of the same results, the field is left without a consensus on the structure of WM. How is it that multiple accounts are supported? One possibility, explored here, is that the ability to measure the structure of WM may vary with the specifics of the assessment task. Specifically task-demands could interact with our ability to measure the architecture of WM in a variety of ways. First, different tasks could change the actual structure of information in WM; therefore, one task may require information in two distinct states while another requires information in 3 distinct states. Second, task-demands could change the properties of a given state, for example, the focus of attention could be allocated to 1 or several items depending on the task. Last, the structure of WM may be fixed but WM assessments may be more or less suitable for characterizing the properties of different states. For example, maybe the focus of attention can always hold 4 items, but some
tasks only require the focus of attention to store a single item. One step towards adjudicating between these possibilities is determination of whether measurement of WM shifts across task-demands.

Serial Position Curves and Measurement of the Focus of Attention

Measurement of the size and content of the focus of attention is central to development of WM theories and can be applied to cognitive assessments for clinical and educational purposes. Multiple experimental measures have been used to judge the characteristics of the focus of attention (see Cowan, 2001). One approach is to examine performance on memory tasks of increasing cognitive load and to note overall trends or discontinuities. The logic here follows that, when the capacity of the focus of attention is exceeded, performance should sharply decline. For example, Luck and Vogel (1997) found diminished performance with arrays of more than 4 items, which suggests a roughly 4-item capacity.

Another approach to measurement of WM and the focus of attention requires comparison of items presented in different serial positions within a list. This approach was classically used to analyze free recall data, and results show more accurate performance for early items and late items when compared to middle items (Glanzer & Cunitz, 1966; Postman & Phillips, 1965). In one interpretation, the primacy effect (i.e., advantage for early items) reflects that early items were more thoroughly rehearsed and encoded into long-term memory than items in the middle of the list. The recency effect (i.e., an advantage for later items) reflects that late items are in a heightened state of activation, WM.

Primacy and recency effects are consistently observed in the study of memory, and have been noted in memory for a large range of list length (e.g., 3 items, Nee & Jonides, 2008; 12 items Nee & Jonides 2011; 20 items; Glanzer & Cunitz, 1966). Primacy and recency have been
reported in both recall (Jahnke, 1963, 1965) and recognition (McElree & Dosher, 1993; Monsell, 1978) and with memory for verbal (McElree & Dosher, 1989) and spatial items (Avons, 1998; Smyth & Scholey, 1996). Notably, there is ongoing debate regarding the source of primacy and recency effects. By some accounts primacy and recency effects suggest separate memory stores (Talmi, et al., 2005) or states (Nee & Jonides, 2011). Others attribute heightened memory for earlier or later items in a list to varying levels of interference (Nairne, 1988), temporal distinctiveness of items at the beginning or end of the list (Brown, Preece, & Hulme, 2000), or a primacy effect driven by greater attention (and subsequently better encoding) for the first item (Oberauer, 2003).

Of central interest to the current work is a group of studies examining the neural and behavioral correlates of the serial position curve (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010; Oztekin, et al., 2009; Talmi, et al., 2005). These studies compare retrieval performance between trials divided by serial position, and use differences in the characteristics of retrieval as evidence that items reside in separate memory states. This group of recent studies used tightly controlled paradigms in an attempt to measure the size and content of the focus of attention. The studies detailed below (with one exception), employ verbal item recognition tasks. All studies include a very fast presentation time (500 ms) and a limited interval between encoding and retrieval (e.g., 750 ms) in an effort to limit supplementary maintenance processes, like phonological rehearsal (Oztekin, et al., 2009).

Talmi and others (2005) conducted an fMRI investigation of the serial position curve to inform the debate between multistore and unitary store memory accounts. Subjects viewed lists of 12 words and completed a recognition task. Trials were divided by the serial position of the probe, and central analyses compared retrieval of early probes (items 1 & 2) and late probes
Behavioral results demonstrated higher accuracy and lower reaction times on late items when compared to early items. Late probes were associated with higher inferior parietal activation, while early probes showed higher activation of left hippocampus and regions of the frontal lobe such as the bilateral inferior frontal gyri (BA, 45 & 47) and the bilateral middle frontal gyri (BA 8 & 9). The authors argued that while both early and late items showed activation of frontal and parietal areas implicated in WM (when compared to control items not on the list), only early items revealed activation in the left hippocampus, an area associated with long-term memory for words (Golby, et al., 2001; Hermann, et al., 1996; Schacter & Wagner, 1999). Therefore, these findings were presented as support for distinct neural correlates of early versus late items, and for multistore models of memory.

A subsequent study with a similar procedure examined two competing hypotheses—McElree’s single item focus of attention and Oberauer’s three-level model (Oztekin, et al., 2010). These models both assume a single item focus of attention, but vary over whether one (McElree, 2006) or two (Oberauer, 2002) memory states exist outside of the focus of attention. Words were split by serial positions into early items (1-8), later items (9-11), and the most recent item (12). Results showed higher accuracy, faster reaction times, and less hippocampal activation for the most recent item when compared to all other items. Hippocampal activation did not vary between early and later items. These comparisons were taken as evidence for a single item focus of attention tied to the final item.

Notably, Cowan (2011) argues for a different interpretation of the results from Oztekin and others (2010). An area of the parietal lobe (BA 40) differed between early and later items. This is an area consistent with the one that varies by load in a WM task in a recent imaging study (Cowan, et al., 2011). Cowan suggests that differences in engagement of this region indicate a
difference between retrieval of early and middle items on a list. This in turn supports accounts where more than one item is maintained in a state that is distinct from other information in long-term memory.

Nee and Jonides considered the size and correlates of the focus of attention, first in a short list of 3 items (Jonides, et al., 2008), and later with a longer list of 6 items (Nee & Jonides, 2011). Both studies showed distinct characteristics of retrieval of the final serial position. Moreover, Nee & Jonides (2011) tested the predictions of Oberauer’s three-tiered model by grouping a 6-item recognition task into three groups of items (items 2-3, items 4-5, item 6). Results showed distinct neural correlates for retrieval of each of the three different groups of items. Specifically, when compared to retrieval of other items: the last item was associated with left inferior parietal, left posterior temporal, and left inferior temporal activation; items 4-5 were associated with greater right hippocampal activity, and items 2-3 were associated with higher left inferior frontal activation. The three distinct activation patterns for the three item groups provided support for a three tiered model of WM, where item 6 resides in the focus of attention, 4 and 5 in short-term memory, and items 2-3 in long-term memory. Importantly, Nee and Jonides’ behavioral findings included both primacy and recency effects, but the authors did not report analysis of trials probing item 1. Instead item 1 trials were omitted due to a concern that the primacy effect made the cognitive state of these items difficult to categorize.

A final study, which most closely motivated the present study, compared retrieval of items in different serial positions in a judgment of recency task (Oztekin, et al., 2009). Here, subjects were presented with 5 letters, 1 at a time. After a short mask, a probe appeared with 2 of the items, and subjects were asked which item came later in the list. In order to measure performance by serial position, trials were grouped by the serial position of the correct probe.
Trials were collapsed in this manner as performance did not vary with the position of the incorrect probe. When the item presented in the final serial position was the answer, performance was more accurate and faster. An fMRI contrast revealed less left hippocampal and left inferior frontal activation (BA 45) for items presented in the final serial position. Again, this was interpreted as support for a single item focus of attention.

On the Stability of Primacy and Recency Effects

The results above demonstrate distinct neural correlates for retrieval of the most recent item in a list, and this result has been interpreted as indicative of a one item focus of attention. Notably, in the relevant body of work, a small subset of memory tasks were employed, all requiring memory for verbal items and requiring either item recognition or judgment of recency (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010; Oztekin, et al., 2009; Talmi, et al., 2005). Importantly, both of these tasks tend to show exaggerated recency effects and attenuated primacy effects, in comparison to other memory tasks (McElree & Dosher, 1989), whereas tasks like immediate serial recall tend to reveal exaggerated primacy effects and attenuated recency effects (Jahnke, 1963, 1965). Here, I question whether the qualities of the recency effects in these studies are specific to verbal judgment of recency and item recognition tasks or are general aspects of memory retrieval across contexts. Results inform whether there is evidence for a single item focus of attention in a wider range of WM tasks.

The present study examined primacy and recency effects across several manipulations. Specifically, performance by serial position was examined as a function of task-demand (judgment of recency (JOR), judgment of primacy (JOP)), information type (verbal vs. spatial), and strategic approach (maintenance-based, retrieval-based). Task-demands are considered here because past work indicates that primacy and recency effects might vary based on the specific
demands and assessment parameters of a task (Oberauer, 2003). Specifically, I examine whether the findings in Oztekin et al., (2009) are tied to the specific processes required for successful completion of a JOR task (but not necessarily all situations taxing WM). In addition to a JOR task, a novel judgment of primacy task was tested. In a judgment of primacy task, subjects are asked which of two test items was presented earlier in a list of items. JOR and JOP are identical tasks except for the requirement of choosing the later (JOR) or earlier (JOP) item of the two items in the retrieval probe. This allows determination of whether cognitive resources (e.g., attention, encoding) are differentially allocated to different items in a list depending on the demands of the task. While the JOR task arguably places a premium on retention of later items in the list, the JOP task might place a premium on retention of earlier items. This logic prompts the prediction that a JOR yields stronger recency effects, while a judgment of primacy yields stronger primacy. If correct, this pattern contradicts that notion that the focus of attention (measured by a retrieval advantage) is invariably tied to the last item in a list.

Another debate in the WM literature concerns whether verbal and spatial information are remembered with similar or different memory operations (Kane, et al., 2004; Miyake, Friedman, Rettinger, Shah, & Hegarty, 2001; Shah & Miyake, 1996). Some empirical evidence suggests that verbal and spatial WM involve different memory systems (Handley, Capon, Copp, & Harper, 2002; Miyake, et al., 2001; Shah & Miyake, 1996). Other evidence suggests that WM contains both domain general components (i.e., processes not tied to a specific type of information) and domain specific components (i.e., processes tied to verbal or spatial information) (Baddeley, 2000; Baddeley & Hitch, 1974; Conway, Kane, & Engle, 2003; Kane, et al., 2004; Turner & Engle, 1989). Moreover, the strength of domain general components is more
predictive of complex cognitive performance than the strength of domain specific components (Kane, et al., 2004).

