THE NEURAL MECHANISMS OF VISUAL SHORT-TERM MEMORY CAPACITY

By

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Dissertation

Submitted to the Faculty of the

Graduate School of Vanderbilt University

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

in

Psychology

December, 2008

Nashville, Tennessee

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ACKNOWLEDGEMENTS

This dissertation represents the culmination of my intellectual development as a member of the Human Information Processing Laboratory, under the leadership of Dr. René Marois. I remain indebted to Dr. Marois for his commitment to my future in cognitive neuroscience. I am also grateful for the opportunity to have worked with a world-class community of psychologists and neuroscientists at Vanderbilt University.

Thank you to my family and friends, who followed and encouraged me through the years. It was during the course of my education that I learned the true value of my grandfather's sage words, "Think nice thoughts and don't grow old." Garrison Keillor paraphrased this advice in a personal correspondence, and I believe it captures the quintessence of all things great and small, including graduate school: "Onward."

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PREFACE

OVERVIEW OF THE DISSERTATION

The goal of this dissertation is to provide insight into the neural mechanisms of visual short-term memory (VSTM) capacity. VSTM refers to the holding of information in mind for a brief period of time. Although we generally behave as if we are able to store a comprehensive representation of a visual scene in memory, these representations are anything but detailed (Intraub, 1997; Mack & Rock, 1998; Simons & Levin, 1997). This is partly due to some of this information being held in VSTM, which is capacity-limited. In fact, we can only maintain about four objects in VSTM (Cowan, 2001; Luck & Vogel, 1997; Pashler, 1988; Todd & Marois, 2004). Besides maintenance, VSTM is also limited by the speed by which representations are consolidated into storage (Vogel, Woodman, & Luck, 2006). This has been implicated as the locus of deficits in information processing in the temporal domain (Chun & Potter, 1995; Jolicoeur, 1998). Using functional magnetic resonance imaging (fMRI), a number of studies have investigated the neural network supporting these two capacity-limited VSTM phases (e.g., Cohen et al., 1997; Jha & McCarthy, 2000; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Linden et al., 2003; Marois, Chun, & Gore, 2000); however, the question still remains: What brain regions are sensitive to the amount of information that is being consolidated to, and held in, VSTM?

CHAPTER I explores the neural correlates of VSTM maintenance capacity limits. Through a series of experiments, it is revealed that only one region, in the parietal cortex, consistently tracks the amount of information held in VSTM. Although other brain regions support maintenance-related processes, this parietal region appears to be the only

one indexing VSTM capacity. Several control experiments rule out alternative explanations for its load-sensitive activation profile.

CHAPTER II explores the relationship of VSTM maintenance and selective attention. Neuroimaging studies show a close relationship between the neural correlates of attention and STM (Corbetta, Kincade, & Shulman, 2002; LaBar, Gitelman, Parrish, & Mesulam, 1999). Here, it is shown that a brain region that supports attentional capture by unexpected and task-irrelevant stimuli is also modulated by VSTM maintenance capacity. Whereas the activity of the region localized in CHAPTER I is positively correlated with VSTM capacity, this other region's response is negatively correlated with the amount of information held in VSTM. This led to an explicit hypothesis linking VSTM maintenance load and attentional capture, which was validated in a behavioral experiment.

In CHAPTER III, the role of VSTM consolidation capacity in limiting our explicit experience is explored. Previous work has shown that our ability to detect the second of two serially presented targets is severely impaired when the second target (T2) is presented shortly after the first target (T1) (Raymond, Arnell, & Shapiro, 1992). Coined the "attentional blink", one prominent model attempting to account for this deficit argues that the time-dependent process of STM consolidation plays a crucial role in causing T2 to pass by unnoticed (Chun & Potter, 1995; Jolicoeur, 1998). This chapter explores the relationship of VSTM consolidation and our awareness of briefly presented, temporally proximate events.

After demonstrating how the duration of consolidation can limit our experience of transient events, CHAPTER IV presents a series of fMRI experiments focused on identifying brain regions that are sensitive to the amount of information consolidated into

VSTM. Two difference approaches are employed. The first approach takes advantage of evidence for the dissociation of VSTM consolidation and maintenance (CHAPTER III; Woodman & Vogel, 2005). The brain was probed for regions whose peak amplitudes of activation reflect the amount of information consolidated into VSTM, while also being insensitive to maintenance-related processes. The second approach takes advantage of consolidation being a time-consuming process (CHAPTER III). Using time-resolved fMRI, brains regions sensitive to the duration of consolidation are isolated. These regions are involved a host of processes related to processing task-relevant information (Duncan & Owen, 2000; Dux, Ivanoff, Asplund, & Marois, 2006). These regions have been shown to play key roles in the detection of the second target in the AB (Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004). Thus, this study is taken as neural support for a role of consolidation in limiting our awareness of temporally proximate events.

CHAPTER V provides an integrative review of the findings from Chapters I–IV, as well as a discussion of the implications of this body of research on VSTM capacity limits. I conclude with an examination of possible future directions of research based upon these findings.

CHAPTER I

THE NEURAL CORRELATES OF VSTM STORAGE AND CAPACITY LIMITS

Introduction

An exhaustive body of behavioral research demonstrates the existence of visual

short-term memory (VSTM) capacity limits (e.g., Cowan, 2001; Luck & Vogel, 1997;

Pashler, 1988; Phillips, 1974). While a vast network of cortical and subcortical brain

regions supports VSTM mechanisms (e.g., J. D. Cohen et al., 1997; Linden et al., 2003;

Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002), it is hitherto unknown which regions

track the amount of information being maintained in VSTM. Without supporting neural

evidence, it is unknown whether the limitation in our ability to explicitly recall our visual

experience (e.g., Rensink, O'Regan, & Clark, 1997; Simons & Levin, 1997) reflects a

global neural network property, or whether a subset of this neural network responds in a

capacity-limited manner.

For a brain area to index VSTM capacity, its activity must be proportional to the

amount of information held in VSTM. A demonstration of a symmetry between changes

in the activity of an area of the brain and a behavioral metric of the quantity of

information stored in VSTM will provide evidence for a neural underpinning of VSTM

capacity. That an area tracks VSTM capacity does not necessitate that the content of

VSTM is stored in that area. This area could retain a quantitative estimate of the

information being stored in VSTM, with qualitative values being stored elsewhere, such

as in the feature and category sensitive regions of ventral occipital-temporal cortex

(Epstein, Graham, & Downing, 2003; Kanwisher, McDermott, & Chun, 1997; Zeki et al., 1991). It could also coordinate these ventral brain regions, keeping track of what feature contribute to the information held in memory.

Substantial evidence supports the contribution of category-selective ventral posterior cortical regions in VSTM maintenance. The stimulus-selective recruitment of these and other ventral areas (Baylis & Rolls, 1987; Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, & Caan, 1982) during VSTM maintenance was first demonstrated in neurophysiological studies on non-human primates (Fuster, 1990; Fuster & Jervey, 1982; E. K. Miller, Li, & Desimone, 1991, 1993; Miyashita & Chang, 1988). Human neuroimaging studies using fMRI have localized category-sensitive modulation of maintenance related activity in a similar collection of regions. Ranganath, DeGutis, and D'Esposito (2004) showed that human inferior temporal (IT) brain regions increased and sustained their activity when observers were instructed to maintain the category-relevant feature in VSTM: When they were instructed to maintain pictures of different faces in memory, a region in the fusiform gyrus that is highly sensitive to faces (the fusiform face area (FFA); Kanwisher, McDermott, & Chun, 1997) was strongly recruited, but a more anterior region, lying within the parahippocampal gyrus (the parahippocampal place area (PPA); Epstein, Graham, & Downing, 2003), which is sensitive to representations of visual scenes (e.g., landscapes and houses), was suppressed during this task. In the same study, when subjects were instructed to remember pictures of visual scenes (photographs of landscapes), the PPA was strongly modulated by the task, but the FFA was not (Ranganath, DeGutis, & D'Esposito, 2004). Other studies have also demonstrated a role for ventral occipital and temporal regions in storage-related processes (Courtney,

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Ungerleider, Keil, & Haxby, 1997).

Non-human primate studies have also shown that prefrontal regions are critical to the maintenance of these stored representations. The recruitment of prefrontal regions appears to be related more to the processes of organizing and manipulating the content of STM than maintaining stimulus representations in memory (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Corbetta & Shulman, 2002; D'Esposito et al., 1995). Work by Miller and colleagues showed that competing and task-irrelevant stimuli can disrupt activity of IT neurons during the maintenance delay (E. K. Miller & Desimone, 1994; E. K. Miller, Erickson, & Desimone, 1996). Neuroimaging research using human participants corroborated these findings, showing that lateral prefrontal cortex is involved in the active maintenance and organization of VSTM content: Prefrontal regions play a more active role of maintaining and organizing information in VSTM, while ventral visual regions are more involved in processing perceptual information (Cornette, Dupont, Salmon, & Orban, 2001; Courtney, Ungerleider, Keil, & Haxby, 1997; Linden et al., 2003), which is consistent with the above neurophysiological studies. Specifically, an fMRI study showed that prefrontal and parietal, but not occipito-temporal, regions were sensitive to the amount of information that subjects had to actively maintain and organize in VSTM (J. D. Cohen et al., 1997), and prefrontal activity is positively correlated with task performance (Sakai, Rowe, & Passingham, 2002). To conclude, whereas IT areas are involved in perceptual VSTM processes such as feature and category processing, prefrontal areas play a more active role in organization and maintenance of VSTM content, especially when the observer must maintain information over an extended period of time or suppress or ignore possible distracting stimuli (Curtis & D'Esposito, 2003).

Parietal regions have also been implicated in tracking the amount of information maintained in STM, although a critical examination of the contribution of parietal regions in STM maintenance has not been performed. Unlike prefrontal areas, which are sensitive to the active maintenance of information in memory, activity in the parietal lobe may be sensitive to the passive (un-rehearsed) online maintenance of information (Linden et al., 2003; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). Within the parietal lobe, the intraparietal sulcus has been identified as a region whose activity may be sensitive to memory load (e.g., J. D. Cohen et al., 1997; Jha & McCarthy, 2000; Linden et al., 2003), and the amplitude of its maintenance-related activity predicts subjects' performance in VSTM tasks (Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). It is also sensitive to the detection of changes across visual scenes separated by brief lags in time, suggesting it may index memory load over time in attention-demanding tasks (Beck, Rees, Frith, & Lavie, 2001; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). Taken together, the parietal lobe may be the brain region most well-situated to index VSTM capacity for visual scenes.

A metric to index VSTM capacity limits.

Numerous brain regions are involved in supporting the maintenance of VSTM content, but no study has effectively proven that any region *indexes* VSTM maintenance load. The following set of experiments were designed to explore this by probing for regions whose activity is sensitive to how much information is being maintained in VSTM. To this end, VSTM capacity itself must be estimated. Most studies have used percent accuracy or *d'* to measure STM capacity (e.g., Jackson & Raymond, 2008; Luck

& Vogel, 1997; Sperling, 1960), but they have a major limitation. Treating memory load as the dependent variable, performance should reach asymptote at the memory load where the capacity limit is reached and level off with further increases in memory load (G. A. Miller, 1956); however, the magnitude of these two statistics typically continues to decrease as memory load increases.

To estimate the amount of information consolidated to memory (k), Pashler (1988) proposed a formula that was later modified by Cowan (2001). Cowan's (2001) k considers the probability that an observer is able to correctly encode the identity of information to memory (hit rate), distinguish it from information that was not to be encoded to memory (correct rejection rate), as well as correctly guess to-be-encoded from not-to-be-encoded information.[1] This k formula produces capacity estimates that tend to remain constant across capacity and supracapacity memory loads. This pattern applies to situations during which performance is affected only by consolidation and maintenance capacity limits.

Regardless of the strategy used to estimate VSTM capacity, there are limitations. First, by themselves, these formulae cannot distinguish between the amount of information consolidated into memory relative to the amount of information maintained in memory. This is an important distinction because the focus of this chapter is to localize brain regions that index VSTM maintenance capacity. The difficulty of separating consolidation and maintenance STM phases reflects these phases occuring prior to the reporting VSTM content and they are also temporally contiguous: Maintenance begins when consolidation ends (Woodman & Vogel, 2005). A simple solution to ruling out

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[1] k = (Hit Rate + Correct Rejection Rate − 1)*Set size

limitations in consolidation is to compare capacity estimates when the memory array's presentation duration is increased (Luck & Vogel, 1997). If there is a difference between performance when the memory array is presented briefly relative to very long (e.g., a doubling of its presentation duration), then this difference may be attributed to a limitation in the amount of time that is necessary to consolidate a given quantity of information into memory. A null effect of a difference in k values between short and long durations would preclude assertions that consolidating limitations resulted from abbreviated processing of the sensory or perceptual representations, because the amount of information transferred to memory was independent of how long the to-be-remembered stimuli were presented. If limitations in consolidation can be controlled, the factor most likely to define the capacity limit is maintenance capacity.

In the following set of experiments, the neural correlates of VSTM maintenance capacity limits are investigated. Acknowledging the distinction of consolidation and maintenance processes, considerable effort was made to investigate the maintenance component. Through careful control of numerous experimental parameters, VSTM maintenance capacity limits can be successfully investigated, at both the behavioral (e.g., Curby & Gauthier, 2007) and neural (e.g., Todd & Marois, 2004, 2005) levels. By determining k for different memory loads, brain regions whose activity indexes differences in the amount of content stored in VSTM can be localized.

Experiment 1: Fast-event related fMRI study to localize VSTM capacity-modulated brain regions

In this first experiment, the whole brain was probed for regions that were sensitive to the amount of information from an array of stimuli that was consolidated into, and

maintained in, VSTM. In an fMRI scanner, subjects performed a delayed match-to-sample task in which they were instructed to remember the identity and spatial location of a varying number of stimuli (referred to as memory load or set size), and following a brief delay, they were probed on the conjunction of identity and location of one of those stimuli (Luck & Vogel, 1997). To minimize the risk of subjects verbally encoding as much of the memory array as possible, which would inflate VSTM capacity estimates, subjects performed an articulatory suppression task (Baddeley, 1986, 1992). The resulting k values were estimated in order to determine subjects' capacity limits.

Following the analysis of behavioral data, the brain was probed for regions whose activity correlated with behavioral performance. By using the set of behavioral k values, i.e., the k function, as a model of changes in VSTM capacity, brain regions were localized that showed the same pattern of activity as the k function. Following this initial voxel-wise analysis, a region-of-interest (ROI) analysis was performed to examine the behavior of this candidate capacity-modulated region, in which the behavior of the ROI was subjected to multiple statistical tests. If a region is modulated by k, then the ROI analysis should reveal a load-modulated pattern of behavior in terms of the amount of activity, i.e., peak amplitude of activation, for each set size. Specifically, changes in the peak-of-activation across the different set sizes should resemble the behavioral k function. The details from this experiment have been published elsewhere (Todd, Fougnie, & Marois, 2005; Todd & Marois, 2004, 2005).

Methods

Participants. Seventeen individuals (8 males) from the Vanderbilt community

participated in this experiment for paid compensation. All subjects provided written,

informed consent. All had normal or corrected-to-normal visual acuity and reported that

they were not colorblind.

Behavioral task. Figure 1 shows a schematic of the trial design for this fast event-related

trial design. In the VSTM task, subjects were instructed to maintain as many of the

colored discs in memory as possible across a retention interval of 1,200 ms, after which

they were tested on the identity of one of the discs from the sample array. In order to

estimate visual VSTM capacities across sub- and supra-capacities, 1, 2, 3, 4, 6, or 8

colored discs were presented in the sample array for 150 ms. The discs were 0.38° visual

angle in diameter and were randomly distributed among nine possible locations in a 3 x 3
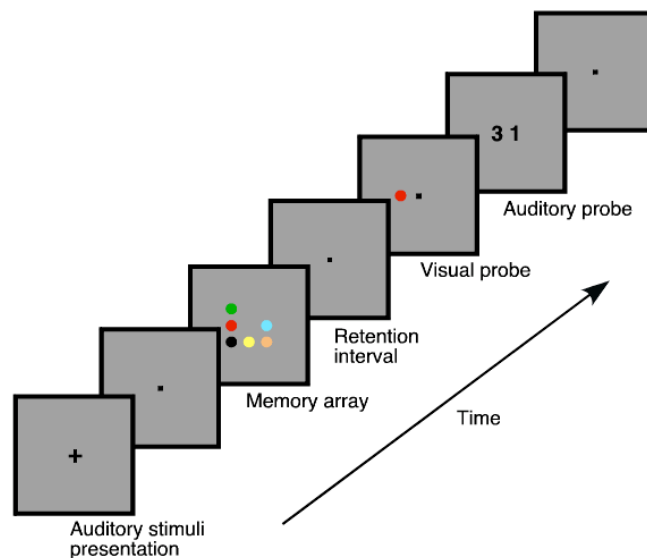
Figure 1. Sample trial for the fast event-related VSTM experiment. At trial onset, the
subject begins rehearsing two digits and continues throughout the trial. The subject
then encodes the colors and locations of a varying number of discs to memory.
Following a 1,200-ms retention interval, the subject decides if the probe disc's color
matches the color of that disc from the memory array. Finally, the subject indicates if
two digits presented at fixation match the two presented at trial onset.

matrix subtending 1.38° x 1.38°. The disc colors were randomly selected, without replacement, from a set of 10 distinct colors: white, black, dark blue, light blue, orange, yellow, red, pink, dark green, light green. Because a large color palette was used in this and the following experiments, luminance was not controlled, thus the inclusion of black and white. After a 1,200-ms retention interval, a probe colored disc appeared for 1,750 ms in one of the positions occupied by a disc in the sample display. Subjects indicated by button press whether the probe's color matched the sample color. When the probe's color was "different," it was randomly sampled from the nine remaining colors; half the probes' colors were from a disc in a different position in the memory array. The probability of the probe being "same" was 50%. Responses were made with the right index finger ("same") and middle finger ("different").

To discourage the verbal encoding of the colors and locations of the memory array stimuli, subjects concurrently performed an articulatory suppression task (Baddeley, 1992). At the beginning of each trial, prior to the presentation of the visual memory array, subjects heard two digits, which were randomly selected without replacement, from a set of ten possible digits (0–9). Each digit was presented for 250 ms, followed by a 250-ms blank interval and a 250-ms auditory mask. The mask was a composite of the ten digits presented in forward and reverse. A 1,400-ms fixation period followed the mask and preceded the visual memory array, in order to give subjects time to begin rehearsing the digits and prepare for the visual memory array. The articulatory suppression task was to subvocally rehearse (i.e., say to oneself) the digits individually and throughout the trial at a fast, but comfortable rate, approximately 2–3 times per second. After the subjects responded to the visual probe, two digits appeared in the center

of the display for 1,500 ms. Before the offset of the digits, subjects indicated if the two

digits were the same as, or different from, the two digits presented at the trial's onset.

Responses were made with the right index finger ("same") and middle finger

("different"). Following each trial there was a 1-s period of fixation before the onset of

the next trial.

In addition to the six set sizes, a no-event trial was included, during which only a

fixation dot was presented throughout the trial. The duration of this condition was 8 s, the

same as for the conventional trials. These seven conditions were counterbalanced: each

condition was equally preceded and followed by all possible conditions. This allows

differences between the conditions' responses to reflect event-related activity, as opposed

to effects of condition presentation order (Buckner et al., 1998; Dale & Buckner, 1997;

Kourtzi & Kanwisher, 2000, 2001). Inclusion of the no-event condition jitters the

intertrial intervals, increases the sampling rate of the hemodynamic response, and

increases the efficacy of extracting the hemodynamic response time courses for the

conditions (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Finally,

counterbalancing allows for the trial length to be shorter than the duration of the

conventional blood-oxygen-level-dependent (BOLD) time course (10-12 s), allowing for

more trials to be collected per unit time, which increases the statistical power (Dale &

Buckner, 1997).

FMRI parameters. The fMRI parameters used in all the studies presented herein are very

similar. For this reason, they will be presented in detail here, and only changes found in

later experiments will be presented in those methods sections. A 3-T GE MRI scanner

(GE Medical Systems, Milwaukee, WI) was used to acquire two-dimensional and three-dimensional (3-D) high-resolution T1-weighted (anatomical) images. In each functional run, 220 T2*-weighted echoplanar images were acquired in nineteen, 7-mm thick, axial slices covering the whole brain and prescribed parallel to the anterior-posterior commissural plane. In-plan resolution was 3.75 x 3.75 mm, with 0-mm skip. Repetition time (TR) was 2,000 ms, with a 25-ms echo time, 24-cm FOV, 64 x 64 matrix. Trial presentation was synchronized to TR onset by scanner trigger pulses. Trial stimulus presentation was controlled by an Apple G4 Macintosh using PsychToolBox for MatLab. Stimuli were back-projected onto a screen viewed by the subject lying supine in the MR scanner through a prism mirror.

Data analysis

Behavioral analysis. Memory capacity was estimated for each set size using Cowan's (2001) *k* formula.

FMRI analysis. Brain Voyager 4.9.1 (Brain Innovation, Maastricht, The Netherlands) was employed for the complete fMRI data analysis. Preprocessing included intrasession image realignment, 3-D motion correction, correction for slice scan acquisition order used sinc interpolation, and linear trend removal was applied to control for linear drift in the MR signal unrelated to task manipulation. Spatial smoothing used an 8-mm Gaussian kernel, full-width at half-max. The anatomical and functional series were co-registered and standardized to Talairach space (Talairach & Tournoux, 1988).

 <u>Voxel-wise analysis</u>. Using multiple regression analysis, group-level statistical

parametric maps (SPMs) were created to localize regions sensitive to changes in VSTM

capacity. Regressors were defined for each set size of each subject and convolved with a

canonical hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996).

Regressor coefficients were weighted by the respective k value, which was standardized

by subtracting the mean k value, yielding a balanced k-weighted contrast. The resulting

SPMs were superimposed to create cluster-filtered composite maps (equivalent of 6

contiguous 100-mm^3 voxels). The overall model fit was assessed using a t value, and the

obtained p values were corrected for the number of comparisons (Ward, 2000,

Simultaneous Inference for fMRI Data; http://afni.nimh.nih.gov/afni/) using a random-

effects model.

     Region-of-interest (ROI) analysis. Regions localized in the voxel-wise analysis as

candidate regions indexing VSTM capacity were subjected to a more sensitive ROI

analysis. This analysis allows for the relative brain activity of the set size conditions to be

statistically quantified. For each ROI, time courses were extracted on a per-run basis for

each of the set size conditions and percent signal-change was calculated using the no-

event condition as the activation baseline. The conditions' time courses were averaged

across the runs for each subject, and a group mean time course was estimated by

averaging across the subjects. Each time course was composed of eight time points,

where each time point, or volume, represented 2 s (the duration of acquisition of the T2*-

weighted (functional) images): 2 s prior to, and 14 s from, the onset of the visual memory

array. This 14-s post-stimulus interval is long enough to accommodate the falling phase

of the hemodynamic response to consolidation and maintenance of information from the

memory array to VSTM. One subject was removed from the time course analysis because

this subject failed to demonstrate canonical hemodynamic responses across the ROIs that were probed.

To quantify the sensitivity to changes in memory load, peak response functions were defined for each ROI by taking the peak activation amplitude for each set size. The volume used to represent the peak amplitude was determined for each ROI by averaging the set size time courses and using the volume with the largest signal.

If a region behaves in a capacity-limited manner, then its peak response function should increase with increasing subcapacity memory loads and be at asymptote at supracapacity memory loads. In other words, the peak response function should be more similar to that of a quadratic function than a linear function. This was tested by comparing the fit of the ROI's peak hemodynamic response function to that of the best-fit linear and quadratic functions (Rosnow & Rosenthal, 1996).

Results and discussion

Behavioral results. Behavioral performance in the articulatory suppression was near ceiling and unchanging across VSTM set sizes (accuracy > 95% across all set sizes; $F < 1$; Figure 2). Accuracy in the VSTM task decreased with increasing set size ($F(5,80) = 72.95, p < 0.001$; Figure 2), while reaction time increased ($F(5,80) = 63.45, p < 0.001$). The estimated amount of information consolidated to, and stored in, memory increased with increasing set size, leveling off around set size 4 ($k_{\text{set size 4}} \approx 3$ items; Figure 3A).[2]

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[2] A pilot experiment using a very similar trial design was run outside the scanner to verify that 150 ms is ample time to consolidate to VSTM as much of the memory array as possible. Here, the memory array duration could be either 150- or 450-ms, randomized within each run, and loads of 2, 3, 4, 6, or 8 colored discs were used. There was no effect of memory array duration ($F(1,15) = 1.26, p = 0.28$), even when looking at high memory

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Demonstrating that a capacity limit was reached by set size 4, while there was a difference in *k* values between set sizes 1 and 4 ($t(15) = 6.09, p < 0.01$, two-tail paired *t* test), there was no difference between 4 and 8 ($t(15) = 0.68, p = 0.51$).

Voxel-wise and ROI results. Only one region was activated above the statistical threshold ($t(16) = 4.35, p = 0.05$), the bilateral intraparietal and intraoccipital sulci (IPS/IOS; peak left/right voxel Talairach coordinates (*x, y, z*): –22/+23, –65/–59, +42/+45; Figure 3B). Time course analysis of this region of interest (ROI) showed that the magnitude of the activation peak for each set size increased until around set size 4 (set size 1 vs. 4, $t(15) = 6.09, p < 0.001$), at which point activation leveled off with increasing set size (set size 4 vs. 8, $t(15) = 0.68, p = 0.51$) (Figure 3A,C). This pattern closely overlaps the behavioral *k* function (Figure 3A). This response amplitude function is better fit by a quadratic
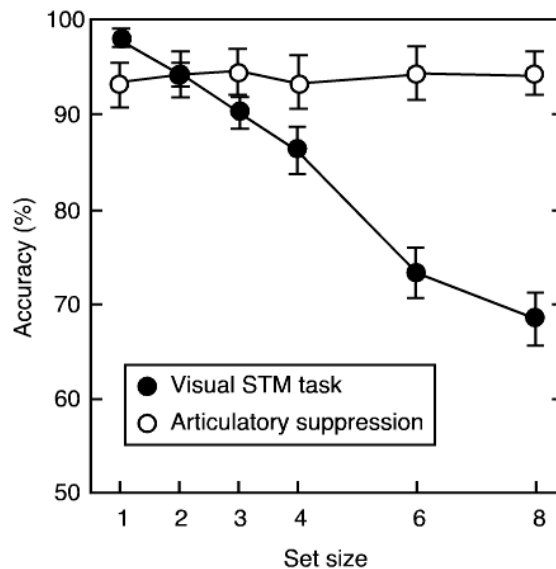
Figure 2. Performance accuracy in the articulatory suppression task (empty circles) and VSTM task (filled circles). Error bars represent the standard error of the mean (SEM).

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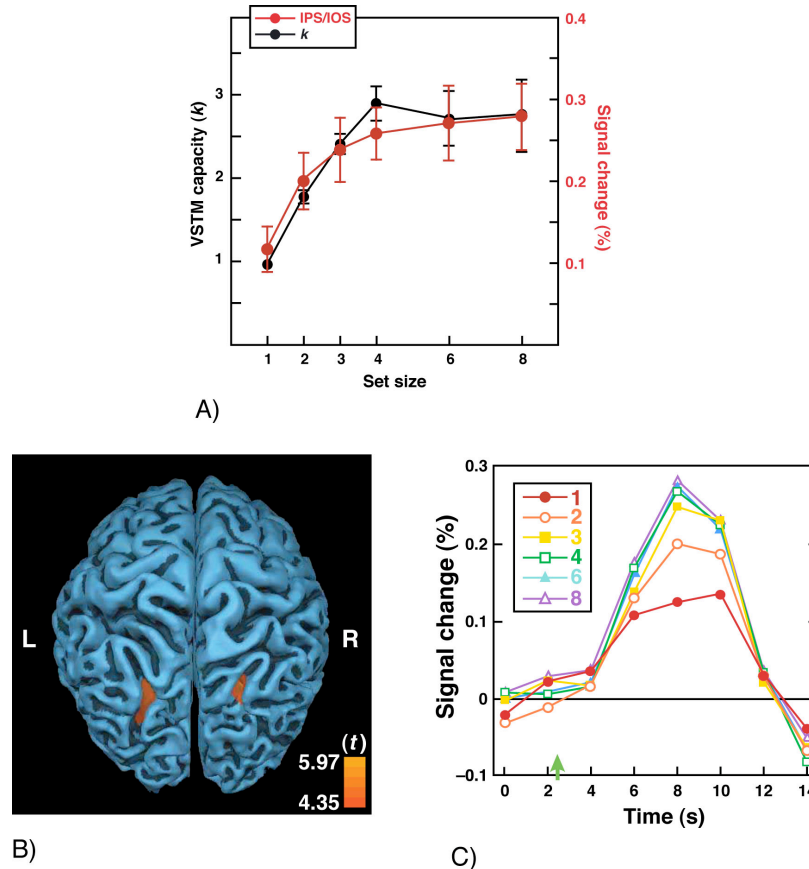
Figure 3. (A) Group mean estimated number of objects stored in VSTM at each set size (black plot). VSTM capacity limit is reached around set size 4. The response function of the IPS/IOS (red plot) overlaps closely with group performance. (B) The results of the voxel-wise analysis revealed activity only in the IPS/IOS that was correlated with behavioral changes in VSTM capacity estimates. (C) IPS/IOS time courses of activity for each set size. Green arrow is the onset of the VSTM memory array.

function than a linear function ($F(1,15) = 8.62, p = 0.01$) (Rosnow & Rosenthal, 1996), consistent with both the behavioral results and the argument that this region behaves in a capacity-limited manner.

The goal of this study was to identify brain regions that store the content of our explicit past immediate experience of this rich and dynamic visual world. The content is presumably held in capacity-limited STM (Atkinson & Shiffrin, 1968; Baddeley, 1986; Cowan, 2001; James, 1890). Despite strong evidence from behavioral research

supporting the existence of a capacity-limited VSTM (Alvarez & Cavanagh, 2004; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001), the neural substrates of its capacity limit have hitherto been unknown. This experiment provides the first rigorous full-brain analysis for regions that are intimately involved VSTM's capacity-limited behavior. While earlier work has implicated the IPS in maintenance (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000) and load-sensitive behavior (Callicott et al., 1999; J. D. Cohen et al., 1997; Linden et al., 2003; Olesen, Westerberg, & Klingberg, 2004), this is the first instance in which it has been shown that the activity of the IPS/IOS (or simply IPS) is critical to the indexing of VSTM content.

Showing that only the IPS tracks VSTM capacity in this experiment should not be taken as indisputable evidence for the existence of *only* one VSTM capacity-indexing region, although an independent electrophysiological study appears to provide converging evidence that the IPS is the only region indexing VSTM capacity. There may be other areas, but fMRI and the task design used do not reveal additional areas besides the IPS. For example, prefrontal cortical regions are known to be sensitive to memory load (Callicott et al., 1999; Clark et al., 1997; Jha & McCarthy, 2000; Linden et al., 2003). A study using a "passive" maintenance task, as the current experiment employs, was not able to identify load-sensitive behavior in prefrontal regions (Rypma & D'Esposito, 1999). D'Esposito and his colleagues (Curtis & D'Esposito, 2003; Rypma & D'Esposito, 1999) argue that load-sensitive prefrontal cortex reflects the active manipulation of memory content.

This experiment used a group-based approach in which the group-average k

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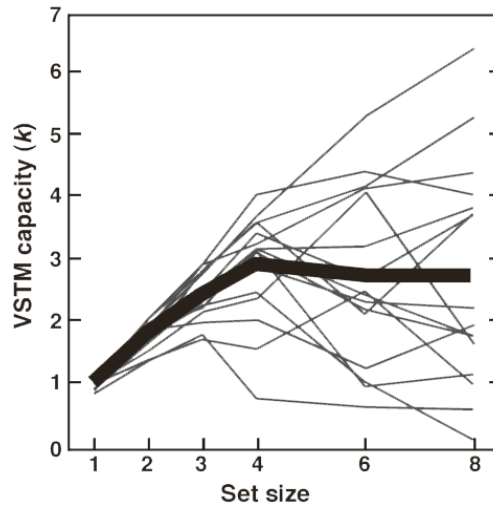
Figure 4. Individual differences in VSTM capacity estimates. Group mean *k* values peaked around set size 4 and leveled off with further increases in memory load. Yet, individuals' performance (thin, gray lines) showed substantial variance in terms of when their capacity limits were reached.

response function was used to localize VSTM capacity-modulated IPS. As Figure 4

shows, there was inter-individual variance composing the group-level *k* function. This

was particularly true at larger set sizes, which a group-level analysis treats as error, hence

the magnitude of the between-subjects error bars in Figure 3A. Furthermore, not all

subjects had the same maximum *k* value (capacity limit): it ranged from 1.74 to 6.37.

Given this variance, IPS activity may not actually reflect subjects' VSTM capacity;

rather, the IPS may serendipitously reflect the group *k* function. If the IPS really does

index VSTM capacity, it should track individual differences in capacity limits (Vogel &

Awh, 2008).

Capitalizing upon an individual differences approach to identifying brain regions

that predict subjects' VSTM capacity limits will, *ipso facto*, provide an estimate of the

variability that that region's activity captures. Multiple factors may collectively account

for the remaining variability in the VSTM capacity-indexing activity pattern, such as

genetics, gender, age, and the complexity of the information stored in memory (Cornoldi & Vecchi, 2003; Tiitinen, 2001). Regardless, electrophysiological work suggests that IPS activity may account for a significant proportion of individual differences in VSTM capacity limits. Measuring event-related potentials (ERPs) at posterior electrode sites on the scalp in the vicinity of the IPS/IOS, Vogel and Machizawa (2004) showed that ERP amplitude was sensitive to differences in VSTM maintenance capacity, corroborating the argument that IPS activity indexes VSTM capacity limits (Todd & Marois, 2004). To determine if the IPS tracks individual performance, the functional data set of the present experiment was re-analyzed using an individual differences approach.

Experiment 2: Individual Differences Analysis of the Fast Event-Related Study

The rationale of this re-analysis followed the logic of Vogel and Machizawa (2004): If a brain area tracks VSTM capacity limits at the individual level, then this area should evoke greater activity for high capacity individuals than low capacity individuals at the individuals' respective capacity limits.

Methods and analysis

Only deviations from the methods in Experiment 1 will be reviewed. These results have been published (Todd & Marois, 2005).

