Neural mechanisms underlying the flexible and continuous allocation of visual short-term memory resources.

Holly Ann Lockhart

Psychology

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Department of Psychology
Faculty of Social Science, Brock University
St Catharines, Ontario

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Abstract

It has long been debated whether objects stored in visual short-term memory (VSTM) are maintained as discrete items or as a continuous resource. While much recent behavioral evidence has supported a continuous resource model, neurological support has lagged behind. In the current study, participants underwent fMRI while they completed a delayed-estimation task with probabilistic cues directing flexible allocation of resources across four items. Behavioural evidence replicated the finding that participants could flexibly allocate memory resources between items, contrary to discrete models of VSTM. Neural activity demonstrated that participants were maintaining multiple items on trials in which one item had a high probability of being cued, consistent with continuous resource models. Whole brain analysis revealed frontal areas play a role in controlling the flexible allocation of memory resources in response to probabilistic cues. The results suggest a mechanism of frontal top-down attentional control over the flexible allocation of memory resources.
# Table of Contents

Abstract

List of Tables

List of Figures

List of Abbreviations

Introduction

Discrete-Item Models of Visual Working Memory

Continuous Resource Models of Visual Working Memory

Neural Evidence in Support of a Discrete Resource Model

Neural Evidence Against a Discrete Resource Model.

Contribution of a Fronto-parietal Attention Network

The Current Study

Methods

Participants

Procedure and Stimuli

Behavioural Task Analysis

fMRI Pre-processing

Planned ROI Analysis

Whole Brain Cluster analysis

Results

Behavioural Models

Planned ROI Analysis

IPS activity

dlPFC activity

Bilateral middle frontal gyri activity

Whole Brain Cluster Analysis

Whole-brain cluster analysis: dlPFC.

Whole-brain cluster analysis: Right middle frontal gyrus.

Whole-brain cluster analysis: Bilateral insula

Exploratory Analysis: Precision and Neural Activity.

Discussion

IPS: Load-dependent activity

Regions of the dlPFC: Contribution of attentional network

Middle frontal Gyri: General and specific role in VSTM

Bilateral Insula: Maintenance activity management

An evolutionary theory for VSTM.

Conclusions

References

Appendix A – Table of study conditions

Appendix B – ROI and Cluster Coordinates

Appendix C – Summary of linear multilevel output of behavioral data

Appendix D – Plot of residuals versus actual value from behavioral data models
List of Tables

Table 1. Summary of test conditions.

Table 2. Summary of Planned ROI and Cluster Coordinates.

Table 3. Summary of linear multilevel model output for absolute error.

Table 4. Summary of linear multilevel model for three-component mixture model output.

Table 5. Summary of linear multilevel model for two-component mixture model output.

Table 6. Summary of one-sample t-test statistics for IPS activity above baseline.

Table 7. Summary of one-sample t-test statistics for dIPFC activity above baseline.

Table 8. Summary of one-sample t-test statistics for bilateral middle frontal activity above baseline.

Table 9. Summary of one-sample t-test statistics for cluster extracted dIPFC activity from baseline.

Table 10. Summary of one-sample t-test statistics for cluster extracted rMF activity from baseline.

Table 11. Summary of one-sample t-test statistics for cluster extracted bilateral insula activity from baseline.
List of Figures

Figure 1. Trial design for delayed-estimation experiment.

Figure 2. Plots linear multilevel model fits of mean absolute error data.

Figure 3. Power-law plot of untransformed absolute error and proportion resources.

Figure 4. Bar chart of IPS mean activity by trial condition.

Figure 5. Bar chart of right dLPFC mean activity by trial condition.

Figure 6. Bar chart of bilateral middle frontal gyri mean activity by trial condition.

Figure 7. Bar chart of right dLPFC mean activity by trial condition.

Figure 8. Bar chart of rMF mean activity by trial condition.

Figure 9. Bar chart of bilateral insula mean activity by trial condition.

Figure D-1. Predicted versus actual values for linear multilevel models of absolute error.
### List of Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AIC</td>
<td>Akaike’s information criterion</td>
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<tr>
<td>BET</td>
<td>brain extraction tool</td>
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<tr>
<td>BIS/BAS</td>
<td>behavioural inhibition scale/behavioural avoidance scale</td>
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<td>BOLD</td>
<td>blood oxygenation level dependent</td>
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<td>CDA</td>
<td>contralateral delay activity</td>
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<td>dlPFC</td>
<td>dorsolateral prefrontal cortex</td>
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<td>EEG</td>
<td>electroencephalography</td>
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<td>EPI</td>
<td>echo planar imaging</td>
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<td>ERP</td>
<td>event related potential</td>
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<td>FA</td>
<td>flexible allocation</td>
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<tr>
<td>FEAT</td>
<td>FMRIB’s expert analysis tool</td>
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<td>FILM</td>
<td>FMRIB’s improved linear model</td>
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<td>FLAME</td>
<td>FMRIB’s local analysis of mixed effects</td>
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<td>FLIRT</td>
<td>FMRIB’s linear image registration tool</td>
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<td>fMRI</td>
<td>functional magnetic resonance imaging</td>
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<td>FNIRT</td>
<td>FMRIB’s non-linear image registration tool</td>
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<tr>
<td>FO</td>
<td>frontal operculum</td>
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<tr>
<td>FOV</td>
<td>field of view</td>
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<td>FWE</td>
<td>family-wise error</td>
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<td>FWHM</td>
<td>full width half maximum</td>
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<td>HRF</td>
<td>hemodynamic response formula</td>
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<td>IOS</td>
<td>intra-occipital sulcus</td>
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<td>Abbreviation</td>
<td>Description</td>
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<tr>
<td>IPS</td>
<td>intra-parietal sulcus</td>
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<td>K</td>
<td>estimated capacity</td>
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<td>LIP</td>
<td>lateral intra-parietal cortex</td>
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<tr>
<td>LOC</td>
<td>lateral occipital complex</td>
</tr>
<tr>
<td>MCFLIRT</td>
<td>motion corrected FMRIB’s linear image registration tool</td>
</tr>
<tr>
<td>MNI</td>
<td>Montreal Neurological Institute</td>
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<td>MRI</td>
<td>magnetic resonance imaging</td>
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<tr>
<td>RIO</td>
<td>region of interest</td>
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<td>rMF</td>
<td>right middle frontal gyrus</td>
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<td>SE</td>
<td>standard error</td>
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<tr>
<td>SNR</td>
<td>signal to noise ratio</td>
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<td>SSR</td>
<td>residual sum of squares</td>
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<td>TE</td>
<td>time to echo</td>
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<td>TR</td>
<td>time to repetition</td>
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<td>V1-V5</td>
<td>early visual cortex</td>
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<td>VSTM</td>
<td>visual working memory</td>
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Introduction

Visual short-term memory is a critical component of cognitive function. Humans are primarily a visually dominant species, meaning they rely on their visual senses to move around the world more than any other sense. Of course everything is not always in view when you need it so you must be able to hold objects actively in memory for short periods of time. The ability to remember items out of view, or to manipulate items in memory is known as visual short-term memory (or visual working memory). It is a valuable skill for everyday functioning, whether its remembering a car has moved from your rear view to your blind spot, remembering if it was your teammate or opponent jersey colour on your right, or where the hands on the clock were pointing. For example, measures of visual short-term memory (VSTM) are correlated with higher-order cognitive abilities such as fluid intelligence (Fukuda, Vogel, Mayr, & Awh, 2010); VSTM ability measured in kindergarten-age children was shown to predict later school success (Alloway & Alloway, 2010).

Despite the fundamental importance of VSTM to cognition the overarching neural mechanism is not known. As well, the processes limiting VSTM are debated, leading to multiple models with varying assumptions about the underlying neural mechanism of VSTM. Broadly there are two classes of these models: discrete resource models and continuous resource models. While discrete models have had much support from both behavioral and neurological data the continuous models have out-performed discrete models in direct comparison. One reason for this trend may be new research methods and increases in computational power have allowed for better assessment of VSTM performance. Converging neurological evidence is also required to fully support these
continuous models. Informed by the latest models of VSTM performance, the aim of the current thesis is to use functional magnetic resonance imaging (fMRI) to investigate the neural mechanisms associated with the continuous and flexible allocation of working memory resources.

**Discrete-Item Models of Visual Working Memory**

Although work had previously identified a capacity limit of short-term visual memory (Philips, 1974), the modern concept of a discrete item limit began with Luck and Vogel (1997). Traditional models conceptualized working memory as having a fixed number of discrete slots to store high-resolution memory items (Luck & Vogel, 1997; Zhang & Luck, 2008). The primary task used to measure VSTM is the change detection task. In this task participants view a number of objects on the screen for a brief period and after a delay, the feature (e.g., color, orientation) of one object can potentially change. There are three variants of change detection: only the target object returns in the same location as in the memory display (single probe), only the target object returns in the center of the display (center probe), all of the objects return in the change-display (whole probe). The ability to report whether a change in the target display took place is taken as an absolute measure of whether the item was in memory or not.