Most relevant to the present work is whether the focus of attention can hold only verbal information or can sustain both verbal and spatial items, either at different points in time or concurrently. Accounts of the focus of attention vary in their consideration of different types of information. According to McElree (2006), the focus of attention is a memory state for verbal information only, and different operations are necessary for spatial memory. In contrast, evidence from Oberauer & Bialkova (2009) suggests that both digits and spatial locations can be maintained in the focus of attention, but only one item or chunk of items at a time. Last, evidence from Cowan and others (2011) suggests that the focus of attention can accommodate verbal items, spatial items, or a combination of material types. Importantly, the group of highlighted studies measure memory performance for verbal information only (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010; Oztekin, et al., 2009; Talmi, et al., 2005). Here, both verbal and spatial tasks were administered. This tests whether a large retrieval advantage for the final item in a list (i.e., the focus of attention) is found for both verbal and spatial WM tasks.

In a further effort to explore the qualities of serial position effects, recency and primacy effects were examined across variations in subjects’ strategies (or approach to a task). Task approach was measured in Oztekin (2009) by looking at an individual’s reaction times data (Hacker, 1980; McElree & Dosher, 1993; Muter, 1979). Oztekin and others (2009) identified two patterns of reaction times across serial positions, forward scanners and backward scanners. Eight subjects revealed a backward serial search pattern (i.e., faster performance on items where the more recent items were correct, and slower performance as the correct answer was earlier in the list). Four subjects revealed a forward serial search. Here reaction times increased as the correct
trial was later in the list, until the final serial position, when there was a decrease in reaction times. While both of these strategies show recency effects, only forward scanners show primacy effects, therefore, the prevalence of backward scanners likely contributes to the large recency effect and small primacy effect.

In the present study, strategy use was measured through reaction times across variation in serial position (like Oztekin, et al., 2009) and also by asking subjects to report their strategy following a group of trials (Dunlosky & Kane, 2007). While the approach used by Oztekin et al., (2009) suggests the order in which items were maintained, it is less informative about the processes employed to maintain or retrieve information (e.g., rehearsal, semantic encoding, visual imagery). This two-pronged approach to measurement of strategy tested the prediction that primacy and recency effects vary with strategy use by subjects. Two broad classes of strategy were measures, maintenance-based strategies and retrieval-based strategies. While both maintenance and retrieval processes are shown to support WM (Unsworth & Engle, 2007, Chein, Moore, & Conway, 2011), one’s approach to a task might emphasize one of these processes over the other. Maintenance-based strategies emphasize active maintenance of information during the encoding-maintenance phase. Recent work proposes two refreshing processes that support retention of information in the short-term, one by sub-vocal pronunciation of items, phonological rehearsal, and one by allocation of attention, attentional refreshing, (Camos, Mora, & Oberauer, 2010). In retrieval based-strategies subjects attend to items at encoding but complete the task with either scanning through the items at test or familiarity-based judgments, two separate processes that might operate during retrieval (Jacoby, 1991; McElree, Dolan, & Jacoby, 1999).

Importantly forward and backward scanners might vary not just in the order with which items are maintained, but also with their approach to retaining the set of items. Arguably,
forward scanning seems more likely if a subject was rehearsing some or all of the items during encoding (maintenance–based), while backward scanning is more likely if subjects perform less repetition and think back to the set of items at test (i.e., retrieval-based). The present study will examine whether serial position effects vary by reported strategy. For example, is the recency effect reported in a past study (Oztekin et al., 2009) tied to the presence of backward scanners?

In addition to testing the stability of a reaction time advantage for the final serial position, there are two other aims of the present work. First, although primacy effects are frequently reported in the study of WM, they are largely ignored in the studies examining recency as a correlate of the focus of attention. Moreover, none of the theoretical accounts above place an emphasis on primacy effects. In fact in a recent examination, the primacy item “was excluded in neural analyses due to ambiguity surrounding the primacy effect” (Nee & Jonides, 2011). In other words, the present framework leaves unclear the memory or attentional state of the primacy item. Both the characteristics of primacy effects and also their role on the structure of WM are probed in the current work.

A final motivation of the current work is investigation of the role of the hippocampus and surrounding medial temporal lobe (MTL) in WM and the focus of attention. Historically, the MTL has not been implicated in WM, in large part because damage to the MTL is associated with profound long-term memory deficits but typically leaves short-term memory intact (Squire & Schacter, 2002). Most neuroimaging studies of short-term and working memory have, consistent with earlier neuropsychological findings, failed to elicit activation of the MTL (Owen, McMillan, Laird, & Bullmore, 2005; Wager & Smith, 2003). However, recent studies implicate the hippocampus in the retrieval period of JOR and item recognition tasks (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010; Oztekin, et al., 2009; Talmi, et al., 2005). Other recent,
neuroimaging studies illustrate that so-called “WM tasks” engage many of the same neural regions engaged by more traditional episodic memory tasks (Axmacher, Elger, & Fell, 2009; Cabeza, Dolcos, Graham, & Nyberg, 2002; Ranganath, Cohen, Dam, & D'Esposito, 2004; Talmi, et al., 2005). These recent developments suggest that, under certain conditions, WM tasks engage brain structures that underlie retrieval from long-term memory, including the anterior prefrontal cortex and MTL (Polyn, Norman, & Kahana, 2009). These conditions include when items are unfamiliar, complex, or require relational processing (Cabeza, et al., 2002; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006; Ranganath & D'Esposito, 2001). Moreover, recent fMRI experiments illustrate increased recruitment of MTL during the recall period of trials in complex WM span tasks, when compared to a memory task requiring storage only (Chein, et al., 2011; Faraco et al., 2010). The present work study examines the role of the MTL in retrieval of items in different serial positions across task-demands and strategy.

In sum, there are competing accounts of the structure of WM (see figure 1). While recent papers argue that a single item recency effect is indicative of the focus of attention, this phenomenon has only been examined a limited set of tasks. Here, the generalizability of recency effects and their neural correlates is revisited in order to inform the use of recency effects as a marker of the focus of attention. Of primary interest to the current paper are the following questions. Is the magnitude of primacy and recency effects dependent of task-demands? Do they have unique neural signatures? Results will be discussed as they inform the structure of WM and the construct of the focus of attention.
CHAPTER 2

BEHAVIORAL CORRELATES OF THE FOCUS OF ATTENTION

In a prior neuroimaging study, Oztekin and others (2009) administered a JOR task and reported faster reaction times and a unique pattern of neural activity for trials on which the most recent item was the correct answer. The present experiment was designed as a replication and extension of that earlier study. Specifically, this experiment explores whether retrieval patterns depend on the serial position of the correct response (as in earlier studies), but also investigates whether serial position effects vary according to task-demands, the type of information that is being tested (verbal or spatial), and self-reported strategies utilized by individual subjects.

Towards this goal, a novel judgment-of-primacy (JOP) task was developed, and performance in this task was contrasted to performance in a JOR task. The inclusion of a JOP task allowed for determination of whether a retrieval advantage for the final item, observed previously in both JOR and item recognition tasks, might be shifted in a task emphasizing earlier rather than later items. Thus, the design could inform whether the retrieval advantage for the final serial position, which is often interpreted as the focus of attention, is in fact tied to particular aspects of experimental methodology. The comparison of JOP with JOR performance patterns was also expected to provide evidence informative in the interpretation of primacy phenomena in short-term retrieval.

Subjects

Forty individuals (29 female) ages 18 – 26 years old ($M = 20.22$, $SD = 1.72$) participated in this experiment. Subjects were Temple University Undergraduates and given course credit for participation.
Experimental Tasks and Strategy Assessment

Four task types were included in the study, verbal JOR, spatial JOR, verbal JOP, and spatial JOP. Figure 2 depicts the JOR and JOP trials. Trials were presented blocked by task type so that subjects would not be required to rapidly switch task-demands between trials. Verbal trials tested memory for letters. Sixteen consonants (B, C, F, H, J, K, L, M, N, Q, R, S, V, W, X, and Z) were used in order to parallel 16 spatial locations used in the spatial task. In order to encourage verbal phonological coding, and to discourage simple perceptual matching of the encoded and probed items, capital letters were used for item presentation while lowercase letters were used for retrieval probes. Spatial trials tested memory for locations (marked by a green circle) on a 4 by 4 grid. In both tasks, a brief mask was presented between the encoding and probe periods so that information would be displaced from sensory buffers.

Figure 2 Schematic of Verbal and Spatial Working Memory Tasks.
Trial presentation was identical across the JOR and JOP tasks, except for the requirement that subjects report the earlier (JOP) or later item (JOR) item. Each trial followed the same sequence: trial initiated by a subject key press, a 500 ms fixation, 5 items presented sequentially for 500 ms each, a 750 ms mask, and a 3-second probe period in which subjects selected the earlier or later item between two alternatives. After 3 seconds, whether or not the subject responded, the trial ended.

Each retrieval probe included two items, both from the list (an incorrect, and a correct response). Specific trials were constructed prior to the experiment in order to control the serial position of the correct and incorrect probes. A practical constraint in these tasks is that in JOR only serial positions 2, 3, 4, and 5 can be the most recent item, while in JOP only serial positions 1, 2, 3, and 4 can be the earlier item. Accordingly, trials were constructed so that each of the four possible correct serial positions in each task was probed as the correct response 24 times, and this scheme resulted in 96 total trials. Incorrect items were also equally distributed between the possible incorrect answers. Importantly, although item 1 is never the correct answer in JOR, any time item 2 is the correct item, item 1 is necessarily the incorrect item (i.e., item 1 must be presented as the incorrect probe). Similarly, in JOP, if item 4 is the earlier probe then the incorrect probe is necessarily serial position 5 (i.e., item 5 must be presented as the later, incorrect, probe).

Strategy self-report questionnaires were administered following each task type (see appendix A). The strategy questionnaire was developed on the basis of an extensive pilot study exploring strategy use across a range of WM tasks. Questionnaires first probed two broad categories of strategy, maintenance-based and retrieval-based, and all strategies were described in laymen’s terms. Alternate forms were created in order to counterbalance the order of the
strategies on the questionnaire. The first broad strategy involved maintenance of some or all of the items during item presentation (maintenance-based) while the alternative base strategy emphasized refreshing of some or all items at the time of test (retrieval-based). Subjects who reported a maintenance-based strategy were asked about an emphasis on phonological rehearsal or attentional refreshing, while those reporting a retrieval-based strategy were asked about an emphasis on either explicit retrieval of items or reliance on simple familiarity.