Voxel-wise data analysis. Brain regions that predicted differences in VSTM capacity limits were identified using a voxel-wise analysis. First, for each subject, the VSTM capacity limit (k_{max}) and the percent BOLD signal change (relative to the signal of the no-

18

event condition) obtained at the k_{max}'s set size was determined. The percent BOLD signal

at set size k_{max} was then standardized to the set size 1 percent BOLD signal for each

subject, since all the subjects had virtually the same k value at set size 1 (mean $k = 0.95$;

Figure 4) but very different levels of activation. This standardization increased sensitivity

for detecting brain regions whose activity correlated with individual differences in VSTM

capacity (Vogel & Machizawa, 2004). Using a general linear model, for each individual,

regressors were then defined for set size k_{max} and set size 1 and were weighted by the

individual's maximum k value. Voxels whose activity covaried with the magnitude of the

difference between set size k_{max} and set size 1 across individuals were localized as

candidate VSTM capacity indexing regions.

Region-of-interest analysis. The ROI approach was used to determine whether brain

regions previously implicated in VSTM storage capacity on the basis of a group average

analysis (Todd & Marois, 2004) contributed to individual differences in VSTM capacity.

For each individual, the difference in peak activity between set size k_{max} and set size 1

conditions was computed. These activation differences were subsequently correlated with

the respective individuals' k_{max} values. A threshold of $\alpha = 0.05$ (one-tail) was set for the

IPS ROI correlation analysis, on the basis of an a priori expectation of a positive linear

relationship between VSTM capacity and brain activity.

Outliers were isolated and removed in ROIs using *DFFITS* with a cutoff threshold

equal to ±1 (J. Cohen, Cohen, West, & Aiken, 2003). No more than two outliers were

removed from any given ROI analysis.
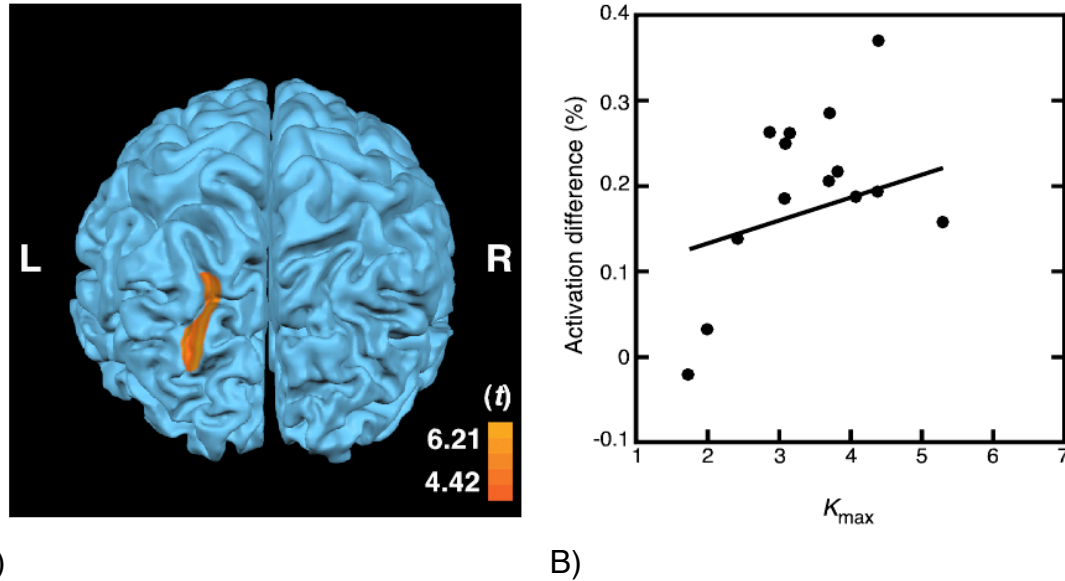
Figure 5. (A) The left IPS/IOS was the only region whose activity was significantly correlated with individual differences in VSTM capacity limit. (B) Correlation analysis of IPS/IOS activation amplitude and individuals' capacity limits.

Results and discussion

The voxel-wise analysis revealed above-threshold activation only within the left IPS/IOS (Figure 5A; $t(15) = 4.42, p = 0.05$, corrected for multiple comparisons). This IPS region showed considered overlap with the IPS/IOS region localized in the group-level analysis in Experiment 1 (Figure 5A; Todd & Marois, 2004): group-level ROI Talairach coordinates, x, -14 to -30; y, -81 to -58; z, $+17$ to $+49$; individual-level ROI coordinates, x, -17 to -29; y, -81 to -61; z, $+21$ to $+45$. Reducing the threshold ten-fold revealed activity along the contralateral IPS/IOS.

An ROI analysis for this IPS region reaffirmed the relationship of individuals' k_{max} and the activation difference between set size k_{max} and set size 1 ($r(12) = 0.56, p = 0.05$; Figure 5B). Because k_{max} is correlated with set size k_{max} activity, which was standardized to set size 1 activity, this correlation cannot be explained by high-capacity subjects

showing overall greater activity than low-capacity subjects (Vogel & Machizawa, 2004). Furthermore, this correlation does not exist using supracapacity memory loads: There was no correlation between individuals' k_{max} and the activation difference of set sizes 8 and 1 (using subjects who reached k_{max} below set size 8, $r(7) = 0.19$, $p = 0.31$).

Using a VSTM task, other studies showed capacity-modulated behavior in a region along the IPS that predicted performance (Linden et al., 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). It must be noted that those studies' experimental designs share a common feature that distinguishes them from the current experiment: They used retention intervals that were much longer than the current experiment's maintenance period of 1.2 s (Linden et al. (2003), 6-s retention; Pessoa, Gutierrez, Bandettini, & Ungerleider (2002), 12-s retention). Consequently, maintenance-related activity could be distinguished from activity associated with consolidation or retrieval (Postle, Zarahn, & D'Esposito, 2000; Zarahn, Aguirre, & D'Esposito, 1997). This is important because the focus of this individual differences analysis is to explore the role of brain regions in *maintaining* the content of our explicit visual experience. The contribution of the three STM phases to subject performance cannot be distinguished in the current experiment, because of the sluggish nature of the hemodynamic response and the short retention interval (Zarahn, Aguirre, & D'Esposito, 1997). Thus, no firm conclusions can be made regarding the contribution of memory storage in the activation pattern of any ROI. In the next experiment the retention interval is increased, thereby allowing more direct claims to be made about the role of each ROI across the three STM phases.

Experiment 3: VSTM phase analysis of candidate capacity-indexing ROIs

The short retention interval used in the previous experiment permitted a relatively extensive sampling of memory loads to be used in the fMRI scanner, allowing brain regions that are sensitive to VSTM capacity limits to be localized. However, because of the short memory retention interval (1200 ms), activity related to VSTM maintenance could not be distinguished from consolidation- or retrieval-related activity (Postle, Zarahn, & D'Esposito, 2000; Zarahn, Aguirre, & D'Esposito, 1997). Measuring ERPs at posterior electrode sites on the scalp (in the vicinity of the IPS/IOS), Vogel and Machizawa (2004) showed that the amplitude of ERPs were sensitive to differences in VSTM storage load. Interestingly, at the onset of the ERPs waves, the amplitude differences were concurrent with peak latency differences (Figure 2 in Vogel & Machizawa, 2004). This may represent the transfer of information to VSTM maintenance, i.e., consolidation-related processing. For these reasons, IPS's load-indexing behavior in the fast event-related experiment may result from consolidation or retrieval, but not maintenance, processes. This is a viable argument, given that a recent neuroimaging study showed that the IPS to be sensitive to the consolidation load, not simply the storage load (Linden et al., 2003).

While other studies provide evidence that the IPS is involved in tracking the storage content of VSTM (J. D. Cohen et al., 1997; Linden et al., 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002), their tasks are substantially different from the current one. For example, subjects had to manipulate and update the memory representation of verbal working memory throughout each trial in Cohen and colleagues' (1997) study, but in the current study, the task does not require subjects to perform any

manipulation on, or updating of, the content held in memory. Unlike the current study, in which all the items to hold in memory were presented simultaneously, Linden et al. (2003) presented subjects with complex stimuli in a sequential manner, like in Cohen et al. (1997). As a result, prefrontal regions were needed to monitor, reorganize, and update stored memory representations during consolidation and maintenance, and areas involved in the control of attention may have supported the storage of memories (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Linden et al., 2003; Rypma & D'Esposito, 1999). Finally, while the focus of Pessoa et al. (2002) was to determine which regions predicted behavioral performance in a VSTM task across the different STM phases, they did not parametrically manipulate the memory load, as was done in the current study.

Thus, this current study is unique relative to past studies in its goal to identify the regions that track the VSTM storage load. To this end, the following experiments address the load-modulated nature of the IPS during VSTM encoding, maintenance, and retrieval.

Two fMRI experiments were run in which the retention interval was increased so the maintenance-related activity could be distinguished from encoding and retrieval STM phases (Leung, Gore, & Goldman-Rakic, 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Zarahn, Aguirre, & D'Esposito, 1997). Experiment 3A demonstrates that the IPS is modulated by memory load during maintenance using set sizes equivalent to subcapacity and capacity loads. Experiment 3B extends these findings by showing that the IPS behaves in a load-modulated manner by adding a third memory load, which represents a supracapacity load. In each experiment, ROI analyses are performed using

both ROIs defined in the group-level analysis and the individual differences analysis.

Experiment 3A: Measuring VSTM storage capacity using two loads

Methods

With the following exceptions, the experimental design (for both the behavioral task & fMRI parameters) was the same as that of Experiment 1.

Fourteen young adults (6 males; 12 right-handed) from the Vanderbilt community provided written informed consent to volunteer in this experiment for paid compensation.

The retention interval was extended from 1,200 to 9,200 ms (trial duration, 18 s). Because each trial in this experiment was more than twice as long as the trial duration in the first experiment, and in order to maintain a high statistical power, only two memory loads were used, set sizes 1 and 3, which respectively correspond to subcapacity and capacity loads. Additionally, there were no non-event trials. The details of Experiment 3A have been published elsewhere (Todd, Fougnie, & Marois, 2005; Todd & Marois, 2004, 2005).

Data analysis

FMRI data analysis. Region-of-interest analysis was performed on the IPS ROI localized in Experiment 1. Time courses were created in a manner similar to that used in Experiment 1, with several exceptions: Percent signal change was standardized to the volume occuring after memory array presentation (the baseline condition), because the signal from the preceding trial related to the falling phase of retrieval-related activity carried over into the rising signal of encoding-related activity (Figure 6). The signal

related to encoding, maintenance, and retrieval was measured at 5.5–7.5, 9.5–11.5, and

15.5–17.5 s (or 4, 6, and 9 volumes) from the onset of the memory array, respectively

(Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). The encoding and retrieval

intervals occur approximately 6 s from the onset of the memory and probe arrays, which

is consistent with the modeled time-of-peak signal amplitude in the hemodynamic

response function used in BrainVoyager 4.9.1 (Boynton, Engel, Glover, & Heeger, 1996).

The volume used to estimate maintenance-related activity is far enough away from the

time at which the consolidation-related signal would peak, so the amplitude of activity

during this "maintenance" volume would most likely reflect VSTM storage processes

(Zarahn, Aguirre, & D'Esposito, 1997).

Result and discussion

Behavioral results. The k value for set size 1 was 0.89 (standard error the mean (SEM) =

0.03), and the set size 3 k value was 2.00 (SEM = 0.20). The difference between the

number of items stored in memory was significant ($t(13) = 6.24, p < 0.001$). This is

consistent with the behavioral results from the fast event-related experiment in

Experiments 1 and 2.

ROI analyses. The left IPS ROI defined using an individual differences analysis (IPS$_{Ind}$

$_{diffs}$) predicted behavioral performance during maintenance ($r(12) = 0.54, p = 0.05$) and

retrieval ($r(11) = 0.63, p = 0.02$), but not during consolidation ($r(11) = 0.50, p = 0.08$). A

comparison of maintenance activity at set sizes 3 and 1 in the group-level IPS ROI

(IPS$_{Group}$), did not show a load effect ($t(13) = 1.27, p = 0.23$), but there were effects of
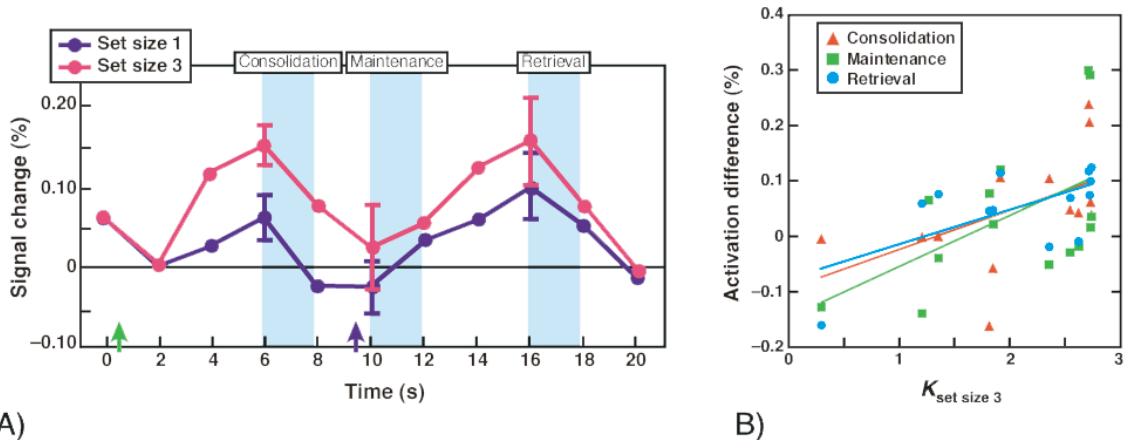
Figure 6. Increasing the VSTM retention interval allowed for maintenance-related activity to be dissociated from encoding- and retrieval-related activity. (A) Time courses for low (set size 1) and high (set size 3) memory loads. Activity attributed to STM phases are labeled appropriately, with error bars showing between-subject variance. Green arrow represents onset of memory array. Purple arrow, onset of the VSTM probe. (B) Individual differences analysis showing a significant correlation of activity with individuals' VSTM capacity limits during the three STM phases. Red, consolidation; green, maintenance; blue, retrieval.

memory load during encoding ($t(13) = 3.25$, $p = 0.006$) and retrieval ($t(13) = 2.13$, $p = 0.05$). Although there was no effect of load during maintenance in the IPS_{Group}, this null result may reflect this analysis being unable to capitalize upon interindividual variance.

A limitation of this slow-event experiment is that it did not use a supracapacity load. Thus, it was unknown how the IPS would behave during maintenance when the memory load exceeds the VSTM capacity limit. To explore this, a second slow-event fMRI experiment was run, and it included subcapacity, capacity, and supracapacity memory loads.

Experiment 3B: Measuring VSTM storage at supracapacity loads

Methods

Twelve right-handed individuals (8 males) from the Vanderbilt community

provided written informed consent to volunteer in this experiment for paid compensation.

The design of the experiment was the same as in Experiment 3A, with several

differences. The intertrial interval was increased from 3 to 5 s, in order to reduce the

carry-over the falling signal from retrieval-related activity on the rising phase of

encoding-related activity (Todd, Fougnie, & Marois, 2005; Todd & Marois, 2004, 2005).

If the IPS tracks VSTM capacity, then its maintenance-related activity should level off

once memory is filled to capacity (Todd & Marois, 2004). To this end, three memory

loads (set sizes 1, 4, and 7) were presented to subjects (presentation was counterbalanced

within each run) to understand the progress of IPS activity as the amount of information

to maintain in memory changes from a subcapacity load (set size 1) to a supracapacity

load (set size 7).

Because there were two high memory loads in this experiment, individual

differences analysis used the set size where the subject had the largest capacity estimate

(k_{max}), which is consistent with the analytical method used in individual differences

analysis the fast event-related fMRI experiment (Todd & Marois, 2005). Three subjects'

k_{max} was reached at set size 1, so individual differences analysis could not be performed

on these subjects, because activity at set size k_{max} is standardized to set size 1 activity.

Results and discussion

Behavioral results. It was anticipated that behavioral performance would be greater for

set size 4 than 1, reflecting the filling of storage to capacity, but there would be no

difference between set sizes 4 and 7, when the capacity limit will have been reached. The

behavioral data reflected this pattern. Behavioral performance peaked at set size 4 (k
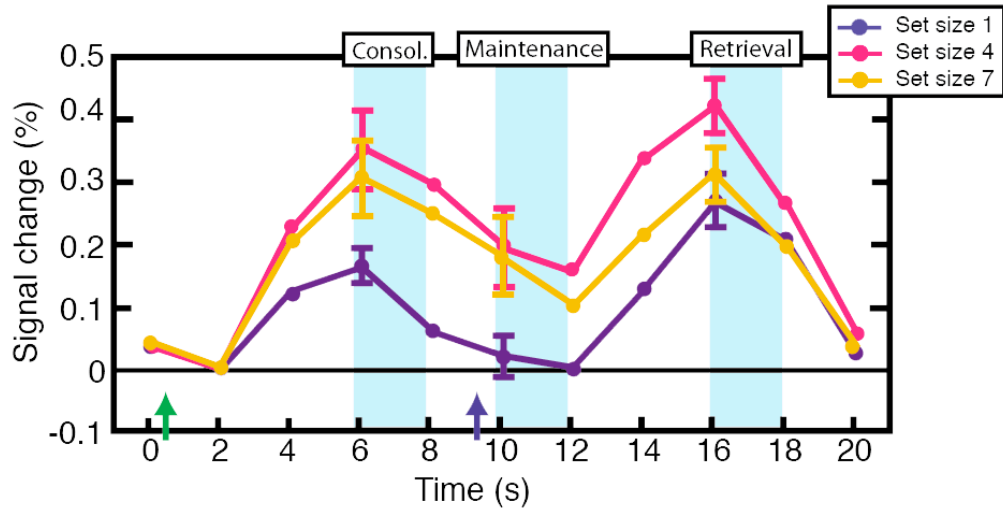
Figure 7. Activity during maintenance behaves in a capacity-limited manner. Green arrow, onset of memory array. Purple arrow, visual probe.

values: set size 1 = 0.78, set size 4 = 1.48, set size 7 = 1.02). Pair-wise comparisons revealed differences between set sizes 1 and 4 ($t(11) = 2.03, p = 0.03$, 1-tail), but not between loads 4 and 7 ($t(11) = 1.52, p = 0.08$), demonstrating that STM was filled to capacity by set size 4.

ROI analyses. As expected, IPS_{Group} activity during maintenance was greater for set size 4 than 1 ($t(11) = 3.39, p = 0.003$, one-tail), but there was no significant difference between set sizes 4 and 7 (Figure 7; $t(11) = 0.38, p = 0.71$, 2-tail). Consistent with the fast-ER experiment (Experiment 1), IPS_{Group} activity responded in a capacity-limited fashion.

Similar to Experiment 2, $IPS_{Ind\ diffs}$ activity during maintenance was marginally predictive of individuals' k_{max} ($r(7) = 0.55, p = 0.06$, 1-tail). Consolidation was *negatively* correlated with performance ($r(6) = -0.71, p = 0.05$, 2-tail). Retrieval activity was not correlated with inter-subject changes in capacity limits ($r(5) = 0.60, p = 0.15$). The sample sizes used were roughly half the size as those in Experiment 3A—this may

contribute to the anomalous findings during consolidation and retrieval STM phases—but the IPS was still able to predict individual capacity limits, with a relatively high degree of authority.

Experiment 4: The IPS is not strongly modulated by iconic memory load

Sperling (1960) and Phillips (1974) showed that our memory of a transient event is initially represented at a very high resolution, but within about one second our explicit experience of that event is diluted to a meager representation of the original event, which is stored in short-term memory. This short-lived sensory memory is referred to as *iconic memory* in the visual domain (Neisser, 1967).

It is possible that the capacity-indexing activity of the IPS in Experiments 1 and 2 may be sensitive to the iconic memory load of the visual scene, rather or instead of VSTM capacity. This seems unlikely, given that there were no differences in IPS activity between capacity and supracapacity loads in Experiment 1, and especially during maintenance in Experiment 3B. Experiment 4 provides an empirical test of this "sensory load" argument, by placing minimum demands on VSTM processes while parametrically manipulating the perceptual load.

Methods

Six right-handed subjects (3 male) with normal or corrected-to-normal vision participated in this experiment. The experiment was identical to the fast event-related experiment (Experiments 1 and 2), with notable exceptions. Rather than encoding all the stimuli in the memory array, they were instructed to indicate when they were confident in

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their decision, if a colored disc appeared in the center location of the memory array. "Present" trials occurred 50% of the trials for each set size (1, 2, 3, 4, 6, and 8 colored discs). Because this was not a memory task, the visual memory probe array was not presented. This experiment has been presented elsewhere (Todd & Marois, 2004).

Results and discussion

Behavioral results. Performance accuracy in the target localization task was near ceiling and unchanging across all the set sizes (97–99%; $F < 1$).

ROI analysis. Neither the IPS_{Group} nor the $IPS_{Ind\ diffs}$ ROIs were not strongly modulated by the iconic memory representation (both, $F < 1$). This provides further support for the argument that the IPS indexes the amount of information being held in VSTM, as opposed to the amount of information that we experience immediately upon perceiving an event (Figure 8).

While this experiment discounts a sensory load explanation for the IPS's behavior, there is an alternative explanation for the capacity-limited behavior of the IPS. The IPS's hemodynamic response might have saturated at the 0.3% signal change amplitude in Experiment 1 (Figure 3A,C) because of limitations in the underlying neurovasculature supporting this activity. This hemodynamic saturation hypothesis seems unlikely for two obvious reasons. First, in Experiment 1, a quarter of the subjects had a peak amplitude of activation greater than 0.3% at set size 8, the load with the largest mean peak amplitude (Figure 3A,C). Second, in Experiment 3B, the same ROI had a mean amplitude greater than 0.3% during the encoding and retrieval phases (Figure 7),
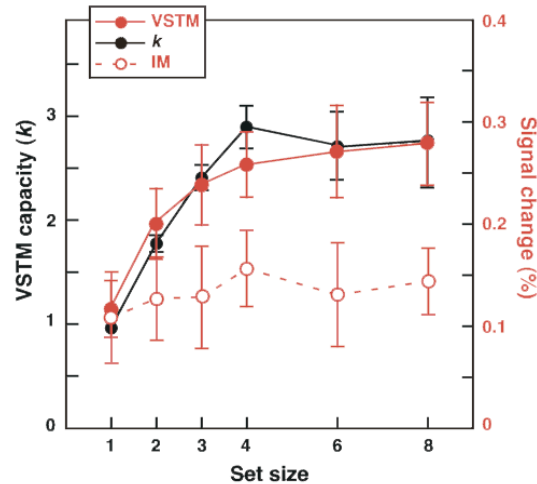
Figure 8. Peak response amplitude functions demonstrating that activity in the group-defined IPS region is sensitive to capacity limits in Experiment 1 (filled red circles, from Figure 3A), but it was not strongly modulated by the amount of information in the visual scene (empty circles). For reference, capacity estimates from Experiment 1 (Figure 3A) are presented in black.

and at least a third of the subjects had a signal amplitude greater than 0.3% during

encoding or retrieval. Thus, the asymptote in the amplitude of the IPS's response function

(Figure 3A) is unlikely to be due to a hemodynamic "ceiling effect".

Experiment 5: The IPS indexes capacity in spatial and non-spatial VSTM tasks

The IPS's sensitivity to the binding of location and identity in these VSTM tasks

puts it in an ideal position to integrate the visual scene for conscious perception

(Friedman-Hill, Robertson, & Treisman, 1995; Shafritz, Gore, & Marois, 2002). There is

also a large body of behavioral (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999;

Klauer & Zhao, 2004; Logie, 1995; Logie & Marchetti, 1991; Tresch, Sinnamon, &

Seamon, 1993), neuroimaging (Courtney, Ungerleider, Keil, & Haxby, 1996; Haxby et

al., 1991; Owen, Milner, Petrides, & Evans, 1996; Postle & D'Esposito, 1999),

neurophysiological (Goldman-Rakic, 1995; Goodale & Milner, 1992), and neurological

(Baddeley, Della Sala, & Spinnler, 1991) evidence supporting a partial dissociation of VSTM processes sensitive to location and identity information. Several neuroimaging studies have documented a preference for parietal regions to process spatial information in memory, while occipito-temporal areas, lying ventral, are selective for processing object identity in STM (Haxby et al., 1991; Owen, Milner, Petrides, & Evans, 1996; Sala, Rämä, & Courtney, 2003). Thus, it possible that the IPS's capacity-indexing behavior reflects the spatial component of the VSTM task, rather than the conjunction of both spatial and identity information? This was tested in a brief control experiment by rendering the spatial location of the VSTM task in Experiment 1 task-irrelevant by placing the probe disc at fixation and instructing subjects to consolidate only the colors of the memory array.

Methods

Four right-handed subjects (3 male) with normal or corrected-to-normal vision participated in this experiment. The experiment was identical to the fast event-related experiment (Experiments 1 and 2), with the notable exception that the visual probe disc was presented in the center of the display, at fixation. Subjects were instructed to ignore the locations of the stimuli and to remember only the colors of the discs to presented. The results of experiment have been presented elsewhere (Todd & Marois, 2004).

Results and discussion

Even with four subjects, activation in the IPS_{Group} was still correlated with performance at the individual level ($r = 0.70$, $t(3) = 3.67$, $p = 0.04$). Thus, the IPS also

tracks non-spatial information held in VSTM.

Xu and Chun (2006) replicated this finding in a set of experiments wherein subjects maintained a varying number of objects in VSTM that were presented simultaneously (the task includes a spatial component) or sequentially (the task has no spatial information), although they showed that the IPS was more strongly activated when spatial information had to be maintained in VSTM. Regardless of the task, the IPS's response reflected the amount of information maintained in VSTM.

Experiment 6: Generalizing the IPS's role to non-color stimuli

These experiments used only one stimulus class: colored discs. To test the generalizability of the IPS in tracking VSTM content, a control was run in which subjects performed the same fast event-related VSTM task used in Experiments 1 and 2, but the colored discs were changed to differently oriented bar stimuli, which are known to recruit the parietal cortex in short-term memory tasks (Cornette, Dupont, Salmon, & Orban, 2001).

Methods

Four right-handed subjects (2 male) with normal or corrected-to-normal vision participated in this experiment. The experiment was identical to the fast event-related experiment (Experiments 1 and 2), except that the stimuli were white bars rotated to 0°, 45°, 90°, and 135°. Organization of the stimuli in the memory array display was controlled to minimize perceptual grouping, which could artificially inflate VSTM capacity estimates. These results have been presented previously (Todd & Marois, 2004).

Results and discussion

IPS_{Group} activity was significantly correlated with behavioral performance ($r = 0.63$, $t(3) = 6.90$, $p < 0.001$). This finding has been replicated using very different stimuli (e.g., outlines of elongated nonsensical objects, mushroom- or umbrella-like stimuli in Xu & Chun, 2006). This impassiveness to the type of stimuli being indexed is consistent with a role for the IPS in supporting the general storage of VSTM content.

General Discussion

The amount of information that the brain is able to extract from our visual experience and keep track of in memory for the short-term is severely limited (Baddeley & Andrade, 2000; Luck & Vogel, 1997; G. A. Miller, 1956; Pashler, 1988; Rensink, O'Regan, & Clark, 1997; Simons & Levin, 1997; Sperling, 1960). Parietal and frontal brain regions have been shown to be sensitive to the amount of information held in STM (J. D. Cohen et al., 1997; Linden et al., 2003), as have ventral occipital-temporal areas (Ranganath, DeGutis, & D'Esposito, 2004). To date, none of the studies implicating frontal or occipital-temporal regions in STM processes have shown that they track maintenance capacity across a large distribution of memory loads. In the above experiments, I showed that when information is held in VSTM, without a need for manipulation or organization, the IPS is the brain region that consistently behaves in a VSTM capacity-limited manner (Todd & Marois, 2004, 2005).

There is some neurological evidence suggesting that parietal lesions result in the impairment of general STM capacity (Baldo & Dronkers, 2006; Duncan et al., 2003;

Habekost & Rostrup, 2007; Schooler, Caplan, Revell, Salazar, & Grafman, 2008).

Patients with a unilateral right IPS lesions exhibit a significant reduction in memory capacity (Habekost & Rostrup, 2007; Peers et al., 2005). STM capacity deficits occur with lesions to any of number of non-parietal brain regions (Schooler, Caplan, Revell, Salazar, & Grafman, 2008), including underlying white matter connecting the parietal cortex to other cortical areas (Habekost & Rostrupt, 2007). This suggests that disruption of any part of the VSTM network with connections with the posterior parietal lobule (PPL) may incur a VSTM capacity deficit if the PPL is the only region that indexes VSTM maintenance, which neuroimaging (Todd & Marois, 2004, 2005) and electrophysiological (Vogel & Machizawa, 2004) evidence suggests.

Showing a specific involvement of the parietal cortex in VSTM storage capacity does not imply that other brain regions do not contribute to VSTM storage. In particular, prefrontal regions might play other roles involved in the indexing of VSTM maintenance capacity. They have been implicated in controlling the focus of attention during consolidation and maintenance (Awh & Jonides, 2001; Marois, Chun, & Gore, 2000; Wheeler & Treisman, 2002), consolidating and actively maintaining content in STM (Courtney, Ungerleider, Keil, & Haxby, 1997; Curtis & D'Esposito, 2003; Fuster, 1990; Jha & McCarthy, 2000; E. K. Miller, Li, & Desimone, 1993), minimizing distractor interference (Sakai, Rowe, & Passingham, 2002), reducing conflict due to task difficulty increasing with memory load (Barch et al., 1997; Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001), and performance-monitoring necessary for accurate retrieval of information from memory (Carter et al., 1998; Todd & Marois, 2004).

Category-selective regions within the inferior temporal lobule are also involved in

supporting VSTM, but current evidence suggests that these areas are not critical to either

storage or indexing VSTM capacity (Druzgal & D'Esposito, 2003; Jha & McCarthy,

2000; Linden et al., 2003; E. K. Miller & Desimone, 1994). Recent neuroimaging work,

using time-resolved fMRI, suggests these regions supply information for VSTM

consolidation and maintenance to prefrontal regions, because activity related to the

presentation of the memory array peaks sooner in the fusiform face area than in prefrontal

areas involved in processing target-relevant information for storage in STM (Druzgal &

D'Esposito, 2003; B. T. Miller, Deouell, Dam, Knight, & D'Esposito, 2008). Despite the

diverse processes that all these non-parietal areas contribute to, it appears that one region

consistently tracks the amount of information being maintained in VSTM (Curtis &

D'Esposito, 2003; Todd & Marois, 2004, 2005).

The IPS/IOS showed sensitivity to VSTM storage capacity, but this region is

composed of numerous subregions, each preferentially sensitive to a particular cognitive

function (Culham & Kanwisher, 2001). The IPS/IOS may be subdivided into different

storage-related processes. Work by Xu and Chun showed that this IPS region may be

functionally divided into two ROIs (Xu & Chun, 2006). The area in the vicinity of the

activation peak in the ROI indexing VSTM capacity forms one ROI, the superior IPS

(sIPS). The second region lies inferior. Unlike the sIPS, whose activity parallels the

behavioral k function, the inferior IPS's (iIPS) response function reaches an asymptote at

a set size of four objects, regardless of behavioral performance.

The experiments presented herein used simple features, such as color and

orientation, to explore capacity modulated behavior in the brain; however, our visual

experience of the world is viewed in terms of complex objects. The sIPS appears to track

the number of features, not the number of bound features (or complex objects), stored in memory (Xu, 2007). Subjects performed equally well maintaining two features (color and shape), regardless of whether they formed one object or two different objects. Even though the memory loads differed, sIPS activation amplitude was the same for both loads. This would not be expected if the sIPS stores bound object representations, in which case greater activation would be expected for a load of two items. Unfortunately, Xu (2007) used a retention interval of 1,000 ms, so maintenance-related activity could not be distinguished from that of other VSTM phases; this effect may have been carried by consolidation-related processes (Todd & Marois, 2004, 2005). Regardless, Xu's (2007) findings are still consistent with IPS's activity being modulated by the amount of information held in VSTM.

The IPS does not simply index how much information we are holding in VSTM, it is also involved in constructing coherent representations of our visual experience. The inferior extent of the IPS may automatically parse a visual scene into spatially defined objects, independent of task relevance (Xu, 2007, 2008; Xu & Chun, 2006). Interestingly, the iIPS was less activated by a complex object than when that object was split into its constituents, suggesting it can process a complex object more efficiently than when it is broken into pieces (Xu, 2008). Accordingly, lesioning the iIPS should result in less of an impairment in perceiving a single, complex object rather than multiple objects that are composed of the constituents of the bound object. In fact, Bálint's syndrome patients, who have bilateral parietal-occipito lesions, exhibit this deficit (Coslett & Saffran, 1991; Xu, 2008).

The posterior parietal lobule (PPL), which includes the IPS, is in an ideal position

to support representations of our conscious experience. Besides indexing the content of VSTM (Todd & Marois, 2004, 2005), the PPL supports the binding of features and complex objects (Coslett & Saffran, 1991; Robertson, 2003). It is also involved in the control of spatial (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) and non-spatial (Marois, Chun, & Gore, 2000; Wojciulik & Kanwisher, 1999) attention in anticipation of a target. Its behavior is also correlated with detecting changes in a visual scene (Beck, Rees, Frith, & Lavie, 2001), as well as salient visual events (Gottlieb, Kusunoki, & Goldberg, 1998). Together, these findings manifest a prominent role of the PPL in the construction and maintenance of our visual experience.

CHAPTER II

THE NEURAL AND BEHAVIORAL CONSEQUENCES OF FILLING VISUAL
SHORT-TERM MEMORY TO CAPACITY.

Introduction

In CHAPTER I, the voxel-wise analysis that probed for regions indexing VSTM

storage capacity revealed activity in an area besides the IPS/IOS. The response profile of

this second region was very different from that of the IPS. Lying at the intersection of the

temporal and parietal cortices, this region, the right temporo-parietal junction (rTPJ;

Figure 9A), is interesting on at least two accounts. First, its response profile is negatively

correlated with VSTM capacity (Figure 9) (Todd, Fougnie, & Marois, 2005). The second

reason concerns the relationship of the rTPJ and IPS to selective attention. Selective

attention refers to the selective, focused processing of an event or events at the expense of

processing other events, and it is generally accepted that selective attention is supported

by two different cortical networks, depending on whether attention is being deliberately

controlled or if the focus of attention is unintentionally oriented away from the task at

hand to another, salient event (Corbetta & Shulman, 2002).