During change detection tasks participants tend to have fewer correct trials as set size increases, with a rapid drop in performance around 3 - 4 items. Depending on the variant of change-detection task, different formulae can be used to estimate the number of items stored in memory, with the peak number of items taken as an estimate of an individual’s capacity (\(K\)). Luck & Vogel (1997) showed that when the number of objects in memory is a calculated, capacity or \(K\) plateaus at around set size four. Based on this
finding, they proposed a slot model that explained that objects would be held in a limited number of “slots” of working memory in an all-or-none fashion. When objects were successfully stored in memory, changes would be reported accurately; by contrast, when objects can were not in a slot, participants’ ability to detect a change would be at chance as there is no information stored about that object.

In their original paper, Luck and Vogel (1997) indicated that items with multiple features could be remembered as well objects with single features. This suggested that if items are stored in memory, they are encoded with high resolution, and are unaffected by the number of features to be remembered. However, the question remained whether memory is limited to a few high-resolution objects, or whether many more low-resolution objects be held in VSTM. To address the question of memory resolution, a delayed-estimation task has been used (Wilken & Ma, 2004). In a typical delayed-estimation task, participants report the colour of an object in memory on a continuous colour-wheel. The error – the distance between the target value and the selected color value – provides a measure of the resolution or precision of memory. Because of the circular space on the colour wheel, the error over many trials takes the form of a circular normal distribution known as the von Mises distribution, and the standard deviation of the von Mises distribution can be interpreted as the inverse of precision. Behavioural evidence from these tasks supported a gradual decrease in memory precision (Wilken & Ma, 2004) – termed the precision set-size tradeoff – instead of an abrupt decline at a fixed capacity (Luck & Vogel, 1997).

Although some studies have examined response error alone as a measure of memory precision (Wilken & Ma, 2004), Zhang and Luck (2008) argued that there is a
second distribution that can be separated from the target responses: random guessing – a flat distribution that would result from randomly reported colour values. Thus, Zhang and Luck (2008) used a mixture model of these two distributions – a uniform distribution, and a von Mises distribution – to examine whether changes in precision could be accommodated by one of two alternatives to the existing slot model, the ‘slot + resource’ model and the ‘slot + averaging’ model. The ‘slot + resource’ model proposed that there was a fixed number of discrete slots that could hold items in memory, but that the fidelity of those items was determined by a continuous resources that could be distributed among the fixed slots. The ‘slot + averaging’ model proposed that there would be a fixed number of slots, and that any unused slots could be given to an item already in memory to boost the representation of that item in memory. Thus, if there were three slots and only one item in memory it could be represented in all three slots and reported with greater precision. For both models the precision of object could be improved below capacity but not above capacity. The models differed in predicting the minimum fidelity of an item; whether precision of a reported item could be less than when a single item is held in a slot.

An alternative to the discrete “slot” models, the continuous resource model, was also examined. The continuous resource model, initially proposed by Wilken and Ma (2004), was completely flexible, able to allocate memory resources to any number of items with no minimum precision and no maximum capacity. Using the continuous response task and the two-distribution mixture-model, Zhang and Luck (2008) found that as the number of objects in memory increased beyond three items, the proportion of guesses (i.e., the height of the uniform distribution) increased but the standard deviation
did not significantly change. Secondly, objects from memory loads below three items were reported with moderately increased precision as fewer objects were maintained in memory. This finding supported the ‘slot + averaging’ model, as resources could be pooled amongst slots.

Measures of VSTM have so far focused on whether an object was in memory, and how well an object in memory is remembered but there is still another feature of memory that is debated: flexibility. What determines the resolution of an object in memory? The traditional slot model did not allow for any flexibility of memory allocation: one item would be stored in one slot. The ‘slot + averaging’ model increased the amount of flexibility so that objects in memory below capacity could use multiple slots or even share a slot. To further test the flexibility of resource allocation in VSTM, Zhang and Luck (2008) added cues to the delayed-estimation task to prioritize one item in memory that would be probed 70% of the time. If a continuous resource was distributed among the objects in memory this object should take memory resources away from the other objects in memory, but if objects in memory shared slots then there would be limited room to gain precision for the cued item while holding all the items in memory. While precision was significantly better for valid cued compared with invalid and neutral trials, neutral trials did not differ from invalid trials. Thus, the benefit to the single cued item was not at the loss of resources to the other items, providing further support for the ‘slot + averaging’ model. Thus, while resources could be allocated flexibly according to the ‘slot + averaging’ model, this model is not completely flexible, as items were limited to the resolution of a single slot.
**Continuous Resource Models of Visual Working Memory**

Despite the success of the discrete resource model, there has been long standing opposition to it (Bays & Husain, 2008; Frick, 1988; Wilken & Ma, 2004). An alternative to the discrete resource model is the category of continuous resource models. These models propose a limited pool of resources that can be flexibly distributed among objects in memory with no fixed upper bound (Bays & Husain, 2008; van den Berg, Shin, Chou, George, & Ma, 2012; Wilken & Ma, 2004). There is growing support that the continuous resource models better explain performance on both change-detection and delayed-estimation tasks than do discrete resource models (Ma, Husain, & Bays, 2014). For example, empirical evidence has shown that precision of memory report is proportional to the number of items held in memory past estimated capacity limits (Fougnie, Suchow, & Alvarez, 2012), proportional to the complexity of items in memory (Alvarez & Cavanagh, 2004; but see Awh, Barton, & Vogel, 2007), and greater for objects of expertise (Curby, Glazek, & Gauthier, 2009). These findings are inconsistent with a fixed capacity and a limitedly-flexible resource as proposed by discrete resource models like the ‘slots + averaging’ model. Critically, in direct mathematic comparisons, behavioural data supports a continuous resource models by significantly out performing discrete models (van den Berg, Awh, & Ma, 2014; (Emrich, Lockhart, & Al-Aidroos, 2017).

In addition, although, Zhang and Luck (2008) suggested that there was limited flexibility in memory representations, recent studies have shown that when cues are given to participants, they can be used to prioritize objects in memory accordingly, demonstrating that memory allocation is continuously flexible. Specifically, Emrich et al. (2017) tested the extent of memory allocation flexibility using several levels of probe-
likelihood. They reasoned that in a flexible resource model, if one item was given 50% of memory resources, performance (i.e., memory precision) for that item should be equivalent to conditions in which two items are held in memory (i.e., when memory resources are split across both items); moreover, the remaining (i.e., uncued) items should get an equal portion of the remaining 50% of memory resources, resulting in a proportional decrease in memory precision. When the flexibility of memory representations is tested in this way, results support a continuous resource model in which the flexibility of memory allocation was tied to the attentional priority given to each item, rather than by the number of items held in memory. Moreover, this effect has been demonstrated with both spatially-predictive cues (Emrich et al., 2017) featured-based attention (Dube, Emrich, & Al-Aidroos, in press), and incentive-associated guided attention (Klyszejko, Rahmati, & Curtis, 2014). Together, the results of these studies support the conclusion that VSTM is both a flexible and continuous resource, rather than an inflexible and discrete one.

**Neural Evidence in Support of a Discrete Resource Model**

Although behavioural models support the conclusion that VSTM is a continuous resource, neurological data supporting this model has lagged behind. By contrast, strong evidence supporting a discrete model has come from converging electroencephalography (EEG) and magnetic resonance imaging (MRI) studies. Vogel & Machizawa (2004) reported an event-related potential (ERP) marker of load-dependent sustained activity during the delay period of a change detection task they termed the contralateral delay activity (CDA). This activity demonstrated a number of attributes consistent with a discrete resource model. First, the CDA amplitude increased as participants had to
remember more items, consistent with a storage mechanism for discrete units. Second, the activity plateaued at the predicted fixed item capacity limit of 3 - 4 items. Further, for low-capacity subjects the difference between load four and load two activity is less than that of high-capacity subjects, which suggests that low-capacity subjects reach their peak activity sooner, storing fewer items in fewer “slots”. Based on this study, the CDA has been considered a hallmark of memory maintenance in a wide variety of studies of VSTM, such as during updating and resetting memory (as more items are stored; Balaban & Luria, 2017), visual search (as locations of already visited items are remembered; Emrich, Al-Aidroos, Pratt, & Ferber, 2009), and face recognition (trustworthy faces are better remembered; Meconi, Luria, & Sessa, 2014).

Similarly, fMRI data has produced a robust region of load-depend activity in support of a discrete resource model. Todd & Marois (2004) reported load-dependent activity in the intra-parietal sulcus (IPS) and intra-occipital sulcus (IOS) during the delay period of a change detection task, but not during an iconic memory task. This activity also plateaued at the predicted fixed item capacity of 3 – 4 items. Similarly, difference in high-load and low-load activity was predictive of capacity estimates just as the difference in CDA activity had been (Todd & Marois, 2005). In fact, evidence suggests that the IPS is the generator location for the CDA (Robitaille et al., 2010), further suggesting a role for this region in VSTM capacity limits.