Procedure

Subjects came to the lab for a one-hour experimental session. Upon entering the lab, subjects signed the consent form and were instructed on the overall layout of the study “i.e. we will be administering memory tasks and asking you some questions about the strategies you used to remember the information”. The behavioral session lasted roughly one hour. In the session, subjects completed 3 of the 4 task types (verbal JOR, spatial JOR, verbal JOP, spatial JOP), and order was counterbalanced. Therefore, 30 subjects completed each task, and 10 subjects began with each of the 4 tasks.

Five practice trials and ninety-six experimental trials were completed within blocks of each task type. Each task block lasted roughly 15 minutes (each trial was 6.75 seconds, and the inter-trial intervals were subject-paced). Within each block of 96 trials, the order of trials probing different serial positions was randomized, as was the identity of the items (letter, location) presented in each serial position. Following each of the task blocks, the strategy interview was administered. During the strategy interview, the experimenter read the strategy questionnaire out loud to the subject while the subject read along. The subject rendered his or her response verbally, and the response was recorded by the experimenter.
Results

Initial analyses probed performance metrics across the different task types. Behavioral outcomes included both accuracy and reaction times for correct trials. Accuracy for all four task-types was above chance (verbal JOR $M = .85, SD = .08$; spatial JOR $M = .73, SD = .12$; verbal JOP $M = .85, SD = .11$, spatial JOP $M = .72, SD = .16$). Average reaction times in milliseconds (ms) for correct trials were as follows: verbal JOR ($M = 1544.22, SD = 210.46$); spatial JOR ($M = 1317.70, SD = 245.00$); verbal JOP ($M = 1427.15, SD = 199.43$); spatial JOP ($M = 1280.84, SD = 287.84$). Analysis of accuracy by task-demand (JOR and JOP) and item type (verbal and spatial) showed a main effect of item type ($F_{(1,116)} = 32.71, p < .005, \eta^2_p = .22$) with higher accuracy in verbal than spatial conditions, but no main effect of task-demand ($F_{(1,116)} = .04, p = .84, \eta^2_p = .00$), or interaction between task-demand and information type ($F_{(1,116)} = .13, p = .72, \eta^2_p = .001$). Results from average reaction times on correct trials indicated a main effect of item type ($F_{(1,116)} = 16.60, p < .005, \eta^2_p = .13$), and no effect of task-demand ($F_{(1,116)} = 2.02, p = .16, \eta^2_p = .017$), or interaction ($F_{(1,116)} = 2.02, p = .16, \eta^2_p = .02$). Response times were faster in the spatial tasks than in the verbal tasks. Together these results indicate strong consistency between performance in JOP and JOR (within an information type), but differences between verbal and spatial performance. Also of note, although accuracy was high overall, there were a few cases where accuracy was below .60. These cases were removed from subsequent analyses.

Next, in order to gauge performance across serial positions, analyses compared performance as a function of the serial position of the correct response. This approach is consistent with the extant literature on JOR where performance has been shown to vary by the serial position of the correct probe but does not change with the position of the incorrect probe.
(McElree, 1993; Oztekin et al., 2009). Supplemental analyses grouped trials according to the serial position of both probes (correct and incorrect) (Appendix B).

In an effort to explore both recency and primacy effects, trials were grouped into three types: primacy item trials, middle item trials, and recency item trials. The definition of these trials varies between tasks (due to the constraint of asking for the more recent or earlier item) as explained in Table 1.

Table 1: Definition of trial types across tasks.

<table>
<thead>
<tr>
<th>Trial Type</th>
<th>Judgment of Recency</th>
<th>Judgment of Primacy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Serial Position</td>
<td>Serial Position</td>
</tr>
<tr>
<td>Primacy Trial</td>
<td>of the Correct</td>
<td>of the Correct</td>
</tr>
<tr>
<td></td>
<td>Answer</td>
<td>Answer</td>
</tr>
<tr>
<td>Middle Trial</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Recency Trial</td>
<td>3 or 4</td>
<td>2 or 3</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>4</td>
</tr>
</tbody>
</table>

Analyses continued in two main steps. First, analyses evaluated the presence of primacy and recency effects within each of the four task types (verbal JOR and JOP, spatial JOR and JOP). Both primacy and recency effects are pervasive phenomena in the study of memory (Glanzer & Cunitz, 1966; Oberauer, 2003; Talmi, et al., 2005), and these analyses essentially tested the consistency of the present data set with past findings. The second and central set of analyses tested the hypothesis that the size of primacy and recency effects varies in accordance with task-demand and strategy. Here, the following predictions were tested: 1) JOR will produce a larger recency effect than JOP; 2) JOP will produce a larger primacy effect than JOR; 3) the engagement of maintenance-based strategies will be associated with larger primacy effects than retrieval-based strategies; and 4) the use of retrieval-based strategies will produce larger recency effects than maintenance-based strategies. If supported, these predictions suggest that heightened retention of specific items in a list varies with aspects of the WM task.
Primacy and Recency Effects within Each Task

Figure 3 presents accuracy and reaction time data split by serial position, for all four task types. Based on an extensive prior literature on serial position effects, a series of planned contrasts were conducted to address the following questions: 1) Was there a primacy effect (difference between primacy item trials and middle item trials)? 2) Was there a recency effect (difference between recency item trials and middle item trials)? and 3) Was there a performance difference between the primacy and recency items? Contrasts tested accuracy and reaction times for all four task types. Results of these contrasts are reported in Table 2.

Figure 3. Exp. 1: Mean Accuracy and Reaction Times for Verbal and Spatial JOR and JOP.
Instances of both primacy and recency effects were shown in tasks of immediate memory. In fact, each of the four conditions produced evidence of primacy and recency (through accuracy and/or reaction times on correct trials). A primacy effect marked by both speed and accuracy was found in verbal and spatial JOP, while a recency effect marked by both speed and accuracy was found in verbal and spatial JOR and Spatial JOP.

**Primacy and Recency Effects across Task**

Crucial to the aims of the present paper is whether the presence and magnitude of primacy and recency effects varies across task-demands. Metrics of primacy and recency were calculated to test the size of these effects across task and strategy. In both JOR and JOP, separately, primacy effects were calculated with the following procedure: 1) reaction times on middle items trials were averaged; 2) the average of the reaction times of primacy item trials was subtracted from this average; and 3) this product was divided by the average of the middle items. Recency effects were calculated with the following, analogous, procedure: 1) reaction times on
middle item trials were averaged; 2) the average of the reaction times for recency item trials was subtracted from this average; 3) the product was divided by the average of the middle items. The procedure produces an index of the advantage (or decrement) for the retrieval of the primacy/recency item in proportion to the overall reaction times.

The resulting indices of the serial position effects were entered into a 2 by 2 repeated measures ANOVA examining task-demand (JOR, JOP) by effect-type (recency effect, primacy effect) with the size of the primacy or recency effect as the dependent variable. These analyses were run separately for verbal and spatial tasks (due to the fact that subjects did not complete all four conditions, the models had to be run separately on the subsets of subjects completing the relevant task). For verbal tasks, the analysis showed no main effect of task-demand \((F_{(1,19)} = 1.13 , \, p = .302 , \, \eta^2_p = .06)\) or of serial position effect \((F_{(1,19)} = 2.10 , \, p = .17 , \, \eta^2_p = .10)\), but a significant effect-type by task-demand interaction \((F_{(1,19)} = 26.64 , \, p < .005 , \, \eta^2_p = .58)\). As predicted above, this interaction was driven by a larger primacy effect in JOP than JOR \((t_{(19)} = 2.76 , \, p = .01)\), accompanied by a larger recency effect in JOR than JOP \((t_{(19)} = 4.48 , \, p < .005)\).

For spatial tasks, there was no main effect of task-demand \((F_{(1,16)} = .12 , \, p = .73 , \, \eta^2_p = .01)\), but a main effect of effect-type demonstrating an overall larger recency than primacy effect \((F_{(1,16)} = 5.39 , \, p = .034 , \, \eta^2_p = .25)\), and an effect-type by task-demand interaction \((F_{(1,16)} = 9.40 , \, p = .01 , \, \eta^2_p = .37)\). In the spatial realm, this interaction indicates a larger recency effect than primacy effect in JOR \((t_{(26)} = 3.051 , \, p = .005)\), and no difference between the size of the primacy and recency effect in JOP \((t_{(26)} = .004 , \, p = .99)\) (Figure 5).
JOR and JOP included trials with the same two items in the probe, but different correct answers. This permitted a more nuanced analysis of how performance varied across tasks for trials involving the same exact probe positions. These analyses focused on trials showing items 1 and 2 in the retrieval probe, and trials showing items 4 and 5 in the retrieval probe. If JOP promotes better performance on early items than JOR, and JOR promotes better performance on later items than JOP, this direct comparison should uncover differences.

Dependant samples t-tests were conducted separately for verbal and spatial item types. In memory for verbal items, when items 1 and 2 were shown, performance was significantly faster in the JOP task than the JOR task ($t_{(19)} = 6.00, p < .005$). However, performance did not differ across tasks on trials where items 4 and 5 were shown ($t_{(19)} = 1.12, p = .28$). In the case of spatial items neither probes showing items 1 and 2 ($t_{(16)} = .338, p = .74$) or probes showing item 4 and 5 differed between tasks ($t_{(19)} = 1.78, p = .09$). Therefore, the strongest case for differential
performance across tasks was found in the verbal tasks, where performance differs for the same exact probes (those showing positions 1 and 2) across task.

Comparison of Primacy and Recency Effects Across Strategy

Strategy was assessed in two manners: by examining individual reaction times patterns, and through self-reported strategies. Findings from the self-reported strategy questionnaire, split by task, are presented in Table 3. Results show that subjects reported both retrospective and prospective strategies. Analysis of self-report strategy use focused on two primary questions. First, did strategy vary as a function of task, and second, did performance vary by strategy. A Chi-Square test demonstrated that the frequency of reporting a prospective or retrospective strategy did not vary significantly as a function of task ($\chi^2_{(3)} = 2.83, p = .42$, Cramer's V=.15).

The second level of strategy report included 4 strategies: phonological rehearsal, attentional refreshing, retrieval of all or some of the list, and familiarity. Again, reported strategy use did not vary as a function of task ($\chi^2_{(9)} = 8.43, p = .49$, Cramer's V=.16).