Multiple neuroimaging studies show the recruitment of regions in the dorsal

parietal and prefrontal regions during goal-driven attention (Corbetta & Shulman, 2002),

which is the voluntary orienting of attention to a potentially task-relevant stimulus or

event. Goal-driven attention recruits a network of dorsal frontal and parietal regions

(Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd,

Desimone, & Ungerleider, 1999; Nobre, Gitelman, Dias, & Mesulam, 2000; Shulman et

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al., 2003). These regions are also recruited in STM processes, such as during the maintenance and manipulation of memory content (Corbetta & Shulman, 2002; LaBar, Gitelman, Parrish, & Mesulam, 1999; Mayer et al., 2007). As discussed in CHAPTER I, and shown by others, the activity of these areas is correlated with subjects' task performance (Cohen et al., 1997; Culham, Cavanagh, & Kanwisher, 2001; Linden et al., 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Todd & Marois, 2004, 2005). These common anatomical activations suggests that STM and goal-driven attention may engage some mutual process or processes, such as controlling what content is consolidated into, and maintained in, STM and maintaining bound features of complex objects in STM (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Cowan, 2001; Wheeler & Treisman, 2002).

In addition to goal-driven attention, attention may also be controlled in a bottom-up, or stimulus-driven, manner, in which attention is reflexively oriented ("captured") to a salient stimulus that may have behavioral relevance (Egeth & Yantis, 1997). Relative to goal-driven attention, stimulus-driven attention predominantly recruits ventral frontal and parietal areas, such as the rTPJ (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Downar, Crawley, Mikulis, & Davis, 2000, 2002; Marois, Leung, & Gore, 2000). Lesions to this ventral network (particularly the rTPJ) from strokes, for example, lead to hemispatial neglect (Driver & Vuilleumier, 2001). Hemispatial neglect patients are impaired in detecting stimuli presented opposite of the lesion site. In the case of damage to the rTPJ, patients will likely show an unawareness of stimuli presented in the left visual field. The neuroimaging and neuropsychological work suggests that the rTPJ has an important role in bringing outside, i.e., previously unnoticed, events into our focus of

attention. These events may undergo additional processing so they enter STM for conscious processing (Baars, 1988; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006).

Functional MRI studies have shown that performance improvement in attention-demanding tasks (e.g., detecting two targets presented briefly and in close temporal proximity, or identifying the direction of coherent motion in an otherwise field of random motion) coincides with increased activation in goal-driven regions and suppression in stimulus-driven regions (Marois, Yi, & Chun, 2004; Shulman et al., 2003; Zacks, Vettel, & Michelon, 2003). Thus, the behavior of these two attentional control networks appears to co-vary: As an observer increases the amount of attention that he commits to a task, goal-driven attention areas become more active and stimulus-driven areas, particularly in the rTPJ, show increased suppression.

Relating the mechanistic differences between stimulus- and goal-driven selective attention to changes in their neural correlates, and considering the voxel-wise analysis showing a possible reciprocal relationship of the IPS and TPJ in VSTM, a specific hypothesis can be made regarding the relationship of the IPS and TPJ in VSTM: The greater the cognitive demands of a task, the less likely the TPJ will process an unexpected and task-irrelevant stimulus, and, consequently, the less likely that attention will captured by that stimulus. Using attention-demanding tasks, it has been shown that increasing the demands of a task prevent unexpected stimuli from reaching awareness (Mack & Rock, 1998). For example, tracking the number of ball passes that one of two intermixed groups of basketball players are making significantly impairs the ability to notice an unexpected event appear in that scene, such as a woman with an umbrella or a person in a gorilla suit

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walking through the playing area (Neisser, 1979; Simons & Chabris, 1999). However, it is unknown if a similar deficit may arise from taxing VSTM storage.

Before this hypothesis can be tested, the nature of the relationship between the rTPJ and the IPS must be tested. To this end, the activation pattern of the rTPJ in VSTM is quantified and compared to the IPS region using the same ROI approach discussed previously (Todd & Marois, 2004). It is shown that the rTPJ is overly sensitive to maintenance load, like the IPS is, but the rTPJ undergoes increased suppression during maintenance, unlike the IPS. Next, evidence is provided that supports a relationship between a deficit in stimulus-driven selective attention and filling VSTM to capacity. The results of this chapter have been presented elsewhere (Todd, Fougnie, & Marois, 2005).

Experiment 1:A near reciprocal relationship of the right TPJ and IPS in VSTM

This experiment was a re-analysis of Experiment 1, in CHAPTER I. Rather than testing for brain regions positively correlated with VSTM load, this experiment now looks for regions whose activity is negatively correlated with changes in VSTM capacity.

Methods

The methods are the same as those in CHAPTER I, Experiment 1 (Figure 1, with two exceptions. First, a voxel-wise approach was used to create a statistical parametric map (SPM) of activity negatively correlated with VSTM load. Second, in the subsequent ROI analysis of the rTPJ, after estimating the signal change relative to the no-event condition, the time courses were standardized to the mean of the volumes directly preceding and containing the presentation of the sample array (time = 0 s and 2 s), in

order to minimize the variance occuring in the signal prior to the onset of the memory array.

Results and discussion

The voxel-wise approach revealed supra-threshold activity whose activity was inversely correlated with VSTM capacity estimates only in the right TPJ (Figure 9A; Talairach coordinates of peak of activity (x, y, z): +59 –47 +24).

In a subsequent time course analysis, it was confirmed that the rTPJ's peak response amplitude was modulated by changes VSTM load (Figure 9B) ($F(5, 75) = 2.28$, $p = 0.05$). It appears that the effect of load on rTPJ activity extends temporally, even during the post-activation undershoot period (Figure 9B). This is in contrast to the IPS, in which the signal for each set size converges to a common amplitude at baseline (0%

A)   B)
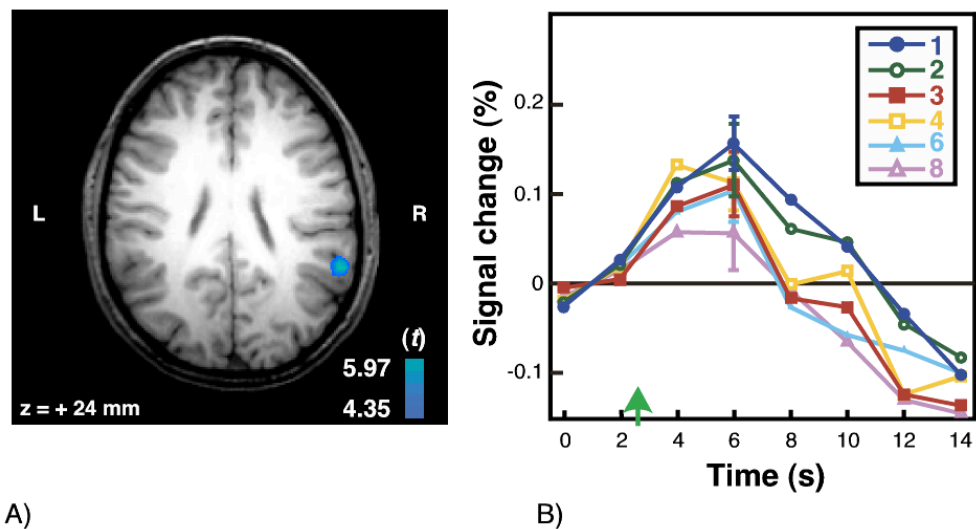
Figure 9. Right TPJ activity is inversely proportional to VSTM capacity. (A) SPM showing the locus of activity in the rTPJ. (B) Time courses for the rTPJ demonstrating that it undergoes increased suppression as VSTM capacity increases. Green arrow, memory array onset. SEM error bars are represented only for the volume of the peak of activation.

signal change; Figure 3C). Because of the continued load-modulation of the rTPJ, there was insufficient statistical power to determine whether its behavior in this VSTM task was better described as linear or quadratic (Rosnow & Rosenthal, 1996; Todd & Marois, 2004).

Experiment 2: VSTM phase analysis of the right TPJ's hemodynamic response

In the previous experiment, the voxel-wise analysis showed that the rTPJ's hemodynamic response is negatively correlated with memory load. The ROI analysis quantified the rTPJ's relationship with memory load, and while it was modulated by load, it could not be described as behaving in a capacity-limited manner, as the IPS does, or simply modulated by increasing cognitive demands. The rTPJ may undergo increased suppression as set size increases, which would mean that its activity reflects the increasing difficulty of the task, rather than increasing memory demands. To determine if the rTPJ is modulated by VSTM maintenance load, the maintenance-related signal of this region was probed in the data set from the two-load slow-ER experiment from CHAPTER I (Experiment 3A).

Methods

Refer to Experiment 3A in CHAPTER I for details on the methods. As a brief review of the task, subjects performed a VSTM task with a concurrent articulatory suppression task. In the VSTM task, subjects were presented 1 or 3 different colored discs for 150 ms, and were instructed to maintain those discs in memory for 9,200 ms, after which they performed a color-location recognition task on one of the discs from the

memory array.

Results and discussion

VSTM capacity estimate was larger for set size 3 than 1 (set size 3, 2.00; set size 1, 0.88; one-tailed t test, $t(13) = 6.24, p < 0.0001$), as discussed in the previous chapter. Activity during the maintenance phase of VSTM showed significantly greater suppression for set size 3 than 1 below baseline activity (Figure 10; $t(13) = 2.84, p = 0.007$). As with the IPS, the rTPJ is modulated by memory load. In contrast to the IPS, the rTPJ's activity is suppressed while information is being maintained in memory.

Experiment 3: VSTM Capacity-Modulated Behavior of the rTPJ

This experiment explores the rTPJ's sensitive to memory storage load further by taxing the observer's VSTM with a supracapacity memory load. If the rTPJ is sensitive to
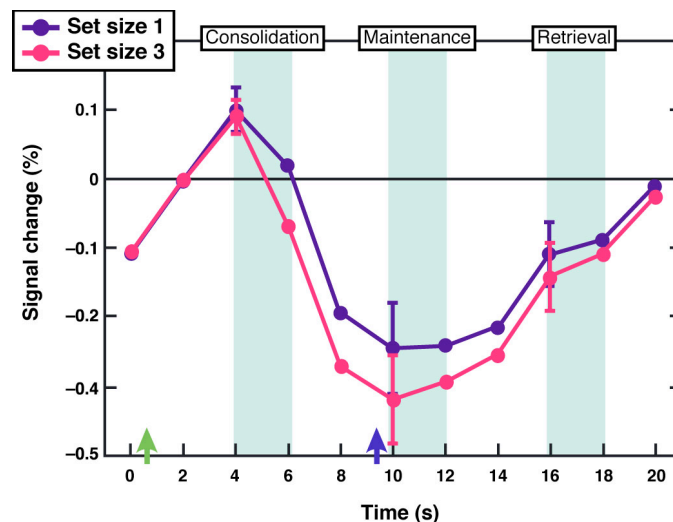
Figure 10. Right TPJ activity is modulated by memory load during maintenance. Green arrow, memory array onset. Purple arrow, probe array.

the amount of information held in memory, then activity should remain relatively constant across supracapacity memory loads, e.g., at memory loads greater than three items. However, if the rTPJ is more sensitive to the task demands, then it should undergo increased suppression because maintaining 6 items in memory is more difficult that storing 3 (Figure 2).

Methods

This experiment is the same as Experiment 2, above, or Experiment 3A in CHAPTER I, with the exception that six of the subjects from that experiment were presented three different memory loads, rather than two. Data analysis followed the same protocol as in the 2-load experiment.

Results and discussion

Behavioral performance was greater at set size 3 than 1 (1.99 vs. 0.90 k units, $t(5) = 6.05$, $p < 0.01$, 1-tailed t test), but there was no difference in the number of items stored in memory between set sizes 3 and 6 (1.99 vs. 1.68, $t(5) = 0.76$, $p = 0.48$). This capacity-modulated pattern was also observed in the hemodynamic response of the rTPJ, which was increasingly suppressed between loads 1 and 3 ($t(5) = 2.34$, $p = 0.03$, 1-tailed, Figure 11), but not between loads 3 and 6 ($t(5) = 0.79$, $p = 0.23$, 1-tailed). This maintenance load-sensitive suppression of the rTPJ could reflect the attentional demands of VSTM maintenance, as the rTPJ is suppressed in attention-demanding tasks (Marois, Yi, & Chun, 2004; Shulman et al., 2003; Zacks, Vettel, & Michelon, 2003).
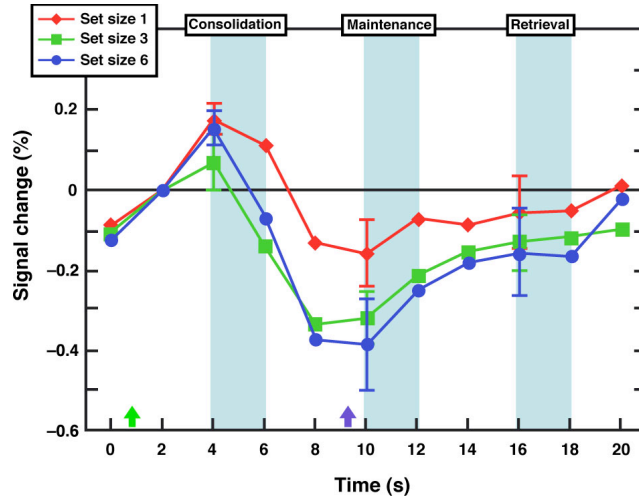
Figure 11. The rTPJ is modulated by VSTM capacity during maintenance. Green arrow, sample array onset. Purple arrow, probe array.

Experiment 4: TPJ activity is insensitive to a perceptual difficulty manipulation

The rTPJ's response to changes in VSTM capacity in the preceding experiments may have reflected increased difficulty in perceptually encoding increasingly complex, multi-element memory arrays. If this is the case, then the rTPJ's response might reflect changes in general difficulty. This possibility seems unlikely given that Experiments 3A, B demonstrated that rTPJ activity tracks VSTM storage load, instead of the difficulty of the task (set size 6 was more difficult than set size 3, yet activity levels were the same). To address this issue directly, an additional experiment was performed in which subjects were instructed to discriminate the color of a large disc presented at fixation (Figure 12). Task difficulty was manipulated by varying the contrast of the disc, which embedded in a field of colored noise.

Methods

Twelve subjects (6 females, 11 right-handed) from the Vanderbilt University

community, with correct or corrected-to-normal vision, participated in this experiment for financial compensation.

On each trial, a fixation cross was presented for 900 ms, followed by a 100-ms blank screen and then an equiluminant red or green colored disc (1.1° visual angle) for 150 ms. The disc was overlapped by a 3.3° x 3.3° field of randomly colored noise masking 20% of pixels in its region (Figure 12). The stimulus display was followed by a 250-ms blank screen then a 2,600-ms fixation screen, during which subjects identified the disc color as red or green. On each trial, disc contrast was set to one of three possible values, with equal probability, which were defined prior to each fMRI run in order to obtain three different performance levels (easy, moderate, hard), evidenced by the subject's reaction time and accuracy. Each fMRI run was composed of four conditions (3 difficulty manipulations and a no-event condition), and presentation order was counterbalanced within each run. FMRI parameters and the rTPJ ROI analysis were identical to Experiment 1, above and in CHAPTER I.

Results and discussion

Accuracy decreased and RT increased with decreasing target contrast (accuracy, $F(2,22) = 26.37, p < 0.001$; RT, $F(2,22) = 17.26, p < 0.001$). The accuracy difference between the Easy and Hard conditions (17% points) is larger than that between set sizes 1 and 3 in the VSTM tasks (Figure 2, Todd & Marois, 2004). Yet, there was no effect of perceptual difficulty on rTPJ activity (Figure 12; either 5 s or 7 s after stimulus presentation; 5 s, $F(2,11) = 2.70, p = 0.11$; 7 s, $F(2,11) = 2.30, p = 0.15$). Even though task difficulty increased with decreasing contrast (reflected by decreasing accuracy and
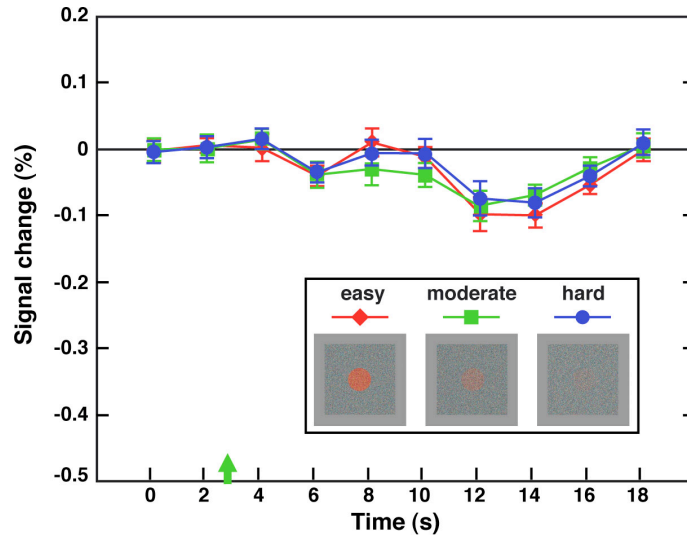
Figure 12. The rTPJ is weakly modulated by perceptual difficulty. Inset, difficulty was manipulated by adjusting the contrast of a colored disc embedded in a field of random colored noise. Subjects determined if the disc was red or green. The time course of activity was not significantly modulated by difficulty. Green arrow, stimulus onset.

increasing response time), the rTPJ response was not robustly modulated by the general task difficulty.

Experiment 5: VSTM Load induces Inattentional Blindness

The rTPJ is strongly activated when attention is captured by infrequent or unanticipated, yet perceptually salient, stimuli (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002; Downar, Crawley, Mikulis, & Davis, 2000, 2002; Marois, Leung, & Gore, 2000), and, as noted above, rTPJ activity is suppressed during goal-driven attention and VSTM tasks. Consequently, if the rTPJ is suppressed during the presentation of salient, task-irrelevant stimuli, the observer might not perceive them. This line of reasoning predicts that increasing VSTM load may impair attentional capture by a task-irrelevant stimulus. To test this hypothesis, the paradigm of

inattentional blindness (IB) was incorporated into a VSTM task. IB refers to a lack of awareness of the presentation of an unexpected and task-irrelevant stimulus as a result of the observer's inattention to that stimulus. To achieve IB, the observer's attention is drawn to a primary, attention-demanding task (Mack & Rock, 1998; Most et al., 2001; Neisser & Becklen, 1975; Simons & Chabris, 1999). Thus, IB experiments test the ability of an unexpected stimulus to capture the observer's attention (Simons, 2000).

Methods

Participants. Ninety-one young adults (41 males) from the Vanderbilt community, with normal or corrected-to-normal visual acuity and normal color vision, participated for financial compensation. A total of 15 subjects were discarded because they failed to detect the critical stimulus in the full attention trial (see below). Results are presented for the remaining 76 subjects.

Task design. Subjects performed a VSTM task as described in Experiment 2, except that the retention interval was 5 s and the set sizes were 1 and 4 (Low and High VSTM loads, respectively). The 76 participants were split evenly into the High load and Low load groups (between-subject design). As with other VSTM tasks, subjects were instructed to maintain fixation throughout the trial, with all colored discs shown within 2° of fixation (see Figure 1; Todd & Marois, 2004, 2005). After a brief practice session, participants performed six experimental trials. The final three experimental trials consisted of the *inattention*, *divided attention*, and *full attention* trials, described below.

Inattention (4th) Trial. On the fourth trial, 2 s into the retention interval, the

unexpected "critical stimulus" (1° white clover from Zapf Dingbats font) was presented

for 60 ms, 9.9° from fixation, in one of the four quadrants of the screen. Subjects were

not informed of the critical stimulus's presentation. Thirty-six of the subjects (18 for each

memory load) were questioned about the detection of the critical stimulus after the

completion of the trial, i.e., following the VSTM and verbal working memory responses.

To ascertain that critical stimulus detection performance reflected IB instead of memory

loss of the critical stimulus (i.e., *inattentional amnesia*; Wolfe, 1999), the other 40

participants (20 for each load) were probed immediately after critical stimulus

presentation by interrupting the trial. There were no effects of critical probe delay on

detection performance (Fisher's exact test, $p = 0.47$, 2-tailed), with the two delay groups

showing comparable load effects. These results suggest that deficits in detecting the

critical stimulus reflected IB as opposed to inattentional amnesia, and justify the

combination of the data from the two probe delay groups for the main analysis.

All participants were presented with three questions regarding the critical

stimulus. The questions were self-paced and presented on the computer monitor. The first

question assessed whether subjects had seen anything unusual during the trial, which

participants responded by "yes" or "no". The second question asked to select which

stimulus participants might have seen among twelve possible symbols selected from

MacIntosh font databases (❑✏➥✚√ ♣ ♫ ⌛✌✈⊕ 🗒 ⚙). The third question asked

participants to select the quadrant on the computer monitor in which the critical stimulus

may have appeared. Adopting the convention of past studies (e.g., Most et al., 2001),

critical stimulus detection was considered successful if the subject 1) reported "yes" to

the presence of the unexpected stimulus and 2) correctly selected the quadrant location.

The object identity test was too difficult even under full attention conditions (performance was at chance), likely owing to the brief and peripheral presentation of the unexpected stimulus, so performance with this question was excluded from analysis.

Performance differences between VSTM load groups are unlikely to be due to eye movements or eye blinks. Twelve subjects from both memory load groups performed the VSTM experiment while being filmed on video camera to monitor for eye movements or blinks during the inattention trial. Neither eye movements nor blinks were detected for any of these participants during the presentation of the unexpected stimulus.

Divided Attention (5th) Trial. At trial onset, subjects were visually instructed to do as well possible in the VSTM task, but to also look for a stimulus appearing during the retention interval. The VSTM display and critical stimulus appeared as described in the inattention trial, followed by an additional 2,940-ms retention interval, and then by the VSTM and verbal working memory response screens. After both responses were recorded, participants were given the three questions regarding detection of the critical stimulus.

Full Attention (6th) Trial. Prior to trial onset, participants were visually instructed to ignore the memory task and instead to look for a stimulus appearing during the retention interval. The trial proceeded as described for the 5th trial except that only the three critical stimulus questions were presented 2,940 ms following the critical stimulus.

Results and discussion

The first three, i.e., "normal", trials were used to estimate VSTM capacity, which was greater for set size 4 than 1 ($k = 2.61$ vs. 0.91; $t(33) = 5.67$, $p < .0001$). In the critical
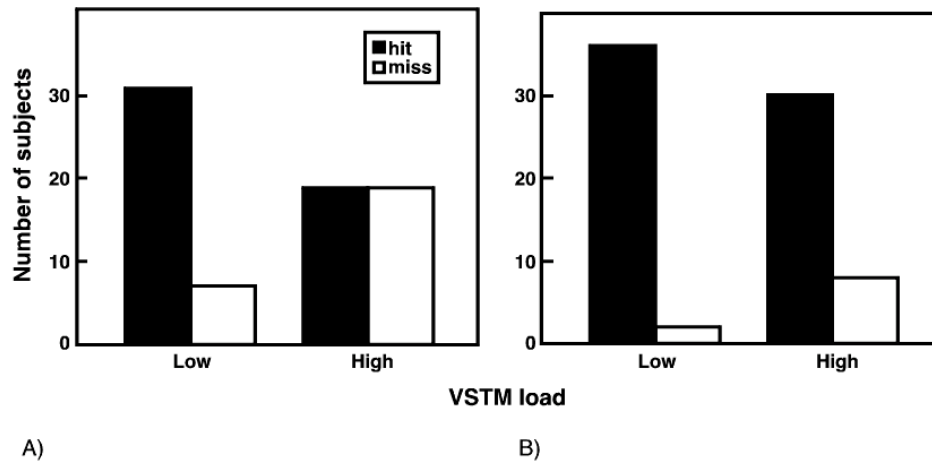
Figure 13. Filling VSTM to capacity induces inattentional blindness. (A) While most of the individuals storing a low load in VSTM detected the unexpected critical stimulus, filling VSTM to capacity significantly increased the number of individuals who were not aware of the critical stimulus. (B) Instructing subjects to divide their attention between the VSTM task and detecting the oddball stimulus improved performance, but the high load group still showed a slight impairment in the oddball detection task. Hits (correctly detecting the critical stimulus) are represented by black bars. Misses are white bars.

trial, fewer subjects detected the critical stimulus in the high VSTM load condition than in the low load condition (Figure 13A, Fisher's exact test, $p < 0.01$). While critical stimulus detection both improved and was much higher in the divided attention condition for the high memory load group, detection performance was still slightly impaired (Figure 13B; Fisher's exact test, $p = 0.08$). This residual impairment likely reflects subjects having to divide attention between the two tasks, as this impairment was absent in the final, full-attention trial when they only attended to the presentation of the critical stimulus (Most et al., 2001).

General Discussion

Heavily taxing VSTM storage demands may allow an unexpected stimulus presented during VSTM storage to pass undetected. It is likely that this unawareness

resulted from the goal-driven demands of the VSTM task preventing the rTPJ from registering unexpected events by suppressing the rTPJ's activity. Because support for this hypothesis is grounded on circumstantial evidence, it will be important in a future study to directly test if suppression of rTPJ activity by a VSTM task prevents the rTPJ from being activated by a task-irrelevant, critical stimulus as used in the experiment above. Doing so would provide the missing link between the neuroimaging finding that VSTM load suppresses TPJ activity and the behavioral finding that VSTM load leads to inattentional blindness.

The interaction between VSTM demands and stimulus-driven attention observed in the present behavioral experiment does not seem to occur just during the maintenance of information that this experiment tested. Active manipulation of VSTM content will also disrupt attentional capture by an unexpected stimulus, rendering it subliminal (Fougnie & Marois, 2007). A contemporary study also explored the interaction of goal-driven processes and explicit attentional capture. It was shown that a perceptually difficult task (e.g., deciding which of two arms of similar length forming a cross was longer) led to a reduction in attentional capture by an unexpected, task-irrelevant stimulus relative to a perceptually easier task (Cartwright-Finch & Lavie, 2007).

By straining the cognitive system, whether by heavily loading VSTM storage (Todd, Fougnie, & Marois, 2005), actively maintaining and organizing a large VSTM load (Fougnie & Marois, 2007), or performing a perceptually demanding task (Cartwright-Finch & Lavie, 2007), our experience of events in the world will be largely restricted to those that are most behaviorally-relevant (Most, Scholl, Clifford, & Simons, 2005; Most et al., 2001), even if those events are ones that must be filtered from the focus

of attention in order to perform well (de Fockert, Rees, Frith, & Lavie, 2001; Lavie, Hirts, de Fockert, & Viding, 2004). Although it has yet to be experimentally proven, the rTPJ appears to play an integral role in the passage of rare or unexpected events into the stream of consciousness (Driver & Mattingley, 1998). Suppression of the rTPJ may thus act in concert with the STM capacity-modulated IPS to limit our experience of the world to the task at hand by simultaneously focusing our goal-driven attention and STM mechanisms to task-relevant events, and preventing perceptually salient, but task-irrelevant, stimuli from drawing on these limited attentional resources (Haines, 1991; Strayer, Drews, & Johnston, 2003).

CHAPTER III

TEMPORAL CAPACITY LIMITS IN VISUAL SHORT-TERM MEMORY

Introduction

CHAPTER II showed that taxing visual short-term memory (VSTM) load can prevent the explicit perception of an unexpected, task-irrelevant stimulus (Todd, Fougnie, & Marois, 2005). These results indicated that the maintenance of information in VSTM can limit our awareness of other visual events. In this chapter, the focus is changed to asking whether our explicit experience of the world is also restricted by the consolidation of information into VSTM. Consolidation refers to the transfer of a durable representation of an event to short-term memory (STM) storage (Jolicoeur & Dell'Acqua, 1998). It is not to be confused with *encoding*, which is the coding of a stimulus for subsequent processing, with no assumptions made about the durability of these encoded representations. Consolidation can be defined as encoding information into STM (Jolicoeur & Dell'Acqua, 1998).

Until fairly recently, little was known about the relationship between VSTM consolidation and awareness. One paradigm in which this issue can been explored is the attentional blink (AB). The AB refers to a subject's impaired ability to detect the second of two targets (T2) in a rapid serial visual presentation (RSVP) stream of distractors if it appears within 200–600 ms of the first target (T1), with each stimulus presented for about 100 ms (Chun & Potter, 1995; Shapiro, Hillstrom, & Husain, 2002). Several models hypothesize that the T2 deficit is the product of capacity-limits in STM consolidation

(Chun & Potter, 1995; Giesbrecht & Di Lollo, 1998; Jolicoeur, 1998). For example, one prominent theory asserts that attention selects information to advance it from a perceptual/conceptual stage, where stimuli are detected and identified as targets, into STM storage (Chun & Potter, 1995). In these models, consolidation of information in STM is time-consuming, typically lasting upwards of 500 ms, and cannot take place for a second target if the consolidation stage is currently occupied by another target. A "blink" is experienced if the T2 representation decays or is replaced by a following distractor before it can be passed into the consolidation stage. In an initial examination of the effect of manipulating T1 VSTM load on T2 performance, Ward, Duncan, and Shapiro (1996) showed that as the number of items in the first target (T1) array is increased from one to two, T2 performance decreases. This deficit was strongest when the T1 and T2 targets were presented within about 500 ms of one another, and T2 performance improved significantly as the delay between T1 and T2 increased. The authors argued that the T2 performance impairment reflected the sluggish speed of the allocation of attention resources to each item necessary to consolidate T1 into STM (Duncan, Ward, & Shapiro, 1994; Ward, Duncan, & Shapiro, 1996).

There is other evidence exploring the relationship of STM load and the AB. Akyürek and Hommel (2005) reported a study in which subjects maintained a varying amount of information in STM while they performed an AB task. Results showed a T2 deficit typical of AB studies. When STM load was manipulated, T2 performance was modulated by STM load, generally decreasing with increasing load. Critically, there was no interaction of T2 performance with STM load and T1-T2 lag. The main effect of STM load in this study may be explained by the need for a capacity-limited central resource

supporting storage of the STM load during the AB task. As more information is transferred to the central resource, less of this resource is available for other tasks, such as consolidation. Support for this comes from a study demonstrating that performance in a VSTM task was impaired when subjects' verbal working memory was taxed by rehearsing a large amount of verbalizable information, but not when the verbal load was small (Morey & Cowan, 2004). Thus, while STM storage does not cause the AB, the study by Akyürek and Hommel (2005) shows that simply storing information in VSTM will not affect the magnitude of the T2 deficit, without also causing a general T2 performance impairment across all lags.

Additional support for a capacity-limited process affecting T2 performance in the AB comes from the finding that when STM content must be scanned for an item matching the T1 stimulus, T2 performance is adversely affected (Akyürek, Hommel, & Jolicoeur, 2007). Critically, this interference only occurred within the temporal window of the AB and it was modulated by the amount of information held in STM. This interaction of STM load and T1-T2 lag supports a role for a capacity-limited central resource in the manipulation of information held in STM (Heil, Wahl, & Herbst, 1999; Jolicoeur, 1998).

A study by Ouimet and Jolicoeur (2007) manipulated T1 load without changing the physical number of items that composed the T1 stimulus: They manipulated the difficulty of storing T1 items in STM by having subjects either remember the T1 items as an ascending sequence of digits "01234" (low T1 load) or a random ordering of those digits (high T1 load). An interaction of T2 performance with T1 load and lag was observed. The authors argued that by increasing the difficulty of T1, T1 consolidation

duration was increased, and when T2 was presented temporally close to T1 in the high load condition, T2 performance was impaired because T1 consolidation had not yet completed. The study by Ward et al. (1996), discussed above, found similar results when they manipulated T1 set size (1 vs. 2 items); however, the interaction of lag and T1 load on T2 performance was only a trend towards significance ($p = 0.08$). Nonetheless, these two studies show that manipulating the amount of T1 information that must be consolidated into STM can modulate T2 performance, and once T1 has been consolidated, T2 consolidation can operate unhindered by the T1 items, which are now being maintained in STM.

Despite support for the role of consolidation in the AB, it wasn't until fairly recently that researchers attempted to measure the speed of STM consolidation in a single-task experimental design. Using a task similar to that in Figure 1, the consolidation rate for colors (bound to specific locations) was estimated to be about 50 ms/item (Vogel, Woodman, & Luck, 2006). A separate study suggested that letters may be consolidated at an even faster rate (Gegenfurtner & Sperling, 1993). In the AB, T1 is typically a single-item stimulus, so a 50-ms/item consolidation rate conflicts with the time course of the AB by almost an order of magnitude. Because of this large difference, the several hundredths of a second that occur outside the estimated 50-ms window of consolidation in the AB may reflect other capacity-limited processes, such as dividing resources between processing T1 and preparing for the subsequent T2 stimulus (Jolicoeur, 1998; Jolicoeur & Dell'Acqua, 1998), and switching attention from T1 to T2.

The aim of this chapter is to determine the contribution of VSTM consolidation in

limiting awareness of transient and temporally proximate events. As has already been shown, the magnitude of the T2 deficit increases as the STM load of T1 in increased (Ward, Duncan, & Shapiro, 1996), but it is unknown what happens to T2 performance at VSTM capacity and supracapacity loads. Such an experiment would provide a more direct test of the role of VSTM in the AB, as Ward et al.'s (1996) results could be accounted for by general attentional demands required for T1 processing, as opposed to T1 VSTM consolidation. According to models identifying STM consolidation as a significant component of the processing bottleneck that underlies the AB (Chun & Potter, 1995; Jolicoeur, 1998), T2 accuracy is expected to worsen with increasing VSTM load until STM is filled to capacity, and remain at asymptote thereafter across supra-capacity loads, since no further information can be transferred into STM maintenance (Woodman & Vogel, 2005). If STM consolidation plays little-to-no role in the AB, T2 performance would be expected to be constant across varying memory loads, regardless of the T1-T2 lag. Alternatively, if T2 performance is regulated by Task-1 difficulty or perceptual load rather than VSTM consolidation *per se*, then one would predict that T2 performance should decrease linearly as the number of T1 items increase, even beyond VSTM capacity.