Extending this finding to complex objects, Xu and Chun (2006) demonstrated that the plateau for complex objects was reached at two items instead of four. Their behavioral evidence, as well as evidence from other studies (e.g. Luria, Sessa, Gotler, Jolicœur, & Dell’Acqua, 2010) suggests fewer complex objects are held in memory than
simple items. As well, this finding suggests the mechanism for maintaining complex items is limited by the same mechanism as simple objects.

fMRI studies have been able to further classify the role of the IPS by splitting up the IPS into superior and inferior regions that uniquely contribute to VSTM maintenance. In four experiments Xu and Chun, (2006) had participants remember simple objects simultaneously presented, complex objects simultaneously present, or intermixed trials of simple and complex objects sequentially presented. This series of experiments determined that regions in the inferior IPS were sensitive to the number of locations of remembered stimuli while the superior IPS was sensitive to the complexity of remembered objects regardless of the number of locations.

Evidence from the CDA in EEG and IPS in fMRI has been taken as converging support for a discrete resource model. Both measures show a monotonic increase with load that plateaus at capacity. The difference between activity at high-load versus low-load –but not absolute activity – is predictive of capacity estimates in both measures. Moreover, both measures are also sensitive to a difference in capacity for complex versus simple items.

**Neural Evidence Against a Discrete Resource Model.**

At face value, the converging results of CDA and IPS activity make a strong case for a discrete load dependent mechanism in the brain. Particularly finding a plateau at a fixed set-size in both measures is best explained by a discrete resource model with fixed capacity limit. However, Ma, Husain, & Bays, (2014) questioned whether the activity reported by Todd & Marois (2004) was actually plateauing at all. Todd and Marois determined that there was not a significant difference between loads four, six, and eight
but Ma et al. report that a continually increasing exponential saturation function fit the data and would be incorrectly identified as a plateau using the method of Todd and Marois. This suggestion casts doubt for a discrete resource explanation in favour of a continuous resource mechanism.

Neural support for a discrete resource model has focused on one type of neural activity: sustained synchronous firing. VSTM is understood as a sustained “online” process, which has lead to the assumption that the neural signature should also be a sustained process of elevated persistent neural firing. Sustained synchronous firing produces a large signal that can be measured by EEG and fMRI; however, to understand the neural mechanism from the cell to systems level, other types of neural activity can be considered. Single cell recording studies are one method that has demonstrated that memory is not held in an all-or none fashion. Buschman, Siegel, Roy, & Miller, (2011) trained two monkeys to perform a change localization task while they recorded from single neurons in the lateral intra-parietal area (LIP), the frontal eye fields (FEF), and lateral prefrontal cortex (LPFC). If objects existed in memory in an all or none fashion it would be expected that there would be no memory trace for objects that were not reported; however, significant LPFC activity was shown in single cell recordings in monkeys for incorrect change localization trials (Buschman et al., 2011).

It is apparent at the cellular level that even poorly remembered objects might have information stored about them. This finding maybe explained through a population coding account of VSTM, consistent with continuous resource models. Population coding refers to a group of neurons coding for related features that together relay information to higher order areas of the brain. In lower order perceptual areas, population coding sends
information about simple features such as line orientation. Individual neurons are tuned to specific orientations and fire preferentially to their orientation and will fire to a lesser degree as the line is tilted away from their preferred orientation. When the population of neurons fires together, the frequency of action potentials are greatest from the neuron that most closely matches the presented orientation, creating a Gaussian function around the true orientation. Paul Bays (2015) recently proposed that population coding may account for performance in VSTM tasks. In memory the neurons are more flexible than at the level of perception and the population of neurons can dedicate firing to encode any object in memory rather than specific features as in perception. Each population code is the signal relaying the object in memory: as more objects are held in memory fewer neurons are devoted to the object and the ratio of signal to noise (SNR) decreases. This noise in the system is related to the variability in responses. Even when only one object is held in memory there is a baseline level of noise in the system, and this accounts for the non-normal distribution of errors even when holding one item in memory (Bays, 2014). The explanatory power of a population code theory stems from the fact that that changes in the SNR can account for a wide variety of empirical evidence from VSTM tasks: increasing response error with load (e.g. Wilken & Ma, 2004), increasing binding errors with load (e.g. Bays, Catalao, & Husain, 2009), degradation of the memory over time (e.g. Pertzov, Bays, Joseph, & Husain, 2013), and increased latency to report items at higher loads (e.g. Pearson, Raskevicius, Bays, Pertzov, & Husain, 2014).

Another feature of a population code theory is that the signal being maintained by the neurons creates a pattern of spiking activity that can be decoded using trained classifiers. In human research one form of decoding for neural activation is multi-voxel
pattern analysis (MVPA) applied to fMRI data. Harrison and Tong (2009) had participants remember one of two oriented gratings and reported whether the test grating was rotated clockwise or counterclockwise. A classifier was trained on the oriented gratings from a separate task and applied to the VSTM task. Early visual areas (e.g. V1-V5) appeared to hold information about the content of memory even in the absence of elevated blood oxygenation level dependent activity (BOLD; Harrison & Tong, 2009). This finding supports a sensory-recruitment theory that proposed that sensory areas hold information about the content of memory.

In the study by Harrison and Tong (2009) half of the subjects did not have elevated activity in the early visual areas but the classifier was no less accurate at identifying which grating was held in memory. This finding is in contrast to a typical fMRI task that would only look for elevated activity in a region. Similarly, a study by (Emrich, Riggall, LaRocque, & Postle, 2013) had participants remember the direction of moving dot patterns presented sequentially to constitute loads one, two, and three. Participants reported the orientation of motion after a delay period. Just as in the study by Harrison and Tong (2009) there was not elevated activation in early visual cortex but the trained classifier was able to reliably decode the content of VSTM from these regions. Further, the classifier was not able to decode the contents of VSTM from the IPS despite robust elevated activation. These findings suggest that elevated activity is not the only marker of memory storage. Recall that Xu & Chun (2006) suggested that the inferior IPS was sensitive to the number of locations of objects in memory, and further the IPS had been previously shown to be active when remembering spatial information without necessarily storing a object from that location (e.g. Curtis, Rao, & D’Esposito, 2004).
Taken together the elevated activity in the IPS may not reflect the contents of VSTM but only the locations of objects in memory.

Evidence presented thus far questioned the mechanisms of VSTM that support a discrete resource model; however, each finding individually does not support a continuous resource model. One primary marker of a continuous resource model is the relationship between resources and memory precision. A population coding theory would suggest this ‘resource’ is cellular activity whether that is in the density of spiking activity or a pattern of activity. The studies by Harrison & Tong (2009), Emrich et al. (2013), and others (Rose et al., 2016) demonstrated that patterns of activity but not necessarily, increases in overall firing, was predictive of the contents of working memory. Additionally, in the study by Emrich et al., (2013) classification accuracy was significantly related to within-subject changes in mnemonic accuracy across load conditions. This finding demonstrates a mechanism of memory precision whereby a pattern of activity rather than a region of activity codes for the content of memory representations. Moreover, this finding is in line with the predictions of a population coding mechanism of VSTM as patterns of cellular activity code for the contents and precision of objects in memory. Although not definitive, this finding provided the support for an alternative mechanism of memory representations that could support the predictions of a continuous resource model of VSTM in human subjects.

**Contributions of a Fronto-parietal Attention Network**

In addition to the potential roles of the IPS and sensory cortex in VSTM maintenance, numerous studies have examined the role of frontal regions in VSTM, particularly in their contribution to attentional control. Fronto-parietal networks are
implicated in broad attention control processes, including goal-directed attention, inhibition, and gating access to working memory. The right dorsolateral prefrontal cortex (dLPFC; Rypma & D’Esposito, 1999; Edin et al., 2009), dorsomedial prefrontal cortex (Nelissen, Stokes, Nobre, & Rushworth, 2013), insula/frontal operculum (FO; Nelissen et al., 2013), and bilateral middle frontal gyri (McNab & Klingberg, 2008) have all been implicated in some way to control access to working memory. Frontal activity is not necessarily load dependent but may have a broader role in gating and relaying preparatory signals during the memory task. For instance, bilateral middle frontal activation was associated with preparing to filter distractors during memory encoding, suggesting the bilateral middle frontal gyri play a role in inhibiting items from being encoded into working memory (McNab & Klingberg, 2008).

The dLPFC has also been implicated in studies of working memory. Specifically, the right dLPFC was found to have activation at high memory load conditions but not low memory load conditions in a letter memory task (Rypma & D’Esposito, 1999). Linden et al., (2003) found evidence for dLPFC activation at high memory load and suggest that this may reflect a strategy, such as rehearsal, that participants need at high-loads but not at a low-load. Alternatively, Edin et al. (2009) suggest that the role of the dLPFC is to increasing subjects’ capacity by sending a boosting current to the IPS that reduces lateral inhibition. At high-loads, reducing lateral inhibition can increase the maximum capacity of the subject but at low-loads the same activity causes more confusion between items or swap errors (Edin, et al. 2009). A similar mechanism may be at play in both boosting and inhibiting items in visual working memory. Edin et al. (2009) noted that this boost signal was not specific to the dLPFC during a whole-brain analysis; additional activity consistent
with boosting was found in the right middle frontal gyrus (rMF) and middle superior frontal gyrus. Thus, although frontal regions appear important for controlling access to VSTM and may provide a mechanism for prioritization, it is not clear whether these roles contribute to the flexible and continuous allocation of resources observed in behavioural studies of VSTM.