<table>
<thead>
<tr>
<th>Table 3 Self-Report Strategy.</th>
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<tbody>
<tr>
<td>Strategy Questionaire Level 1</td>
</tr>
<tr>
<td>Maintenance-Based</td>
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<tr>
<td>Verbal JOR</td>
</tr>
<tr>
<td>Spatial JOR</td>
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<tr>
<td>Verbal JOP</td>
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<tr>
<td>Spatial JOP</td>
</tr>
</tbody>
</table>

| Strategy Questionaire Level 2 | |
|-------------------------------|
| Rehearsal | Attentional Refreshing | Retrieving Items | Familiarity |
| Verbal JOR | 13 | 3 | 11 | 3 |
| Spatial JOR | 12 | 5 | 10 | 3 |
| Verbal JOP | 17 | 5 | 6 | 2 |
| Spatial JOP | 2 | 10 | 5 | 11 | 3 |

Table Notes: 1 Level 2 was nested in level 1. For example, participants who answered maintenance-based were then asked to select between rehearsal and attentional refreshing. 2 One person left Level 2 of the strategy questionnaire blank for spatial JOR.
A series of repeated measures ANOVA (one for each task-type) examined serial position of the correct probe as a within subjects factor, and strategy as a between subjects factor. Strategy did not have a significant impact on reaction times, as there was neither a main effect of strategy or serial position, nor an interaction between these variables in any of the four task-types (all $F < 1.5$, $p > .20$). Performance was not examined across the second tier of strategy choices (phonological rehearsal, attentional refreshing, retrieval of the list of items, familiarity) as several of the options were very infrequently reported (see Table 3).

Oztekin et al., (2009) identified two scanning patterns, forward scanners (who show patterns consistent with a forward serial search through the list until the most recent item which is retrieved faster than other others) and backwards scanners (who show patterns consistent with a backward serial search through the list). In verbal JOR there were 15 forward scanners, 1 backward scanner and 14 subjects who could not be classified. In spatial JOR there were 5 forward scanners, 0 backward scanners and 25 who could not be classified. In verbal JOP there were 15 forward scanners, 1 backward scanner and 14 who could not be classified. In spatial JOP there were 7 forward scanners, 1 backward scanner and 22 who could not be classified. A different type of forward scanner is one whose reaction times increases with the recency of the correct response and do not show a recency effect. Of those unclassified, 3 of the verbal JOR subjects, 1 of the spatial JOR 2, and 1 of the verbal JOP fit this pattern.

Discussion

In order to evaluate primacy and recency effects and their comparative size in different task contexts, these effects were examined as a function of task-demand (JOR, JOP), item type (verbal, spatial), and strategy (maintenance-based, retrieval-based). Significant primacy and recency effects (measured by accuracy, reaction times or both) were found in all four
task/material-type combinations (verbal JOR, spatial JOR, verbal JOP, and spatial JOP). More importantly, the magnitude of primacy and recency effects varied as a function of task-demands, suggesting that phenomena do not reflect fixed components of WM (e.g., a focus of attention tied to the last item in a list), but the flexible allocation of WM resources to best accommodate task-demands.

Prior studies of verbal JOR tasks have reported a small primacy effect and larger recency effect (Oztekin et al., 2009; McElree & Dosher, 1993). Here, this pattern did not generalize across tasks. Instead, the comparative size of primacy and recency effects differed between JOR and JOP. In the verbal conditions, there was a larger primacy affect in JOP than JOR, and a larger recency effect in JOR than JOP. In the spatial conditions there was a larger recency effect than primacy effect in JOR, but no difference between the recency and primacy effects in JOP. Importantly, this pattern of results demonstrates an impact of task-demand on the size of primacy and recency effects, even when the two tasks are as similar as JOR and JOP. These tasks shared every feature except for the requirement to identify the earlier or later of the two items presented in the probe. Arguably, tasks differing in more extensive ways would also produce differential serial position effects (although not necessarily in a single direction or additive fashion).

Comparison across verbal and spatial conditions revealed a few notable differences. Accuracy was significantly higher in the verbal conditions than the spatial condition, while reaction times were faster in the spatial relative to verbal conditions. For the spatial tasks, analysis of accuracy by serial position of the correct probe showed very low (near chance level) accuracy in item 3 in JOR and item 2 in JOP. Low performance in the spatial domain for a single item (in the middle of the list) can be interpreted as either a failure to encode, maintain, or retrieve this item. Whatever the cause, it appears that subjects had difficulty accommodating the
entire set of five items in the spatial task, and may have accordingly adopted a strategy that sacrificed accuracy for middle items. In contrast to the spatial conditions, verbal JOR and JOP showed accuracy of above 75% on all items. A final difference between the verbal and spatial conditions regards primacy effects. Primacy effects were smaller in verbal than spatial tasks, and in JOP there were similar sized recency and primacy effects (rather than a larger primacy effect). Due to some distinct qualities of spatial performance (smaller primacy effect and chance level performance on the 2\textsuperscript{nd} or 3\textsuperscript{rd} item) in the subsequent fMRI experiment performance was tested in only the verbal realm.

Examination of forward and backward scanning strategies indicated that the overwhelming majority of subjects followed a forward scanning pattern or could not be classified as a forward or backward scanner. Unlike the prior study (Oztekin et al., 2009) where there were twice as many forward scanners as backwards scanners, here, there were only 3 instances of backward scanning across all conditions. Examination of self-report strategy revealed that strategy distribution was similar across tasks, and that performance did not vary according to the reported strategy. This finding (or lack thereof) could be interpreted in several ways. A straightforward interpretation would suggest that there was simply an even distribution of strategies and comparable performance between individuals with differing strategies. A related possibility is that even without performance differences, strategic differences might be reflected in the engagement of differing neural substrates (e.g., differences in brain activations in areas tied to phonological rehearsal). Lastly, it is also possible that strategic differences that effect performance do exist, but the strategy questionnaire failed to uncover true differences in subject strategy.
In sum, this experiment demonstrated strong behavioral evidence of primacy and recency effects, and more importantly, it established that the size of these effects is dependent upon task conditions. This finding is important in that it is informative in adjudicating between alternative views of the inherent structure of states within WM. Rather than supporting a single current model of the structure of WM, these results show that the size and allocation of the focus of attention may be more flexible than is suggested by some models, and is dependent on the very specific structure of the task. Specifically, in some instances (e.g., verbal JOR) a retrieval advantage is found for the last item in a list, while other instances (e.g., verbal JOP) show an advantage for earlier items in the list. This may suggest flexible allocation of the focus of attention according to task-demands.
CHAPTER 3

NEUROIMAGING OF THE STRUCTURE OF WM

The experiment above demonstrated both primacy and recency effects and differences in the size of primacy and recency effects across task contexts. The prior fMRI literature explores the neural underpinnings of a recency effect, but does not examine primacy effects, or compare the neural markers of primacy and recency effects. While Experiment 1 showed behavioral indexes of recency and primacy, it is unclear whether these retrieval advantages come about from the same or different cognitive and neural processes. For example, each of these advantages could be indicative of the focus of attention or the recency effect could come about from one cognitive process (e.g., the focus of attention) and primacy effect another (e.g., phonological rehearsal). Here, fMRI was used to explore the neural correlates of both recency and primacy effects, and to examine whether these neural correlates are stable across task (JOR, JOP) and strategy (maintenance-based, retrieval-based).

Subjects

Twenty-eight individuals (18 female) ages 18 to 27 years old ($M = 21.5$, $SD = 2.8$) participated in this experiment. Subjects were recruited from Princeton University, and the greater Princeton, NJ community through a website advertising paid experiments at Princeton University. Each subject was paid $30 for the 90-minute session.

Experimental Tasks and Strategy Assessment

Verbal JOR and JOP tasks identical to the ones from the behavioral study described in Chapter 2 were also used here (see Figure 2). Subjects completed the same 96 trials of JOR and 96 trials of JOP constructed for the behavioral experiment. However, unlike in the behavioral experiment, the inter-trial interval (ITI) was experimenter-paced, and varied between the trials
(like Oztekin, et al., 2009). The length of the ITI varied from 2 to 16 seconds, with a mean of 6.625 seconds. A variation (or jittering) of the length of this interval allows easier differentiation between fMRI signal for separate trials, and limits habituation and expectation effects. Both the length of the inter-trial interval (ITI) and the order of the varying ITI were determined using Optseq2, a tool designed for optimal stimulus presentation for fMRI designs. A trial order using the same trials from the first experiment was created, and trials were assigned to inter-trial intervals. The same trial randomization was used for all subjects in order to take advantage of the Optseq2 optimizations. Strategy questionnaires identical to those used in the behavioral study were administered (Appendix A).

**fMRI Acquisition and Behavioral Data Collection**

Subjects were scanned using a Siemens Skyra 3-Tesla scanner equipped with a 16 channel phased array head coil. Stimuli were projected onto a visual display in the magnet’s bore and viewed by the subject through a mirror above his or her eyes. Subjects responded with a handheld response box, and the experimental onset was synchronized with scanner activity through a trigger system.

Structural images were collected via T1-weighted three dimensional magnetization-prepared rapid acquisition with gradient echo (MPRAGE) collected in the sagittal plane (TR=2300 ms, TE=3.08 ms, flip angle =9°). Functional data was collected during participation in the two memory tasks, JOR and JOP. A total of 6 functional runs were collected with three runs for each task. Each run was roughly 7 minutes and included 210 whole-brain acquisitions (i.e., TRs). Functional T2*-weighted images were collected using an echoplanar image (EPI) sequence. Thirty-four 3 mm slices with 2.97 mm by 2.97 mm in-plane resolution were acquired in an interleaved fashion (TR=2000 ms, TE= 34 ms, flip angle 71°).
Procedure

Subjects arrived at Princeton University for a 90-minute session. They signed a consent form, and were then screened to insure safety to be in the MRI environment. Screening included a questionnaire to confirm there was no metal in the subject’s body, and two metal detectors (a wand and an “airport” style metal detector”) were used as further safety measures. The experimenter explained both the broad layout of the experiment (“you will complete two tasks with memory for letters and respond to questions about your strategy use”), and the details of the MRI environment. The subjects were shown the first task they would complete (either JOP or JOR) and given 5 practice trials. It was also explained that later in the session they would complete the other task. Once in the scanner a series of structural images were acquired (see above). During the structural sequence the subject completed 20 more practice trials.