The current set of experiments is intended to extend the current body of research and explore the role of STM consolidation in limiting awareness of the second of two temporally proximate events. Benefits of this work over past studies include the parametric manipulation of the amount of T1 information to be consolidated into VSTM before T2 is presented. The delay between T1 and T2 presentations was also manipulated in order to estimate the time course of T1 consolidation-related processes on T2. If, as

others argue, STM maintenance and consolidation are distinct processes (Woodman & Vogel, 2005), then when T2 is presented at longer lags, when all of T1 should have been transferred into maintenance, T2 performance is not expected to be modulated by T1 consolidation load.

Experiment 1: The relationship of T1 VSTM load and T2 performance, and measuring VSTM capacity

Typical AB experiments use a memory load of one item for T1, so T1 performance is measured as accuracy (Raymond, Shapiro, & Arnell, 1992). In the current study, the interest is in determining how the quantity of T1 information being consolidated into VSTM affects T2 performance. To estimate T1 VSTM capacity (k), two different response procedures were used: a full report of T1 (all memorized T1 stimuli were reported by subjects) and a partial recognition of T1 (subjects were probed on the identity of one of the T1 stimuli). Full report is considered a direct measurement of subjects' memory, because the number of items recalled from memory should represent the number of items held in memory. A drawback to a full report task it can lead to underestimates in STM capacity because memory may rapidly deteriorate while being reported (Sperling, 1960). In contrast, while partial recognition tasks provide more accurate assessments of subjects' memory (Sperling, 1960), they do not provide direct assessments of memory capacity, because only a subset of the information held in memory is reported. To circumvent this limitation in this study, Cowan's k was used to estimate VSTM capacity (Cowan, 2001). Thus, in addition to measuring the influence of T1 memory load on T2 performance, this experiment will test different methods for estimating VSTM capacity, which has only rarely been done (Cowan, 2001).

Methods

Participants. Eleven Vanderbilt undergraduate students (7 females), with normal or corrected-to-normal visual acuity, participated in this experiments for credit in undergraduate psychology courses.

Stimuli and general procedure. The experiment was presented on an Apple G3 iMac computer. All stimuli were white presented on a dark gray background. Each subject participated in the partial recognition and full report sessions. Both sessions were identical in all respects except during the response period. A schematic of the trial design for the partial recognition session is shown in Figure 14. Each trial began with a fixation cross in the center of the screen for 1,500 ms. While attending to the center of the display, subjects were presented a varying set size (1, 2, 3, 4, 5, or 6) of T1 stimuli (each 0.73° x 0.63°) randomly sampled without replacement from a set of consonant letters (B, D, L, M, N, P, R, T, X, Y). These stimuli were randomly presented in any of six possible positions in a circle subtending 3.33° in the center of the screen. Following a 300, 375, 450, 600 or 900 ms delay from the onset of T1, a T2 stimulus was presented. The T2 stimulus could be the target ("F") or a distractor (one of the following letters: J, K, H, V). The T2 stimulus was followed by two masks: the "at" (@) and ampersand (&) symbols. The T2 stimulus and its masks were large (1.35° x 1.56°), in order to reduce the possibility that shifts of spatial attention from the peripheral T1 circle to the T2 location would contribute to the T2 deficit (Visser, Zuvic, Bischof, & Di Lollo, 1999). T2 stimulus size was small enough to fit within the inner diameter of the T1 display and not suffer from meta-contrast masking by the T1 stimuli (see below). The range of T1-T2
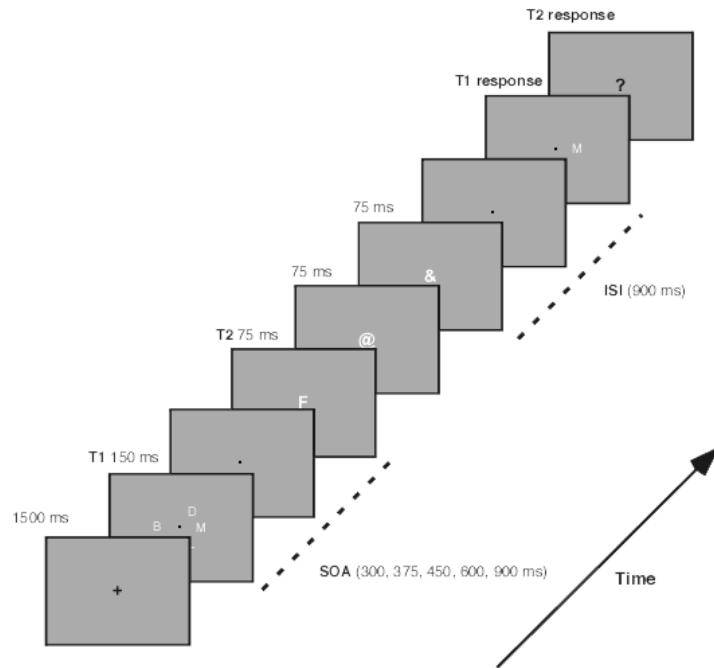
Figure 14. Trial design of the partial recognition experiment. Subjects were instructed to remember the letters from T1. After a varying delay, a letter and two symbols were presented at fixation, and the task was to take note if the letter was "F" or not. After a 900-ms delay, a probe letter appeared in one of the positions from the T1 array and the subject reported if the probe was identical to the letter at that position in the T1 memory array. After responding to the T1 probe, a question mark appeared at fixation and the subject indicated if T2 was present or absent.

stimulus onset asynchronies (SOAs) encompassed the time window during which the AB

is typically very large (300 ms), as well as later lags (e.g., 900 ms) during which all the

T1 stimuli should be consolidated into VSTM before T2 is presented and T2 performance

should be unaffected by T1 load (Chun & Potter, 1995; Raymond, Shapiro, & Arnell,

1992). The T2 stimulus and masks presentations were followed by a 900-ms period

fixation period, which was itself followed by a response probe for the T1 array, and then

by the response probe for the T2 stimulus.

Partial recognition session response period. In the partial recognition session,

after the 900-ms fixation period following the final T2 mask, a single T1 probe letter was

presented in one of the positions occupied by the T1 sample array (Figure 14). The probe

matched the T1 letter at that position in 50% of the trials. When the probe did not match

the T1 stimulus, the probe stimulus was taken from the set of stimuli not used in the T1

memory array for that trial. Subjects were not informed of the relationship of the T1

probe and the respective T1 stimulus identity. When a T1 probe appeared, subjects made

an unspeeded two-alternative forced-choice response regarding whether the T1 probe

letter matched the sample letter at that position or if it was different from the letter

presented in the same position in the T1 memory array.

After responding to the T1 probe, a single question mark appeared at fixation and

subjects made an unspeeded two-alternative forced-choice decision, reporting if the T2

target was present or absent in that trial (Figure 14). The T2 target stimulus was presented

in two-thirds of all trials. Three-quarters of trials in which the T2 target was presented

had a T1 probe from the memory array, and one-quarter of the T2 target "present" trials

had a T1 probe that did not appear in the memory array.

Full report session response period. In the full report session, two question marks

appeared in the center of the screen and participants were instructed to type all the letters

that they were confident were presented in the T1 array. Following the T1 response,

subjects were required to press the space bar to continue to the T2 report. T2 report was

the same as in the partial recognition session: A single question mark appeared at fixation

and participants indicated by unspeeded button press if the T2 target was present or

absent in the trial. As in the partial report sessions, the T2 target appeared in two-thirds of

all trials.

Session presentation order. Report session presentation order was

counterbalanced between participants. Before each session, the instructions were reviewed to the subjects, who were also instructed to maintain fixation on the center of the screen throughout each trial and emphasize accuracy over speed. Twenty practice trials were given before each session. The six T1 set sizes were crossed with the five SOAs, and repeated six times, yielding a total or 180 trials/block. Trial presentation order was randomly intermixed. Each subject performed six blocks of 30 trials. Rest periods were provided at the conclusion of each block of trials. Following the conclusion of the final block of trials, a message appeared on the computer monitor instructing the subject to get the experimenter.

Data analysis

Because subjects were instructed to emphasize accuracy over speed when responding to both T1 and T2 probes, reaction time was not assessed in this study.

In the partial recognition session, the estimated number of objects consolidated was calculated using Cowan's k formula (Cowan, 2001). In the full report session, k was calculated by summing the total number of T1 stimuli correctly recalled from memory. The convention in AB studies is to measure T2 performance using trials where the subject accurately detected T1, i.e., to use T1 "hit" trials in partial report experiments (Raymond, Shapiro, & Arnell, 1992). In the current study, T2 performance was calculated in the partial recognition sessions of the current study by using trials with correct T1 responses only (hits and correct rejections). By using all T1-correct trials in reporting T2 performance, more accurate conclusions can be made between the relationship of VSTM processes and the detection of a subsequent target, because only

the proportions of T1-correct trials are used to calculate Cowan's k. In the full report

session, because subjects were not expected to have encoded every T1 stimulus at high

memory loads (e.g., set sizes 5 and 6), trials were used for T2 analysis if the subject

reported correctly at least one T1 item.

Results and discussion

T1 performance. A repeated measures ANOVA with set size and report mode as factors

was run to determine if the report modes produced different T1 k values. There was a

significant effect of set size ($F(5,50)=62.17, p < 0.0001$), but no main effect of report

mode ($F < 1$). Despite this null effect, each report mode's T1 results will be presented

separately because, as will be shown, there was an effect of report mode on T2

performance.

T1 Performance diverged from what is expected from a capacity-*un*limited

process around set size 4 (Figure 15B) for both report modes. Based on previous studies

indicating that the VSTM capacity limit is around 3–4 items (Alvarez & Cavanagh, 2004;

Cowan, 2001; Luck & Vogel, 1997; Todd & Marois, 2004; Vogel, Woodman, & Luck,

2001), it was expected that the number of objects consolidated would significantly

increase between set sizes 2 and 4, but not between set sizes 4 and 6. This was confirmed

in paired *t* tests for the partial recognition (set size 2 vs. 4, $t(10) = 6.16, p < 0.001$; set size

4 vs. 6, $t(10) = 0.65, p = 0.53$). In the full report condition, there was a significant

increase in VSTM capacity between set sizes 2 and 4 ($t(10) = 11.21, p < 0.001$), but a

decrease between set sizes 4 and 6 ($t(10) = 4.55, p = 0.001$). The decrease in capacity at

larger set sizes in the full report condition is consistent with past studies using full report
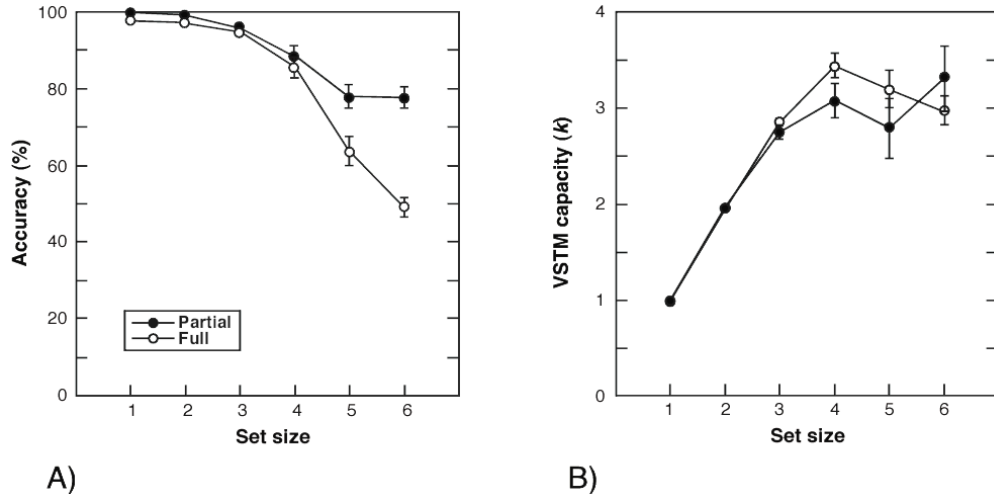
Figure 15. T1 performance in Experiment 1. (A) T1 accuracy for partial recognition (filled circles) and full (empty circles) report tasks. (B) Memory capacity estimates showing the capacity limit was reached around set size 4, for both tasks. Error bars represent SEM.

(Sperling, 1960), and it likely reflects interference incurred during retrieval (Nairne, 2002). Regardless, the VSTM capacity limit was reached around set size 4 for both report modes, thereby validating the use of either a full report or partial recognition T1 task in the present study to estimate VSTM capacity limits.

T2 performance. An ANOVA with set size, T1-T2 SOA, and report mode as factors revealed main effects of set size ($F(5,50) = 34.50$, $p < 0.001$), SOA ($F(4,40) = 10.65$, $p < 0.001$), and report mode ($F(1,10) = 5.92$, $p = 0.04$) (Figure 16). There was also an interaction of set size and report mode ($F(5,50) = 7.22$, $p < 0.001$). There was no interaction between set size and SOA ($F(20,200) = 1.17$, $p = 0.28$). All other interactions were not significant ($F < 1$). The interaction of report mode and set size may be attributed to differences in performance between report modes at supracapacity VSTM loads (T1 set size greater than 4). An ANOVA for low memory loads (set sizes 1–4) revealed no

main effect of report mode ($F < 1$), but there was an effect at supracapacity loads (set sizes 5 and 6) ($F(1,10) = 13.88, p = 0.003$). This effect at large loads, showing overall poorer T2 performance in the full report than partial recognition session (Figure 16), may reflect memory decay of the T2 stimulus as memorized T1 stimuli are being individually reported during T1 report (Sperling, 1960). This in unlikely to occur for large memory loads in the partial recognition session, because the subject only has to recognize one item from the T1 stimulus array.

The lack of an interaction of set size and SOA is consistent with other studies showing STM load affecting the magnitude of T2 detection performance at large SOAs, e.g., 720 ms in Akyürek and Hommel (2006) and 1200 ms in Ouimet and Jolicoeur (2007). It is also possible that the use of longer SOAs would have revealed such interaction, as explored later in Experiment 5. Finally, T2 accuracy was significantly
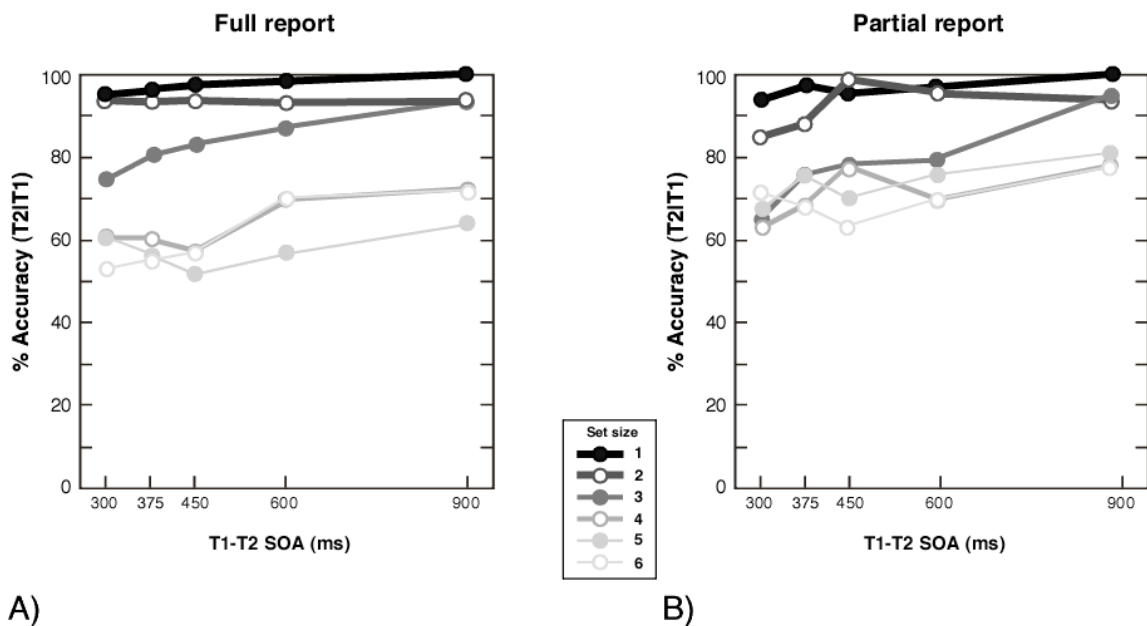
Figure 16. T2 performance by set size and SOA in Experiment 1. (A) Performance in the full report task. (B) Performance in the partial report task.

greater than the FA rates (less than 8% for all conditions) for both partial recognition ($F(1,10) = 710.34, p < 0.001$) and full report ($F(1,10) = 684.03, p < 0.001$) tasks. Thus, T2 performance is not due to subjects adopting a guessing strategy during T2 report.

If T2 detection is modulated by consolidation load, then increasing the T1 memory load should lead to increased impairment in detecting T2, until the storage capacity limit is reached. This hypothesis was tested at the 300-ms T1-T2 SOA, which encompasses the T1-T2 temporal window where the T2 deficit is frequently maximal (Shapiro, Arnell, & Raymond, 1997). An ANOVA of set size and report mode for T2 accuracy at this SOA showed a significant main effect of set size ($F(5,50) = 12.29, p < 0.001$), but no effect for report mode ($F < 1$) (Figure 17). Indeed, T2 accuracy decreased between set sizes 2 and 4 (partial recognition, $t(10) = 3.89, p = 0.003$; full report, $t(10) = 6.07, p < 0.001$), but leveled off at set size 4 (set size 4 vs. 6: partial recognition, $t(10) = 1.11, p = 0.29$; full report, $t(10) = 0.85, p = 0.41$).
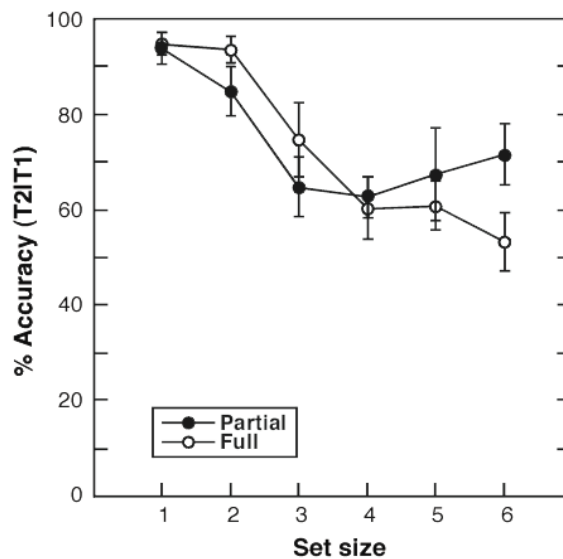
Figure 17. Results for Experiment 1. T2 accuracy on trials where T1 report was correct. The pattern of T2 detection accuracy (300-ms SOA) was opposite of that for T1: Accuracy decreased until the capacity limit for T1 items was reached.

To summarize, T2 performance is modulated by the amount of T1 information consolidated into STM, not simply the amount of information presented in the T1 display, i.e., the perceptual load. If overall Task 1 difficulty underlies the AB, then subjects should show continued T2 impairment through set size 6, because T1 performance was worse at set size 6 than 4 (partial recognition, $t(10) = 3.31, p = 0.008$; full report, $t(10) = 16.45, p < 0.001$) (Figure 15A). This was clearly not the case: When VSTM was filled to capacity with T1 array items (Figure 15B), T2 performance leveled off with further increases in T1 memory load (Figure 16).

Experiment 2: A control for verbal working memory

Experiment 1 used letters as T1 and T2 stimuli. A possible limitation of using these stimuli is that subjects may have consolidated them into verbal short-term memory, in addition to visual short-term memory (Baddeley, 1986, 1992; Vogel, Woodman, & Luck, 2001). This could affect T1 k values, as well as T2 accuracy. To address this, a second experiment was run in which performance was compared between VSTM-AB tasks that differ in the use of a concurrent articulatory suppression task (Todd & Marois, 2004).

Methods

Thirteen Vanderbilt undergraduate students (10 females), with normal or corrected-to-normal visual acuity, participated in this experiments for credit in undergraduate psychology courses. The task design was exactly like that in the partial

recognition task of Experiment 1, with the exception that the 375-ms SOA was not used and subjects performed an articulatory suppression task for half of the trials. This experiment was divided into two parts: "rehearsal" and "non-rehearsal". In the rehearsal session, subjects performed the articulatory suppression task used previously in the fMRI experiments of CHAPTERS I and II (Todd, Fougnie, & Marois, 2005; Todd & Marois, 2004, 2005). After the fixation period at the beginning of each trial (Figure 14), two different, randomly selected single digits (0–9) were presented auditorily through headphones for 250 ms each. After a 500-ms delay, an auditory mask (a composite of the ten digit sound files played in forward and reverse) was presented for 500 ms. Participants were instructed to subvocally rehearse the pair of digits throughout the entire trial, at a fast but comfortable rate (2–3 times/second).[3] A 1500-ms period followed the offset of the auditory mask before the trial proceeded normally with T1 and T2 stimulus arrays. After the T2 response, participants were prompted to type the two digits they rehearsed. Presentation order of the sessions was counterbalanced between subjects. In each session, there were 144 total trials (6 set sizes x 4 SOAs x 6 repetitions). Subjects performed six blocks of 24 trials and trials were randomly intermixed across the six blocks. Subjects were given the opportunity to take a break after every block of trials. There were twenty practice trials at the onset of each session.

Because the 300-ms SOA is the time at which ABs are typically very strong (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992; Shapiro, Arnell, & Raymond, 1997), figures for T2 performance will be shown only for this SOA, in this experiment and the remaining ones as well (except for Experiment 5, which carefully explores the

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[3] Performing the articulatory suppression task aloud does not change the pattern of results, as Experiment 4 demonstrates (see below).
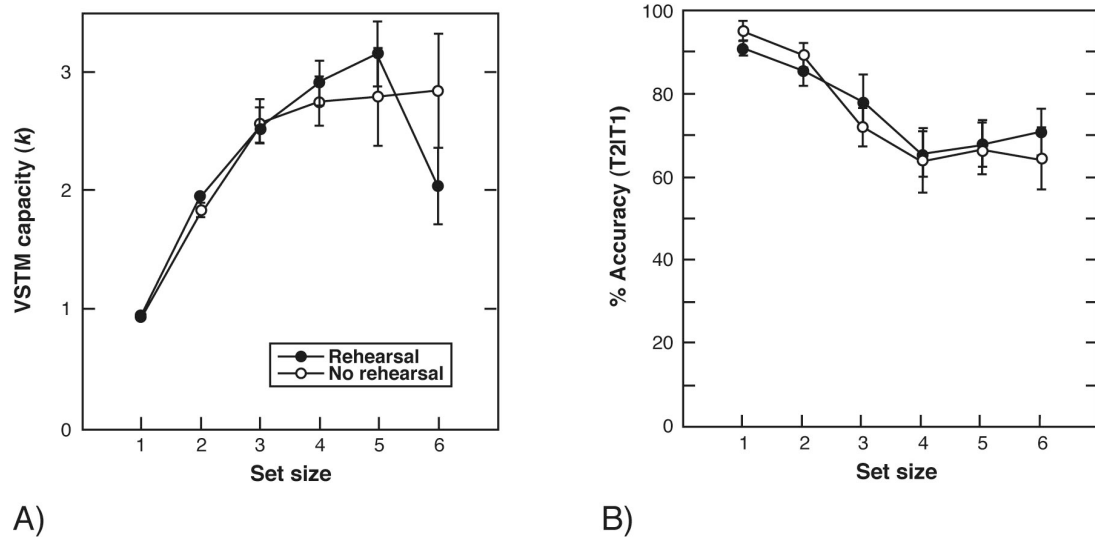
Figure 18. Results for Experiment 2. Rehearsal of verbal information, filled circles. No rehearsal, empty circles (A) T1 performance when subjects performed an articulatory suppression task and when it was absent. (B) T2 detection performance is not affected by the auditory-verbal control.

time course of T2 performance). For all these experiments, ANOVAs of T2 performance by set size and SOA will still be reported.

Results and discussion

One subject was removed from analysis because that subject did not complete the rehearsal session. Results are presented for the remaining twelve subjects.

Accuracy in the articulatory suppression task was consistently high across set sizes (accuracy > 87% across all set sizes; $F(5,55) = 1.69, p = 0.15$). The effect of digit rehearsal on the number of T1 objects encoded per set size was examined in an ANOVA with set sizes and rehearsal mode as factors. The results demonstrated an effect of set size ($F(5,55) = 17.83, p < 0.001$) but no effect of rehearsal mode ($F(1,11) = 0.07, p = 0.80$). As Figure 18A shows, T1 performance reached a capacity limit by set size 4. While

capacity increased from set size 1 to 4 (rehearsal: $t(11) = 11.03, p < 0.001$; no rehearsal: $t(11) = 2.85, p = 0.02$), it remained stable at larger memory loads in the rehearsal condition ($t(11) = 1.66, p = 0.12$), and there was actually a drop in k when subjects performed the articulatory suppression task ($t(11) = 3.09, p = 0.01$); however, performance was stable between set sizes 4 and 5 in the rehearsal condition. ($t(11) = 0.97$, $p = 0.35$). It is concluded that the T1 task primarily measures visual STM, not verbal working memory, and a capacity limit was reached around set size 4, consistent with Experiment 1.

An ANOVA of T2 performance with set size, SOA, and rehearsal mode as factors showed significant effects of set size ($F(5,55) = 18.70, p < 0.001$) and SOA ($F(3,33) = 18.27, p < 0.001$). T2 performance was not significantly influenced by the articulatory suppression task ($F < 1$), and none of the interactions were significant ($F\text{s} < 1.3, p\text{s} > 0.24$). A more focused analysis on T2 performance for the 300-ms SOA, when the AB T2 deficit is typically very robust, showed an effect of set size ($F(5,55) = 5.87, p < 0.001$), but no effect of rehearsal mode ($F < 1$). As shown in Figure 17B, performance was worse at set size 4 than 2 (rehearsal, $t(11) = 2.86, p = 0.02$; no rehearsal, $t(11) = 2.84, p = 0.02$), but there was no significant difference in T2 accuracy between set sizes 4 and 6 (rehearsal, $t(11) = 0.94, p = 0.37$; no rehearsal, $t(11) = 0.26, p = 0.80$).

A lack of an effect of the articulatory suppression task on T2 performance contradicts a previous study's finding (Akyürek & Hommel, 2005). However, that study was more demanding, as it included three different tasks: 1) an articulatory suppression task designed to interfere with the AB task, 2) a VSTM load presented at trial onset and maintained throughout the trial, and 3) an AB task (T1 and T2 were presented in an

RSVP and their memory loads were always one item). It is possible that the addition of the articulatory suppression task in that study taxed the subjects' ability to perform all three tasks concurrently, resulting in a general poorer performance in detecting T2 (Morey & Cowan, 2004). In any event, the VSTM load-modulated T2 results in the current experiment are unlikely to primarily reflect the contribution of verbal working memory. Instead, they are consistent with the hypothesis that T2 performance is modulated by T1 VSTM consolidation load.

Experiment 3: A control for verbal encoding of T2

Despite Experiment 2's findings, one may still argue that the low auditory-verbal STM load of the articulatory suppression task still allowed subjects to verbally encode T1 and T2 targets, and thus the results may not primarily reflect visual STM processes. This third experiment was designed to address this issue further by using a T2 stimulus that is not easily verbalized. If the results from the previous experiments depended on verbal working memory, then rendering the T2 task more perceptual should affect the trade-off relationship between T1 consolidation and T2 performance. To address this possibility, the T2 stimulus was changed to a box that could have a gap on any side, forming a Landolt "C", a stimulus that has been used extensively in visual perception tasks (Davis, Shikano, Peterson, & Michel, 2003; Nazir, 1991; Woodman, Vogel, & Luck, 2001). The T2 task consisted of reporting if the T2 box had a gap (on any side) or not. Thus, any modulation in T2 accuracy by T1 load is unlikely to result from limitations in verbally consolidating the T2 stimulus.

Methods

Sixteen Vanderbilt undergraduate students (7 females), with normal or corrected-to-normal visual acuity, participated in this experiment for credit in undergraduate psychology courses. The experimental design was exactly like that of the full report task of Experiment 1, with the exception that the T2 stimulus was a white box (1.56° square) and subjects determined if a gap (1°) appeared on any side of the box, forming a Landolt figure, or if a solid box was presented.

Results and discussion

T1 performance was capacity-limited. The effect of set size ($F(5,75) = 140.87$, $p < 0.001$) reflected the increasing capacity of T1 stimuli from set size 2 to 4 ($t(15) = 2.40$, $p = 0.03$), and performance reached asymptote at higher memory loads (set size 4 vs. 6: $t(15) = 1.93$, $p = 0.17$) (Figure 19A).
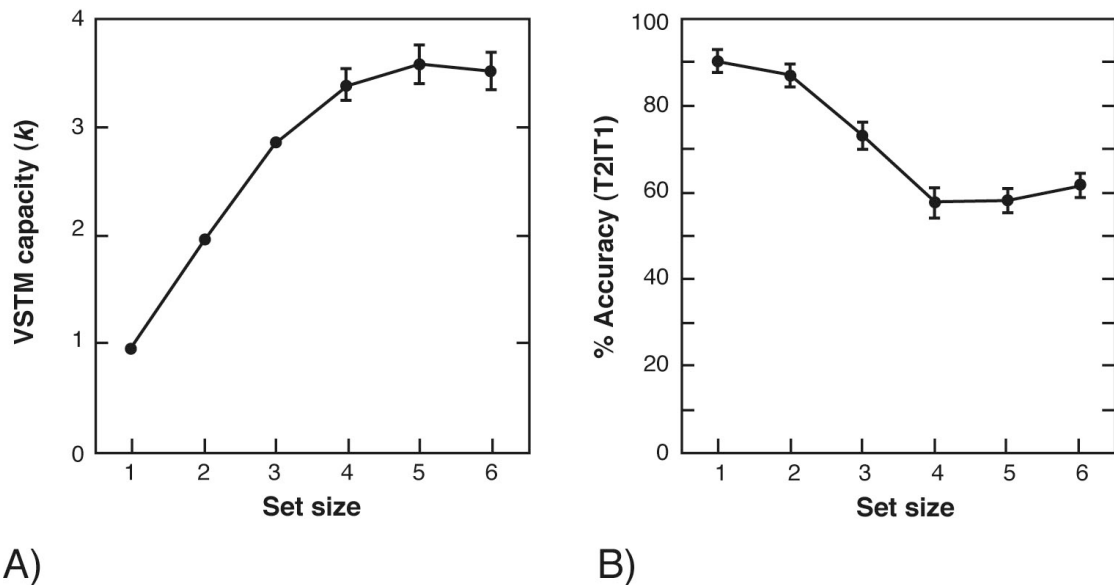
Figure 19. Experiment 3 performance. (A) T1 k values. (B) T2 performance.

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Even when using a stimulus that was more difficult to verbalize, T2 performance still showed an effect of T1 set size ($F(5,75) = 26.39, p < 0.001$) and SOA ($F(4,60) = 14.02, p < 0.001$), but the interaction was not significant ($F(20,300) = 1.26, p = 0.21$). At the 300-ms SOA, there was an effect of T1 set size ($F(5,75) = 7.98, p < 0.001$). More importantly, and indicative of a capacity-limited pattern of results, T2 performance dropped from set size 2 to 4 ($t(15) = 2.40, p = 0.03$), and leveled off with further increases in memory load (set size 4 vs. 6, $t(15) = 0.62, p = 0.54$) (Figure 19B). This provides further supporting evidence that the deficit in reporting T2 reflects predominantly visual, not simply verbal, processes.

Experiment 4: Effect of masking T1

Because the T1 display was not masked in the preceding experiments, subjects may have used their iconic memory representations of T1 targets to facilitate T1 consolidation, which would artificially inflate VSTM capacity estimates (Neisser, 1967; Vogel, Woodman, & Luck, 2006); however, in typical AB experiments, T1 is masked, which would erase the iconic memory trace of T1 (Raymond et al., 1992; Chun & Potter, 1995). Hence, in the present experiment, a mask composed of an annulus of randomly oriented lines was presented immediately after T1 for 75 ms.

In addition to examining the effect of a T1 mask on VSTM capacity, the present experiment also assessed the possibility that this mask, or the T1 display itself, could perceptually interfere with T2 processing. Given that T2 was presented within the fovea and did not spatially overlap with either the T1 display or T1 mask, it seems improbable that T2 processing would be affected by forward or lateral masking (Bouma & Leigen,

1977, 1980; Breitmeyer, 1984; Nazir, 1991; Raymond, Shapiro, & Arnell, 1992). To address this issue explicitly, subjects were also tested on their ability to perform the T2 task alone. If the T1 display and mask do not perceptually interfere with T2, then T2 performance should not be affected by the presence of the T1 display and mask when subjects are told to ignore them.

Methods

Twenty-one participants from the Vanderbilt community (9 females), with normal or corrected-to-normal visual acuity, volunteered in this experiment for paid compensation.

This experiment was similar to Experiment 2 with the articulatory suppression task, except for the following changes. Immediately following the T1 presentation, a mask (an annulus subtending 0.63° thick with an outer diameter of 3.33°) composed of randomly oriented white bars on a gray background was presented for 75 ms. The mask did not spatially overlap with the T2 stimulus sequence: The diameter of the mask's inner contour subtended 2.07°, which is at least 0.25° peripheral to the T2 stimulus, on any given side of the T2 target. (The size of the foveated T2 stimulus and its distance from T1 and the mask should make T2 immune from lateral masking: Using smaller stimuli with a shorter gap between the target and its peripheral masks, Nazir (1991) found that subjects performed at near-ceiling levels in a task requiring them to identify the foveated target stimulus). After a varying T1-T2 SOA (225, 300, 450, or 750 ms), T2 was presented. In this experiment, the T2 target stimulus was the digit "6" (digits 3, 5, or 8 were presented as foils in non-matching trials) presented for 50 ms, followed by the same masks as in

Experiment 1 (the "at" (@) and ampersand (&) symbols), with each mask presented for 75 ms.

The experiment was divided into two sessions, with 20 practice trials provided at the onset of each session. Trials for each session began with the same stimuli (a T1 display and mask followed by the T2 sequence of stimuli), but the probe screens differed between the sessions. In the first session, referred to as the "T2-control" session, subjects performed only the T2 detection task, even though T1 and its mask were presented (subjects were instructed to ignore these task-irrelevant stimuli). Because there was no T1 response period for these trials, the T2 masks were immediately followed by the T2 response period. After the T2-control session, subjects performed the "experimental" session. Here, subjects made responses to both tasks while concurrently performing an articulatory suppression task. Subjects rehearsed "the" aloud at a fast but comfortable rate, about 2–3 times a second (Baddeley, 1992). Before each trial, there was a 2,500-ms fixation period to give the subject time to begin the articulatory suppression task. The experimenter monitored the rehearsal from another room through speakers to verify that the subject was actively rehearsing throughout the experimental session. The absence of the articulatory suppression task in the control session was unlikely to have affected T2 performance, given that it did not affect T2 performance in Experiment 2.