**The Current Study**

The purpose of this thesis is to understand the neural mechanisms mediating the flexible allocation of a continuous memory resource. That is, although a plethora of studies have examined the contribution of parietal, sensory, and frontal areas to VSTM, none of these studies have identified the continuous and flexible nature of this resource, as the majority of these studies were performed with the discrete resource model in mind. To address this, the current study had participants perform a delayed-estimation task with probabilistic cues while undergoing fMRI. The memory task is similar to the one used in Emrich et al., (2017) with memory loads one, two, four set by cuing with 100% likelihood a subset of four presented items, and a flexible allocation (FA) condition. In the FA condition, one item was cued, which had 50% likelihood of being probed. Performance on this task has been shown to reflect a flexible and continuous allocation of memory resources, such that performance on this FA condition resembled conditions with two items (in which each item receives 50% of memory resources). Consequently, by comparing the FA condition to the high memory load condition, it should be possible to identify the source of this flexible control.

To examine the neural markers of VSTM storage under a continuous resource model, a region of interest analysis based on the location of Todd and Marois (2004) will
be used to localize the activity in the IPS. At memory loads one, two and four it is hypothesized that IPS activity should replicate the monotonic increase observed by Todd & Marois (2004). It is unclear whether the IPS would track cued and uncued memory objects in the same trial the same way it tracks overall load. Although all four items should be in memory during the FA trials, it may be that items allocated memory resources below a certain threshold (i.e. the uncued items) will not elicit the same level of IPS activity; however, high-load trials did elicit IPS activity in the study by Todd & Marois (2004) of which each object would have received a similarly low proportion of resources as the uncued items (i.e. $1/6 = 0.167$). As well some evidence suggests the IPS – at lest the inferior IPS (Linden et al., 2003; Xu & Chun, 2006)– tracks locations of memory items rather than overall memory load. Taken together, the FA condition activity is hypothesized to most resemble load four conditions, since four items are in memory. Thus, this study will attempt to extend the findings of Todd & Marois (2004) to better account for continuous resource allocation.

To understand the mechanism for flexible and continuous resource allocation, candidate regions in the frontal lobe have been identified. Regions in the frontal attentional network are of particular interest as attention is thought to be the executive modulating activity that determines the proportion of resources allocated to each item in memory encoding and maintenance (Emrich et al., 2017). Frontal regions play a critical role in working memory tasks to filter, inhibit, and focus attention. Regions identified include the dlPFC for it’s role in gating control of the working memory and special role at high memory loads to maintain performance (Edin et al. 2009), and the bilateral middle frontal gyri for their role in preparatory activity suggested to bias encoding (McNab &
Klingberg, 2008). Activity for each trial condition was analyzed in these regions. Additionally a whole brain analysis will be done to identify any regions contributing to the difference between the critical FA and load four (i.e. the source of resource allocation).

Neural activity should predict behavioral performance within individuals. Although the dataset is small, exploratory correlations will be carried out to investigate the association between each region and behavior. Correlational data is not expected to have enough power at this number of participants so any trending data may be explored in the future based on a sequential stopping rule proposed to improve the efficiency of data collection while maintaining type one error rates at 0.05 levels which is particularly relevant for costly data collection (Fitts, 2010; Frick, 1998; but see Yu, Sprenger, Thomas, & Dougherty, 2014).

The precision of responses is a measure of memory fidelity and as such should correlate with regions that support the content of working memory. As such, the relationship between neural measures and behavioral performance will be carried out between absolute error and neural activity in the dLPFC and IPS. Todd and Marios (2005) analyzed IPS activity correlated with individuals estimated capacity; however, with a delay-estimation task the behavioral outcome of interest is memory precision. If elevated signal in the IPS reflect representations of the contents of VSTM there should be a measurable relationship in with behavioral performance. Edin et al. (2009) carried out similar correlations with the prediction that dLPFC activity would be more strongly correlated at high memory loads in accordance with their proposed signal boost mechanism. As well Edin et al. (2009) predicted that dLPFC activity would decrease
lateral inhibition in the IPS, which would allow more items to be stored in memory at the
cost of increased competition between items. It is predicted that this would correlate with
the rate of non-target errors since greater competition between items should be associated
with more confusion and thus non-target reports.

Methods

Participants

Sixteen participants were recruited from Brock University and the University of
Toronto. Three subjects only completed the orientation session leaving thirteen
participants in the final sample (8 female, 12 right handed, ages 18-35 M=24.7).
Participants were paid honorarium of $10/hour for the orientation session and $25/hour
for the scanning session. Participants were screened for normal or corrected to normal
vision and normal colour vision, no history of serious psychiatric difficulty and were not
taking medications that affected their nervous system. All participants met MRI safety
criteria. All procedures were approved by the Research Ethics Boards at Brock University
and the University of Toronto.

Procedure and Stimuli

delayed-estimation colour memory task was used to test VSTM while in the
scanner. Each trial contained four coloured squares on the display and one, two, or four
spatial line cues simultaneously on the display for 500ms (see Figure 1). In the FA
condition, the single line cue was only 50% valid. Each condition can be described by the
total memory load or alternatively they can be described by the proportion of resources
allocated to each item in the display. On 100% validly cued conditions each item in the
display receives a proportion of total recourse equal to 1/(number of cued items) (i.e. 1/2
Figure 1. Trial design for delayed-estimation experiment. Each trial began with a shape cue to signal the cue condition presented for 500ms. A sample display consisted of four coloured squares with line cues directing which of the squares was likely to be a target at memory report was presented for 500ms followed by a 1000ms retention interval. Participants reported the colour value of a target colour during the 6500ms report period cue will result in the cued item receiving a proportion of resources equal to 50% of the total resources (i.e. 0.50), and the uncued items will receive a proportion equal to the remaining 50% of total resources divided among the remaining items (i.e. 0.50/3 = 0.167). See Table 1 in Appendix A for a summary of load and proportion of resource by condition.

Participants were instructed as to the cue validity or visual control condition on each trial by a shape cue that appeared for 1500ms. A target colour was reported after a 1000ms delay using a button-box in the scanner to move the colour value on a colour wheel. The colour value changed by increments of 5° clockwise or counter-clockwise or 90° clockwise to jump quadrants of the colour wheel. The target position was randomly
chosen among the possible locations by condition. The orientation of the colour wheel was randomly jittered between trials, and the starting colour location was jittered between trials with the constraint that it had to be a multiple of five degrees from the colour value. Participants had 6500ms to choose their colour value before the next trial began. No participants reported having difficulty with the timing in the scanner. In the visual control condition participants did not have to report a remembered colour value, in all other conditions participants reported the colour value of a probed-item. Trial order was optimized for event related fMRI experiments using optseq2 to create a unique condition schedule for trials each of the six runs in the scanner. Blank trials lasting one TR (2 seconds) were interspersed to optimize the trial sequence.

Trials were presented on a MRI safe high-resolution (1920 x 1080) BOLDscreen monitor located behind the bore of scanner. Participants could view the screen through a mirror placed over their eyes angled at the screen behind them. Each coloured square was designed to be one visual degree in length. The squares were presented around the fixation point at a radius of 4 visual degrees. The colour wheel was 12 visual degrees from the fixation point.

An orientation session, lasting one hour, was completed at either Brock University or the University of Toronto prior to scanning. Participants filled out a MRI safety screening form and had their colour vision tested. To assess participants’ capacity a change detection task with set sizes two, four, six was performed. Participants saw two, four, or six uniquely coloured squares for 500ms followed by fixation for 1000ms before the display returned with zero or one changed colour until participants reported whether
they saw a change at any location in the display (whole-probe). Capacity was calculated using Pashler’s formula for whole-probe change detection (Pashler, 1988).

\[ K = (\text{set size})^{hit \, rate - false \, alarm \, rate} \times \frac{hit \, rate - false \, alarm \, rate}{1 - false \, alarm \, rate} \]

Each participant completed 60 trials of the task as practice, equivalent to a single run in the scanner. During practice trials participants used the keyboard to move their reported colour value. Lastly, each participant completed the behavioural avoidance and inhibition scale (BIS/BAS scale; Carver & White, 1994). Results of the BIS/BAS analysis were not analyzed for the purposes of this thesis.

All participants came to the Toronto Neuroimaging Facility for their scanning session. The scans were acquired using a Siemens Prisma 3T Full Body Scanner and 32-channel head coil at the Toronto Neuroimaging Facility. Participants performed 360 trials of the memory task in the scanner in six runs each lasting ten minutes. Participants then underwent a retinotopic-mapping scan to map the quadrants of their visual field (not analyzed for the purpose of this thesis). Functional images were acquired by a T2*-weighted echo planar imaging (EPI) sequence (33 slices, field of view (FOV) = 220mm, resolution matrix = 64 x 64 x 34, voxel size = 3.44mm x 3.44mm x 4.25mm, TR = 2000ms, TE = 30ms, flip angle = 90°, interleaved). The first three TRs from each run were removed from analysis to have consistent steady state tissue magnetization. Lastly a high-resolution anatomical scan was acquired using a T1 weighted anatomical sequence (175 sagittal slices, FOV = 240mm, resolution matrix = 176 x 236 x 213, voxel size = 0.94mm x 0.94mm x 0.94mm, TR = 2300ms, TE = 229ms, flip angle = 8°).