Each of the 6 functional runs was composed of 32 task trials, and subjects completed 96 total trials of each task. The order of the tasks was counterbalanced, so that 14 subjects began the session with JOR and 14 began with JOP. Subjects completed 3 runs of one task, then were administered the strategy questionnaire while still in the scanner, and then completed 3 runs of the other task. The first strategy questionnaire was completed while in the scanner for two reasons: 1) in order to give the subjects a break between the two task types; and (2) to assess strategy after each task type without removing subjects from the scanner. The strategy questionnaire was projected onto the screen, and the subjects spoke their response to the experimenter. Before the second task began, subjects were reminded about the nature of the new task requirements and were probed to make sure they understood the change in task-demand. Following the 3 runs of the second task, subjects were removed from the scanner and the second questionnaire was administered. Here again, subjects were read the form as they read along, and
gave verbal responses that were recorded by the experimenter. After removal from the scanner, and completion of the strategy questionnaire, subjects were debriefed about the aims of the study.

**Image Analysis and Preprocessing**

Preprocessing and analysis were conducted using AFNI (Cox, 1996). Data underwent the follow preprocessing steps prior to statistical analysis. Individual slice time-series were shifted to compensate for interleaved collection of slices, and both functional and structural images were re-sampled from oblique to cardinal coordinates. A despiking procedure was used to reduce the impact of artifactual outliers on the dataset. Both structural and functional data were aligned through a procedure that registered each of the functional volumes to the 4th volume of the first functional run using a 6-parameter affine motion-correction algorithm, and then aligned all functional acquisitions to the individual subject’s high-resolution structural image. Spatial smoothing was applied to functional images with a 6-mm full-width half-maximum Gaussian kernel. Signal was also converted into a percent using the mean value of each run in order to interpret beta weights as percent signal change. For group analyses, structural data were converted into a normalized template from the Montreal Neurologic Institute that was manually transformed into Talairach space.

Analyses were implemented using a general linear model (GLM) approach. This approach uses an ordinary least squares method to estimate fMRI BOLD signal, and allows for contrasting of signal changes during different conditions or stages of a task to be assessed. Models included regressors of non-interest for the six motion parameters resulting from the motion correction step, as well as for the cubic polynomial trends in the run-wise data. To model task events, separate regressors were entered for the encoding-maintenance phase (the interval
from presentation of the first item through the end of the mask), retrieval phase (including a separate regressor for each correct serial position), and for extended baseline periods associated with the ITI (specifically, the final 4 seconds of ITIs exceeding 10 seconds were modeled in order to establish an estimate of baseline activity). Retrieval events were modeled using a single parameter gamma-variate function approximating the shape of the canonical hemodynamic response. Encoding-maintenance regressors were modeled using a one parameter block stimulus of duration 3.75 seconds that was also convolved with a gamma-variate model. The ITI was modeled as a block period of 4 seconds with no convolution.

Individual subject data were analyzed with a subject-specific fixed-effect model, and contrasts of interest were submitted to a second-level random effects group analysis. The criterion for significant clusters was calculated using AFNI’s 3dclustsim program with 10,000 Monte Carlo simulations to establish family-wise error rates. Correction to a .05 level required an uncorrected voxel-wise threshold of $p < .001$, with a cluster size of 17 contiguous voxels. For both the encoding and retrieval phase data, this correction resulted in several very large clusters containing multiple local maxima. To identify more specific peak loci within these large clusters, the voxel-wise statistical threshold was extended upward to more stringent levels ($p < .001$, $p < .0001$, $p < .00001$).

As detailed in the results section, several contrasts were conducted on the encoding and retrieval periods of the task. Contrasts separately compared the encoding/maintenance-related activity to the ITI, and retrieval-related activity (collapsed over all serial positions) to the ITI. Contrasts in the retrieval period focused on comparison of the retrieval period for trials where the correct response was in different serial positions (e.g., trials where item 5 was correct vs. trials where items 2 or 3 were correct).
Behavioral Results

Overall accuracy was quite high (JOR: $M = .92, SD = .06$; JOP: $M = .90, SD = .06$), and was significantly higher in JOR than JOP ($t_{(27)} = 2.10, p = .046$). Performance on JOP ($M = 1491.95, SD = 257.43$) was significantly faster than JOR ($M = 1608.77, SD = 229.43$) ($t_{(27)} = 4.84, p < .005$).

Primacy and Recency Effects within Each Task

In order to probe serial position effects within tasks, trials were averaged by the serial position of the correct probe (see Figure 5). Additionally, planned contrasts mirroring those in Experiment 1 were conducted and are summarized in Table 4. These contrasts examined primacy effects, recency effects, and whether there were differences in retrieval of the primacy and recency item. Evidence of primacy effects was found for both JOR and JOP, but evidence of recency effects was found in JOR only. Moreover, it was faster for primacy items trials than recency item trials in both JOR and JOP.

Figure 5. Exp. 2: Average Accuracy and Reaction Times for Verbal JOR and JOP.
Comparison of serial position effects across task

Again primacy and recency effects were compared across JOR and JOP to test whether the items with the quickest retrieval speed (and arguably the most heightened memory state) were consistent across task. Metrics of primacy and recency effects were calculated in the same manner as in Experiment 1. An ANOVA with task (JOR, JOP) and effect-type (primacy, recency) as within-subjects independent variables revealed that the main effect of task was not significant ($F(1,27) = .02, p = .90, \eta^2_p = .00$), but the main effect of effect-type was significant, and showed overall larger primacy effects than recency effects ($F(1,27) = .32.33, p < .005, \eta^2_p = .55$).

Similar to Experiment 1 there was a significant task by serial position interaction ($F(1,27) = 9.86, p < .005, \eta^2_p = .27$). This interaction indicates a comparatively larger primacy effect in JOP than JOR ($t(27) = 2.19, p = .04$), and larger recency effect in JOR than JOP ($t(27) = 2.53, p = .02$) (see Figure 6). Therefore, like Experiment 1 the magnitude of serial position effects was task-depandanent, indicating that the size of the retrieval advantage for primacy or recency items shifted with task instructions.
Individual subject reaction times were used to classify subjects as forward or backward scanners. In JOR, there were 15 forward scanners, 0 backward scanners and 13 that could not be classified. In JOP, there were 9 forward scanners, 0 backward scanners, and 19 who could not be classified. Importantly, forward scanners were categorized according to the same criteria as in Oztekin et al., (2009) and included only those who had monotonically increasing reaction times across correct position probes in the first positions and showed a recency effect. A different type of forward scanner is one who shows increased reaction times for all of the 4 possible probe types. Of those unclassified, 1 of the JOR subjects and 8 of the JOP subjects fit this pattern.
Regarding self-report strategy, subjects overwhelmingly reported maintenance-based strategies over retrieval-based strategies. In JOR 24 subjects reported a maintenance based strategy while 4 subjects reported a retrieval-based strategy. In JOP, 23 subjects reported a maintenance based strategy while 5 subjects reported a retrieval-based strategy. Splitting each into secondary categories revealed that in JOR, 20 subjects reported phonological rehearsal, 4 reported attention based strategies, 3 reported an emphasis on scanning items at retrieval, and 1 reported an emphasis on familiarity of the probe. In JOP, 19 subjects reported phonological rehearsal, 4 attention based strategies, 5 an emphasis on scanning items at retrieval, and no one reported emphasis on familiarity of the probe. As self-report strategy was so biased towards a single category (creating substantial differences in group sizes), neither behavioral performance nor imaging contrasts were examined across strategy.

Imaging Results

Separate analyses probed activation patterns during two segments of the task: 1) the encoding-maintenance period, which included item presentation and the mask between encoding and retrieval, and 2) the retrieval period, based on the moment at which the test probe was shown. For each task (JOR, JOP), contrasts compared activation during each of these periods to baseline activation during the ITI (Figure 7, Table C1, Table C2). Tables listing the full set of imaging contrasts are provided in Appendix C.

The encoding-maintenance period of the both JOR and JOP were marked by significant positive activations (when compared to the ITI) in several regions, including: bilateral premotor cortices, extending through lateral portions of BA 6 and 4, the left supplementary motor area (SMA) including medial regions of BA 6 extending down to BA 32 in the dorsal anterior cingulate cortex, and bilateral activations in the posterior parietal lobe that extended through the
superior and inferior parietal lobes (BA 7 and 40) via the intraparietal sulcus. Areas showing higher activation for the ITI relative to the encoding-maintenance period (i.e. deactivation) also included areas of the posterior parietal lobe, specifically (BA 40, 7), and also medial regions of the right lateral prefrontal cortex (BA 8). Nearly identical patterns of activation were found for the encoding-maintenance across tasks, and in fact, not a single cluster of activation reached significance in a direct comparison of encoding-maintenance activity during JOR vs. JOP.

The retrieval period was also investigated in comparison to the ITI, separately for each task, and between tasks. The retrieval period of both JOR and JOP yielded increased activations in several areas when compared to the ITI. These areas included bilateral regions of the premotor cortex (BA 4, 6), the right prefrontal cortex (BA 9), and the posterior portion of the left cingulate gyrus (BA 23). A few regions also showed higher activity levels during the ITI than retrieval, including the medial temporal lobe, the inferior frontal gyrus (in BA 47), and posterior parietal

Figure 7. Exp. 2: Encoding- Maintenance and Retrieval Activation Patterns.
lobe (BA 7, 40). Again, activations were highly consistent across the JOR and JOP tasks, and there were no significant clusters of activation that varied significantly in a direct comparison of retrieval-related activity between tasks. Notably, overall activation patterns in both the encoding-maintenance and retrieval periods were consistent across tasks, and also consistent with a network of regions in the frontal and parietal lobes observed in numerous other fMRI examinations of WM (Chein et al., 2003; Owen et al., 2005; Wager & Smith, 2003).

FMRI Examination of Primacy and Recency Effects within Tasks

The neural correlates of the behavioral primacy and recency effects were examined by analysis of trial activity dependent on the serial position of the correct probe. FMRI analysis of primacy and recency effects focused on activation during the retrieval period of the task. Primacy and recency effects were defined in the same manner as the behavioral analyses. Recency effects compared fMRI signal on recency item trials and middle item trials primacy while primacy effects compared fMRI signal on primacy item trials and middle items trials (see Table 1). Importantly, fMRI contrasts exploring recency effects showed no above threshold differences between recent and middle item trials in either the JOR or JOP task. Additional analyses were conducted in order to further probe recency effects. These included comparison of the recency item to only the immediate item preceding it (i.e., item 3 in JOP and item 4 in JOR), and comparing recency items trials to all other trials. These analyses also failed to show above threshold clusters of activation. Therefore, in this pool of subjects, there were not distinct neural correlates of trials probing the most recent item when compared to trials probing other items.