In the experimental session, there were 144 total trials (6 set sizes x 4 SOAs x 6 repetitions). Subjects performed six blocks of 24 trials and trials were randomly intermixed across the six blocks. Subjects could take a break between blocks of trials.

In the T2-control session, there were 50 total trials, randomly selected from 144 total trials (6 set sizes x 4 SOAs x 6 repetitions), resulting in an average of 7.6–9.3 trials

per set size per subject. Subjects were given the opportunity to take a break after 25 trials.

Results and discussion

Experimental session. T1 k values revealed a main effect of set size ($F(5,100) = 14.3, p < 0.001$), and performance peaked at set size 4 (set size 2 vs. 4, $t(20) = 3.29, p = 0.003$; set size 4 vs. 6, $t(20) = 2.93, p = 0.08$; Figure 20A). This drop in performance at high T1 loads is attributed to the mask rather than to interference from the T2 array, as there is no effect of SOA ($F(3,60) = 1.25, p = 0.30$) or an interaction of set size and T1-T2 SOA on T1 performance ($F(15,300) = 1.34, p = 0.18$).

As in Experiment 1, an ANOVA with set size and SOA as factors showed that T2 performance was modulated by set size ($F(5,100) = 9.60, p < 0.001$) and SOA ($F(3,60) = 21.00, p < 0.001$), but the interaction was not significant ($F(15,300) = 0.85, p = 0.62$; Figure 20B). T2 performance still showed an effect of set size at the longest SOA (750

A)   B)
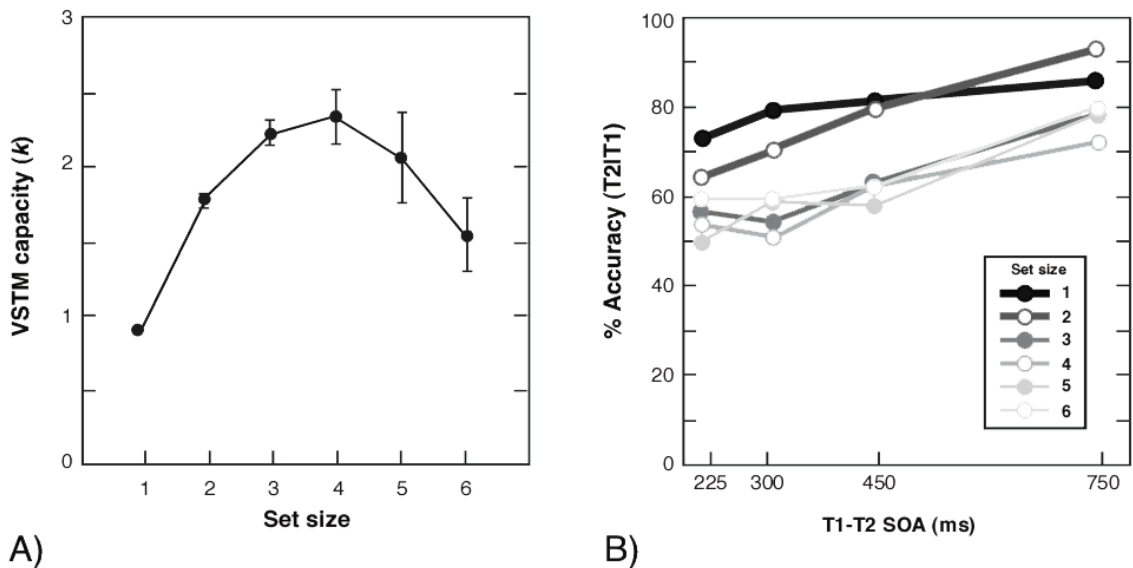
Figure 20. (A) T1 k values. (B) T2 performance for each set size and SOA. For illustrative purposes, error bars are not presented.

ms, $F(5,100) = 4.14, p = 0.02$). Given that the consolidation rate of letters is less than 100

ms/letter (Gegenfurtner & Sperling, 1993), and subjects could not store more than about

3 items in memory, consolidation of the T1 display might have been expected to finish by

300 ms. The impairment in reporting T2 at this long SOA suggests that maintaining

information in VSTM might also interfere with forming a durable representation of T2 in

VSTM (Akyürek, Hommel, & Jolicoeur, 2007). Alternatively, consolidation of T1 items

may be much slower in the AB. Consequently, T1 consolidation may not have been

completed by 750 ms. Experiment 5 addresses this issue.

T2 performance at the 300-ms SOA showed a capacity-limited pattern of results

(Figure 21). An effect of set size ($F(5,100) = 4.08, p = 0.002$) reflected the drop in

performance from set size 2 to 4 ($t(20) = 2.42, p = 0.043$), and T2 performance did not

change significantly at larger T1 set sizes (set size 4 to 6, $t(20) = 1.09, p = 0.29$).
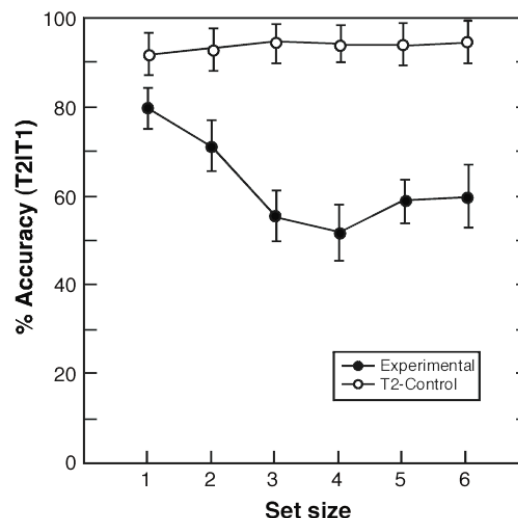
Figure 21. Controlling for perceptual memory does not affect the pattern of results. The T2 stimulus was easily detected when subjects only had to detect T2 (empty circles), but awareness of T2 at the 300-ms SOA was impaired when subjects accurately identified the T1 probe (filled circles).

T2-Control session. T2 performance was consistently high across all set sizes when it was performed alone (92–95% accuracy; $F(5,100) = 1.30$, $p = 0.27$; Figure 21), unlike in the experimental session. The results of the T2-control task show that difficulty in detecting the second target in the T1-T2 task was not due to perceptual interference from the T1 display and mask on T2 perception.

Experiment 5: Filling VSTM storage does not impair T2 detection

The first four experiments failed to find an interaction between T1 VSTM load and SOA, perhaps because the SOAs that were used were not large enough to avoid the T1 task from interfering with T2 performance (Ouimet & Jolicoeur, 2007). In this experiment, T2 performance was tested at T1-T2 SOAs of 450, 950, and 1,450 ms. Given that the longest of these SOAs is well beyond the range of memory consolidation and iconic memory (Gegenfurtner & Sperling, 1993; Phillips, 1974; Vogel, Woodman, & Luck, 2006), any effect of T1 load on T2 performance at that SOA should be caused by VSTM maintenance rather than consolidation.

Methods

Twelve participants from the Vanderbilt community, with normal or corrected-to-normal visual acuity, volunteered in this experiment for paid compensation. This experiment was identical to Experiment 3, except that 1) subjects performed the articulatory suppression task from Experiment 1, 2) the T1 response was a partial recognition task, like the partial report task in Experiment 1, and 3) only three T1-T2 SOAs were used: 450, 950, and 1,450 ms. As a result the selection of these SOAs, no

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300-ms SOA results can be included.

Results and discussion

Performance in the articulatory suppression task was high (accuracy was 92% across all set sizes), and there was no effect of set size ($F(5,55) = 2.04, p = 0.09$). T1 performance showed an effect of set size ($F(5,55) = 32.17, p < 0.001$), and a capacity limit around set size 4 (set size 2 vs. 4, $t(11) = 6.41, p < 0.001$; set size 4 vs. 6, $t(11) = 0.37, p < 0.71$; Figure 22A).

T2 detection was again modulated by set size ($F(5,55) = 6.81, p < 0.001$) and SOA ($F(2,22) = 17.80, p < 0.001$), but there was now also a significant interaction of these two factors ($F(10,110) = 2.59, p = 0.007$; Figure 22B). Specifically, there were set size effects at the 450-ms SOA ($F(5,55) = 4.94, p = 0.001$) and the 950-ms SOA ($F(5,55)$

A)   B)
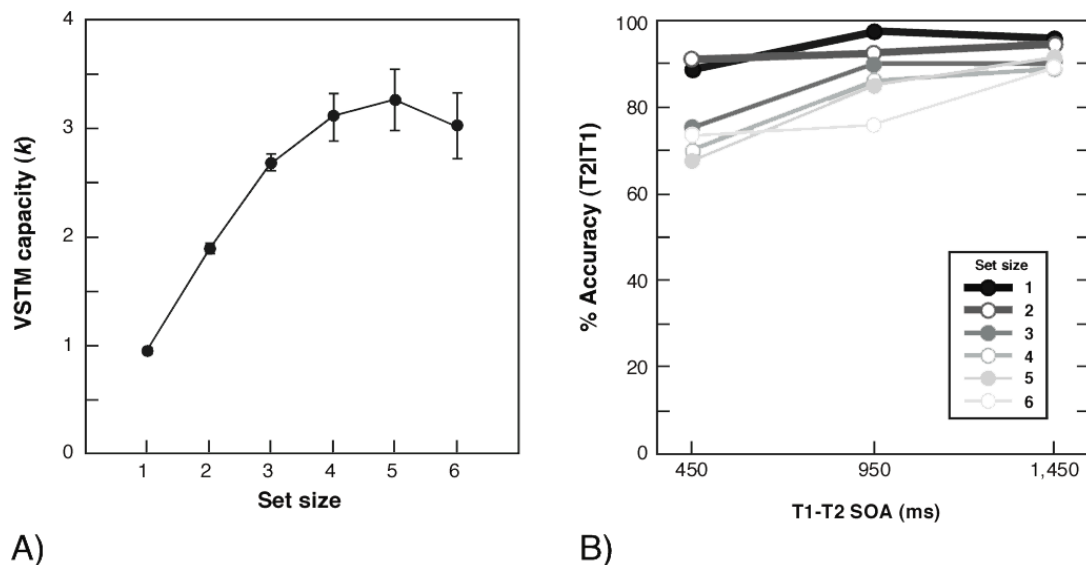
Figure 22. Performance at extended T1-T2 SOAs. (A) T1 k values. (B) T2 detection performance increased with increasing T1-T2 SOA and set size. While there was an effect of T1 set size in the shorter SOAs, there was no effect of T1 load at the 1,450-ms SOA, when consolidation of the T1 information should be complete.

$= 6.65, p < 0.001$), but performance was not significantly modulated by memory load at the longest (1,450-ms) T1-T2 SOA ($F(5,55) = 1.20, p = 0.32$).

A null effect of VSTM maintenance load on the magnitude of the AB dovetails with studies exploring the relationship of VSTM maintenance and the AB (Ouimet & Jolicoeur, 2007). As already discussed, the maintenance of T1 information in VSTM is not enough to produce a T2 deficit within the AB window of about 500 ms from T1 onset. Akyürek and Hommel (2005) showed that increasing STM load will interfere with T2 performance across all SOAs. The interaction of T1 set size and SOA, as well as the null effect of T1 set size at the 1450-ms SOA would seem to be inconsistent with Akyürek and Hommel (2005)'s findings. However, the longest SOA used in that study (720 ms) may not have been long enough in order to dissociate the consolidation of T1 and T2 stimuli. In the current experiment, even a 950-ms SOA was not long enough for T2 processing to proceed without interference from T1 processing (Jolicoeur, 1999). It is possible that the Akyürek and Hommel (2005) study would have found an interaction of STM load and SOA on T2 performance had they used much longer SOAs, such as 1,450 ms (Experiment 5) or 2,200 ms (Ouimet & Jolicoeur, 2007).

General Discussion

The basic design of the experiments presented here is consistent with other studies that explored the role of STM processes in the AB, in that all these studies required subjects to consciously register targets appearing temporally proximate to one another (Akyürek & Hommel, 2005, 2006; Akyürek, Hommel, & Jolicoeur, 2007; Jolicoeur & Dell'Acqua, 1998; Ouimet & Jolicoeur, 2007; Ward, Duncan, & Shapiro, 1996). Most

studies exploring the role of STM load and the AB have required subjects to maintain a set of items in memory while monitoring an RSVP for T1 and T2 stimuli (Akyürek & Hommel, 2005, 2006; Akyürek, Hommel, & Jolicoeur, 2007). Such a task design negates any direct evaluation of the role of STM consolidation in the AB. By contrast, other studies manipulated T1 memory load to explore the relationship of T1 STM processes on T2 performance. However, these studies used sub-capacity memory loads (fewer than 4 items) (Jolicoeur & Dell'Acqua, 1998; Ward, Duncan, & Shapiro, 1996), which makes it difficult to draw firm conclusions about whether T2 impairments co-occuring with increased T1 load are specifically related to STM load, as discussed earlier.

The current study avoided these limitations by parametrically manipulating T1 memory load from sub- to supra-capacity VSTM limits, and along with the inclusion of sufficiently long T1-T2 SOAs, the time course of the interaction of T1-related STM processes with the conscious processing of subsequently presented targets could be estimated. The resulting experimental design was able to provide direct support for a key role of STM consolidation in limiting our awareness of temporally proximate events. In particular, T1 consolidation-related interference with T2 awareness is very strong at a 300-ms T1-T2 SOA (Experiments 1–4), but this effect diminishes with increasing T1-T2 SOA (Experiment 5). These effects likely measured limitations in VSTM, rather than verbal working memory (Experiments 2 and 3) or perceptual interference by either T1 or its mask (Experiment 4).

The AB is classically defined as a transient deficit of the second of two targets when distractors are presented between the targets (Raymond, Shapiro, & Arnell, 1992). However, recent studies have shown relatively weak deficits in identifying multiple (e.g.,

three) consecutively presented targets in a trial (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Kawahara, Kumada, & Di Lollo, 2006; Nieuwenstein & Potter, 2006). To accommodate the discrepancy in these findings, a model was proposed arguing that the T2 deficit in typical AB studies results from a disruption of attentional set for selecting targets by intervening distractor stimuli (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Olivers, van der Stigchel, & Hulleman, 2007). Recent studies have experimentally challenged the conclusion that the three-target paradigm reveals that the AB is caused by distractor-based modulations of attentional control, suggesting instead that the results can be accounted for by a trade-off in attentional processing between T1 and subsequent targets (Dell'Acqua, Jolicoeur, Luria, & Pluchino, in press; Dux, Asplund, & Marois, 2008). Similarly, the present experiments (except for Experiment 4) had no stimuli presented between the T1 and T2 arrays that could disrupt the selection of target stimuli for consolidation, yet T2 performance was consistently impaired when it followed T1 within about 1,000 ms. This T2 deficit without a preceding distractor to interfere with target processing is inconsistent with these distractor-based accounts of the AB. It is worth noting that higher T2 performance was observed at low T1 loads, when there was no distractor following T1 (e.g., Experiment 1, Figure 16B), compared to when T1 was followed by a mask (Experiment 4, Figure 20B). Thus, a distractor presented between T1 and T2 may disrupt T2 processing, in addition to STM consolidation, although it is currently unclear whether this additional deficit results from disrupting the attentional control set (Di Lollo, Kawahara, Ghorashi, & Enns, 2005) or from the T1 mask increasing the attentional demands to T1 by making its identification more difficult (Potter, Staub, & O'Connor, 2002).

In typical AB studies, when T1 and T2 are presented in immediate succession and at the same location, with no intervening stimulus, T2 performance is very high (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992; Visser, Zuvic, Bischof, & Di Lollo, 1999). This *Lag-1 sparing* is considered a hallmark feature of the attentional blink. In all of the present experiments, there is no evidence of Lag-1 sparing. Because the T2 target never immediately followed T1 in any of the experiments (the shortest T1-T2 SOA was typically twice as long as T1 duration), Lag-1 sparing was not expected. It is hypothesized that Lag-1 sparing will not occur at shorter SOAs with this experimental design. Even though the size and central location of the T2 stimulus were selected to minimize any contribution of spatial attention in identifying that target, T1 and T2 stimuli were not presented at the same location, and it is known that Lag-1 sparing is largely abolished when a spatial shift of attention is required from the location of T1 to the location of T2 (Visser, Bischoff, & Di Lollo, 1999; Visser, Zuvic, Bischof, & Di Lollo, 1999). Nonetheless, whether Lag-1 sparing occurs or not in this experimental design deserves further attention in future research.

In sum, the body of results in this study is broadly consistent with AB models in which T1 and T2 processing compete for a capacity-limited resource (Chun & Potter, 1995; Jolicoeur, 1998). This resource likely corresponds to, or encompasses, STM consolidation. At low T1 loads, T2 is moderately impaired because STM consolidation takes place on only a few T1 stimuli before processing T2. In contrast, increasing the number of T1 stimuli prolongs the duration of consolidation, making it more likely that T2 will have been erased by the subsequent distractors in the RSVP stream before it can be consolidated to STM. However, the T1 load effect on T2 performance stabilizes at

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supracapacity loads. Under such conditions, more stimuli are presented in the T1 array than can be consolidated into VSTM. Hence, these supracapacity T1 loads cannot further influence T2 processing. Finally, these results suggest that VSTM consolidation, but not maintenance, affects the AB, because T2 detection is not modulated by T1 memory load at very long lags. Presumably, the consolidation of T1 stimuli is completed before the presentation of T2 at these prolonged lags. This finding is consistent with evidence that VSTM consolidation and maintenance are dissociable processes (Vogel & Woodman, 2005).

Vogel and colleagues (2006) showed that it takes about 50 ms to consolidate the conjunction of a single color and its location to VSTM. In the above experiments, T2 identification was strongly hampered when T1 preceded it with an SOA of around 300 ms (the SOA typically showing a strong T2 deficit (Chun & Potter, 1995)), although T2 deficits were also observed at longer SOAs. This result suggests that consolidation rate in the above experiments was at least 100 ms per item (assuming a capacity limit of 3–4 items). This consolidation rate estimate is larger than that for color (Vogel, Woodman, & Luck, 2006) and letters (Gegenfurtner & Sperling, 1993). In AB studies, while subjects are consolidating T1 into memory, they are also preparing for the presentation of the second task-relevant stimulus (Weichselgartner & Sperling, 1987), and they may also need to switch some attentional set between T1 and T2 for optimal target processing (see above). These additional cognitive processes may add to T1 consolidation to account for the prolonged stages of information processing that must take place before the cognitive system is optimally tuned to process T2 (Jolicoeur, 1999; Ouimet & Jolicoeur, 2007). The implication is that the consolidation duration for each T1 item is not upwards of 100

ms, but increasing the number of T1 targets (and/or their perceptual difficulty) will increase the total duration of T1 consolidation (Akyürek & Hommel, 2005; Ward, Duncan, & Shapiro, 1996). Regardless of the correct estimate of VSTM consolidation duration, the present findings demonstrate a grave consequence of engaging such a mechanism in dual-target search in RSVP: increased difficulty in consolidating and becoming aware of subsequently presented, behaviorally-relevant events.

CHAPTER IV

NEURAL CORRELATES OF VISUAL SHORT-TERM MEMORY
CONSOLIDATION

Introduction

CHAPTER III showed that the capacity-limited process of VSTM consolidation

can result in a deficit in identifying the second of two temporally proximate targets, but

when the lag between the two targets is sufficiently long, such that the second target is

presented after the first target has presumably completed VSTM consolidation, the

second target may be consolidated into VSTM. This lag effect not only supports models

of the attentional blink (AB) that implicate STM consolidation as a bottleneck

responsible for temporal deficits in conscious target perception (Chun & Potter, 1995;

Jolicoeur, 1999), it also corroborates previous work on VSTM showing a dissociation

between VSTM consolidation and maintenance (Woodman & Vogel, 2005). The

independence of these two VSTM processes suggests that the neural substrates of

consolidation and maintenance should be at least partly dissociable. While behavioral

evidence is accumulating supporting the division of consolidation and maintenance, there

is a paucity of neuroimaging research that has attempted to identify brain regions

involved in consolidation (Ranganath, DeGutis, & D'Esposito, 2004), let alone regions

whose activation patterns support behavioral models dissociating consolidation and

maintenance.

As discussed in CHAPTER I, considerable work has gone into identifying the

neural correlates of VSTM maintenance. While IPS/IOS activity tracks VSTM

maintenance load, regardless of the type of information held in memory (Todd & Marois,

2004, 2005; Xu & Chun, 2006), processes associated with VSTM maintenance also appear to be supported by prefrontal/frontal (D'Esposito et al., 1995; Postle, 2006; Postle, Berger, & D'Esposito, 1999) and temporal (Courtney, Ungerleider, Keil, & Haxby, 1996; Ranganath, DeGutis, & D'Esposito, 2004) brain regions. Thus, a vast network of brain regions is recruited to help maintain durable representations in memory over the short-term, and each of these regions uniquely contributes to maintenance (CHAPTER I).

In contrast to the body of neuroimaging studies focused on maintenance-related processes, the dearth of studies exploring the neural substrates of VSTM consolidation make supporting a dissociation of consolidation and maintenance unattainable at the neural level. Neuroimaging studies have proposed that prefrontal and parietal regions are recruited during STM consolidation, and the plurality of these areas also partake in maintenance (Linden et al., 2003; Majerus et al., 2007; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rypma & D'Esposito, 1999, 2003; Todd & Marois, 2004, 2005). Because VSTM maintenance begins immediately after consolidation, the sluggish time course of the hemodynamic response does not have the temporal resolution necessary to isolate consolidation-specific activity that is uncontaminated by maintenance-related activity (Postle, Zarahn, & D'Esposito, 2000; Zarahn, Aguirre, & D'Esposito, 1997). Thus, much of the hemodynamic evidence for consolidation-sensitive regions conflates consolidation- and maintenance-related activity (Linden et al., 2003; Majerus et al., 2007; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Todd & Marois, 2004, 2005). It remains to be shown which of these regions are truly sensitive to the amount of information consolidated into STM, which is the goal of CHAPTER IV.

Given its involvement in processing visual features and objects, the ventral

occipito-temporal cortex is another area that may be associated with consolidation (Druzgal & D'Esposito, 2003; Jha & McCarthy, 2000; Linden et al., 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Ranganath, DeGutis, & D'Esposito, 2004). Analysis of the time course of ventral brain regions shows them reaching their peak of activity sooner than prefrontal and parietal regions (Druzgal & D'Esposito, 2003; Leung, Gore, & Goldman-Rakic, 2002; Miller, Deouell, Dam, Knight, & D'Esposito, 2008), which has led some to suggest that these ventral areas supply prefrontal regions with visual representations necessary for consolidating events to memory (Druzgal & D'Esposito, 2003). It is not clear whether ventral cortical activity more accurately reflects perceptual processing, or whether it genuinely reflects VSTM consolidation.

In this chapter, two experimental approaches were used to isolate the neural substrates of VSTM consolidation. First, a parametric manipulation of VSTM load is used to identify brain regions associated with VSTM consolidation, in the absence of a measurable contribution to VSTM maintenance. The analysis is founded upon work showing load-modulated activation amplitude during consolidation (Linden et al., 2003) and maintenance (Linden et al., 2003; Todd & Marois, 2004, 2005). Consolidation-specific brain regions will be selected for their sensitivity to VSTM load during consolidation while showing a null effect during storage load.

The second approach consists of identifying brain regions whose duration of activity, as indicated by the latency in the peak of activity, reflects the amount of time it takes to consolidate information into VSTM. The logic follows that, as the cognitive demands of consolidation increases, so too should the duration of consolidation (Chun & Potter, 1995; Jolicoeur & Dell'Acqua, 1998; Ouimet & Jolicoeur, 2007). One of the

neural fingerprints of manipulating consolidation duration is that the time-of-peak activity should be increasingly delayed as consolidation itself lasts longer (Henson, Price, Rugg, Turner, & Friston, 2002). The following experiments used these two approaches in order to identify brain regions sensitive to the amount of information consolidated into VSTM.

These two approaches are complementary and address different, yet related, components of the hemodynamic response to VSTM consolidation. If a region is involved in consolidation-specific behavior, then it should demonstrate load-dependent amplitude modulation during consolidation but not during maintenance, and it should also be sensitive to the amount of time spent encoding representations into VSTM. However, even if a region demonstrates storage-related activity, it is still possible to determine if it is sensitive to consolidation load using fMRI: The latency of its peak response peak during the consolidation phase of its hemodynamic time course should reflect differences in consolidation duration. Thus, with these two approaches, consolidation-sensitive regions can be identified and their involvement in maintenance can be assessed in an attempt to relate the neural substrates of consolidation and maintenance to behavioral models (e.g., Woodman & Vogel, 2005).

Experiment 1: Using peak amplitude differences to localize consolidation-specific brain regions

If a brain region tracks the amount of information encoded into VSTM, then differences in consolidated memory load should be reflected in changes in the region's response amplitude. This is regardless of whether increasing VSTM load increases the intensity of neural activity, or whether it increases neural activity duration. Because the

hemodynamic signal represents the integral of neural activity over time, changes in hemodynamic response amplitude may reflect changes in the amplitude and/or duration of neural activity (Henson, Price, Rugg, Turner, & Friston, 2002; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Using this blood-oxygen-level-dependent (BOLD) signal peak amplitude as a measure, the present experiment aims to determine whether any brain regions are specifically associated with VSTM consolidation by contrasting activity during consolidation and maintenance VSTM phases. Identifying regions that are sensitive to memory load during consolidation but not maintenance would support behavioral evidence dissociating STM consolidation and maintenance (Woodman & Vogel, 2005; see also CHAPTER III).

Experiment 1 is a re-analysis of the slow event-related (slow-ER) experiment from CHAPTER I (Experiment 3B) wherein subjects held 1, 4, or 7 different colored discs in VSTM over the course of a 9,200-ms delay. This experiment was selected for the current analysis because its long retention interval allows for maintenance-related activity to be distinguished from the consolidation-related activity. In order to isolate candidate memory load- and consolidation-sensitive brain regions, the voxel-wise analysis concurrently employed two independent models of hemodynamic activity. The first model used the three different memory loads to isolate brain regions that behave in a capacity-limited manner during consolidation. That is, these brain regions should show increased signal amplitude with VSTM load until subjects' VSTM capacity is reached, because no further information can be consolidated into VSTM if VSTM is filled to capacity (Woodman & Vogel, 2005). To determine whether these brain regions are specifically involved in VSTM consolidation, the second model assessed if this load-

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modulated pattern of activation is absent during VSTM maintenance. After localizing

regions whose behavior is consistent these models, a region-of-interest analysis was

employed to rigorously quantify the behavior of these regions.

Methods

The task design and fMRI methods for this experiment are described in

CHAPTER I, Experiment 3B.

Voxel-wise analysis. A set of stringent criteria was established to determine if a brain

region is specifically sensitive to the amount of information consolidated into VSTM.

Such a region should demonstrate the following pattern of activity: 1) above-baseline

activity during consolidation, 2) an effect of memory load during consolidation, and 3) a

baseline activity level during maintenance with no load effect. This approach will ensure

that any memory load effects are due to consolidation processes rather than VSTM

maintenance. In the voxel-wise analysis, loads 1 and 4 were used to probe for load effects

because the largest k value was obtained at set sizes 4 (see Behavioral Results of

CHAPTER I, Experiment 3B). The results were qualitatively the same when the analysis

employed set size 7 rather than 4.

Data were preprocessed using BrainVoyager 4.9.1, and the voxel-wise analysis

was performed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands).

To localize consolidation load-sensitive regions, boxcar regressors were defined for set

sizes 1 and 4 for the consolidation phase (defined as the volume containing the

presentation of the memory array; time = 0–2 s in Figure 7) and maintenance phase (two

volumes taken 6–10 s from the onset of the volume containing the memory array (time =

0 s) in Figure 7) for each subject. The maintenance regressor corresponds to the final 3.8

s of the maintenance period was chosen because it models brain activity associated with

maintenance with minimal overlap with consolidation-related activity (Pessoa, Gutierrez,

Bandettini, & Ungerleider, 2002; Zarahn, Aguirre, & D'Esposito, 1997). The

consolidation and maintenance phase regressors were then convolved with a two-gamma

hemodynamic response function (Friston et al., 1998). A group-level voxel-wise

regression analysis using a weighted interaction contrast of consolidation and

maintenance for set sizes 1 and 4 was performed to create statistical parametric maps

(SPMs) of activity correlated with the hypothesized pattern of activity. This interaction

was designed to isolate brain regions that show overall greater peak activity during

consolidation than maintenance and sensitivity to VSTM load during consolidation but

not maintenance (Figure 23A). The balanced contrast weights were: consolidation-set

size 1 = +1; consolidation-set size 4 = +5; maintenance-set size 1 = –3; maintenance-set

size 4 = –3. Using similarly weighted interaction contrasts did not qualitatively alter the

SPMs. The overall model fit was thresholded using q(FDR) < 0.05, which restricted the

false discovery rate (FDR) to an estimated 5% of activated voxels. Above-threshold

activated regions were isolated for ROI analysis using a cluster threshold of 10

contiguous voxels of activity around the peak-activated voxel.

Region-of-interest (ROI) analysis. After candidate regions were localized in the voxel-

wise analysis, time courses were extracted for each set size and tests were performed on

the hemodynamic signal associated with the consolidation and maintenance phases, as

discussed in the introduction to this experiment.

Besides contrasting load effects during consolidation and maintenance, another analysis was carried out to provide further evidence of the specific relationship between a given ROI's activation profile and VSTM consolidation. This analysis tests the hypothesis that the shape of the hemodynamic response profile during consolidation should be sensitive to activity occurring during maintenance, because these phases are contiguous (Zarahn, Aguirre, & D'Esposito, 1997). The rising phase of the hemodynamic response in regions sensitive to consolidation and maintenance and in regions sensitive to just consolidation should be similar, reflecting the encoding of information into VSTM. In contrast, their falling phases (representing the return of activity to baseline) should be very different: While maintenance-sensitive regions should show a shallow negative slope, reflecting the ongoing maintenance of information in VSTM, consolidation-specific regions should show a much steeper falling slope of the hemodynamic response because this brain's region's level of activity should return to baseline after consolidation has completed (Figure 23B). The group-defined IPS was used as a VSTM-maintenance standard in the slope analysis because of its prominent role in VSTM maintenance (Todd & Marois, 2004, 2005). The rising slope was estimated by measuring the slope of the signal from the volume directly preceding the volume of peak consolidation activity to that peak-of-activation volume. The falling slope was defined as the slope from the volume of the consolidation peak-of-activation to the immediately following volume (Figure 23B). The slope analysis used was performed on set size 4 activity, because it represents the VSTM capacity limit for the conjunction of color and location and thus it maximally taxes VSTM consolidation, avoiding the concern that consolidation-related

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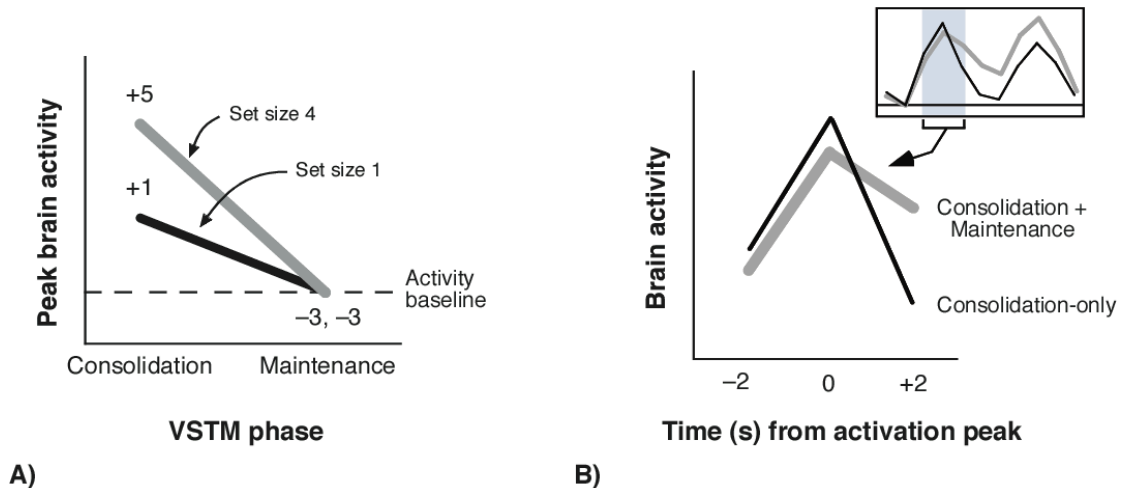
Figure 23. (A) Interaction contrast of VSTM phase and memory load used in the voxel-wise analysis. Regressor coefficient weights are beside each condition. Represented by the difference in coefficient weights for each set size, peak activation amplitude during consolidation should be greater than activity during maintenance. Activation should be greater for set size 4 than 1 during consolidation, but there should be no load effect during maintenance, shown by the differences in coefficient weights at consolidation and maintenance, respectively. (B) Slope analysis. Inset shows sample slow-event time courses from two different regions, and the volumes used in slope analysis are highlighted blue. The volume directly preceding and following the peak of activation during consolidation are represented in the primary figure and are used to estimate the rising and falling slopes, respectively.

activity for set size 1 would not be very robust for either consolidation or maintenance

(e.g., Figure 23A showing weak modulation of set size 1 in the IPS during consolidation

and maintenance).