**Behavioural Task Analysis**

Analysis will first seek to replicate the behavioral findings of Emrich et al. (2017)
to ensure this task is reflecting flexible resource allocation. The primary measure for behavioural analysis was response error (i.e., the difference between the target colour and the reported colour). Paired-sample t-tests were done to check that the manipulation of the FA condition was successful. Resource model (i.e. power-law) and discrete model fits (linear) to absolute error in degrees from the target were compared. Response error data was modeled using the three-component mixture model (Bays et al., 2009) and a two-component mixture model (Zhang & Luck, 2008) with maximum likelihood estimates performed in MATLAB with MemToolBox (Suchow, Brady, Fougnie, & Alvarez, 2013). The two-component mixture model consists of a flat distribution of errors (random guessing) and a von Mise distribution centered on the true value as used by Zhang and Luck (2008). The output of this model is the rate of guessing and the standard deviation of the von Mise distribution (precision). The three-component mixture model included additional von Mise distribution centered on the values of the non-target items in the memory display (Bays et al. 2009). The output from this model is the rate of guessing, the rate of non-target errors, and the deviation from the true value in degrees (precision).

**fMRI Pre-processing**

Each subject’s anatomical image was skull stripped by first pre-masking the images to standard space and then skull stripping performed with the brain extraction tool (BET) with a fractional intensity threshold at -0.15 (Smith, 2002). This produced a reliably clean brain extraction that did not remove frontal brain matter.

FMRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, [www.fmrib.ox.ac.uk/fsl](http://www.fmrib.ox.ac.uk/fsl)). Registration of the functional data to the high-resolution structural image was carried out
using the boundary based registration algorithm (Greve & Fischl, 2009). Registration of
the high resolution structural to standard space was carried out using FLIRT (FMRIB’s
Linear Image Registration Tool; Jenkinson & Smith, 2001; Jenkinson, Bannister, Brady,
& Smith, 2002) and was then further refined using FNIRT nonlinear registration
(Andersson, Jenkinson, & Smith, 2007a; Andersson, Jenkinson, & Smith, 2007b). The
following pre-statistics processing was applied; motion correction using MCFLIRT
(Motion Corrected FLIRT) (Jenkinson et al., 2002) non-brain removal using BET (Smith,
2002); spatial smoothing using a Gaussian kernel of Full width at half maximum
(FWHM) 5mm; grand-mean intensity normalization of the entire 4D dataset by a single
multiplicative factor; high-pass temporal filtering (Gaussian-weighted least-squares
straight line fitting, with sigma = 50.0s). Time-series statistical analysis was carried out
using FILM (FRMIB’s improved linear model) with local autocorrelation correction
(Woolrich, Ripley, Brady, & Smith, 2001). The time series model included each task
condition modeled by double gamma HRF (hemodynamic response formula), with
temporal derivative and temporal filtering. Extended motion parameters were applied as
nuisance regressors. Further, TRs with frame-wise displacement greater than 0.9mm were
modeled out. Experimental trials each lasted ten seconds (visual control trials lasted 6
seconds) but events were modeled for two TRs (four seconds) to capture memory activity
including encoding, and maintenance activity during the task. The second-level analysis,
combining EPI runs within subject, was carried out using a fixed effects model, by
forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of
Mixed Effects) (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann,
Jenkinson, & Smith 2004; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004;
This model averaged parameter estimates over runs within each participant. Z (Gaussianised T/F) statistic images were threshold at using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = 0.05$ (Worsley, 2001). Third level analysis, averaging parameter estimates from all participants, was carried out using FLAME stage one (Beckmann et al., 2003; Woolrich et al., 2004; Woolrich, 2008). Threshold-free cluster enhancement was performed using Randomise at 5000 permutations for family-wise error (FWE) corrected $p$-values and variance smoothing set to 5mm FWHM (Winkler, Ridgway, Webster, Smith, & Nichols, 2014).

**Planned ROI Analysis**

Regions of interest (ROI) were computed as a sphere around previously identified areas in the bilateral IPS/IOS (Montreal Neurological Institute coordinates (MNI): 22/-22, -63/-69, 49/46; Todd & Marois, 2004), bilateral middle frontal regions (48/-40, -10/-12, 44/50; McNab & Klingberg, 2008), and the right dorsolateral prefrontal cortex (52, 34, 32; Edin et al., 2009). ROIs were 5mm in diameter for the IPS and bilateral middle frontal gyrus, and 10mm in diameter for the dLPFC. See Table 2 in Appendix B for summary of ROI coordinates cluster analysis peak coordinates. The coordinates for the IPS/IOS were converted from Talaraich to MNI space using the Yale BioImage Suite Package (Papademetris, 2014) mapping from Lacadie, Fulbright, Constable, and Papademetris, (2008). Percent signal change was extracted by featquery (FEAT Results Interrogation) in the designated ROI for each subject. Contrasts of interest for ROI comparison were task conditions from baseline, or the contrast between the FA and load four conditions. Contrasts between trial conditions and the visual control were run to
measure the activity specific to memory over perception; however these contrasts are not analysed here to allow for comparison with past studies that did not use a perceptual control (e.g. Todd & Marois 2004). Percent change output was tested to be significant different from zero using a one-sample t-test for each condition contrast. Linear mixed effects analysis determined if activity levels were predicted by trial condition with random intercept for subjects and fixed effects of the trial condition; the “lme4” package in R was used for linear mixed effects analysis (Bates, Maechler, Bolker, & Walker, 2015). Post hoc analysis was done on planned contrasts of the parameter estimates for trial conditions and output a t-ratio of beta values and Satterthwaite approximate degrees of freedom using the lmerTest package in R (Kuznetsova, Brockhoff, & Christensen, 2016).

**Whole Brain Cluster analysis**

A whole brain cluster analysis was performed on the contrast of the FA condition greater than load four. This contrast was chosen because it isolates the effect of the flexible allocation of resources from the effect of memory load: In both the FA and load four trials four objects are in memory but in the FA condition the cued object is prioritized requiring a flexible allocation process to distribute memory resources unevenly. Threshold-free cluster enhancement was performed using Randomise at 5000 permutations for FWE corrected p-values with variance smoothing at 5mm FWHM (Winkler et al., 2014). FWE correction controls the false discovery rate, as it may under represent large clusters of brain activity but is unlikely to identify false positive clusters of activity. Clusters greater than one voxel large at FWE corrected p-values less than 0.05 were considered significant. For post-hoc analysis ROIs were constructed using the
cluster masks, see Table 2 in Appendix B. These clusters were then tested using the same methods applied to the planned ROI regions to characterize the involvement of the region in the flexible allocation of memory resources in VSTM.

**Results**

**Behavioural Models**

Subjects performed the delayed-estimation task in the scanner with four conditions (see Table 1). The measure of interest was response error (i.e. the absolute difference between their response and the true value in degrees). As a manipulation check of the FA condition multiple paired t-tests were performed. Paired t-tests sought to determine if the manipulation in the FA condition differentiated the error report for cued and uncued between each other and trial types as predicted by the flexible allocation of memory resources. Bonferroni corrections were applied to four tests (significance reached at \( p < 0.0125 \)).

Cued and uncued items in the FA condition were significantly different from each other, \( t(12) = 9.59, p < 0.0001 \), such that uncued items were reported with a mean of 46 degrees further from the true value. The FA cued items were marginally better than load two memory report with an average of four degrees less error on memory reports, \( t(12) = 2.30, p = 0.04 \). Cued items in the FA condition were significantly worse than load one with a average of 3.5 degrees more error, \( t(12) = 4.22, p = 0.001 \). The uncued items in the FA condition were significantly worse than load four, \( t(12) = 5.55, p = 0.0001 \), with a mean of 26 degrees increase in error for the uncued items. These comparisons are consistent with the findings of Emrich et al. (2017), demonstrating the flexible allocation manipulation in the FA condition was successful at encouraging participants to prioritize
the cued item at a level similar to the load two and that the uncued item was maintained
with less resolution than load four items as expected.

Further analysis is performed to determine if the error reported is consistent with
the predictions of a continuous and flexible resource model. According to Emrich et al.
(2017) and others (Dube et al., in press; van den Berg et al., 2014) the response error
should be predictable by a power-law according to the proportion of memory resources.
To verify this prediction in the current dataset the data was modeled using a power-law fit
by proportion of resources as a predictor variable and compared to a linear fit by memory
load. Mean absolute error was calculated for each condition and fitted to a linear model
predicted by memory load, a linear model predicted by proportion of resources (i.e., 1/cue
probability, see Table 1), and a power-law fit – transformed into a linear fit for the
purposed of modeling – using the log of absolute error and the log of resource proportion.
The linear fit by proportion of memory resources is not a predicted model but only serves
to demonstrate that a power-law relationship is an improvement over a linear fit. The
proportion of resources was plotted at 1/(proportion of resources) so that the models
would be in a consistent direction (see Figure 2), since data was log-transformed before
modeling, axes of the power-law fit do not reflect the log-linear distance between the
datum (see Figure 3 for untransformed power-law fit of the data). Linear mixed effects
analysis was performed with fixed and random effects. A random intercept controls for
variance between subjects and the fixed effect models the effect of the predictor variable
fit by maximum likelihood estimations. Each model was a significant improvement over
the random intercept model (linear –load model $\chi^2(1) = 53.19, p < 0.0001, \text{AIC} = 524.77$;
linear –resource model $\chi^2(1)= 82.67, p < 0.0001, \text{AIC} = 489.63$; log-linear –resource
model $\chi^2(1) = 94.66, p < 0.0001, AIC = -77.70$; see Figure 2). Since each model has the same degrees of freedom the residual sum of squares (SSR) was calculated as a measure of goodness of fit to the data to determine which model was the best fit to the data. This comparison determined that the log-linear –resource model fit was the best fit to the data since it had the smallest residual sum of squares (linear –load model $SSR = 7725.18 >$ linear –resource model $SSR = 785.88 >$ log-linear –resource model $SSR = 0.41$). See Table 3 for a summary of model output in Appendix C as well as plots actual values against predicted values in Appendix D.