On the other hand, neural correlates of the primacy effect were found in both the JOR and JOP tasks (Table C3, Table C4). In JOR, regions in the right premotor cortex (extending through frontal areas associated with BA 4 and 6), and right occipital/fusiform gyri (BA 18, 19, 37)
displayed higher activation for primacy trials than middle trials. Figure 8 depicts a region in the right premotor cortex exhibiting differential activation across primacy and middle trials. In addition to these regions, a few regions showed significantly different levels of deactivation (i.e., activation below baseline), including the left anterior cingulate (BA 32, BA 24) and the right inferior frontal gyrus (with a peak activation in BA 47 and extending through portions of BA 45). This investigation of primacy effects in a JOR task did not reveal above threshold cluster with higher activation in middle items than the primacy item.

Figure 8. Exp. 2: Neural Correlates of Primacy in a JOR Task.

In the case of JOP, there were also neural markers of the behavioral primacy effect, but importantly, the pattern of results was different from that obtained with the JOR task. For JOP, significantly lower activation for primacy item trials than for middle items trials was found in
several areas, including the left premotor cortex (lateral portions of BA 6 and BA 4), SMA (medial portions of BA 6 and BA 32), and dorsolateral prefrontal cortex (BA 46) (Figure 9).

Figure 9. Exp. 2: Neural Correlates of Primacy in a JOP Task.

Contrasts also compared the retrieval period of primacy and recency item trials to each other (Table B3, Table B4). The purpose of these contrasts was two-fold, to compare the neural mechanisms of retrieval of the earliest and latest items, and also to “complete the set” of comparisons between the three trial types (primacy item trials, middle item trials, and recency item trials). In each case, regions were very consistent between the primacy and recency probe trials, and only areas of the right occipital and fusiform gyrus (BA 17, 18) varied between
primacy and recency items. In JOR, activity was higher for the primacy item than the recency item, and while in JOP it was higher for the recency item than the primacy item.

Serial Position Effects across Tasks

In the above analyses there was no evidence for differential activation of any region in association with the behavioral recency effect. However, investigation of activation differences that might underlie primacy effects within each task suggested task-dependent differences. While JOP showed decreased activation for the primacy item trials relative to middle item trials, JOR revealed a distinct set of areas where there was increased activation for primacy item trials relative to middle item trials. In order to more formally test whether task-demands affect the neural signature of serial position effects, ANOVAs comparing the effects (recency, primacy) observed in each task were conducted. The first ANOVA included recency effects (JOR: items 3, 4, 5; JOP: items 2, 3, 4) across task (JOR, JOP), while the second examined primacy (JOR: items 2, 3, 4; JOP: 1, 2, 3) across task (JOR, JOP). The results of interest regarded the task by effect-type interaction (Table B5, Table B6).

A single inferior frontal region (BA 9/44) showed a significant task by recency effect interaction. The source of this interaction was explored through comparison of fMRI signal change (against baseline) in each of the serial positions of interest. However, contrasts revealed that neither JOR nor JOP showed a difference between the recency trial and the middle trials (JOR: $F_{(1, 27)} = 2.32, p = .14, \eta^2_p = .08$: JOR: $F_{(1, 27)} = 1.78, p = .20, \eta^2_p = .06$). Instead this task by serial position interaction was driven by a difference between performance on middle trials that was found in JOR ($F_{(1, 27)} = 20.60, p < .005, \eta^2_p = .43$) and not in JOP ($F_{(1, 27)} = .12, p = .72, \eta^2_p = .01$). In other words this difference was not driven by a difference in the neural response for retrieval of recency items.
Additional support for the task-dependant nature of the neural correlates of primacy was provided by the serial position by task ANOVA. Specifically, 9 different regions showed a task by effect-type interaction, including a medial frontal cluster extending through the supplementary motor area and the dorsal anterior cingulate cortex (BA 6, 8, 32), bilateral regions in the inferior frontal gyri in BA 46 that extends through BA 9, and a region in the right middle frontal gyrus (extending though BA 6 and 9). Investigation of the source of the task by serial position interaction corroborates the within task findings regarding primacy. In 7 of the regions of the 9 significant clusters of activation, JOP showed less activity associated with retrieval during primacy items trials than retrieval during middle item trials. In JOR one of two patterns emerged, no difference between primacy and middle trials or stronger activation during primacy item trials than middle item trials. This pattern is illustrated in a region of the medial frontal cortex (SMA, Figure 10), in a region overlapping with one implicated in the within task primacy effect analyses. A significant neural primacy effect was found in JOP \( F(1,27)= 15.28, \ p = .001, \eta_p^2 = .26 \), but no such difference was found in JOR \( F(1,27)= .02, \ p = .899, \eta_p^2 = .00 \).

Figure 10. Experiment 2: Neural Correlates of Primacy a cross Task-Demand.
Discussion

Consistent with the findings from the first experiment, the comparative size of the behavioral primacy and recency effects shifted with the demands of the task. Once again, while JOR yielded larger recency effects than JOP, JOP yielded larger primacy effects than JOR. Therefore, both experiments provide evidence that the presence of primacy and recency effects does not signal some immutable trait of WM, but rather, indicates a task-dependent emphasis on different items in the list. Also of note, while in Experiment 1 overall primacy and recency effects were of similar sizes (as revealed by the effect-type by task ANOVA); in Experiment 2 there was a relatively larger primacy effect than recency effect. Therefore, across experiments there was both similarity, and some variation in the profile of behavioral primacy and recency effects. This once again prompts caution when interpreting primacy and recency effects as unyielding factors in WM.

Imaging analysis of the encoding-maintenance and retrieval periods of JOR and JOP showed very consistent patterns of activation across tasks, and only when specific serial positions were considered did differences emerge. Examination of the encoding-maintenance and retrieval periods of JOR and JOP showed bilateral frontal (BA 4, 6, 32), and parietal lobe (BA 7, 40) activations consistent with numerous prior investigations of WM (Owen, et al., 2005; Wager & Smith, 2003). A newer development to the fMRI literature on WM indicates a role of the MTL (Cabeza, et al., 2002; Ranganath, et al., 2004; Ranganath & D'Esposito, 2001). The present study did not find positive activation of the MTL, and in fact, found significantly less activation in bilateral regions of the MTL than at rest.

Crucial to the present work was elucidation of the neural correlates of primacy and recency effects. Importantly, imaging contrasts failed to identify any brain regions where activity
specifically varied in association with retrieval of an item in the recency position (e.g., a recency effect). This finding is consistent with the small behavioral recency effect reported in this cohort of subjects, but is inconsistent with the prior literature on the neural markers of recency effects (Oztekin, et al., 2009). A more thorough comparison of the present and past findings is presented in the general discussion.

In contrast to a null result with respect to recency, contrasts revealed differences in fMRI signal that could be linked to the primacy effect. In the case of JOR, higher activation during primacy item trials than middle item trials was found in regions of the right premotor cortex (BA 6 and 4) and the right fusiform gyrus. Notably, in JOP, fMRI signal was lower for primacy item trials than middle item trials in regions including the left premotor cortex (BA 4, 6) and SMA (BA 6, 32). Consistent with this apparent task-dependent pattern, a direct analysis of the interaction between neural signatures of the primacy effects and task (JOR and JOP) revealed an interaction in a group of regions including the SMA (BA 6, 32), and SMA and right inferior frontal gyri (extending from BA 46 to BA 6 and 9). Further exploration of the SMA (and several other areas) showed that this interaction resulted from weaker activation for primacy item trials than middle item trials in JOP, but no such difference for JOR.

To summarize, neural correlates of a primacy effect appeared in both JOR and JOP, but there was task specificity in the direction and spatial localization of these phenomena. Importantly, both the SMA and premotor cortex (implicated in the analyses above) are associated with sub-vocal repetition or rehearsal of items at encoding, maintenance, and retrieval during WM performance (Awh et al., 1996; Chein & Fiez, 2001; Paulesu, Frith, & Frackowiak, 1993). Therefore, the primacy effect associated with differential activation of these regions may be linked to the dependence on rehearsal processes at the time of retrieval. Specifically, in JOP,
when the first item is the correct answer subjects do not engage rehearsal processes as strongly as they do for middle item trials. This trend appears specific to JOP since in JOR the primacy effect was associated with higher activation the right premotor cortex. In fact, in JOR, the premotor cortex (on the right side) showed more activation during primacy item trials than middle trials, and speculatively, this may suggest stronger rehearsal processes in primacy item trials than middle item trials. Together, these findings support the conclusion that differences in phonological rehearsal of items at test are associated with primacy effects, but the directionality of this effect is task-specific.

Contrasts also compared fMRI signal for retrieval of primacy and recency item trials. These contrasts inform whether the primacy and recency items are retrieved via similar or different neural processes. Retrieval was quite consistent between these two trial types, and the contrast produced above threshold differences in only the right fusiform gyrus. Regarding the finding in the fusiform gyrus, the primacy item showed less activity than a later item in JOP, and more activity than a later item in JOR. The fusiform gyrus has been associated with reading, visual recognition, and access in memory to verbal memoranda (McCandliss, Cohen, & Dehaene, 2003; Pernet, Celsis, & Démonet, 2005). Therefore, this activity could be linked to either processing of the retrieval probe, or accessing of the memory items.

In sum, Experiment 2 yielded two main findings. First, like Experiment 1, there was an effect-type by task interaction showing larger primacy in JOP and larger recency in JOR. Second, FMRI contrasts demonstrated task specific neural correlates of the primacy effect, which differed between JOR and JOP. These findings suggest that models of WM should consider the flexible allocation of WM components according to the demands of the task, and also the
cognitive status of the first item in a list. Specific, statements concerning these findings and specific models of WM are in the General Discussion.
CHAPTER 4
GENERAL DISCUSSION

The present work examines claims that the focus of attention, the most immediate state of WM, is limited to a single item. Evidence for this limited focus of attention is drawn from observation of recency effects (McElree, 2006; McElree & Dosher, 1993; Oztekin, et al., 2009). Here, I investigated both recency and primacy effects and asked the following questions. Are the qualities of recency and primacy effects consistent across different manipulations of assessment (e.g., task-demands, strategy, and information type)? And should recency effects and/or primacy effects be interpreted as indicative of the focus of attention?