Results and discussion

Voxel-wise analysis. Over 20 brain regions were activated at threshold using the

interaction contrast analysis. Of these, only one showed a significant increase in activity

during consolidation, load-modulated behavior during consolidation, and a null effect of

load during maintenance. This region lies on the border of the right middle temporal

gyrus and superior occipital gyrus (MTG-SOG; peak voxel Talairach coordinates (x, y, z):
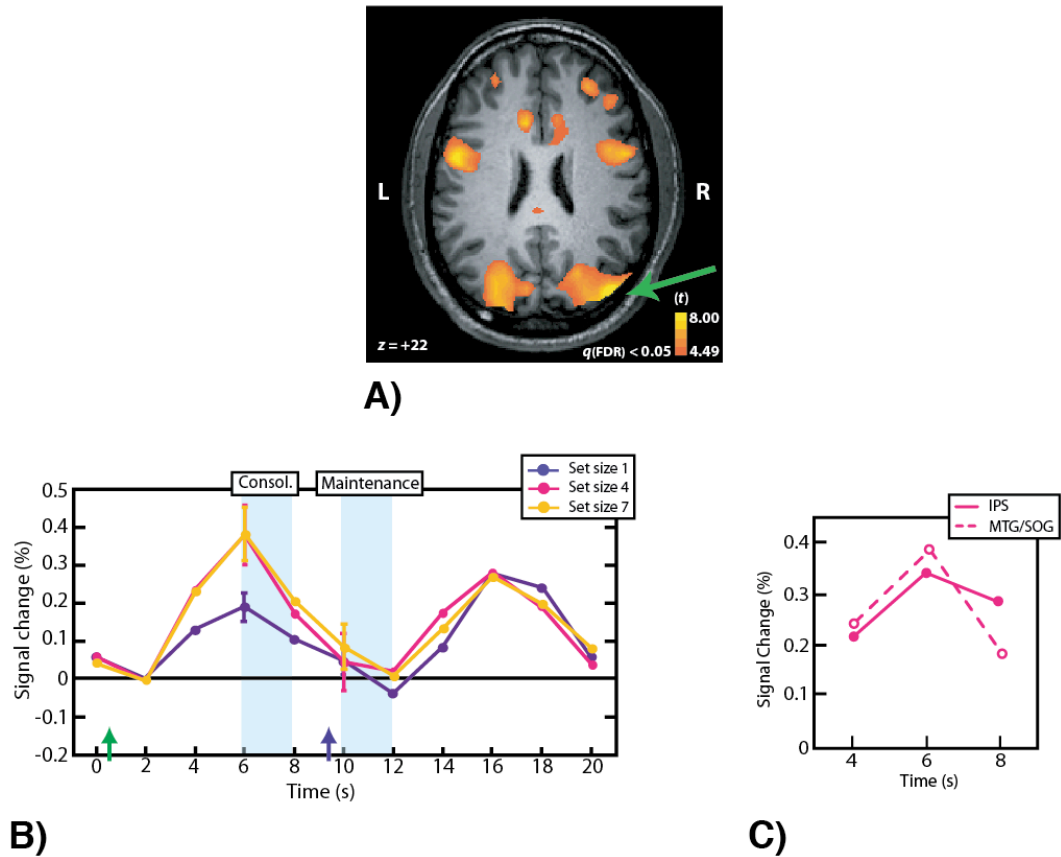
Figure 24. (A) Right MTG-SOG localized in Experiment 1 (green arrow). (B) Time course analysis revealing consolidation-sensitive activity without a measurable contribution during the maintenance phase. Activity most strongly associated with consolidation and maintenance phases is indicated by the respective blue-highlighted periods. Green arrow, memory array onset. Purple arrow, memory probe is presented. Error bars represent SEM. (C) Slope analysis for set size 4-related activity showing a steeper falling slope in the MTG-SOG (solid line) than in the IPS (dashed line), which is modulated by maintenance load.

+42, –76, +22; Figure 24A).

ROI analysis. At the group level, time course analysis of the MTG-SOG ROI showed an effect of load during consolidation ($F(2,22) = 9.59, p = 0.001$), but not maintenance ($F(2,22) < 1$), and maintenance activity did not deviate significantly from baseline (0% signal change) (for all set sizes, $ts < 1.5, ps > 0.18$, 2-tailed individual groups t tests) (Figure 24B). Consolidation-related activity was greater at set size 4 than 1 ($t(11) = 3.66$,

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$p = 0.004$, 2-tailed paired t test), and there was no difference between set sizes 4 and 7 ($t(11) = 0.03, p = 0.97$).

In the slope analysis, there was no difference between the rising slope of the MTG-SOG and the IPS ($t(11) = 0.23, p = 0.82$) (Figure 24C). By contrast, the MTG-SOG's falling slope was significantly steeper than that of the IPS's ($t(11) = 3.69, p = 0.003$). Taken together, of all the regions in the brain that are involved in consolidation, only one region consistently met the criteria of a brain region behaving in a consolidation-specific, and maintenance-insensitive, manner: the right MTG-SOG.

Experiment 2: Replication of Experiment 1's findings

The MTG-SOG ROI was probed in a separate slow-ER experiment that used a different set of subjects in an attempt to replicate the findings from Experiment 1.

Methods

The slow-ER experiment from CHAPTER I (Experiment 3A) with two memory loads (1 and 3 colored discs) was used for this analysis. All analyses were as explained in Experiment 1 above.

Results and discussion

Set size 3 activity was greater than set size 1 during consolidation ($t(13) = 2.53, p = 0.03$), but not maintenance ($t(13) = 0.26, p = 0.80$) in the MTG-SOG ROI (Figure 25), and neither set size's maintenance activity deviated significantly from baseline (set size 1, $t(13) = 1.68, p = 0.12$; set size 3, $t(13) = 1.76, p = 0.10$). Furthermore, the rising slope
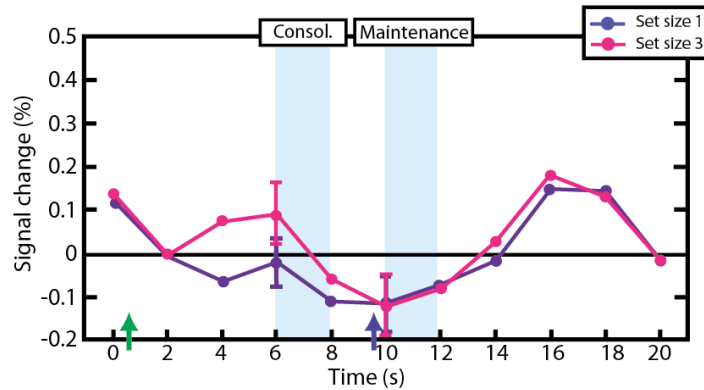
Figure 25. Replication of consolidation-specific activity in the MTG-SOG in Experiment 2, using two memory array set sizes. Green arrow, memory array presentation. Purple arrow, memory probe is presented. Error bars represent SEM.

analysis for set size 3 in the MTG-SOG was not different from that in the IPS for set size 3 ($t(13) = 0.59$, $p = 0.56$). The falling slope was steeper for the MTG-SOG than for the IPS ($t(13) = 3.79$, $p = 0.002$). These results replicate Experiment 1's findings, and support the MTG-SOG as having a distinct role in VSTM consolidation.

Experiment 3: The role of sensory and perceptual processing in the MTG-SOG

Occipito-temporal regions are frequently cited as being sensitive to the sensory or perceptual load of the stimulus array, rather than the transfer of encoding representations to short-term storage (Druzgal & D'Esposito, 2003; Linden et al., 2003; Todd & Marois, 2004). Given that the MTG-SOG lies at the intersection of these cortical areas, the sensitivity of this ROI to a parametric manipulation of sensory and perceptual load was addressed in Experiment 3.

Methods

The MTG-SOG ROI was probed in the perceptual load experiment from CHAPTER I (Experiment 4). As a brief review of the task, six subjects performed a
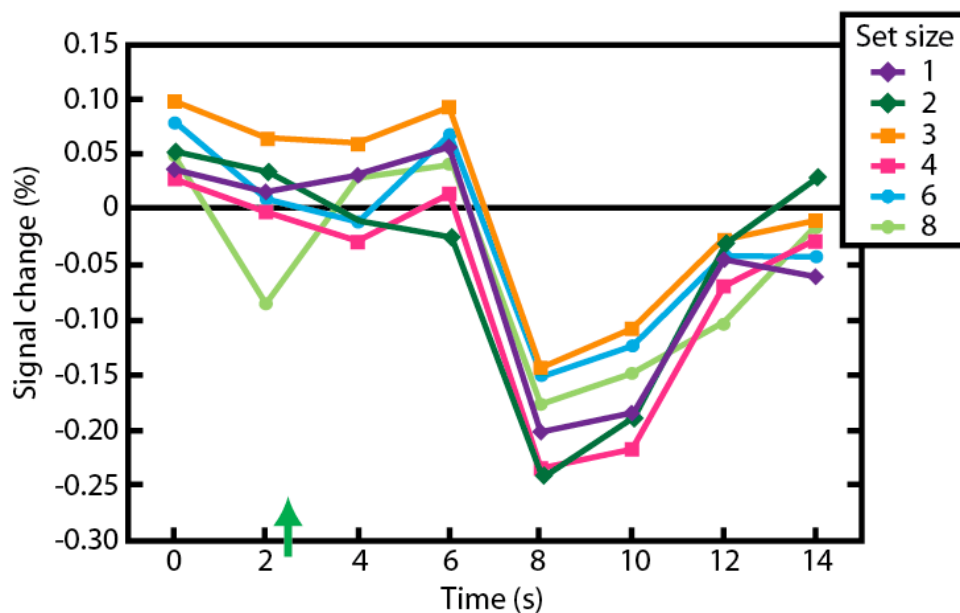
Figure 26. MTG-SOG activity is not load-modulated by manipulations in perceptual load in Experiment 3. Green arrow represents the presentation of the stimulus array.

detection task in which they indicated if a colored disc appeared in the central position of the sample array. Set size varied from 1 to 8 colored discs, and a disc appeared in the target location on half of all trials, for each set size.

Results and discussion

The time course of activity is shown in Figure 26. The MTG-SOG activity was not modulated by set size (4–8 seconds from the search array's onset $Fs < 2.2$, $ps > 0.10$). Furthermore, the MTG-SOG was suppressed below baseline in this task. This pattern of results is inconsistent with areas that are sensitive to the sensory or perceptual load of a visual scene (Todd & Marois, 2004).

Experiment 4: The role of attention during consolidation in the MTG-SOG

The tasks of Experiments 1 and 2 were attention demanding. It is possible that the MTG-SOG activity reflected those tasks' attentional demands, rather than VSTM consolidation *per se*. This issue was not addressed in the perceptual load experiment (Experiment 3), because subjects were instructed to attend to the central position, regardless of the memory array's set size. To address this limitation, a new experiment was performed that assessed whether MTG-SOG activity is modulated by a task that manipulates attentional load without affecting VSTM consolidation. A visual search task was used (Figure 27), because it placed minimal and constant demands on VSTM (subjects only needed to remember the color of a cue presented prior to the search array), yet the task's attentional demands were manipulated by varying the set size of the search array. Visual search performance is well known to be inversely proportional to the number of distractors present in the search array (Duncan & Humphreys, 1989; Treisman & Gelade, 1980). If the MTG-SOG's response during consolidation in Experiments 1 and 2, was simply related to the increased attentional demands of consolidating more items into VSTM, then this brain region should also exhibit greater activity in the search task, when the attentional demands of that task are enhanced with increased set sizes.

Methods

Participants. Ten right-handed subjects (7 females) from the Vanderbilt community with normal or corrected-to-normal vision participated in this experiment for paid compensation. All subjects reported having normal color vision.
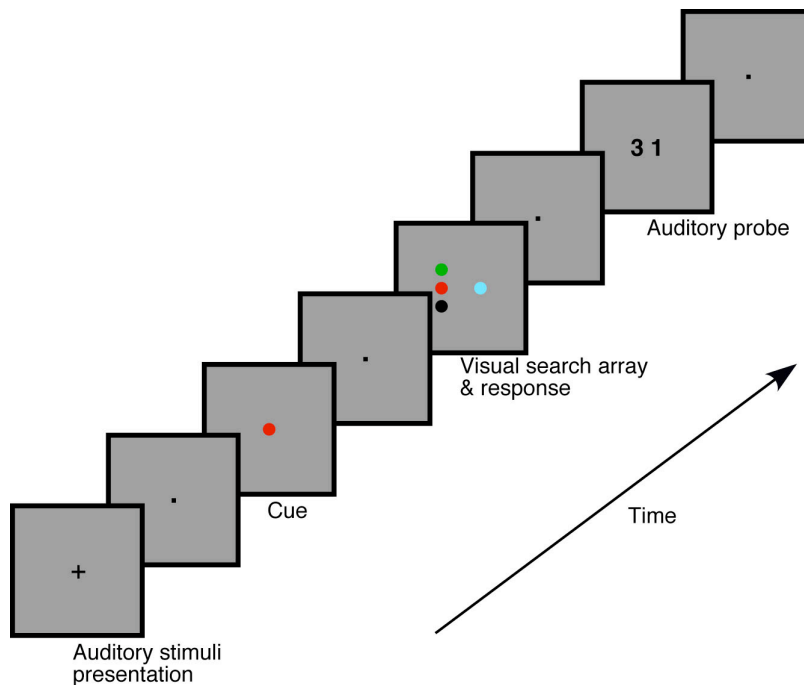
Figure 27. Visual search task trial design for Experiment 4. At trial onset, two digits were presented and the subject began rehearsing them throughout the trial. Next, a single colored disc appeared at fixation for 500 ms. After a 1,200-ms fixation period, an array of a varying number of colored discs appeared and a speeded response was made regarding the presence or absence of the cue disc's color. Finally, the subject was probed on the identity of the two digits rehearsed in auditory-verbal working memory.

Behavioral task. The trial design of this experiment (Figure 27) was adapted from

Experiment 1 of CHAPTER I, and the stimulus parameters (e.g., colors, size, etc.) were

the same as in Experiment 1, CHAPTER I. During each 8-s trial, subjects performed a

visual search task while concurrently performing the articulatory suppression task used in

the previous fMRI experiments studying VSTM capacity limits (CHAPTER I,

Experiment 1; Todd & Marois, 2004): At trial onset, two digits were presented through

earphones followed by an auditory mask, and subjects subvocally rehearsed the digits

throughout the trial, at a fast but comfortable rate (2–3 times per second). Following the

auditory stimuli, and a 1,400 ms fixation period, a colored disc (a "cue") was presented at fixation for 500 ms. After a 1,200-ms fixation period, a visual array of 1, 4, or 7 colored discs was presented for 200 ms. The task was to report if the target color (the cue disc's color) was present or absent in the search array. The target color was present in the search array in half of the trials. Subjects were instructed to report their decision as quickly as possible, and they were given 1,950 ms to make a response, from the onset of the search array. Following this response period, two digits appeared at fixation and subjects indicated if the digits were the same two that they were rehearsing. Each trial concluded with a 400-ms fixation period.

One-quarter of the total trials were no-event trials, in which the normal duration of a trial was replaced by a fixation period. These no-event trials served as a baseline condition during ROI analysis (Todd & Marois, 2004). The four trial conditions (3 set sizes and the no-event trial) were counterbalanced, as in CHAPTER I, Experiment 1.

FMRI parameters. All fMRI parameters were the same as in CHAPTER I, Experiment 1.

Data analysis

Behavioral analysis. In order to quantify task difficulty, the effect of array size on reaction time and accuracy was tested.

FMRI analysis. Preprocessing followed the protocol of Experiment 1, above (see also CHAPTER I, Experiment 1).

Region-of-interest (ROI) analysis. Time courses were extracted on a per-run basis for each search array size and the no-event condition, as in Experiment 1 of CHAPTER
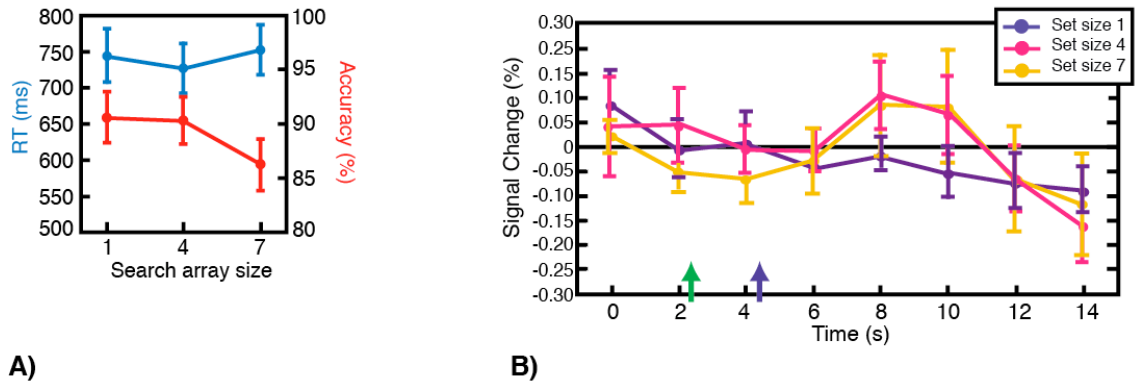
Figure 28. (A) Behavioral results in the visual search task of Experiment 5. Accuracy (red) decreased with increasing search array size, but reaction time (blue) did not change with search array size. (B) Time course for the MTG-SOG. There was no main effect of load during the peak of activation. Also, activity increased from set size 1 to 4, but there were no differences in behavioral performance between set sizes 1 and 4.

1. Each time course was composed of eight time points representing 2 s prior to, and 14 s from, the onset of the visual cue. Each set size's time course was standardized to the no-event condition, in order to calculate percent signal change from this baseline condition.

Results and discussion

Behavioral results. An ANOVA for accuracy revealed an effect of set size (Figure 28A; $F(2,18) = 6.25, p = 0.009$). Accuracy was greater at set size 1 and 4 than at set size 7 (set size 1 vs. 7, $t(9) = 2.83, p = 0.02$; set size 4 vs. 7, $t(9) = 2.83, p = 0.02$). There was no difference between accuracy at set sizes 1 and 4 ($t(9) = 0.25, p = 0.81$). This drop in accuracy at set size 7 is not due to a speed-accuracy tradeoff: there was no effect of set size on reaction time (Figure 28A; $F(2,18) = 1.22, p = 0.32$). While effects of search array set size were expected for both reaction time and accuracy, the accuracy results still demonstrate an effect of set size on task difficulty.

Right MTG-SOG ROI results. Time course analysis showed that activity of this brain region was poorly modulated by the task, as there were no effects of search array set size (time from search array onset: 4 s, $F(2,18) = 1.38$, $p = 0.28$; 6 s, $F(2,18) = 1.83$, $p = 0.19$). As shown in Figure 28B, this pattern of activity does not parallel the behavioral results. While peak amplitude doesn't change between set sizes 4 and 7, the behavioral results show a difference in accuracy between these two set sizes. Thus, it is unlikely that the MTG-SOG is modulated by general attentional load. This is not to say that attention is not involved in consolidating items into VSTM. Attention is considered to play an important role in STM consolidation, particularly with regard to the selection of stimuli for entry into STM storage (Bundesen, 1990; Chun & Potter, 1995; Cowan, 2001; Duncan, Ward, & Shapiro, 1994; Jolicoeur, 1998). Thus, the MTG-SOG load-modulated pattern of activity observed in Experiments 1 and 2 may still reflect an attentional process. Critically, this process is not one that is common to all attention-demanding visual tasks, but rather one that is specific to the consolidation of items into VSTM.

Experiment 5: Indexing the duration of VSTM consolidation for a time-resolved fMRI study

In addition to isolating brains regions involved in VSTM consolidation by tracking amplitude modulation, it is also possible to identify VSTM consolidation regions by tracking the duration of consolidation-related brain activity. Relative to other non-invasive neuroimaging techniques, such as the millisecond resolution of ERPs, fMRI's temporal resolution is much lower, but it has become possible to obtain sub-second temporal resolution using fMRI (Dux, Ivanoff, Asplund, & Marois, 2006; Formisano & Goebel, 2003; Henson, Price, Rugg, Turner, & Friston, 2002; Liao et al., 2002). By

taking advantage of the increased temporal resolution of fMRI, it should be possible to localize brain regions tracking relatively large differences in the amount of time spent consolidating information to VSTM.

A manipulation of VSTM consolidation duration may be achieved by requiring subjects to consolidate objects of varying complexity. Because of temporal resolution limitations in fMRI, the neuroimaging experiment mandates a relatively large difference (about 1 s) in consolidation duration in order to isolate regions sensitive to consolidation duration. Relative to simple stimuli (e.g., colors and letters), complex stimuli (e.g., faces) appear to take much longer to consolidate into VSTM storage (Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Curby & Gauthier, 2007; Ouimet & Jolicoeur, 2007). While a single color can be consolidated within about 50 ms (Vogel, Woodman, & Luck, 2006), face consolidation may take 500 ms/item (Curby & Gauthier, 2007). This difference in consolidation duration (450 ms) is quite large, but still difficult to resolve using fMRI. Doubling the set size would result in an approximately 900-ms difference, which is well-within the temporal limit of fMRI in terms of finding latency differences within an individual brain region (Dux, Ivanoff, Asplund, & Marois, 2006; Henson, Price, Rugg, Turner, & Friston, 2002; Liao et al., 2002). In order to accurately estimate the consolidation duration of stimuli to be used in the fMRI experiment, a behavioral experiment was performed to quantify the consolidation duration of stimuli designed for use in the subsequent neuroimaging latency experiment (Experiment 6).

In this behavioral experiment, subjects were presented a memory array of two different colored faces within the fovea, and they were instructed to remember either the colors or face identities and were probed on the target feature after a delay. The duration

of the memory array was parametrically manipulated to determine the minimum duration necessary to consolidate the maximum amount of information to VSTM, defined by Cowan (2001) k values. From these two k curves (one for colors and one for faces), two memory array durations, representing the consolidation duration of colors and faces, were chosen for the fMRI experiment.

The manipulation of presentation duration and measurement of k values to determine the consolidation duration of stimuli are grounded upon the assumption that more time is needed to consolidate complex than simple stimuli into VSTM. By drastically limiting a subject's experience of a complex stimulus, the amount of available information to consolidated to VSTM will be much smaller than if the subject had ample time to consolidate the perceptual representation of the same complex stimulus (Vogel, Woodman, & Luck, 2006). In contrast, there should be only nominal differences in VSTM capacity estimates when simple stimuli are used. All else being equal, by parametrically manipulating the presentation duration of stimuli, it is possible to determine how much time is spent consolidating stimuli into VSTM: The duration at which no more information can be consolidated into VSTM reflects the duration of consolidation (Vogel, Woodman, & Luck, 2006).

In the current experiment, consolidation durations of two colors and, separately, two faces were estimated by identifying when performance reached asymptote along a continuum of memory array durations, ranging from 30 ms to over 1,500 ms. The consolidation duration for each stimulus condition (color and face) was estimated as the duration after which no further information could be consolidated into VSTM (Luck & Vogel, 1997).

Methods

Participants. Thirty-nine volunteers (27 females, 2 left-handed) from the Vanderbilt and the local Nashville community provided informed consent and participated in this 1-hour long experiment for paid compensation. Twenty-four subjects performed both color and face conditions, and 15 subjects performed only the face condition, discussed in detail below. All subjects reported normal color vision.

Stimuli. To ensure that the color and face stimuli would lead to differences in the duration of VSTM consolidation that could be temporally resolved with fMRI, subjects were presented with two colors or two faces to consolidate. Taking into consideration that these stimuli will be used in an fMRI experiment, in order to ensure that a brain region's activity differences between the two conditions are not driven by low-level sensory differences between the two stimulus classes, colors and faces were integrated within the same display by applying a different color filter to each face stimulus, resulting in colored faces as stimuli (Clark et al., 1997) (see the memory and probe stimuli in Figure 29 for examples). As a result, the same stimuli were presented in the color and face conditions; only the task changed by instructing the subjects to remember either just the colors or just the faces.

Twenty male, affect-neutral faces were selected from a database of faces, with the constraint that their features (eyes, noses, lips, etc.) are similar enough such that subjects had to process the entire face, rather than rely upon a single feature to discriminate the faces. Using similar faces served to prolong the minimum consolidation duration needed to accurately perform the task.
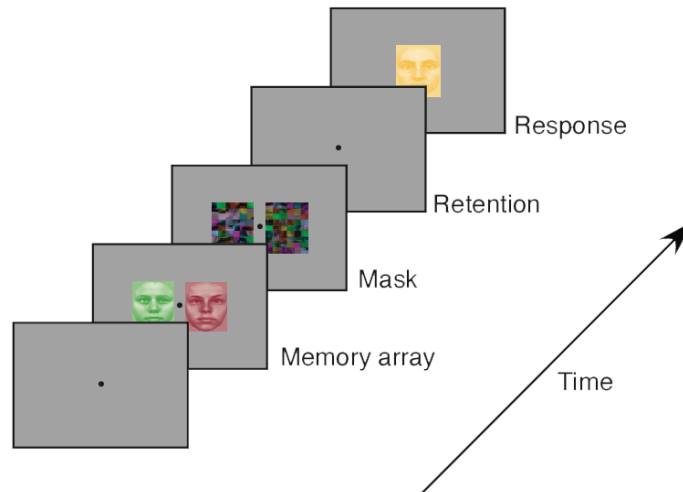
Figure 29. Trial design used to estimate consolidation duration for color and face stimuli in Experiment 5. Subjects are instructed to remember either the colors or faces presented in the memory array. After a varying 1,500-ms retention interval, they are tested on their memory for the task-relevant feature.

In each trial, two grayscale faces were selected randomly without replacement from the sample set of twenty faces. The faces were modified, having their ears, hair, and necks masked for this experiment, and they were resized to measure 0.84° x 0.76° (height x width) visual angle. The average contrast of each face was adjusted to match the group mean contrast, thus minimizing the possibility that subjects used differences in contrast to perform the memory recognition task. In the memory array, the stimuli were positioned on either side of a black fixation point, presented in the center of a dark gray screen (Figure 29). The total visual angle of the memory array was 0.84° x 2°, which places the stimuli within the fovea, thereby minimizing the need for subjects to make eye movements in order to process the fine features of each face.

Similar to the face stimuli, two colors were selected randomly without replacement from a set of seven distinct colors (green, magenta, violet, yellow, cyan, light blue, and red). Using distinct colors would minimize their consolidation time, and thus maximize the difference in consolidation duration between faces and colors. Each

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color was randomly assigned to one of the two faces. The RGB values of each grayscale-face were weighted by a given color's RGB value, thereby making each face colored.

Following each colored face in the memory array was a mask, which was one of the remaining faces randomly selected without replacement. The mask face was partitioned into 54 constituent boxes, and each box was randomly assigned one of the seven colors, with replacement. Each box was flipped along the vertical plane and the order of the boxes was randomized to minimize the risk of subjects misattributing the masks' features with those of the memory array faces.

Following the mask, a colored probe face was presented at fixation, centered over, and occluding, the fixation dot. The probe face matched one of the memory arrays faces on 50% of trials, and the probe's color was found in the memory array on 50% of the trials. The probability that the probe was the conjunction of same face and color features used for one of the memory array stimuli was 25% (50% same color x 50% same face). When present in the memory array, the respective probe target feature (e.g., face identity in the remember face condition) was randomly chosen from the left or right stimulus.

Trial design. Figure 29 shows a schematic of a sample trial. At the onset of each session, the subject is reminded of the task (remember color or face identity). Trial onset was cued by a fixation cross appearing at the center of a computer display. At this point, the subject began an articulatory suppression task: rehearse "the" aloud at a fast but comfortable rate (2–3 times/second) (Baddeley, 1992). The experimenter monitored the subject's rehearsal in a separate room via an audio baby monitor system. After 500 ms, the fixation cross was replaced by a small dot for 500 ms, then the memory array was presented. Because

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consolidation takes longer for faces than colors, 15 of the 39 subjects performed only the face condition. This allowed for presentation durations that lie comfortably outside estimates for color consolidation (Vogel et al., 2006) to be tested in the face condition. Thus, the total set of durations used for the face condition were 30, 50, 100, 300, 600, 900, 1,200, 1,500, 1,800, 2,100, 2,700, and 3,400 ms. The color condition used durations of 30, 50, 100, 300, 600, 900, 1,200, 1,500, and 1,800 ms. Each duration occurred four times in each block of trials, with the total number of trials dependent upon the experiment version (ranging from 32 to 72 trials/block), and subjects performed 8–14 blocks per session (number of blocks was inversely related to the number of trials per block). Immediately following the offset of the memory array, two masks were presented in the same positions as the memory array stimuli, for 500 ms. A 1,500-ms retention period ensued, during which only the fixation dot was presented. A probe stimulus was subsequently presented at fixation until the subject indicated whether the probe's target-relevant feature was present or absent in either of the two memory array stimuli. Subjects made button presses on a standard keyboard using the index and middle fingers of their dominant hand to report whether the target feature was respectively present or absent in the memory array. Subjects were explicitly instructed to ignore the irrelevant feature, because its presence in the memory array was not related to the occurrence of the task-relevant probe feature. Subjects were instructed to emphasize accuracy, but to still respond in a timely manner. After responding to the probe, they could stop rehearsing "the". The intertrial interval was 500-ms.

Every thirty trials, a screen appeared that reminded the subject of the task, and the subject could take a break at that time, To motivate subjects to perform as accurately as

possible, subjects were given the opportunity to win up to $10 in bonus pay for responding accurately. The amount of money that could be won on any given trial was $10 divided by the total number of experimental trials. The prorated reward was rewarded for each correct response, and the "rest-break screen" informed the subject of his or her total bonus reward. Finally, twenty practice trials were administered before each session.

Results and discussion

Performance in the memory task was converted to Cowan (2001) k values (Todd & Marois, 2004). Within each condition, pair-wise comparisons were made between durations to determine when performance reached asymptote. The onset of performance asymptote for a condition was defined as the duration whose k value is not significantly different from three subsequent durations. In the color condition, the amount of information consolidated into VSTM increased between consecutive increases in duration, from 30 to 300 ms (ts > 2.6, ps < 0.01, 2-tailed paired t tests) and leveled off with further increases in presentation duration between 300 and 1,500 ms (all ts < 1.2, ps > 0.28, 2-tailed; blue line in Figure 30). These results are interpreted as evidence for subjects needing approximately 300 ms to consolidate the two stimuli's colors. This estimate of consolidation duration is somewhat larger than that estimated by others, possibly owing to the stimuli used in the present experiment being more complex (colored faces) than the stimuli used in experiments testing only color consolidation, which were composed of a homogenous hue of a particular color (similar to Figure 1) (Vogel, Woodman, & Luck, 2006). Regardless, the important point is that is the current
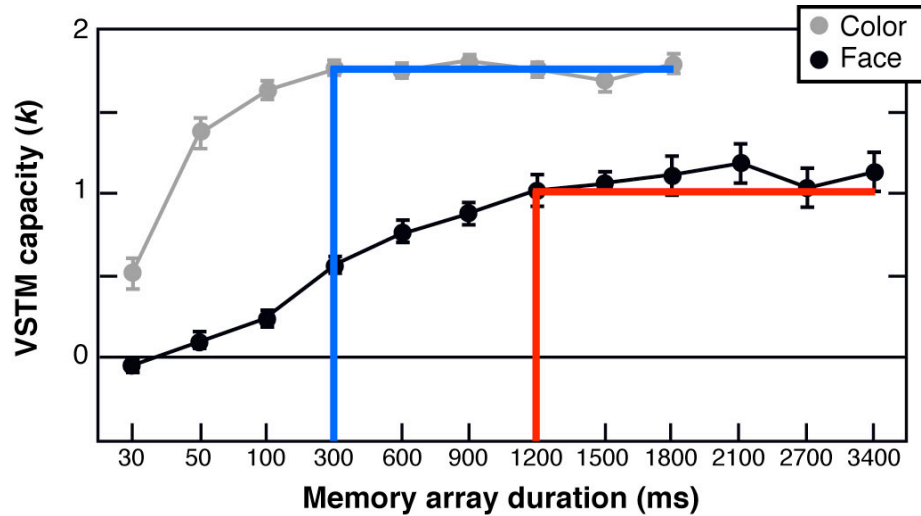
Figure 30. Estimates of consolidation duration of 2 color (gray) and 2 face (black) stimuli reached asymptote in Experiment 5, according to when VSTM capacity estimates (*k*) reached asymptote. Color consolidation took less time (300 ms, blue line marking when performance reached asymptote) than faces (1,200 ms, red line).

consolidation estimate is much shorter than those for more complex stimuli, such as faces, as demonstrated next.

Subjects spent considerably more time consolidating faces into VSTM before their performance reached asymptote (red line in Figure 30). Performance increased up to 1,200 ms, at which point it stabilized with further increases in presentation duration (all pair-wise comparisons from 1,200 to 3,400 ms, $ts < 2$, $ps > 0.06$). Thus, performance reached asymptote when the memory array is presented for about 1,200 ms. Half of this estimate would represent the consolidation duration per single face (600 ms), and it is in-line with Curby and Gauthier's (2007) work showing that memory capacity for a single face doesn't change when it's presentation duration is increased from 1,500 ms to 2,500 ms.

Taken together, the consolidation time courses for colors and faces show that, on average, memory capacity is filled much sooner for colors than for faces, as evidenced by

a shorter consolidation duration for two colors (approximately 300 ms) than for two faces (about 1,200 ms). Functional MRI is capable of resolving this difference (900 ms) within a given brain region (Dux, Ivanoff, Asplund, & Marois, 2006). Thus, these stimuli were used the neuroimaging experiment, in order to isolate regions sensitive to VSTM consolidation duration.

Experiment 6: Peak latency differences during VSTM consolidation

This neuroimaging experiment was designed to identify brain regions that are sensitive to differences in the amount of time spent consolidating the faces and colors from the previous experiment (Experiment 5) into VSTM. In consolidation-sensitive brain regions, differences in the duration of VSTM consolidation should be reflected in the duration of neural activity in brain regions involved in VSTM consolidation. In turn, differences in the duration of neural activity can be inferred in the BOLD signal from the latency of peak activation (Dux, Ivanoff, Asplund, & Marois, 2006). Specifically, objects that take longer to consolidate should yield activation time courses that peak later than objects that can rapidly be consolidated. This logic was used to isolate regions sensitive to the amount of time spent encoding information into VSTM.

Methods

Participants. Twenty-four individuals (13 females, 23 right-handed) from the Vanderbilt community participated in this experiment for paid compensation. All subjects reported normal color vision and had normal or corrected-to-normal visual acuity.

Behavioral methods. Differences from behavioral Experiment 5, and critical features of the current experiment's design will be discussed. Otherwise, Experiments 5 and 6 had the same stimulus and trial parameters.

<u>*Stimuli*</u>. Because of differences in the color gamut of the CRT computer monitors used in Experiment 5 and the LCD video projection system at the MRI scanner, the light blue color from Experiment 5 was removed because it appeared very similar to cyan, leaving six different colors for this experiment. The number of face stimuli used was reduced to six, so each face and color were used with equal probability.