**Planned ROI Analysis**

While behavioral analysis could separate the effects within the FA condition to the cued (prioritized) item and the uncued items at report, neural activity cannot directly assess these conditions separately; consequently, all analyses of fMRI activity in the FA condition are collapsed across cued and uncued trials. Thus, trial conditions differed only by load except for the FA condition, which manipulated the allocation of memory resources such that four items would be in memory but with one item prioritized to reflect flexible allocation of memory resources.

**IPS activity**

The IPS is thought to be involved in memory storage, and a candidate for the location of memory storage (but see Emrich et al. 2013). Robust activity is routinely reported in this region associated with VTSM load. Percent signal change was extracted using the featquery function for contrast estimates from the trial conditions compared to baseline activity. One-sample t-tests were performed on for mean bilateral IPS activity extracted for each trial type to determine if activity was significantly above baseline.
Figure 2. Plots of linear multilevel models for absolute error. Predicted values for individual subjects shown in grey, mean model prediction shown in black, error bars represent 95% confidence intervals. A) Linear –Load model. B) Linear –Resource model. C) Log-Linear –Resource fit. The axes do not reflect the log-linear distance between datum because they were log-transformed before modeling.
Figure 3. Power-law plot of untransformed absolute error and proportion resources. A) Power-law fit by proportion of resources for mean absolute error. B) Linear fit by memory load for mean absolute error.

Signal change was significantly above zero for all conditions ($p < 0.001$), see Table 6.

IPS activity by trial condition was modeled using random intercepts and fixed effects in a linear mixed model fit by maximum likelihood. Random intercepts account for variance between subjects. Fixed effects model the effect of the trial conditions on IPS activity. Multilevel fit of IPS activity by trial condition shows this model is a

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>0.6004</td>
<td>$t(12) = 4.8221$</td>
<td>$p = 0.0004$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>0.6877</td>
<td>$t(12) = 5.0300$</td>
<td>$p = 0.0002$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.7351</td>
<td>$t(12) = 5.6531$</td>
<td>$p = 0.0001$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.6991</td>
<td>$t(12) = 5.7258$</td>
<td>$p &lt; 0.0001$</td>
</tr>
</tbody>
</table>
significant improvement from the random intercept model alone $\chi^2(3) = 34.42$, $p < 0.0001$, AIC = -99.12. Post-hoc analysis of planned contrasts revealed that load two activity was greater than load one activity $\beta = 0.069$, SE = 0.010, $t(39) = 6.78$, $p < 0.0001$; the load 4 condition was greater than load two $\beta = 0.072$, SE = 0.012 $t(39) = 6.11$, $p < 0.0001$; and FA activity was greater than load four activity $\beta = 0.048$, SE = 0.010 $t(39) = 4.71$, $p < 0.001$.

The activity in the IPS was consistent with the findings of Todd & Marois (2004) demonstrating a monotonic increase between loads one, two, and four. IPS activity in the FA condition was greater than at load four. The FA condition could not be separated by cued and uncued probed trials since the participants would not know which trials would probe the cued item when storing items in memory. The elevated activity levels in the FA conditions suggest that participants are holding approximately four items in memory.

**dlPFC activity**

dlPFC activity is suspected to have a supporting role in VSTM maintenance at high memory load conditions (Edin et al., 2009). Percent signal change was extracted using the featquery function for contrast estimates from the trial conditions compared to baseline activity. One-sample t-tests were performed on mean activity to determine if the change in activity was significantly above baseline. Signal change was significantly

<table>
<thead>
<tr>
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<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>0.2290</td>
<td>$t(12) = 1.1768$</td>
<td>$p = 0.2621$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>0.2074</td>
<td>$t(12) = 1.3435$</td>
<td>$p = 0.2040$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.3430</td>
<td>$t(12) = 2.3348$</td>
<td>$p = 0.0038$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.3455</td>
<td>$t(12) = 2.2208$</td>
<td>$p = 0.0046$</td>
</tr>
</tbody>
</table>
above zero only for load four and FA conditions (high-load conditions): load four $t(12) = 2.22, p = 0.046$; FA $t(12) = 2.33, p = 0.038$, see Table 7.

dIPFC activity by condition was modeled using random intercepts and fixed effects in a linear mixed model fit by maximum likelihood. Random intercepts account for variance between subjects. Fixed effects model the effect of the trial conditions on dIPFC activity. Linear multilevel fit of dIPFC activity by trial condition shows this model is a significant improvement from the random intercept model alone $\chi^2(3) = 23.28, p < 0.0001$, AIC = -77.11; see Figure 5. Based on the previous finding that activity in the dIPFC differentiates high and low-load conditions (Edin et al., 2009; Rypma & D’Esposito, 1999), planned comparisons tested whether the FA condition differed from load four, whether load two differed from load one, and whether the average of the FA

![Figure 5](image)

Figure 5. Bar chart of dIPFC mean activity by trial condition, 95% confidence intervals around the mean shown. Individual subjects shown as grey lines.
and load four differed from the average of load one and two. Planned contrasts revealed
that high-load conditions are not different from each other $\beta = 0.002$, $SE = 0.012$, $t(39) = 0.13$, $p = 0.9005$; low-load conditions are not different from each other $\beta = 0.001$, $SE = 0.012$, $t(39) = 0.05$, $p = 0.9606$; but the average of high-load conditions are different from
the average of low-load conditions $\beta = 0.096$, $SE = 0.17$, $t(39) = 5.64$, $p < 0.0001$.

**Bilateral middle frontal gyri activity**

Bilateral middle frontal activity was found to have a role in preparatory activity to
prioritize target items over distractor items (McNab & Klingberg, 2008). This area may
play a role in the flexible allocation of memory resources as an extension of this filtering
role. Percent signal change was extracted using the featquery function for contrast
estimates from the trial conditions compared to baseline activity. One-sample t-tests were
performed on mean activity to determine if the change in activity was significantly above
baseline. Signal change was significantly above zero for all conditions ($ps < 0.001$), see
Table 8.

Bilateral middle frontal activity was modeled using random intercepts and fixed
effects in a linear mixed model fit by maximum likelihood to determine if trial condition
could predict neural activity. Random intercepts account for variance between subjects.
Fixed effects model the effect of the trial conditions on bilateral middle frontal activity.

**Table 8.**

**Summary of One-sample t-test statistics for bilateral middle frontal gyri activity from baseline**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>0.1978</td>
<td>$t(12) = 5.8727$</td>
<td>$p &lt; 0.0001$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>0.2031</td>
<td>$t(12) = 5.8100$</td>
<td>$p &lt; 0.0001$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.2051</td>
<td>$t(12) = 5.7618$</td>
<td>$p &lt; 0.0001$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.2054</td>
<td>$t(12) = 5.6346$</td>
<td>$p = 0.0001$</td>
</tr>
</tbody>
</table>
Linear multilevel fit showed this model is not a significant improvement from the random intercept model alone $\chi^2(3) = 0.52$, $p = 0.91$, AIC = -146.33. Although activity was elevated in each condition, the manipulation of load and flexible allocation did not predict the degree of activity elevation, see Figure 6. This region may play a unique role in preparatory activity – to filter between target and distractor items – not reflected in flexible resource allocation.

**Whole Brain Cluster Analysis**

In order to identify regions of activity responsible for the flexible allocation of memory resources, a whole-brain analysis was performed contrasting the load four and the FA conditions. Critically, although both conditions involved the maintenance of four items in VSTM, the FA condition required allocating resources unevenly across items, and thus requires a greater degree of attentional control. Thus, those areas which show

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*Figure 6. Bar chart of bilateral middle frontal gyri mean by trial condition, 95% confidence intervals around the mean shown. Individual subjects shown as grey lines*
greater activity in the FA compared to load 4 should reveal areas involved in flexible allocation of resources, without necessarily being load-dependent.