The experiments above yielded several main findings. First, simply, behavioral evidence of both primacy and recency effects were found in two WM tasks, JOR and JOP, and in two domains, verbal and spatial. Although both serial position effects were identified, the comparative size of these effects shifted with some of the manipulations in the present study. In the case of verbal information, both experiments indicated a shift in the comparative size of primacy and recency effects across task (larger recency effects in JOR than JOP and larger primacy effects in JOP than JOR). In the spatial realm, the significant task by effect-type interaction indicated a larger recency than primacy effect in JOR but equally sized primacy and recency effects in JOP. Regarding the comparison between verbal and spatial realms, two findings stand out. First, spatial tasks show less evidence of primacy effects than verbal tasks, and second, performance was near chance on middle item trials in the spatial tasks, indicating some trouble maintaining the entire set of five locations. Still, examination of verbal and spatial WM tasks suggests flexible allocation of WM resources, shown by changes in the magnitude of primacy and recency effects, in accordance with task-demands.
Formal statistical analyses were not conducted across the first and second experiments, but the first experiment showed primacy and recency effects of similar sizes, while the second experiment showed larger primacy effects than recency effects. The prominence of primacy effects in only the second experiment could be tied to a few differences between the experiments. Different cohorts of subjects were used (from two different Universities), and therefore, differences in the size of the primacy and recency effects may be related to the characteristics of an individual. Additionally, while the first experiment was conducted in a behavioral testing room, the second experiment was conducted in an MRI scanner, and the allocation of memory processes may vary inside and outside of the MRI environment. Differences in the subjects themselves, the testing environment, or some combination could lead to differences in the size of primacy and recency effects. Regardless of the cause, these results indicate that there can be variation in the magnitude of serial position effects, which raises some doubt that these phenomena alone can be relied upon as markers for fixed properties of WM.

In the case of strategy, neither strategy distribution differences across task nor performance differences across strategy were found. In Experiment 1, performance was equivalent across maintenance-based and retrieval-based strategies. In Experiment 2, there was such a prevalence of maintenance-based strategies that performance and neural correlates could not be fairly compared between strategies. Importantly, several other approaches to studying strategy exist in the WM literature, including: instructing subjects to engage in a predetermined strategy (McNamara & Scott, 2001), allowing subjects to control the pace of item presentation and measuring looking time to infer the amount of strategic processing (Engle, Cantor, & Carullo, 1992), designing stimuli and tasks which promote a particular strategy (Bor, Cumming, Scott, & Owen, 2004), and also questionnaires with different categories of strategy than the
one’s constructed for the present experiments (Dunlosky & Kane, 2007). Further investigations with different methodology may reveal differences in serial position effects across strategy.

Imaging analyses of the encoding-maintenance and retrieval periods of JOR and JOP revealed activation patterns consistent with a network of frontal and parietal regions which is commonly implicated in maintenance, monitoring and updating of information in WM (Chein, et al., 2011; Miller & Cohen, 2001; O'Reilly & Frank, 2006). Moreover, consistent with previous studies (Chein & Fiez, 2001; Kruggel, Zysset, & Von Cramon, 2000; Rypma & D’Esposito, 1999), several of these frontal cortex regions were activated at both the encoding-maintenance phase and also the retrieval phase of the task. Frontal activation in regions such as the SMA and premotor cortices can be interpreted as a reflection of phonological rehearsal of items during the encoding-maintenance phase, and a sub-vocal review of the items at the time of test. Parietal activations may reflect the allocation of attention and/or the load of information present in the task. Posterior parietal activations have been implicated in completion of attentionally demanding tasks (Naghavi & Nyberg, 2005) and the use of attention to maintain task-relevant information in an active state (Berryhill, Chein, & Olson, 2011). Moreover, a region of the parietal lobe, the intraparietal sulcus (BA 40), has been shown to increase in activity as the load of information in a task increases (Cowan, et al., 2011; Todd & Marois, 2004, 2005).

The present study did not reveal increased activation of the MTL during either encoding-maintenance or retrieval (when compared to activity during the ITI). This is inconsistent with recent studies examining both JOR (Oztekin, et al., 2009) and item recognition tasks (Nee & Jonides, 2008, 2011; Oztekin, et al., 2010). Importantly, investigation of the role of the MTL in WM is rather new to the study of WM and its neural underpinnings. Many of the demonstrations of the role of the MTL in WM occurred in studies where items were unfamiliar, complex, or
involved relational processing (Cabeza, et al., 2002; Olson, et al., 2006; Ranganath, et al., 2004). For example, two recent examinations showed MTL activation during performance on complex span tasks, which interweave each item in a list with an unrelated processing task (Chein, et al., 2011; Faraco, et al., 2010).

Together these findings point towards a possible interpretation of the role of the MTL in WM. Perhaps the MTL is recruited when other mechanisms, such as those that support active maintenance, are exhausted. It follows that the tasks here may not have adequately targeted the MTL, because resources used to maintain and rehearse items were not exhausted. High levels of accuracy in these subjects and the reports of an active-maintenance strategy (over a retrieval-based strategy) indicate that subjects were able to actively rehearse or maintain the items. Further research is necessary to elucidate the precise role of the MTL in WM performance and whether there are specific conditions when the MTL is engaged in WM.

Neural Correlates of Recency and Primacy

The most surprising finding in the present study was likely the lack of a neural signature for the behavioral recency effect in either task. This is in stark contrast to earlier studies that show neural correlates of a recency effect and deem the final item in a list present in the focus of attention (Oztekin, et al., 2010; Oztekin, et al., 2009). One conclusion that can be drawn from the absence of neural markers of a recency effect is that the focus of attention is not necessarily tied to last item in a list, and I favor this conclusion.

An opposing explanation is that performance in the present task was not appropriate to measure the focus of attention due to evidence of phonological rehearsal by subjects. Prior literature suggests that the most pure methods of measuring the focus of attention are when rehearsal processes are limited (Cowan, 2001). Accordingly, the JOR task in the present study
was designed by researchers to “eliminate or minimize engagement in maintenance rehearsal operations, so that retrieval specific differences in neural activation across tasks and [serial position] could be examined without confounding effects of encoding and maintenance operations” (Oztekin et al., 2009, p. 583). Importantly, although the JOR task was nearly identical to the one used by Oztekin and others (2009) and the JOP used identical timing procedures, the pattern of brain activation and the reports of rehearsal in the present study suggest that rehearsal operations were present. It follows that one interpretation of the results is that the presence of supplementary rehearsal processes obscured measurement of a single item focus of attention tied to the final item. However, one goal of the present work is illuminate the architecture of WM states, and as rehearsal processes and/or their neural correlates are so often present during WM performance, (Baddeley, Gathercole, & Papagno, 1998; Camos, et al., 2010; Davachi, Maril, & Wagner, 2001; Wager & Smith, 2003), I argue their presence need not invalidate measurement of the underlying structure of WM.

In contrast, neural correlates of the behavioral primacy effect were observed in both JOR and JOP. In JOR, a region in the right premotor cortex (BA 4 and 6) showed greater activation during the retrieval period in primacy item trials than middle item trials; whereas, in JOP, regions of the left premotor cortex and SMA showed less activation during retrieval in primacy item trials than middle item trials. Additional analyses demonstrated a task by effect-type interaction in regions such as the SMA (BA 6, 8, 32) and right and left inferior frontal gyrus in BA 46.

Several of these regions, including the SMA and left premotor cortex, are strongly implicated in phonological rehearsal of items (Awh, et al., 1996; Smith & Jonides, 1998). It follows that one explanation of the primacy effect links it to variation in rehearsal processes at
the time of retrieval. In JOR, activity was higher for the primacy item trials than middle item trials, and in JOP, activity was lower for primacy item trials than middle item trials. Finding either the pattern associated with JOR or the pattern associated with JOP would lead to a directional prediction about the relationship of rehearsal processes to the primacy effect. However, together the findings from JOR and JOP tell a more complex story about the neural correlates of primacy.

At least two accounts could explain these task-related differences, one related to task-demand and another related to capacity limits. In regards to task, the JOR and JOP tasks might engage rehearsal processes differently, leading to differences in the source of the behavioral primacy effect. For example, in JOP, subjects might direct more rehearsal efforts towards earlier items on the list during encoding. If the earliest item is well rehearsed and encoded, it may require less rechecking via rehearsal at test than items that were not as well rehearsed. In contrast, the objective in a JOR task might direct subjects away from rehearsing earlier items, and a primacy effect could emerge from stronger rehearsal processes at test.

In a different but related explanation, the neural correlates of primacy found in JOP might be specific to the very first item in a list, which is not the primacy item in JOP (see Table 1). This interpretation indicates a one item capacity for this sort of primacy effect. If this were so, then the primacy effect in JOR would arise from a separate mechanism. Again, this account could be linked to stronger rehearsal processes for primacy item trials (in JOR) and less a necessity of rehearsal processes for primacy item trials (in JOP).

The present results cannot distinguish between explanations. However, the novel findings above present a hypothesis that primacy effects in WM could be tied to the strength of active-maintenance processes during the retrieval period of WM tasks. Moreover, the task dependant
effects found here suggest that focusing on a single task could lead to a simpler but potentially misleading story.

Comparison of Past and Present Methodologies

While the present experiment was meant to replicate and extend Oztekin et al., (2009), a few differences in methodology across between these two studies should be noted. Importantly, the verbal JOR task in the present study was nearly identical to the task from Oztekin and others (2009). The one exception was that 16 rather than 20 consonants were sampled in the present study. Sixteen consonants were chosen to mirror the 16 spatial locations in the spatial tasks.

The overall experimental sessions differed in two ways, one related to task practice and another related to the ordering of different trial types in the session. In Oztekin et al., (2009) subjects practiced the task for 45 minutes (compared to 5-10 minutes in the present study). Moreover, in many of the earlier behavioral studies of JOR even higher levels of practice were involved (Hacker, 1980; McElree & Dosher, 1993; Muter, 1979). For example, in Experiment 1 of McElree & Dosher (1993), subjects completed 20, 75 minute, sessions, and in Hacker (1980) subjects completed 75, 5 minute sessions. Importantly, larger amounts of practice may have lead to different performance levels and or approaches to the task. For example, extensive practice with a task may prompt subjects to extend less effort to sustain items in a heightened state at encoding. Instead subjects could learn to rely more on retrieving some or the entire list of items during the retrieval period.