Two different presentation durations were used: 500 and 1,500 ms. Experiment 5 demonstrated that 1,500 ms is long enough for performance in the face VSTM task to reach asymptote. By contrast, a 500-ms duration should allow for complete consolidation of the two colors, but not the faces.

<u>*Trial design*</u>. Figure 31 shows a schematic of a trial. Trial onset was cued with a letter presented in the center of the monitor to remind the subject of the stimulus feature to remember, "F" for *face identity* and "C" for *color*. As in Experiment 5, subjects performed an articulatory suppression task throughout each trial (subvocally rehearse "the" at a fast but comfortable rate of about 2–3 times/second) (Baddeley, 1992; Todd & Marois, 2004). Following a 500-ms fixation period, a memory array of two colored faces was presented for 500 or 1,500 ms. The size of memory array (2° visual angle) was small enough to fit within the fovea to minimize subjects' use of eye movements during consolidation. Subjects were instructed to maintain fixation and not move their eyes during each trial.
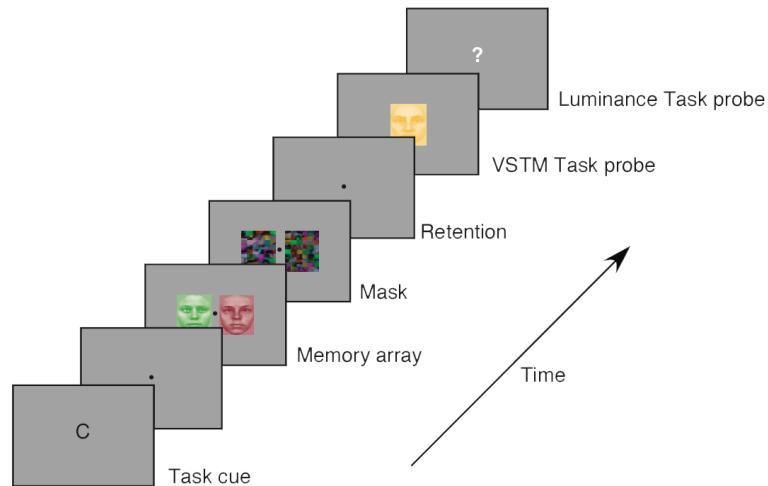
Figure 31. Sample trial for the color condition in Experiment 6. At trial onset, a cue reminds subjects of the task-relevant feature (C, color; F, face). While performing an articulatory suppression task, the subject consolidates the task-relevant feature from the memory array, which is presented for 500 or 1,500 ms. Concurrent with consolidating the memory array, the subject searches for a brief change in the luminance in either memory array stimulus. Following a mask and then a 9,000 ms retention interval, memory for the task-relevant feature is tested. When a question mark appears in the center of the display, the subject indicates if he/she did or did not detect a luminance change in the memory array.

The same style of mask (a scrambled, multicolored face not used in the sample or probe arrays) was presented after the sample array for 500 ms. To dissociate encoding from maintenance and retrieval phases of VSTM, a 9,000-ms retention duration followed the mask's offset (Todd & Marois, 2004). A single probe colored face then appeared at fixation, and the subject was given 3 s to make a present/absent judgment regarding whether the probe's target feature (color or face identity) was present in the sample array. Based upon response times from Experiment 5, the 3-s presentation duration of the probe was long enough for subjects to make an accurate response.

Because consolidation completes sooner for color than face identity, subjects might stop attending to the stimuli sooner in the color than in the face condition. Such differences in attention duration could potentially drive any differences in the duration of

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brain activity, thereby confounding the signal associated with VSTM consolidation. To control for such differences in the amount of time that subjects are attending to the memory arrays, subjects concurrently monitored the memory array for a 500-ms change in luminance (dimming then brightening) that occurred randomly in one of the two stimuli in half of the trials. In the 1,500-ms sample array, the luminance change occurred in one of three temporal bins (0-500, 500-1,000, or 1,000-1,500 ms from array onset). At the offset of the VSTM probe, a question mark appeared for 1,500 ms (Figure 31), and subjects indicated if there was a luminance change in either colored face in the memory array. The magnitude of the luminance change was manipulated after each run in order to keep the mean detection accuracy between 70% and 80%.

Prior to the onset of each run, subjects were instructed of the target feature to remember. Condition order (face vs. color) alternated between runs, and the condition of the first run was counterbalanced between subjects. Subjects performed six runs (16 trials/run) of each condition in each 1-hour training session (in a mock fMRI scanner) and three runs (27 trials/run) of each condition in the 1.5-hour experimental session (in an actual fMRI scanner). Performing the training session in the mock scanner acclimated subjects to the fMRI scanner environment (e.g., lying supine while performing the experiment, the presence of distracting noise from MRI scanner, etc.). This ensured that behavioral performance in the training session would be comparable to that obtained in the fMRI session (Hannula, Simons, & Cohen, 2005). Subjects were trained equally with both tasks until their performance in the color task reached asymptote, typically achieved after two, or three at most, training sessions

Subjects were instructed to respond as accurately as possible, but still respond

within the response period. To motivate subjects to perform as well as possible in the

practice and experimental sessions, they were given the opportunity to win up to $10 for

good performance. For each trial where they performed accurately in both the VSTM and

luminance detection tasks, they were awarded a fraction of the $10, equivalent to about

6¢ ($10 divided by the total number of trials) in the training and experimental sessions.

To facilitate extraction of time courses, a no-event condition was included in 5 of

the 27 (19%) trials of each run, for the fMRI session. In these trials a cue stimulus (face

or color) was still presented at trial onset, but it was followed by 17.5 s of fixation (Todd

& Marois, 2004; Xu & Chun, 2006). In both training and experiment sessions, the

number of trials with a given memory array duration (500 vs. 1,500 ms) and VSTM

probe presence (present vs. absent) were presented equally in each run. In the fMRI

session, the presentation order of these trial conditions and the no-event trials was

counterbalanced (Todd & Marois, 2004). In the training session, trial condition order was

randomized.

FMRI methods. A 3-T Philips Intera Achieva scanner was used to acquire T2*-weighted

echoplanar images (TR, 1,000 msecs; TE, 35 msecs; flip angle, 70°; FOV, 24 cm, matrix,

64 x 64). Each scan consisted of 18 contiguous 5-mm axial slices running parallel to the

AC–PC line (in-plane resolution, 5 x 5 mm, 1 mm skip). Low- and high-resolution T-1

weighted anatomical images were acquired using conventional scan sequences.

Stimuli were presented to the subject, lying supine in the MR scanner, using an

LCD back-projection video system. Stimuli were presented to subjects using

PsychToolBox for MatLab on an Apple MacBook laptop computer. Manual responses

were collected from hand pucks (MRI Devices Corp.), using the right hand puck for responses to the VSTM task and the luminance change task, with the index finger corresponding to VSTM probe "present" and luminance change "present", and the middle finger corresponding to "absent" responses.

Data analysis

Behavioral analysis. VSTM capacity estimates were calculated using Cowan's (2001) k formula. Although response time was not emphasized, VSTM task reaction time was calculated in order to verify that any differences in k were not due to speed-accuracy tradeoffs. Performance accuracy and response time in the luminance detection was were calculated to determine if subjects were focusing attention on the memory array for the full duration of the memory array.

FMRI analysis. All pre-processing and imaging data analysis was performed using BrainVoyager QX software (Brain Innovations, B.V). Raw functional data was preprocessed, and included 3-D motion correction, slice scan-time correction, intra-session image alignment, linear trend removal, and spatial smoothing using a 6-mm FWHM Gaussian kernel. Data were transformed into standardized Talairach space for group, random effects analysis, and individual subject analysis.

     <u>*Voxel-wise analysis.*</u> Regressors were defined for the consolidation phase of VSTM. The consolidation phase was defined as the volumes associated with the presentation of the memory array (1 volume for 500-ms duration, 2 volumes for 1,500-ms duration).

A voxel-wise analysis was performed for each individual subject, and statistic parametric maps (SPMs) were created using multiple regression by convolving the regressors to a canonical, two-gamma hemodynamic response function. An open contrast was defined for the consolidation phase, and the resulting activation map was thresholded using q(FDR) < 0.05.

Region-of-interest analysis. ROIs were defined at the individual level using a cluster threshold of 10 contiguous above-threshold voxels around the peak-activated voxel. For a given ROI, time courses were extracted by calculating that region's mean percent signal change activation for a condition, relative to the no-event condition, on a per-run basis for each participant and averaged across all runs. For each ROI, peak latencies were contrasted between face and color conditions for each memory array duration (500 and 1,500 ms). As a result, any differences in peak latency between the two conditions cannot be due to differences in sensory factors because the stimulus conditions were presented for the same duration.

Results and discussion

A total of six subjects were removed from analysis. Four subjects were removed because their performance in the face condition was not significantly different from chance even at the long stimulus duration (50% accuracy). Two subjects were removed because of improper slice prescription at the fMRI scanner, resulting in signal cutoff in the parietal lobule.

Behavioral results. An ANOVA with condition (color, face) and duration (500 ms, 1,500

ms) as factors revealed main effects for both factors (condition, $F(1,17) = 161.09, p < 0.0001$; duration, $F(1,17) = 21.14, p = 0.0003$) and a significant interaction as well ($F(1,17) = 11.14, p = 0.004$) (Figure 32A). Consistent with the Experiment 5, capacity estimates in the color condition were not different in the two stimulus durations (500 vs. 1,500 ms, $t(17) = 1.30, p = 0.21$), but more information was consolidated to VSTM in the face task at the longer duration than the shorter duration (500 vs. 1,500 ms, $t(17) = 4.16, p < 0.001$).

An ANOVA for reaction time showed an effect of task ($F(1,17) = 63.74, p < 0.0001$): Subjects were faster to respond in the color condition than the face condition. However, there was no effect of memory array duration on reaction time ($F < 1$) (Figure 32B). Thus, the drop in k value in the 500-ms duration relative to the 1,500-ms duration for the face condition does not reflect a speed-accuracy tradeoff.

An ANOVA on luminance detection performance showed that subjects' accuracy in the task was effected by the duration of the memory array ($F(1,17) = 9.18, p < 0.008$;

Figure 32. Memory task performance. (A) Group mean k values for the 500-ms (red bars) and 1,500-ms (blue bars) durations for color and face conditions. (B) Reaction times for the 500-ms (red bars) and 1,500-ms (blue bars) durations for color and face conditions.

Figure 33A): Subjects were more accurate in the 1,500-ms condition than the 500-ms condition (1,500 vs. 500 ms, $t(17) = 3.03$, $p = 0.008$). There was also a main effect of condition ($F(1,17) = 7.61$, $p = 0.01$), as mean accuracy was higher in the color condition than the face condition ($t(17) = 2.76$, $p = 0.01$). Importantly, the interaction between array duration and task condition was not significant ($F < 1$), unlike for the VSTM task (see above). Thus, the VSTM interaction results cannot simply be explained by a trade-off in performance between that task and the luminance detection task. Moreover, performance in the luminance detection task demonstrated that subjects attended to this task throughout the stimulus's presentation.

Finally, an ANOVA on reaction time for the Luminance task showed that the effect of condition on accuracy was not due to a speed-accuracy tradeoff, as there was no main effect of condition on reaction time ($F(1,17) = 1.22$, $p = 0.28$) (Figure 33B). However, there was a main effect of memory array duration on reaction time in the luminance detection task ($F(1,17) = 12.12$, $p = 0.003$), owing to faster reaction times

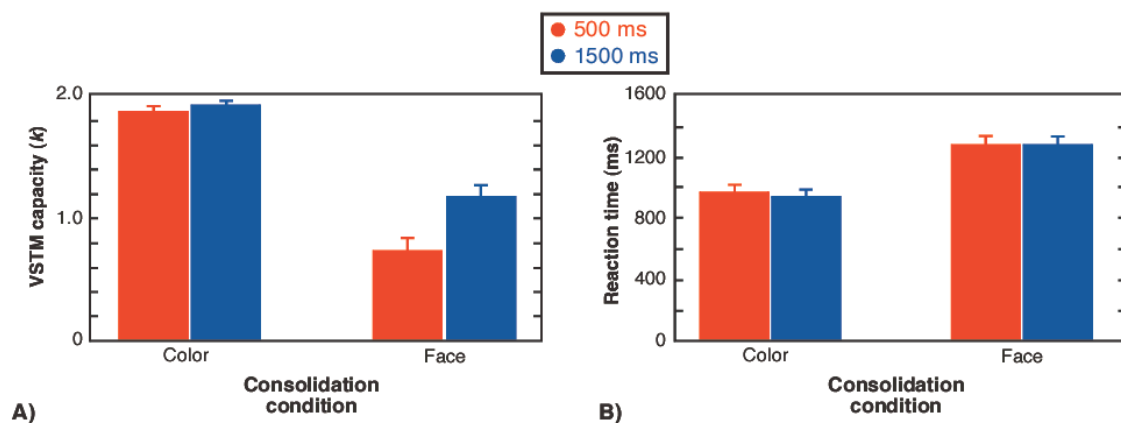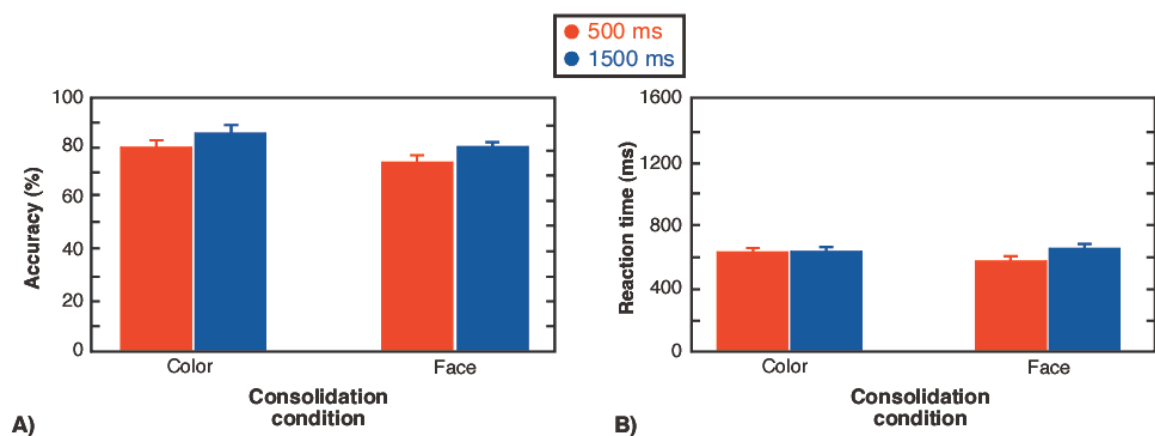*Figure 33*. Luminance detection task performance. (A) Group mean accuracy for the 500-ms (red bars) and 1500-ms (blue bars) durations for color and face conditions. (B) Reaction times for the 500-ms (red bars) and 1500-ms (blue bars) durations for color and face conditions.

when the memory array was presented for 500 ms than 1,500 ms ($t(17) = 3.48, p = 0.003$).

FMRI results. Several brain regions in frontal, parietal, occipital and temporal cortex were isolated with the open consolidation contrast. The hemodynamic response of each region was assessed to test for activation latency effects expected of brain regions involved in VSTM consolidation, namely a peak latency difference between the color and face conditions at the 1,500 ms stimulus duration but not at 500 ms. Of all the ROIs, only the intraparietal sulcus (IPS) and the inferior frontal junction demonstrated sensitivity to the duration of consolidation.

For the bilateral IPS (mean Talairach coordinates of the peak of activity (*x, y, z*), right/left: +26/–25, –53/–53, +48/+46; Figure 34A), an ANOVA of time-of-peak, VSTM condition (color, face), and duration (500, 1,500 ms) revealed a trend towards significance for condition ($F(1,17) = 3.36, p = 0.08$) and a main effect of duration ($F(1,17) = 7.91, p = 0.01$), but no interaction ($F < 1$). A peak latency analysis comparing face and color tasks for the 500-ms duration found no significant difference between the time-of-peak of the color (latency, 7.06 s) and face (latency, 7.22 s) conditions ($t(17) = 0.55, p = 0.59$; Figure 34B). There was a peak latency difference in the 1,500-ms memory array duration (mean latency: color, 7.63 s; face, 8.0 s; $t(17) = 2.37, p = 0.03$; Figure 34C).

The second ROI was in the left inferior frontal junction (IFJ), lying at the intersection of the inferior frontal and precentral sulci (mean Talairach coordinates of the peak of activity (*x, y, z*): –38, +8, +26; Figure 35A) along the lateral prefrontal cortex. An

ANOVA with condition and stimulus duration as factors, showed peak latency effects for condition ($F(1,17) = 7.84$, $p = 0.01$), but neither duration ($F(1,17) = 2.42$, $p = 0.13$) nor the interaction was significant ($F(1,17) = 1.21$, $p = 0.29$). The condition effect reflects longer processing of the face stimuli (latency, 7.92 s) than color stimuli (latency, 7.14 s) ($t(17) = 2.80$, $p = 0.01$). Most importantly, the peak latency analysis showed no effect of task at the 500-ms duration between the face (latency, 7.61 s) and color (latency, 7.0 s) conditions ($t(17) = 1.83$, $p = 0.09$; Figure 35B), but there was an effect at the 1,500-ms duration (color, 7.28 s; face, 8.22 s; $t(17) = 3.18$, $p = 0.005$; Figure 35C).
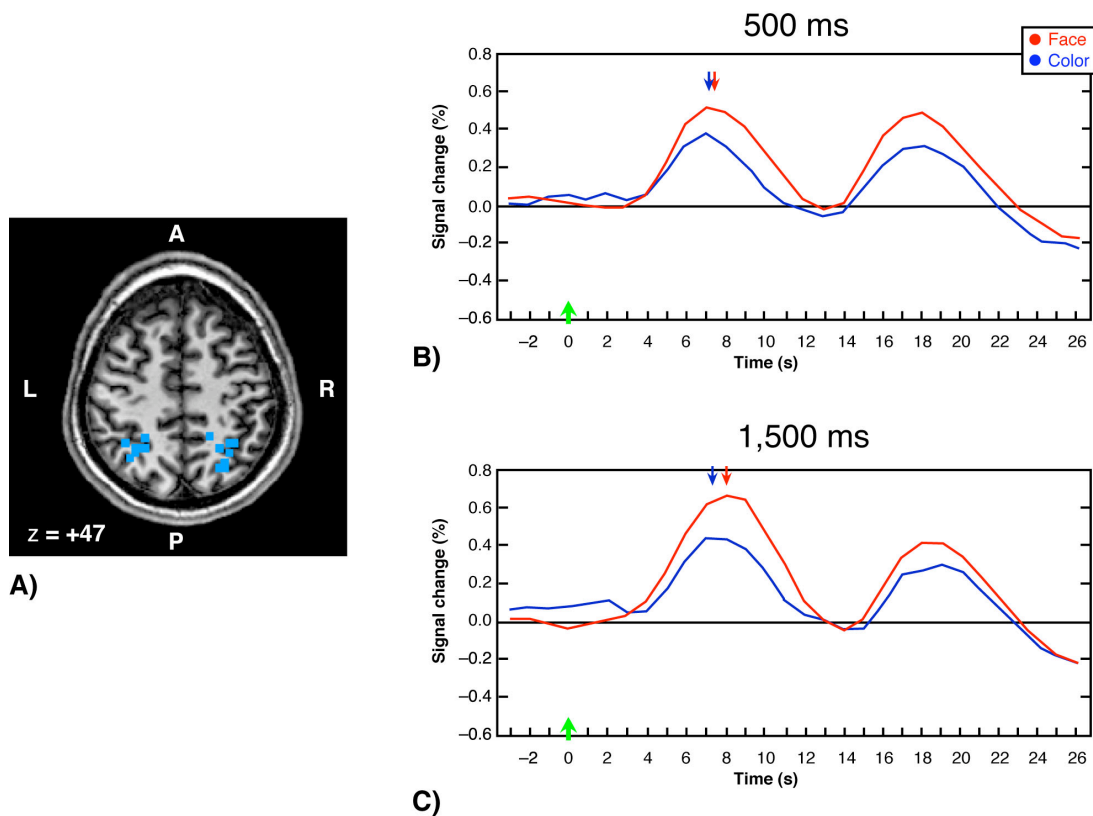
Figure 34. Bilateral IPS ROI peak latency analysis. (A) Distribution of individual subjects' foci of IPS peak activation (blue squares) on an axial slice of a representative subject. R = right, L = left, A = anterior, P = posterior. (B) The 500-ms condition did not show a latency effect during condition. (C) The face condition peaked later than the color condition in the 1,500-ms duration. The time-of-peak for each condition is represented by a red (face condition) or blue (color condition) arrow. Green arrow, onset of memory array.

The MTG-SOG ROI localized in Experiment 1, above, was found to be sensitive to the consolidation load, in terms of signal amplitude. If this region indexes VSTM consolidation load, it should also be sensitive to consolidation duration, and thus show a consolidation latency effect in the present experiment. Peak latency analysis of the MTG-SOG was performed. Owing to poor signal in this brain region for six subjects, which prevented the assessment of time-to-peak during consolidation, these subjects were removed from analysis. Inclusion of these subjects did not qualitatively affect when the
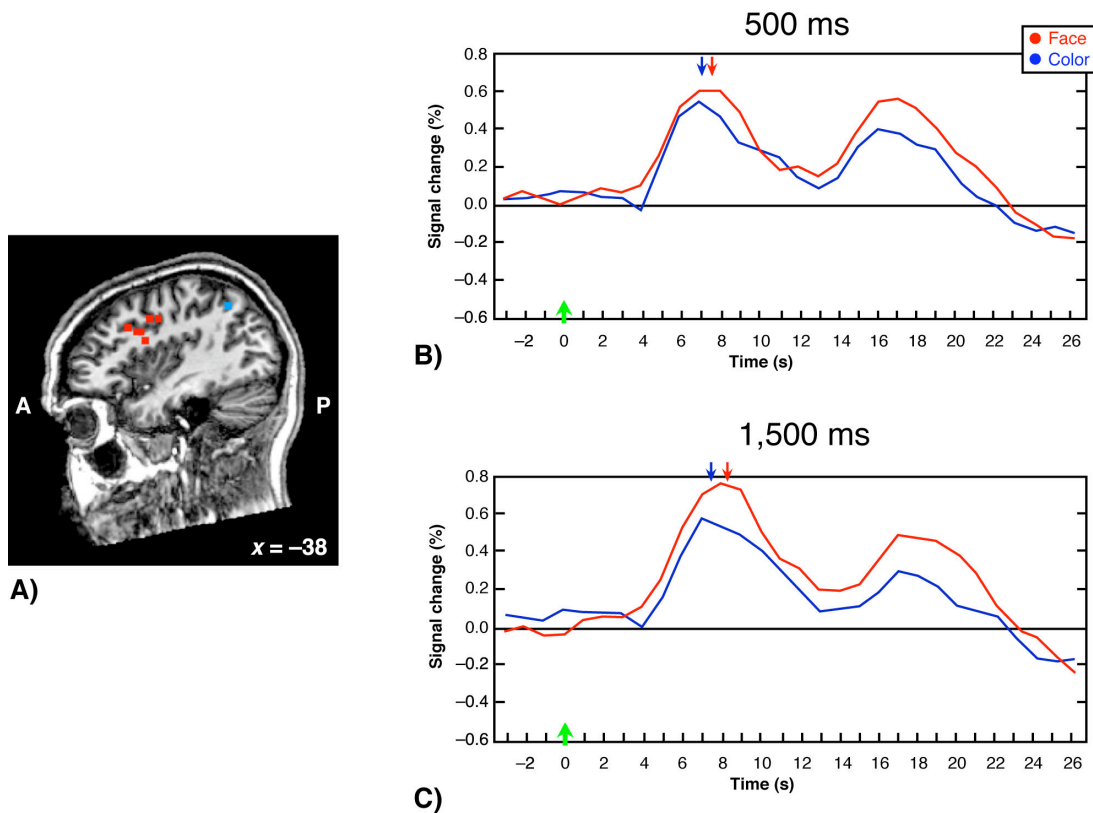
Figure 35. Left IFJ ROI peak latency analysis. (A) Distribution of individual subjects' foci of left IFJ peak activation (red squares) on a sagittal slice of the same subject. The blue square represents an individual subject's IPS peak coordinates. A = anterior, P = posterior. (B) There was no effect of latency in the 500-ms duration between color (blue) and face (red) conditions. (C) The time-of-peak was significantly later for the face than color condition in the 1,500-ms duration condition. The time-of-peak for each condition is represented by a red (face condition) or blue (color condition) arrow. Green arrow, onset of memory array.
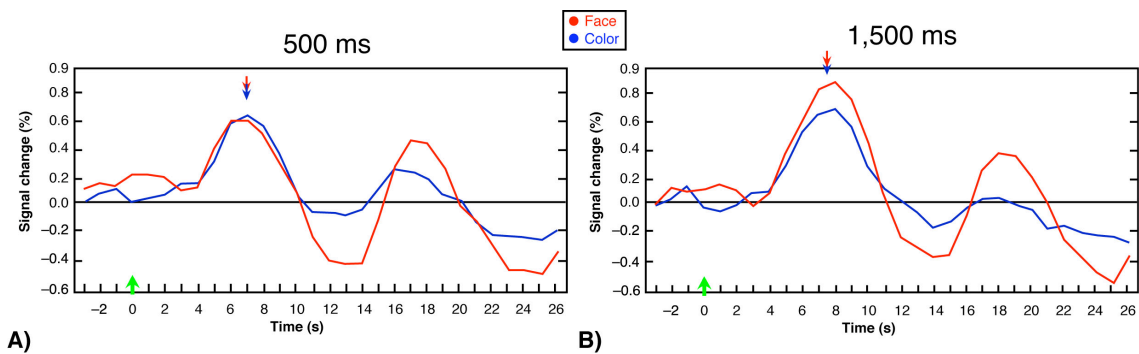
Figure 36. The right MTG-SOG ROI from Experiment 1 is not sensitive to the duration of consolidation. (A) Time course for the 500-ms array for color (blue) and face (red) conditions. (B) Time courses for the 1,500-ms color and face conditions.

time-of-peak occurred in the group-average time course shown in Figure 36. An ANOVA

using the remaining twelve subjects revealed a main effect of duration, owing to a 660-

ms difference in peak latency between the 500-ms (latency, 6,920 ms) and 1,500-ms

(latency, 7,580 ms) memory array durations ($F(1,11) = 11.36$, $p = 0.006$), collapsed

across condition. Unlike in the IPS and IFJ, there was no effect of condition (color vs.

face) and the interaction was also not significant (Fs < 1). Thus, even though this MTG-

SOG region's activation amplitude indexes consolidation load (Experiments 1, 2), it is

insensitive to the duration of consolidation. This evidence is inconsistent with the MTG-

SOG playing a central role in consolidation, and will be discussed below in greater detail.

General Discussion

This chapter focused on isolating brain regions involved in VSTM consolidation.

Two methodological approaches were adopted to investigate the neural substrates of

VSTM consolidation-sensitive processes. The first approach, using a BOLD signal

amplitude measurement, sought to determine if there are any brain regions involved in

VSTM consolidation but not in VSTM storage (Experiment 1). The second approach used a peak latency analysis to identify brain regions involved in the consolidation process (Experiment 6).

Consolidation load modulation reflected by BOLD peak amplitude

This first approach was valuable in demonstrating how few brain regions show consolidation-specific activation. This is not to discount the contribution of brain regions previously implicated in VSTM consolidation (Cohen et al., 1997; Marois, Chun, & Gore, 2000; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rypma & D'Esposito, 1999). Rather, none of those studies precluded the contribution of other processes, such as VSTM maintenance, perceptual processing, or general attentional effects. The present results suggest that most, if not all, of these brain regions are either not involved in VSTM consolidation *per se*, or are involved in cognitive processes in addition to consolidation. A consequence of this latter possibility is that VSTM consolidation is not supported by a specific neural network but may instead be entwined with the neural circuitry mediating VSTM maintenance.

These results suggest that the neural substrates of VSTM consolidation and maintenance are not identical. The right MTG-SOG showed VSTM consolidation-specific activation: It consistently failed to show a maintenance-related response, but exhibited VSTM load-sensitive activation during consolidation. These findings were replicated in Experiment 2, which used a similar experimental design. Follow-up experiments showed this region to be insensitive to both the amount of sensory information in a visual scene (Experiments 3 and 4), as well as to the amount of

information that is attended while searching for a target in that scene (Experiment 4).

The MTG-SOG is not a region typically associated with VSTM consolidation, which makes its behavior in this study all the more interesting. The coordinates of the right MTG-SOG place it superior to the lateral occipital complex (LOC), an area that is sensitive to the perception of objects and shapes (Kourtzi & Kanwisher, 2000; Malach et al., 1995; Xu, 2008). The LOC is also modulated by VSTM capacity during maintenance (Xu & Chun, 2006), behaving in a pattern similar to the IPS (Xu & Chun, 2006, 2007), but it's maintenance-related signal appears to be only weakly activated above baseline. It is possible that the load effect during maintenance is carry-over from the hemodynamic signal related to consolidation (see Figure 3B in Xu & Chun, 2006), since it is difficult to distinguish the hemodynamic signal related to each phase (Todd & Marois, 2004). Given its anatomical location, the MTG-SOG may have functional characteristics similar to those of the LOC. Another neighboring area, visual area 3a (V3a) lies dorsal to the LOC, and it is also sensitive to object perception (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998). Altogether, MTG-SOG's proximity, if not overlap, with the LOC and V3a may indicate that this brain region is involved in object processing. It is therefore tempting to speculate that the MTG-SOG may play a distinct role in the consolidation of objects to VSTM, and acts as an intermediate stage of information processing, sandwiched between the perceptual processing areas in visual cortex and the VSTM storage areas in parietal and frontal cortex (Cohen et al., 1997; Curtis & D'Esposito, 2003; Todd & Marois, 2004). As such, the MTG-SOG would provide neurobiological support for the hypothesis that consolidation and maintenance are dissociable processes (Woodman and Vogel, 2005). The fact that this brain region did not show the expected

activation profile from a region involved in VSTM consolidation in the peak latency analysis casts doubts about the role of the MTG-SOG in VSTM consolidation. It is possible that the null effect in the latency analysis may be related to task differences between this study and the amplitude study, such as the VSTM stimulus categories used subjects not having to remember spatial location of the stimuli in the latency experiment. Until these issues can be resolved with additional experiments, the role of MTG-SOG in VSTM consolidation must be considered speculative.

Consolidation load modulation reflected by time-of-peak activation

The peak latency analysis complemented the amplitude analysis. The latter approach was employed to isolate brain regions sensitive to VSTM consolidation, but not maintenance, as discussed in the behavioral literature (Woodman & Vogel, 2005). The latency analysis, on the other hand was carried out to find regions sensitive to the duration of VSTM consolidation, which behavioral research has characterized as a time-consuming process (Chun & Potter, 1995; Vogel, Woodman, & Luck, 2006). Using time-resolved fMRI, two brain regions, the IPS and IFJ, were found to be sensitive to the duration of consolidation-related activity. While these regions are identified as key neural loci in VSTM consolidation, no strong claim can be made regarding the specific role of these brain regions in consolidation. In particular, some of these regions have been implicated in indexing VSTM maintenance capacity limits (Todd & Marois, 2004, 2005). Moreover, the fact that the IPS and IFJ were not identified as consolidation-specific regions in Experiment 1 suggests that these ROIs may be involved in VSTM maintenance as well as in VSTM consolidation. The proximity of the group mean coordinates of the

IPS from the latency analysis places this region proximate to the storage capacity-modulated IPS from Chapter I (Todd & Marois, 2004), suggesting that this IPS ROI is sensitive to memory load.

To directly test this hypothesis, the IPS and IFJ ROIs from the VSTM consolidation latency experiment were probed in the VSTM consolidation amplitude experiment (Experiments 1 and 2). Specifically, a 1-cm^3 box was defined around the mean Talairach coordinates of the IPS from the latency analysis of Experiment 6, and this ROI was probed in the data set from Experiment 1 (3-load, slow-ER experiment). Consistent with a role for the IPS in VSTM storage, an ANOVA of set size provided evidence that this IPS region is modulated by VSTM load during storage (ANOVA of set size, $F(2,22) = 3.80, p = 0.04$; Figure 37A). As with the load-modulated IPS ROI (see Experiment 3, Chapter I), this latency-defined IPS ROI showed greater activity for set size 4 than 1 ($t(11) = 2.73, p = 0.02$, 2-tailed), but there was no difference between activity for set sizes 4 and 7 ($t(11) = 0.56, p = 0.59$). This was replicated in an analysis of the same ROI using the data set from Experiment 2, which also showed significantly
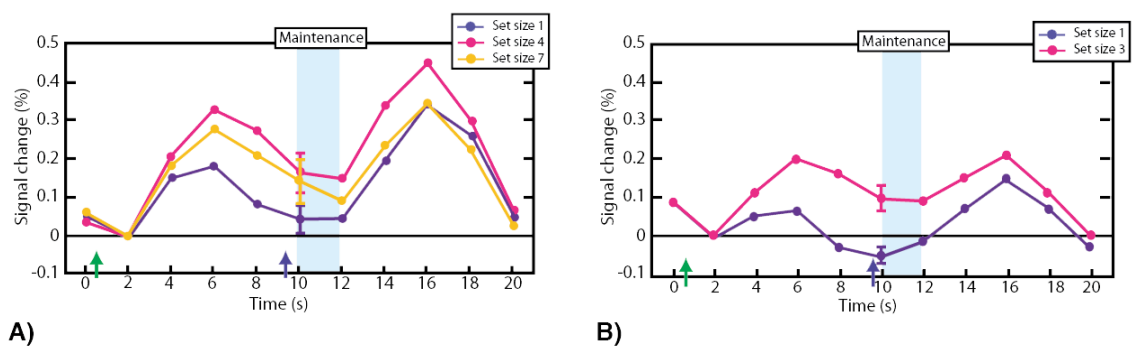
Figure 37. The bilateral IPS ROI from Experiment 6 is sensitive to memory load during maintenance. Time course from (A) Experiment 1 and (B) Experiment 2 data sets The volumes used to estimate IPS's response during maintenance are highlighted blue, and SEM error bars are provided only for these volumes.

greater activity for set size 3 than 1 during maintenance ($t(13) = 3.86$, $p = 0.002$; Figure 37B). These results suggest that the IPS is involved in both consolidating into, and maintaining information in, VSTM. The recruitment of the IPS in the construction of coherent, multi-feature objects (Shafritz, Gore, & Marois, 2002) may reflect its role in the consolidation of coherent representations into VSTM, and with its ability to index VSTM maintenance capacity (Todd & Marois, 2004; Xu, 2007; Xu & Chun, 2006, 2007), this brain region is in a key position to support VSTM.