FWE corrected cluster analysis found significant regions of activity in regions of the right dIPFC ($p = 0.028$), bilateral insula (right $p < 0.001$, left $p = 0.001$), cingulate gyrus ($p = 0.002$), rMF ($p = 0.023$), right middle temporal gyrus ($p = 0.035$, $p = 0.026$), bilateral lateral occipital complex (LOC) (right $p = 0.017$, left $p = 0.011$, $p = 0.034$), right supramarginal gyrus ($p = 0.023$). For full list of significant cluster coordinates see Table 2 in Appendix B. Some of these regions are not uncommon in VSTM or attention network studies but are not of interest to the present design. Clusters in the dIPFC, and middle frontal gyrus have previously been identified as significant regions in a fronto-parietal network and analyzed with planned ROI analysis. Planned ROI of these regions do not completely overlap with the whole-brain defined clusters and so second regions in the dIPFC and rMF were extracted from the FWE corrected cluster analysis. When right and left regions are combined, bilateral insula activity was the largest and most significant cluster identified so this region will be investigated.

Masks were created from the cluster index output by the FWE corrected cluster analysis for the dIPFC, rMF, and bilateral insula. Just as in the planned ROI regions, percent signal change was extracted for each trial condition. One-sample t-tests were performed on the output to determine if activity in this region was significantly above baseline. Since activity in these regions is characterized by the manipulation of flexible allocation, linear multilevel analysis was performed to explore evidence for what role the region has, if any, in the other conditions.
Whole-brain cluster analysis: dlPFC.

The maximum coordinates of the right dlPFC cluster were 10mm more dorsal, and 4mm more anterior than the ROI center coordinates. A second mask in the dlPFC was constructed for the FWE corrected cluster. One-sample t-test revealed activity in this region was only above baseline in the high-load conditions, see Table 9. This pattern is repeated in the planned ROI region in the dlPFC. However, activity in this cluster was greater in the FA condition than at load four. The overall pattern of results is consistent between planned ROI and whole-brain analysis. Linear multilevel model of fixed and random effects was performed to test if the change in dlPFC could be predicted by trial conditions. Random intercepts control for the variance between subjects such that only the change in dlPFC activity is predicted by fixed effects. The model of trial condition was a significant improvement over the intercept model, $\chi^2(3) = 27.56, p < 0.0001$, AIC = -80.47. Planned contrasts identical to the contrasts made in the planned ROI revealed that condition one and condition two did not differ ($p = 0.81$), the FA condition and load four did not differ ($p = 0.79$), but that the mean of the high-load conditions was significantly greater than the mean of the low-load conditions ($\beta = 0.118, SE = 0.019, t(39) = 6.32, p < 0.0001$, see Figure 7. This result replicates the results from the planned ROI for the dlPFC region.

Table 9. Summary of one-sample t-test statistics for cluster extracted dlPFC activity from baseline

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>0.1227</td>
<td>$t(12) = 2.7366$</td>
<td>$p = 0.1227$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>0.1162</td>
<td>$t(12) = 2.8573$</td>
<td>$p = 0.1162$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.2412</td>
<td>$t(12) = 4.7196$</td>
<td>$p = 0.0005$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.2340</td>
<td>$t(12) = 4.0417$</td>
<td>$p = 0.0016$</td>
</tr>
</tbody>
</table>
Figure 7. Bar chart of right dIPFC mean activity by trial condition. A) Bar chart of mean activity by trial type, 95% confidence intervals shown. Grey lines represent individual subject data. B) Location of dIPFC cluster, right presented on the left.

Whole-brain cluster analysis: Right middle frontal gyrus.

The whole-brain cluster analysis defined region in the rMF was 4mm more dorsal than the right portion of the region specified in the planned ROI of the bilateral middle frontal gyrus. One-sample t-test in the regions showed that activity was not above baseline in any of the task condition, all ps > 0.05 see Table 10. This pattern of results does not replicate the activity from the planned ROI in the bilateral middle frontal gyrus that had found activity was above baseline in every task condition. Activity is greater for

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>0.1284</td>
<td>$t(12) = 0.4106$</td>
<td>$p = 0.6886$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>0.1162</td>
<td>$t(12) = 1.5370$</td>
<td>$p = 0.1502$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.2412</td>
<td>$t(12) = 0.6631$</td>
<td>$p = 0.5198$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.2340</td>
<td>$t(12) = 0.1643$</td>
<td>$p = 0.8722$</td>
</tr>
</tbody>
</table>
Although activity is not increased above baseline the difference between trial conditions suggests a role for the rMF in the flexible allocation of memory resources.

Linear multilevel model of fixed and random effects was performed to test if the change in rMF activity could be predicted by trial conditions. Random intercepts control for the variance between subjects such that only the change in rMF is predicted by fixed effects. The model of trial condition was a significant improvement over the intercept model, $\chi^2(3) = 19.44, p = 0.0002, \text{AIC} = -84.29$. Planned contrasts revealed that load two was more negative than load one ($\beta = -0.028, \text{SE} = 0.012, t(39) = 2.35, p = 0.0239$), the FA condition and load four did not significantly differ but were trending ($\beta = -0.023, \text{SE} = 0.012, t(39) = 1.91, p = 0.063$), and that the average of high-load conditions was significantly greater than the average of load two ($\beta = 0.068, \text{SE} = 0.017, t(39) = 4.00, p =$

Figure 8. Bar chart of rMF mean activity by trial condition. A) Bar chart of mean activity by trial type, 95% confidence intervals shown. B) Location of rMF cluster, right presented on the left.
0.0003), see Figure 8. This suggests that the contribution of the rMF is particular to high memory load conditions but inhibition of this region may be important at low memory loads, although activity was not significantly different from baseline levels.

**Whole-brain cluster analysis: Bilateral insula**

The bilateral insula was the largest region identified in the whole-brain analysis, so although previous literature in VSTM storage had not identified this region it may play a role in flexible allocation of memory resources separate from VSTM storage activity or support from fronto-parietal network. One-sample t-tests revealed that only the activity in the load two condition was different from baseline levels in the negative direction, $t(12) = 2.79, p = 0.0165$, all other $ps > 0.05$. Although not significantly different from baseline activity was greatest in the FA condition, see Figure 9. Linear multilevel model of fixed and random effects was performed to test if the change in bilateral insula activity could be predicted by trial conditions. Random intercepts control for the variation between subjects such that only the change in insula activity is predicted by fixed effects. The model of trial condition was a significant improvement over the intercept model, $\chi^2(3) = 25.87, p < 0.0001$, AIC = -124.88. Planned contrasts revealed that condition one and condition two did not differ ($p = 0.12$), the FA condition and load four did not

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean (% signal change)</th>
<th>Test statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Condition 1 (Load 1)</td>
<td>-0.0360</td>
<td>$t(12) = 1.7793$</td>
<td>$p = 0.1005$</td>
</tr>
<tr>
<td>Condition 2 (Load 2)</td>
<td>-0.0684</td>
<td>$t(12) = 2.7874$</td>
<td>$p = 0.0165$</td>
</tr>
<tr>
<td>Condition FA (Load 4/1)</td>
<td>0.0476</td>
<td>$t(12) = 1.6280$</td>
<td>$p = 0.1295$</td>
</tr>
<tr>
<td>Condition 4 (Load 4)</td>
<td>0.0186</td>
<td>$t(12) = 0.8896$</td>
<td>$p = 0.3911$</td>
</tr>
</tbody>
</table>
significantly differ \( (p = 0.28) \), but that the average of high-load conditions was significantly greater than the average of load two \( (\beta = 0.082, \ SE = 0.014 \ t(39) = 5.74, \ p < 0.0001) \). This suggests that the contribution of the bilateral insula is particular to high memory load conditions, although activity was not significantly different from baseline levels, except for load two which was significantly below baseline. This region showed a decrease in activity at low-load conditions but an increase at high-load conditions; inhibition of this region may have a complementary role at low-loads while increased activity is relevant to high-loads. Although these differences are not different from baseline levels the change in activity was predicted by the trial condition. Activity was greatest in the FA condition supporting a role for the insula that contributes to the flexible allocation of memory resources.

**Exploratory Analysis: Precision and Neural Activity.**

In order to determine if neural activity supported precision of memory report within subjects, exploratory correlations were carried out between behavior on the
memory task and neural activity. However given the sample size at present, these analyses should be considered purely exploratory. Chosen tests were guided by the predications of Edin et al. (2009) with regard to the role of dIPFC and IPS activity. Analysis focused on the relationship between behavioral performance and neural activity. Flexible allocation of memory resources is reflected in the precision of memory report so neural areas that contribute to the behavioral performance provide evidence for flexible allocation and a continuous resource model. Since the data set is very small for correlational data this analysis at a trending level of significance may suggest there is a non-zero relationship between these two measures if there was more power.

Linear multilevel modeling was use with fixed and random effects to predict behavioural measures of absolute error and three-component model output for all cued trials from neural activity. Random intercept controlled for variance between subjects. Fixed effects modeled the effect of change in neural activity (dIPFC, or IPS) on each of the behavioral measures specified. The change in dIPFC activity predicted absolute error over the random intercept alone ($\chi^2(1) = 9.62, p = 0.0019, AIC = 39585$). This finding suggests the change in dIPFC activity within subjects was predictive of absolute error. As well the change in dIPFC activity within subjects predicted three-component mixture model precision, ($\chi^2(1) = 6.10, p = 0.014, AIC = 338.92$) but not model guess rate $\chi^2(1) = 1.33, p = 0.2481, AIC = -72.70$ or non-target rate ($\chi^2(1) = 2.63, p = 0.1049, AIC = -96.36$). This provides further support for a role of the dIPFC in flexible allocation of memory resources as precision of memory report can be manipulated by flexible allocation of memory resources biasing resources towards preferred objects in memory. While the associations with guess rate and non-target errors are not significant in this
dataset there may not be enough power to say for certain whether the relationship with these parameters is actually zero.