Another key difference between the present paper and Oztekin et al., (2009) was the intermixing of different trial types. In the present experiment, trial type was always blocked and strategy questionnaires were administered between blocks (giving subjects a short break from the mental set of the task). In contrast, Oztekin and others (2009) intermixed trials of item
recognition and JOR, and subjects did not know the requirement of the task until the retrieval probe was presented. Not knowing whether order or identity would be required at test may have led to a different task approach (or differential emphasis on WM processes). Importantly, Berryhill and others (2011) found that, when two tasks were administered in different blocks, differing strategies could be allocated to each one, whereas when the task varied, subjects reverted to a single strategy. In short, differences in the level of practice and the details of the session may have contributed to the differences in findings reported here and in past studies. If so, this is consistent with the suggestion that neural and behavioral signatures of WM are tied to the specific properties of a memory task.

The Structure of WM

What do these findings contribute to our understanding of the structure of WM and the focus of attention? This question can be broken into two sub-questions: is the primacy effect seen here indicative of the focus of attention? And how do these findings support or refute the three highlighted accounts of the focus of attention?

Here, distinct neural and behavioral characteristics of a primacy effect were reported in a verbal JOR and a JOP task, and behavioral indicators of primacy and recency were found in spatial JOR and JOP. Whether this primacy effect is indicative of the focus of attention is necessarily tied to the definition of the focus of attention. If the focus of attention is marked by a recency effect, and by weaker MTL engagement, then this primacy effect is certainly not the focus of attention. However, a more inclusive definition of the focus of attention defines it as the most immediate state of WM where item(s) are in a heightened state of activation (and can be retrieved faster than items outside of this state). If this more inclusive definition is adopted, then
the primacy effect seen here could in fact indicate a focus of attention, which contains item(s), at the beginning of the list.

The present results contribute to discussion of the three competing accounts of the focus of attention, McElree’s single item focus of attention (McElree, 2006; McElree & Dosher, 1989, 1993), Cowan’s multiple item focus of attention (Cowan, 1995, 1999, 2001), and Oberauer’s three level model of memory (Oberauer, 2002; Oberauer & Lange, 2009). Importantly, both Oberauer’s and McElree’s models suggest a one item focus of attention limited to the final item in a list. Therefore, the evidence of neural correlates of primacy only is inconsistent with the assumptions of these accounts. The behavioral recency effect could be seen as indicative of the focus of attention, but only if two factors were accommodated in Oberauer’s (2002) and McElree’s (2006) models, the presence of the primacy effect and the lack of neural correlates of the recency effects.

If these results do not support a single item focus of attention, do they instead support Cowan’s account of a multiple item of a focus of attention (Cowan, 1999, 1995, 2001)? In some sense these findings are quite in line with a multiple item focus of attention. Subjects responded with high accuracy to trials presenting five different items in an immediate memory task. Moreover, fMRI shows activation of frontal and parietal regions associated with WM task performance (Owen, McMillan, Laird, & Bullmore, 2005; Wager & Smith, 2003) and not regions like the MTL and associated with retrieval from longer term memory (Golby et al., 2001; Hermann, Seidenberg, Wyler, & Davies, 1996; Schacter & Wagner, 1999). Therefore, one interpretation of these results is that several of the items in the JOR and JOP tasks were in the focus of attention, a heightened state of awareness separate from long-term memory. Notably,
this argument involves dismissal of recency or primacy effects as a necessary marker of the focus of attention.

On the other hand, a multiple item focus of attention is plausible even if primacy and recency effects are considered signatures of the focus of attention. For example, the behavioral findings of significant primacy and recency effects within the same task could indicate a focus of attention of more than one. Also, together, these past and present fMRI finding indicate that both neural correlates of recency and primacy can occur in certain memory scenarios. A remaining question is whether distinct neural correlates of both primacy and recency effects can be found within the same task.

The results above do not suggest a distinct cognitive status (e.g., the focus of attention) tied to the last item in a list. Instead these results suggest both primacy and recency effects as well as task-dependent differences in performance metrics. Consequently, as the data here shows a more complex story than prior studies (Oztekin, et al., 2010; Oztekin, et al., 2009), one should proceed with caution when interpreting recency effects as a stable, immutable mark of the architecture of WM.
References


APPENDIX A: SELF-REPORT STRATEGY ASSESSMENT

Strategy Assessment Interview: Form A

Subject Number:
Task:

Individuals differ in the strategies they use to remember information. The following questions are meant to determine the primary strategy you used to perform the task you just completed.

Each question will describe two types of individual. For each question please decide which sort of person you are more like: if you don’t understand I can repeat the descriptions or clarify further. After I read the descriptions, please tell me if you really like the first person, sort of like the first person, sort of like the second person, really like the second person, or cannot answer.

The task can be broken into two components: the part where the letters/dots initially appear, and the part where you see two items and are asked to respond. For this question please focus on the period of time that the letters/dots were initially appearing. Here is the first pair of descriptions.

Person A: I noted the letters/locations as they appeared, and then waited until I was asked to respond before I thought back to them.

Person B: I tried to actively and continuously think about the presented letters/locations so that they would already be in mind when I was asked to respond.

Are you, really like the first person, sort of like the first person, sort of like the second person, really like the second person or cannot answer?

A: Really like A:
A: Sort of like A:
B: Sort of like B:
B: Really like B:
I cannot answer:

Some people may feel they used both strategies but settled into one as their primary strategy. Would you say you used exclusively the strategy you indicated or both? If so, at what stage did you choose your primary strategy?

[Diagram showing time progression from earlier to later, with options for selecting points within Person A]
You just told us: I noted the letters/locations as they appeared, and then waited until I was asked to respond before I thought back to them. I’ll again read two descriptions. After I read the descriptions, please tell me which person you are more like. For this question please focus on the period of time that the letters/dots were initially appearing.

Person A1: When I thought back, I tried to remember the specific sequence of letters/locations.

Person A2: I simply made my response based on which letter/location felt most or least familiar. Are you, really like the first person, sort of like the first person, sort of like the second person, really like the second person, or cannot answer?

A: Really like A1:
A: Sort of like A1:
B: Sort of like A2:
B: Really like A2:
I cannot answer:

Within Person B
You just told us: I tried to actively and continuously think about the presented letters/locations so that they would already be in mind when I was asked to respond. I’ll again read two descriptions. After I read the descriptions, please tell me which person you are more like.
Person B1: I tried to silently repeat (visually imagine) all of, or a portion of, the sequence after each letter/location appeared.
Person B2: I strongly attended to each successive item, and tried to keep attention focused on the sequence of items.

Are you, really like the first person, sort of like the first person, sort of like the second person, really like the second person, or cannot answer?

A: Really like B1:
A: Sort of like B1:
B: Sort of like B2:
B: Really like B2:
I cannot answer:
APPENDIX B: ANALYSES BY THE SERIAL POSITION OF THE CORRECT AND INCORRECT ITEMS

In chapters 2 and 3, performance was shown to vary by the position of the correct probe. This approach was used by Oztekin and others (2009) who found little impact of the serial position of the incorrect probe. Here, the serial position of both probes (correct and incorrect) is considered. Trials were grouped by pairs of probes (i.e., the serial position of the correct and incorrect probe; see Figure 4).

Experiment 1

Average reaction times divided by the serial position of the correct and incorrect probes are provided in Figure B1. Planned contrasts explored whether, holding the correct position constant, differences emerged according to the incorrect serial position. Analysis of the JOR task focused on pairs of trial which included position 5 as the correct probe, while analysis of JOP included position 1 as the correct probe.

Contrast tested whether performance varied by the distance of the two probe items (correct and incorrect) from each other. For JOR, contrasts compared performance on trials presenting positions 5 and 1 (high distance) to trials presenting 5 and 4 (low distance). In the case of verbal JOR performance only trended towards significance \((F_{(1,28)} = 3.48, p = .073, \eta^2_p = .110)\), while in spatial JOR there was a significant difference between performance \((F_{(1,25)} = 8.97, p = .01, \eta^2_p = .26)\). However, while in verbal trials performance was faster for high distance trials than low distance trials, in spatial trials there was significantly faster performance on low distance trials than high distance. In the case of JOP, similar contrasts focused on trials where position 1 was the correct probe. Contrasts compared performance on trials presenting positions
1 and 5 (high distance) to trials presenting 1 and 2 (low distance). For verbal JOP, there was a trend toward significance showing faster performance for items low distance trials \((F(1,26) =3.17 , p=.09 , \eta^2_p = .105)\), and in spatial there was significantly faster performance for high distance trials than low distance trials \((F(1,25) =14.15 , p<.005 , \eta^2_p = .352)\). Together these findings indicate that low distance and high distance pairs sometimes differed in speed, but that sometimes low distance pairs were faster and other times high distance pairs were faster.

**Figure B1. Exp 2: Analysis of mean reaction times by correct and incorrect probe position.**

Experiment 2

Analyses mirroring those in Experiment 1 were conducted on Experiment 2. Figure B2 shows reaction times when trials are divided by the serial positions of both items in the probe.
Analyses also considered whether performance differed by the distance between the correct and incorrect item positions. In JOR, trials with a larger distance between probes (5, 1) did not vary from lower distance probes (5, 4) ($F_{(1,27)}= 2.20$, $p=.15$, $\eta^2_p = .08$). In JOP, performance was faster for low distance trials (1,2) than high distance trials (1,5)($F_{(1,27)}= 8.82$, $p=.01$, $\eta^2_p = .25$). As in Experiment 1, there was not a consistent pattern of either high distance or low distance pairs.

Figure B2. Exp 2: Analysis of items by correct and incorrect probe position.
Table C1. Judgment of Recency: Activations associated with the Encoding-Maintenance and Retrieval periods when compared to the ITI.

### Judgment of Recency

<table>
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<tr>
<th>Location</th>
<th>BA</th>
<th>p-value</th>
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<th>y</th>
<th>z</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Right Fusiform Gyrus</td>
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Table C2. Judgment of Primacy: Activations associated with the Encoding-Maintenance and Retrieval periods when compared to the ITI.

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Table C3. Judgment of Recency: Serial Position Contrasts. Note: Areas in italics denote differing levels of deactivation.

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2 < 3 & 4 (None)

2 > 5

| Right Fusiform Gyrus                          | 18,19,37| 0.001   | 40.5  | -67.5 | -15.5 |

2 < 5 (None)
### Table C4. Judgment of Primacy: Serial Position Contrasts.

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### Table C5. Primacy Effect: Task (JOR, JOP) but serial position (middle and recency item trials) Interaction

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### Table C6. Recency Effect: Task (JOR, JOP) but serial position (middle and primacy item trials) Interaction

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