The latency analysis-defined left IFJ in the lateral prefrontal cortex (LPFC) was found to be weakly modulated by the memory storage load manipulations of Experiments 1 and 2. While the IFJ was not modulated by memory during maintenance in Experiment 1 ($F(2,22) = 2.34$, $p = 0.12$; Figure 38A), maintenance-related activity was greater for set size 3 than 1 in Experiment 2 ($t(13) = 4.35$, $p < 0.001$; Figure 38B). These results are consistent with evidence showing general IFJ recruitment during maintenance (Courtney, Ungerleider, Keil, & Haxby, 1997; Jha, Fabian, & Aguirre, 2004; Linden et al., 2003). However, this activity does not appear to index the amount of information held in VSTM
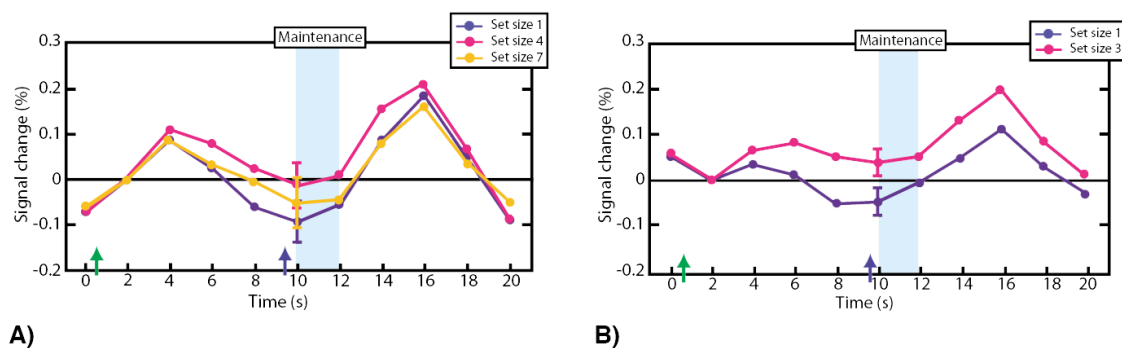
Figure 38. The left IFJ ROI from Experiment 6 is weakly modulated by memory load during maintenance. (A) Experiment 1 activity does not show an effect of maintenance. (B) There is a load effect in Experiment 2. The volumes used to estimate maintenance-related activity are highlighted blue. SEM error bars are only provided for these volumes.

to the same degree as the IPS. This evidenced by a load effect in Experiment 2 but not Experiment 1, and the IFJ's failure to be localized as a storage capacity-modulated region in past studies (Todd & Marois, 2004, 2005).

LPFC involvement in VSTM has often been attributed to non-mnemonic processes contributing to the organization and manipulation of stored VSTM content (Curtis & D'Esposito, 2003; Postle, 2006). In this respect, the weak activation during maintenance may reflect the absence of a need to manipulate the content of VSTM or to preserve the stored representations from distracting stimuli (Blumenfeld & Ranganath, 2006; Brass, Derrfuss, Forstmann, & von Cramon, 2005; Jha, Fabian, & Aguirre, 2004). Taken together, these results suggest that the IFJ tracks the amount of time spent consolidating information into VSTM, and it also contributes to VSTM maintenance.

In addition to the IFJ's sensitive to VSTM consolidation load, the IFJ, and the LPFC, in general, is frequently recruited in long-term memory (LTM) tasks, showing increased activity during the consolidation of novel information to LTM (Kirchoff, Wagner, Maril, & Stern, 2000; Ranganath, Johnson, & D'Esposito, 2003), and its activity is positively correlated with the depth of processing of stimuli encoded into LTM (Blumenfeld & Ranganath, 2006). However, LPFC is not simply involved in the consolidation of selected information, it is also involved in selecting that information. LPFC is recruited during the reconfiguration of one's task-set in order to select task-relevant information (MacDonald, Cohen, Stenger, & Carter, 2000; Yeung, Nystrom, Aronson, & Cohen, 2006). Indeed, it is possible that the LPFC plays a common role in an array of cognitively demanding tasks, supporting the selection of task-relevant information for in-depth processing (Corbetta & Shulman, 2002; Desimone & Duncan,

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1995; Duncan, 2001; Duncan & Owen, 2000). Given this, the role of IFJ in VSTM consolidation is likely one of selecting perceptual representations for entry into VSTM, while the IPS keeps track of the representations being consolidated to, and stored in, VSTM. Thus, the sensitivity of the IFJ to consolidation duration might reflect the amount of time spent selecting each stimulus's features necessary for distinguishing it from relatively similar stimuli (Braver et al., 2001).

This selective processing by the IFJ and IPS involved in the consolidation of target events may contribute to the AB (Marois, Chun, & Gore, 2000). The potential anatomical and conceptual overlap between the present VSTM consolidation study and previous attentional blink (AB) studies is striking. The IFJ and IPS ROIs isolated in the peak latency experiment have both been implicated as core neural nodes underlying the AB, and their activity is correlated with conscious detection of the second of two successive targets (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004). As discussed earlier in detail (CHAPTER III), a prominent model of the AB is that it results from the capacity-limited stage of consolidating information into VSTM (Chun & Potter, 1995; Jolicoeur, 1998). In that model, increasing the duration of consolidation and the amount of resources allocated to consolidating an initial target in the IFJ and IPS limits the availability of resources needed to consolidate other temporally proximate and behaviorally-relevant events, thereby leading to an AB (Chun & Potter, 1995; Jolicoeur & Dell'Acqua, 1998). The present findings provide strong neural support for this hypothesis, as they suggest that brain regions typically associated with the AB are the same as those that demonstrate

a temporal profile of VSTM consolidation.

Although the role of the MTG-SOG in consolidation needs to be assessed in greater depth than what the experiments revealed herein, several conclusions can be made from this consolidation study. The IFJ and the IPS are intimately involved in encoding durable representations into VSTM. This was evidenced by their sensitivity to consolidation duration in Experiment 6, as well as their correlation with awareness of the second target in the AB (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marois, Yi, & Chun, 2004), which is believed to reflect consolidation but not maintenance capacity limits (Chapter III; Chun & Potter, 1995; Jolicoeur, 1999). These brain areas are also involved in maintenance processes, be they tracking VSTM maintenance (IPS) or supporting the maintenance of representations in VSTM (IFJ). Together, these findings suggest that consolidation and maintenance are not completely dissociable processes, which is a conclusion that appears inconsistent with behavioral findings claiming dissociation between these two stages of information processing (Chapter III; Woodman & Vogel, 2005). This interpretation of the neuroimaging results assumes that the same neural populations within each ROI are involved in consolidation and maintenance. It is equally possible that while the same region is recruited in those two STM processes, different neural subpopulations contribute to each process, which would be consistent with Woodman and Vogel's (2005) conclusion. More research will be necessary to elucidate the role of these areas in consolidation, before firm conclusions can be made regarding the dissociation of VSTM consolidation and maintenance. However, these findings provide a road map for guiding such future research.

CHAPTER V

CONCLUDING REMARKS: IMPLICATIONS AND FUTURE DIRECTIONS

Summary and overview

The goal of this dissertation was to understand how the neural mechanisms of

visual short-term memory (VSTM) contribute to capacity limits during consolidation and

maintenance VSTM phases. The body of behavioral research presented in this

dissertation expands the understanding of the role of VSTM consolidation and

maintenance in limiting our conscious experience. Taking this one step further, the brain

regions that likely play critical roles in the manifestation of these capacity limit-

dependent deficits were localized using fMRI. Together, these behavioral and

neuroimaging findings support a model in which VSTM consolidation and maintenance

are distinct processes sharing partially overlapping neural networks, the latter of which

may reflect the contiguous nature of consolidation and maintenance.

CHAPTER I focused on isolating the neural substrates of VSTM maintenance

capacity limits. Past research has determined VSTM maintenance capacity limits to be on

the order of about four objects (Luck & Vogel, 1997; Pashler, 1988; Phillips, 1974).

More recently, there has been extensive research exploring the neural correlates of

VSTM maintenance. Although these neuroimaging studies have localized maintenance-

related activity in all cortical lobes, parietal and frontal areas are consistently recruited

when subjects are maintaining information in VSTM (Cohen et al., 1997; Jha &

McCarthy, 2000; Leung, Gore, & Goldman-Rakic, 2002; Linden et al., 2003; Pessoa,

Gutierrez, Bandettini, & Ungerleider, 2002). Yet, it remained to be shown which regions are sensitive to the amount of information being maintained in VSTM. In the primary experiment of CHAPTER I, VSTM capacity (*k*) was estimated across a range of memory array set sizes, and the resulting group-averaged *k* values were used to probe for regions whose activity paralleled changes in the amount of information maintained in VSTM as memory load increased. Only one region's activity was significantly correlated with the amount of information held in VSTM: the bilateral intraparietal/intraoccipital sulci (IPS/IOS), or simply the posterior parietal cortex (PPC) (Todd & Marois, 2004). This was replicated in an individual differences analysis of the same data set (Todd & Marois, 2005), providing further support for the PPC's role in tracking VSTM load.

Because of the sluggish nature of the hemodynamic response, maintenance-related activity could not be differentiated from activity related to consolidation or retrieval in the primary experiment (Zarahn, Aguirre, & D'Esposito, 1997). Thus, it could only be conjectured that the PPC indexes VSTM capacity during maintenance. To circumvent this limitation, two additional experiments were conducted that used prolonged maintenance intervals, which allowed for the maintenance-related signal to be differentiated from other VSTM phases (Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). Both experiments found load-modulated activity in the PPC during the maintenance phase. In several control experiments, this PPC region was shown to be insensitive to iconic/perceptual memory load, as well as being weakly modulated by general task difficulty associated with having to consolidate an increasingly large amount of information into memory. In two final experiments, it was found that the PPC indexes VSTM maintenance capacity for both spatial and non-spatial memory, which are

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considered to be distinct forms of VSTM (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999; Klauer & Zhao, 2004; Logie, 1995; Logie & Marchetti, 1991; Tresch, Sinnamon, & Seamon, 1993), and the role of the PPC in maintenance generalizes to other classes of visual stimuli, besides the stimuli used throughout the study.

In the voxel-wise analysis employed in the primary experiment of CHAPTER I, along with the PPC, a region within the right temporo-parietal junction (rTPJ) was activated at the statistical threshold. The rTPJ's activation profile was negatively correlated with VSTM capacity, complimenting the PPC's positively correlated response. Subsequent analyses showed the rTPJ's level of suppression during maintenance to negatively correlate with VSTM capacity. This unanticipated load-modulated finding was interesting because the rTPJ has not previously been demonstrated to be sensitive to VSTM capacity. Indeed, the rTPJ has more frequently been associated with selective attention (the deployment of attention to a particular event so it may undergo in-depth processing). Selective attention is frequently divided into two processes, goal-driven and stimulus-driven attention (Corbetta & Shulman, 2002; Egeth & Yantis, 1997). The first is the voluntary or top-down control of selective attention, and relative to stimulus-driven attention, it shows greater recruitment of areas in the parietal lobe, especially the PPC region localized in CHAPTER I, and dorsal frontal cortical regions (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). In contrast, stimulus-driven attention, which is the reflexive orienting or "capture" of attention by a salient stimulus, more strongly recruits ventral prefrontal and parietal areas, in particular the rTPJ (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Downar, Crawley, Mikulis, & Davis, 2000, 2002;

Marois, Leung, & Gore, 2000).

The near-reciprocal relationship of the rTPJ and PPC in both selective attention and VSTM maintenance led to the hypothesis that filling VSTM to capacity should result in the increased suppression of the rTPJ, and as a consequence, its ability to process unexpected information will be impaired, thus reducing the probability that the observer will detect such events (Todd, Fougnie, & Marois, 2005). This was tested in a behavioral experiment by pairing a VSTM task with an inattentional blindness (IB) paradigm. IB occurs when an individual is engaged in an attention-demanding task and misses the presentation of an unexpected, yet otherwise easily detected, stimulus (Mack & Rock, 1998; Neisser & Becklen, 1975). In the VSTM-IB experiment, subjects had to maintain either a small or large number of items in VSTM (respectively representing subcapacity and capacity memory loads) and they were then tested on the identity of one of the items in the memory array. After several trials of performing just the VSTM task, an unexpected stimulus was presented in the periphery during the maintenance phase, and subjects were probed on their detection of this novel event. As predicted, subjects who maintained a large amount of information in VSTM were more likely to be impaired in detecting the critical stimulus presented during the retention interval. Additional analyses demonstrated that this deficit did not reflect limitations related to an inability to perceive the critical stimulus. Thus, it was concluded that VSTM maintenance and selective attention processes can interact to restrict our explicit experience of the visual world. The neural substrates of this interaction is hypothesized to be in PPC and rTPJ, but since the near-reciprocal relationship of the PPC and rTPJ was not directly measured in an VSTM-IB experiment, the conclusion that these regions play key roles in limiting our awareness

of unexpected events during VSTM maintenance is only inferred. The precise roles of these regions in IB remains to be addressed.

After exploring the neural correlates of VSTM maintenance capacity, as well as how filling memory to capacity can constrain our explicit experience, the focus shifted to investigating VSTM consolidation. CHAPTER III presented a series of experiments exploring the consequence of taxing VSTM. The general experimental design was an adaptation of the attentional blink (AB) paradigm, in which the second (T2) of two targets, presented in a rapid serial visual presentation (RSVP) stream of distractors, passes unnoticed if it follows within about 200–500 ms of the first target's (T1) onset (Raymond, Shapiro, & Arnell, 1992). A prominent model of the AB attributes the T2 deficit to limitations in the speed of consolidating information to a durable, short-term store (Chun & Potter, 1995; Jolicoeur, 1998). Research on VSTM consolidation has shown that it is a time-consuming process, even for simple stimuli such as colors (Vogel, Woodman, & Luck, 2006) or letters (Gegenfurtner & Sperling, 1993). Thus, the more information from an event that is to be consolidated to memory, the longer the expected duration of consolidation. If consolidation for one target is long enough, the presentation of a subsequent target may pass by undetected because the resources necessary for consolidating this second target are being used on the first (Chun & Potter, 1995; Jolicoeur, 1998). Put differently, if STM consolidation is involved in limiting an event's entry into VSTM, it is more likely to occur when there is a large, rather than a small, consolidation load.

To test this hypothesis, subjects were presented with two events to consolidate and store in memory. The first, T1, was an array of a varying number of letters presented

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simultaneously. The second event, T2, was a single stimulus that could be either a predefined target, or one of several distractors, and its presentation could occur at one of several lags following T1. The lag manipulation allowed for the role of consolidation to be distinguished from maintenance. Work by Woodman and Vogel (2005) showed that consolidation can operate independent of VSTM maintenance, as long as there is space in VSTM for those to-be consolidated items. Thus, if T1 consolidation can interfere with T2 processing, this should occur only during short T1-T2 lags. After T1 consolidation is complete, at longer lags, T2 consolidation should proceed unimpaired. Integrating the T1 memory load and T1-T2 lag manipulations, the T2 deficit should be greatest for large T1 memory loads, but only when T2 is presented close in time to T1.

This predicted interaction of T2 performance with T1 load and lag was observed in the study. When T2 was presented close to T1, T2 deficits increased with the number of T1 items being consolidated into VSTM. After VSTM maintenance was filled to capacity with T1 items, further increases in the number of T1 array items presented had no influence on either T1 capacity estimates or the magnitude of the T2 deficit at short lags. At longer T1-T2 lags, T2 detection performance was not modulated by T1 consolidation load, presumably because T1 consolidation had finished before T2 was presented. Several control experiments ruled-out the contribution of verbal working memory in consolidating and maintaining T1 and T2 stimuli, as well as the possibility that subjects used sensory representations of T1 stimuli to help them consolidate as much of T1 as possible, thereby exaggerating T1 consolidation duration and T1 VSTM capacity estimates and, consequently, the time course the T2 deficit. In addition, the trial design controlled for perceptual forward masking of T2 by presenting the T1 array in an annulus

surrounding T2. The T2 deficit was even observed when no distractor stimulus was presented between T1 and T2 stimuli, ruling out alternative explanations for the T2 deficit that are associated with processing intervening distractors, such as the possible disruption of attentional set or slowing T1 stimulus processing (Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Potter, Staub, & O'Connor, 2002). In sum, this collection of experiments supports the role of consolidation in limiting our conscious experience of our fast-paced, dynamic visual world.

After demonstrating how limitations in the rate of VSTM consolidation can limit what enters our stream of consciousness, CHAPTER IV focused on identifying brain regions whose activity reflects the amount of information consolidated into VSTM. This was done using two different approaches: Firstly, as behavioral evidence supports the dissociation of consolidation and maintenance phases (CHAPTER III; Woodman & Vogel, 2005), I attempted to identify brain regions whose activation amplitude indexed the amount of information consolidated into VSTM, but not the amount of information maintained in this store. In doing so, only one brain region showed load-modulated activation during consolidation, but not during maintenance. This region was localized to the right middle temporal and superior occipital gyri (MTG-SOG), in the lateral temporo-occipital lobule. The MTG-SOG has not previously implicated as playing a unique role in VSTM consolidation, suggesting this finding may be a false alarm; however, MTG-SOG's consolidation-sensitive behavior was replicated in a separate experiment, and several control experiments ruled out alternative explanations for its behavior, such as sensitivity to attentional load.

The second approach I used to identify brain regions sensitive to VSTM

consolidation load took advantage of the time-dependent nature of consolidation (Chun & Potter, 1995; Jolicoeur, 1998; Vogel, Woodman, & Luck, 2006). If a brain region is involved in consolidation, its hemodynamic response should peak later as the consolidation load increases, thus reflecting the increased duration of consolidation-sensitive neural processing (Henson, Price, Rugg, Turner, & Friston, 2002; Liao et al., 2002). The previous experiments were not designed to probe for such latency effects, so a new experiment was run that could take advantage of the increasing temporal resolution of fMRI (Dux, Ivanoff, Asplund, & Marois, 2006; Formisano & Goebel, 2003; Henson, Price, Rugg, Turner, & Friston, 2002; Liao et al., 2002).

In this time-resolved fMRI experiment, subjects were instructed to remember one of the features of two colored face stimuli. If a region is sensitive to consolidation duration, then it should show a peak latency difference when subjects consolidate face identity relative to color, because there is a substantial (about 1 s) difference in the amount of time spent consolidating colors versus faces into VSTM (CHAPTER IV; Curby & Gauthier, 2007; Vogel, Woodman, & Luck, 2006). In a subsequent ROI analysis of the network of brain regions involved in VSTM consolidation of colors and faces, only two regions were found to be sensitive to the duration of consolidation. The first was the left inferior frontal junction (IFJ), in the lateral prefrontal cortex, which has been implicated in the selection of task-relevant information for in-depth processing (Duncan, 2001; Duncan & Owen, 2000). The second region was the bilateral IPS, lying very close to the IPS/IOS region that tracks how much information is held in VSTM (CHAPTER I; Todd & Marois, 2004, 2005). This experiment was designed to probe for latency effects during consolidation, not load effects during maintenance, so these two

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ROIs were probed in the slow event-related experiments that were employed to investigate VSTM maintenance-related activity in the IPS/IOS and rTPJ regions. It was revealed that both the IFJ and IPS ROIs play a role in maintenance. This was expected for the IPS ROI, given its proximity to the maintenance load sensitive IPS ROI from CHAPTER I. Given that there was no distracting information presented during the maintenance period, the maintenance-sensitive behavior of the IFJ was a relatively novel finding (Jha, Fabian, & Aguirre, 2004; Linden et al., 2003), but it is consistent with a hypothesized role for this region in facilitating the maintenance and organization of VSTM content (Curtis & D'Esposito, 2003; Postle, 2006).

As already discussed, behavioral models of the AB have identified the duration of STM consolidation as playing a key role in limiting our awareness of temporally proximate events (Chun & Potter, 1995; Jolicoeur, 1999). Past work has shown that IFJ and IPS activity is related to target processing and subjects' awareness of stimuli in the AB (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004). Now, by showing that these regions are also sensitive to consolidation duration, the current study provides neural support for the close relationship of VSTM consolidation and the attentional blink.

A peak latency analysis of the "consolidation-specific" MTG-SOG ROI did not show it to be sensitive to the duration of consolidation, which suggests that its role in consolidation needs to be reassessed before its behavior may be confidently attributed to consolidation. Taken together, the findings presented in CHAPTER IV did not support the complete dissociation of consolidation and maintenance processes that behavioral research has proposed (Woodman & Vogel, 2005). To be conservative, this summary of

the results assumes that the same neural populations within each ROI are involved in consolidation and maintenance. Additional work is needed to address these issues.

In sum, the body of work presented in this dissertation not only demonstrates how VSTM capacity limits may operate to define our visual experience, it also has identified brain regions that are most sensitive to these capacity limited processes. Reflecting upon past cognitive neuroscience research exploring the behavior of these regions in VSTM and selective attention processes, very specific hypothesis were made regarding the roles of the fronto-parietal regions in how they may contribute to deficits in awareness while we are consolidating and maintaining information in VSTM. Taken together, the work presented herein proposes central roles for a small number of prefrontal and parietal regions in building and supporting our fleeting memories of our experiences.

Implications and future directions

This dissertation demonstrates a close relationship between the neural correlates of VSTM capacity and selective attention. Work by Awh and his colleagues demonstrated that focusing spatial attention at a particular location facilitates VSTM maintenance of information previously presented at the attended location; but memory performance is impaired when attention is shifted to a location other than that represented by the stimulus maintained in VSTM (Awh, Jonides, & Reuter-Lorenz, 1998; Awh et al., 1999). Similarly, maintaining spatial information in VSTM can impair one's ability to shift attention in search of a target (Oh & Kim, 2004; Soto & Humphreys, 2008; Woodman & Luck, 2004). Together, these findings are consistent with a contribution of the PPC to both the tracking of the content of spatial information held in VSTM (Todd &

Marois, 2004, 2005; Xu & Chun, 2006) and in the control of goal-driven shifts of attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Culham, Cavanagh, & Kanwisher, 2001; Hopfinger, Buonocore, & Mangun, 2000). With respect to the work presented in CHAPTER I, it is probable that as VSTM is filled to capacity, our ability to efficiently and voluntarily control spatial shifts of attention will be increasingly impaired, and performance will level off at supracapacity memory loads. Work by Fougnie and Marois (2006) and Soto and Humphreys (2008) supports the interaction of VSTM maintenance and the ability to control where one is attending: The more information that must be maintained in memory, the greater the impairment in controlling where we are attending (Soto & Humphreys, 2008), and vice versa (Fougnie & Marois, 2007).

How might this capacity-limited deficit be reduced? As shown in CHAPTER I, across subjects, larger VSTM capacity limits were correlated with greater PPC activity (Todd & Marois, 2005; Vogel & Machizawa, 2004), and work by Olesen et al. (2004) suggests that this relationship also applies in conditions of VSTM training. In that study, improvements in VSTM capacity were associated with increased activity across several brain regions, including the PPC region associated with keeping tracking of VSTM content (Olesen, Westerberg, & Klingberg, 2004; Todd & Marois, 2004). Unfortunately, Olesen et al. (2004) did not distinguish activity related to each VSTM phase, so it is unknown whether this PPC activity is correlated with changes in neural activity during consolidation, maintenance, or retrieval. Another limitation is that this study was analyzed at the group level, rather than using an individual difference analysis, so the genuine relationship of individuals' improvements in VSTM capacity with PPC activity can only be inferred (CHAPTER I; Todd & Marois, 2005; Vogel & Machizawa, 2004).

However, if PPC activity increases proportionally with increases in individuals' VSTM capacity limits, it is possible that after extensive training in a VSTM task, storing a memory load equivalent to one's pre-training storage capacity limit will require fewer VSTM resources. This will increase the availability of resources for other processes. A possible consequence of this "freeing-up" of VSTM resources is that tasks that once interfered with VSTM (e.g., goal-driven shifts of spatial attention) may now interact with VSTM much less, resulting in an improvement in performance where there was once a large deficit (Fougnie & Marois, 2006; Soto & Humphreys, 2008).

A corollary of the hypothesis that PPC activity increases proportionally with increasing VSTM capacity during training is that individuals with larger VSTM capacity limits may be less sensitive to interference from task-irrelevant, distracting stimuli than individuals with smaller capacity limits. Discussed in CHAPTER II, neuroimaging findings showed increased TPJ suppression with both increased cognitive load and improved behavioral performance (Shulman et al., 2003; Todd, Fougnie, & Marois, 2005; Zacks, Vettel, & Michelon, 2003). Complimenting this, behavioral work shows that increasing cognitive load reduces subjects' probability of detecting unexpected, task-irrelevant events (Cartwright-Finch & Lavie, 2007; Fougnie & Marois, 2007; Todd, Fougnie, & Marois, 2005). As a consequence, filling VSTM to capacity should result in less interference from unexpected events for high capacity individuals than for low capacity individuals, possibly because the TPJ undergoes greater suppression in high- than low-capacity individuals.

This has been investigated in neither STM tasks, nor in the field of neuroimaging as a whole. However, support for this can be found in behavioral research on working

memory (WM), which includes the active organization and manipulation of information in memory (STM does not entail this "active" maintenance of information in memory). In one particular study (Conway, Cowan, & Bunting, 2001), subjects performed two different tasks. In the one session, subjects were presented a mathematical operation and an unrelated word, and they were instructed to report the validity of the operation while memorizing the word. After a varying number of trials, they were tested on their recall performance of the words. Subjects were divided into four groups, according to their WM capacities, defined by their ability to correctly recall the stored words in the operation span task. In the second session, the same subjects performed a selective listening task. They were presented two streams of words, each to a different ear, and they were instructed to repeat the words presented to one ear and ignore the stream presented to the other ear. Partway through this shadowing task, the subject's name was presented unexpectedly in the unattended stream, and the subject's demonstration of a "cocktail party effect" (here, detecting one's name in the otherwise unattended stream) was assessed. While 65% of subjects who scored in the lowest quartile of WM capacity detected their name, only 20% of subjects in the upper quartile of WM capacity noticed their names. This difference between WM capacity groups was not simply due to the low capacity group being unable to selectively attend to the target stream of words, as there was no difference in shadowing performance for the two words directly preceding the subject's name, and shadowing performance returned to baseline level very quickly after name detection for both groups. Thus, it appears that low WM capacity individuals are more prone to attentional capture by task-irrelevant, yet possibly behaviorally relevant (their names), information than high capacity individuals (Conway, Cowan, & Bunting,

2001). This is consistent with work showing high-capacity individuals being less susceptible to interference from irrelevant information (Kane & Engle, 2000).

What might be the neural substrates of attentional capture by unexpected events in WM tasks, and how might this relate to individual differences in WM capacity? It likely results from ventral parietal and lateral prefrontal cortical (LPFC) regions processing the salience and behavioral relevance of novel or possibly behaviorally relevant information (CHAPTER II; Downar, Crawley, Mikulis, & Davis, 2001, 2002; Marois, Leung, & Gore, 2000). While the ventral parietal lobule, specifically the TPJ, is most strongly activated by potentially behaviorally relevant stimuli, the LPFC is sensitive to general stimulus changes, regardless of task-relevance (Downar, Crawley, Mikulis, & Davis, 2001). In addition, the LPFC is recruited during task-switching and response selection (Duncan, 2001; Duncan & Owen, 2000; Dux, Ivanoff, Asplund, & Marois, 2006). The outcome of these functional attributes of the LPFC is that its in-depth processing of events can lead to awareness of those events (CHAPTER IV; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004). Complimenting the LPFC's role in the selective processing of task-relevant stimuli, the TPJ plays a critical role in the stimulus-driven orienting of attention towards an event of interest (CHAPTER II; Corbetta & Shulman, 2002; Downar, Crawley, Mikulis, & Davis, 2002). Given the dynamic roles of the PPC, TPJ, and LPFC in VSTM/WM and selective attention, it would appear that the LPFC and TPJ are at least partly responsible for the selection of one's name in the cocktail party effect. Hypothetically, the TPJ may exogenously orient attention toward the otherwise unattended auditory stream, upon detection of the meaningful stimulus (the subject's own

name). If the LPFC is engaged in the processing of the name, and the subsequent stimuli, this may be reflected by a decrease in task performance (Conway et al., 2001), as the LPFC is sensitive to processing duration. This deficit reflects LPFC's sensitivity to consolidation duration and its proposed role in the AB (CHAPTERS III, IV).

The relationship of the LPFC and the TPJ with our ability to control the entry of information into STM may apply to much more complex cognitive processes, such as general fluid intelligence (gF), which measures reasoning and novel problem-solving ability. The WM component most strongly correlated with gF is WM's central executive component, which coordinates and actively maintains durable representations in WM (Baddeley, 1986, 1992). Measures of gF are strongly correlated with the central executive's ability to concurrently maintain and process information (Conway, Cowan, Bunting, Therriault, & Minkoff, 2002; Engle, Tuholski, Laughlin, & Conway, 1999). Examples of this WM component include the operation-span task used above by Conway et al. (2001) or the *n*-back task, which requires the continuous updating of memory maintenance with items presented in a sequential stream of stimuli while also making a affirmative response when the current presented stimulus was repeated *n* positions ago. The neural correlates of *n*-back tasks include the LPFC and PPC (Braver et al., 1997; Cohen et al., 1997). Given these and other studies' findings, the neural substrates of central executive processes are believed to reside within the LPFC (D'Esposito et al., 1995; Smith & Jonides, 1999). The strong relationship of these behavioral measures of WM with gF suggests that LPFC also plays a key role in gF (Kane & Engle, 2002). A neuroimaging study using tasks that are significantly correlated with gF contrasted brain activity in high- and low-scoring gF individuals. This comparison revealed greater

activity in LPFC regions, which anatomically overlap with LPFC regions recruited in WM tasks involving maintenance and processing (Duncan et al., 2000). That Duncan and colleagues (2000) did not use a WM task (the stimuli remained visible to the subject until a response was made, and thus memory load was minimal), it is not necessarily surprising that there was a lack of differential recruitment of parietal activation in their study. Given the relationship of performance in WM maintenance-and-processing tasks to gF (Conway, Kane, & Engle, 2003), it is possible that using a memory-demanding task will reveal differences in the level of activity within the storage-load sensitive parietal cortex, as it does in the *n*-back task (Cohen et al., 1997).

A study exploring the relationship of gF and neural activity related to performance in an *n*-back WM task provides more direct evidence that the common neural loci of gF and the WM central executive is in the LPFC (Gray, Chabris, & Braver, 2003). In this study, subjects performed an *n*-back task in an fMRI scanner, and outside the MRI scanner they performed the Raven's Standard Progressive Matrices, which is a spatial reasoning task considered to be highly sensitive to gF (Carroll, 1993). In the behavioral analysis, WM performance was significantly correlated with gF on "lure" trials in the *n*-back task ($r = 0.36$) (Gray, Chabris, & Braver, 2003). In these trials, a stimulus was repeated, but not at the *n*-th stimulus presentation, requiring subjects to inhibit a prepotent response. The correlation between WM lure trials and gF tasks likely reflects a cognitive process related to controlling one's behavior in the presence of interference, in order to accurately perform the task (Duncan et al., 2000). This leads to the question of what brain regions may support this process?

Individual differences analyses correlating brain activity during lure trials with gF

found the strongest relationship in the LPFC and inferior parietal lobule (IPL), the latter of which includes the TPJ region (Gray, Chabris, & Braver, 2003). Even more interesting, the collective activity of these regions accounted for 99% of the shared variance between WM accuracy and gF. Additionally, the average level of right IPL activity throughout the experiment was significantly negatively correlated with gF ($r = -0.31$). More work remains to be done to explore the relationship of WM and gF, such as determining the relationship of brain regions that track individual differences in WM capacity limits with regions sensitive to gF. Another issue that can be addressed includes understanding the relationship of WM load, PPC activity, and gF (discussed above). Also, it will be interesting to use other measures of WM and gF to understand if there is a common network of WM regions involved in gF. Regardless, it would seem that the mechanisms used to limit what information is processed in VSTM and WM may recruit brain regions similar to those used in performing cognitively demanding reasoning and problem solving tasks.

To summarize, it will be interesting to determine if and how the same network of regions involved in VSTM capacity (CHAPTERS I, II, IV) changes with training (Olesen, Westerberg, & Klingberg, 2004), and how these regions interact in selective attention tasks that are correlated with WM capacity, such as the cocktail party effect (Conway, Cowan, & Bunting, 2001). For example, if IPS activity increases at the individual level with training, does the TPJ activity conversely undergo greater suppression? Does the near-reciprocal relationship of the IPS and TPJ found in VSTM maintenance and general changes in task demands (CHAPTER II; Todd, Fougnie, & Marois, 2005; Marois, Yi, & Chun, 2004; Shulman et al., 2003) also play a key role in

tasks requiring the selective filtering of one of multiple sources of stimulation? The LPFC is involved in the selection of task-relevant information (CHAPTER IV; Duncan, 2001; Duncan & Owen, 2000), and its activity is correlated with changes in stimulus awareness and behavioral performance (CHAPTER IV; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004). Thus, does the LPFC behave differently in high- and low-capacity individuals in the selective attention tasks, when a task-irrelevant, yet meaningful, stimulus suddenly captures one's attention (e.g., cocktail party effect)? Finally, if these parieto-frontal regions are involved in filtering out task-irrelevant information from entering the stream of consciousness, do they play similar roles in gF, which involves reasoning and problem solving in novel situations, two processes that require concentrated manipulation of task-relevant information (Engle, Tuholski, Laughlin, & Conway, 1999)?

The limited amount of work that has begun to address these questions suggests that the same brain regions that support VSTM capacity processes such as maintenance and consolidation are also involved in the selective processing of task-relevant and consciously available information in demanding situations. This may occur either directly (e.g., the LPFC and PPC are involved in selecting and maintaining that information in memory) or indirectly (e.g., the TPJ undergoes suppression during cognitively demanding tasks, thereby limiting interference from unexpected or task-irrelevant events). Future research may resolve these issues, but the work presented within this dissertation provides insight into the neural mechanisms that play key roles in limiting our explicit experience and thus necessitate the selective processing of events in this dynamic and fast-paced world.

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