IPS activity was not a significant predictor of absolute error over the random intercept model ($\chi^2(1) = 1.22, p = 0.2687, \text{AIC} = 39593$). Change in IPS activity did not predict three-component mixture model precision, ($\chi^2(1) = 0.71, p = 0.3991, \text{AIC} = 346.31$), guess rate ($\chi^2(1) = 0.002, p = 0.9628, \text{AIC} = -71.37$) or non-target rate ($\chi^2(1) = 0.03, p = 0.869, \text{AIC} = -93.76$). Despite the low power of the analysis, the lack of a trending effect in this data suggest that it is unlikely that there is a non-zero relationship with these behavioral parameters and IPS activity. This may suggest that the activity in the IPS does not reflect the contents of VSTM but it specific to the number or locations of representations (Xu & Chun, 2006); although the analysis of activity over the whole region of the IPS may not be sensitive to localized changes within sub-divisions of the IPS.

**Discussion**

Despite strong behavioural evidence for a continuous resource model of VSTM there has not been much neural evidence that supports a mechanism of flexible and continuous resource allocation. It was previously demonstrated that VSTM resources are more flexible than predicted by a discrete resource model (Zhang & Luck, 2008) by cuing participants to prioritize objects in memory over other (Emrich et al., 2017). The current thesis used the same task to look for regions of activity that would contribute to flexible resource allocation and thus provide neural support for a continuous resource model. Results replicated the behavioral data of Emrich et al. (2017) demonstrating flexible resource allocation. Neural evidence replicated the load-dependent activity in the IPS.
(Todd & Marois, 2004), and high-load dIPFC activity, but not condition dependent filtering activity in the bilateral middle frontal gyri. Further regions were identified which were more active in the FA condition than at load four. In each of these conditions participants hold four objects in memory but in the FA condition memory resources must be flexible allocated to a preferred item. Regions identified include the dIFPC, rMF, and bilateral insula. These regions with greater activity in this condition reflect areas that may provide a unique or supportive role in flexible resource allocation. The current analysis cannot comment on the exact role of the identified regions but bearing past research in mind it is possible to make suggestions as to what contribution these areas make to task performance; however, this type of reverse inference should be read with a level of skepticism until further analysis can directly comment on the specific role these regions have in the flexible allocation of memory resources (see Poldrack, 2011 for a discussion of the use of reverse inference in neuroimaging research).

**Behavioral task: Flexible resource allocation**

Participants completed a delayed-estimation task in the scanner with three conditions that manipulated the memory load and one condition that manipulated attentional demand by requiring flexible allocation of memory resources to cued and uncued items. The absolute error of memory report is a measure of VSTM resolution and has been shown to be associated with these task manipulations (Emrich et al., 2017, Dube et al., *in press*). Behavioral data when modeled by power-law fit to the proportion of resources provides an excellent fit. These data are consistent with the findings of Emrich et al. (2017) and Dube et al. (*in press*) and suggest that participants are flexibly allocating memory resources among the objects. Specifically, because the error in the FA condition
report of the cued item was most similar to the report of load two it suggests that participants had allocated approximately 50% of memory resources to this single item just as each item in load two received 50% of memory resources. Further, the uncued items receive a small portion of memory resources and are reported with precision that would be predicted by receiving only one third of the remaining 50% portion. This portion is less than what would predicted by the ‘slot + averaging’ model for a single slot.

**IPS: Load-dependent activity**

While the cued and uncued trials of the FA condition could not be separated in the analysis of fMRI BOLD signal, these data reveal what attributes of the FA condition the region is sensitive to. At each trial condition IPS activity was significantly above baseline levels, consistent with a role of the IPS in VSTM tasks. Planned ROI analysis of the IPS showed that trial condition (i.e. load) was a significant predictor of the change in activity within subjects replicating the finding by Todd and Marois (2004). Post-hoc tests revealed that load two activity was greater than load one activity but less than the FA condition, and the FA condition activity was greater than load four activity. The difference between load four and the FA condition was small but statistically significant with a mean difference of only 0.036% between the conditions. This suggests that participants are holding multiple objects in memory in the FA condition. Participants’ IPS activity was significantly greater in the FA condition than at load two demonstrates that participants were holding more than two items in memory. Moreover, since activity resembled IPS activity at load four, participants are most likely holding four items in memory. This analysis also demonstrates that the IPS does not track only prioritized items in memory since only one item was prioritized in the FA condition.
Regions of the dlPFC: Contribution of attentional network

Planned ROI analysis of the dlPFC activity showed that only activity in load four and FA conditions were above baseline levels. This finding further suggests that participants are holding four items in memory in the FA condition. Linear multilevel modeling showed that trial condition was a significant predictor of dlPFC signal change. Planned comparisons in post-hoc tests showed that activity in load one and two did not differ (collectively called low-load), and that activity in the load four and FA condition did not differ (collectively called high-load) but that activity was significantly greater in the high-load conditions. It is unclear whether load per se, or other increased task demands present at high-load trials (e.g. increased attentional demand) is responsible for elevating dlPFC activity. This pattern of activity replicates the pattern reported in dlPFC activity by Edin et al. (2009). Edin et al. (2009), found that dlPFC activity was present only in high-load conditions and suggested that the dlPFC sends a boost signal to the IPS to reduced lateral inhibition. The purpose of lateral inhibition is to maintain higher number of objects in memory but would increase the amount of noise between objects in memory. Exploratory correlations did not find an increase in non-target errors associated with greater dlPFC activity but since the data was trending there may not have been sufficient power to find this association. Interestingly, the multilevel model between dlPFC activity and absolute error, as well as between dlPFC activity and three-component mixture model precision were significant compared to intercept models. This suggests a role for the dlPFC in memory precision and flexible resource allocation. As well, whole brain cluster analysis found a significant region of activity in the dlPFC. This analysis identified regions that were characterized by greater activity in the FA condition.
Analysis of this region replicated the findings from the planned ROI. This suggests that the dIPFC has a role in flexible resource allocation as well as supporting maintenance activity in high memory load trials. The mechanism of support from the dIPFC was not investigated so it is uncertain whether it is the same mechanism (i.e. boost signal to the IPS) that would provide increased control during the flexible resource allocation trials. It may be possible that the dIPFC provides subsequent or increased boost activity to the prioritized item to maximize the resolution of the cued item while maintaining each other item with reduced resolution (i.e. less lateral inhibition between uncued items).

**Middle frontal Gyri: General and specific role in VSTM**

Based on the findings of McNab & Klingberg (2008), bilateral middle frontal gyrus activity was investigated for a role in prioritizing items in memory. The window of investigation in the current data did not analyze pre-stimulus activity as in McNab & Klingberg (2008), but hoped to capture controlled filtering activity between the onset of the trial and maintenance period associated with flexible resource allocation (Dube et al., in press). While one-sample t-tests showed that bilateral middle frontal gyri activity was significantly above baseline levels for all conditions of the task (Table 8), linear mixed effects models showed that the activity could not be predicted by trial condition ($p = 0.91$). This suggests that the role of the bilateral middle frontal gyri did not differentiate load conditions or the flexible allocation condition but is more general in VSTM task during this time window. McNab & Klingberg (2008) had identified this region as differentiating target and distractor trials in the pre-stimulus window. In the current task four items were displayed in every condition with cues designating which items were likely to be probed. Participants did not know the number of cues that would be presented
–only the validity of those cues – which may have lead to preparatory filter activity for all trials. In the current window bilateral middle frontal gyri activity does not provide a controlled filter after the stimulus display. Future analysis of this region should include the pre-stimulus window to best capture preparatory filtering activity.

Whole brain FWE corrected cluster analysis found a small but significant cluster in the rMF that was more active in the FA condition than in the high-load condition. This region did not differ significantly from baseline activity but was predicted by trial condition with the greatest activity at high-load trials, and particularly the FA condition. While not the main location of analysis, Edin et al. (2009) had found patterns of activity in the rMF that were consistent with the boost signal activity in the dlPFC. There may be a specific role of the rMF in the flexible allocation of memory resources and high-load VSTM.

The location of the maximum coordinate was 20mm more anterior and 6mm more dorsal than the ROI center constructed from the maximum location specified by McNab & Klingberg (2008), which is entirely outside of the area captured by the ROI. Perhaps the middle frontal gyrus should be split anterior and posterior with the anterior portion having a specific role in flexible allocation of memory resources without necessarily an increase above baseline levels and the posterior section having a more general role in VSTM, associated with pre-stimulus preparatory filtering, that increases above baseline levels but is not load dependent or unique to flexible resource allocation. Future studies may investigate the exact role for this region, as well as look to the pre-stimulus window.
**Bilateral Insula: Maintenance activity management**

Whole-brain analysis identified regions with greater activity in the FA condition than at load four to look for activity that contributes to flexible resource allocation. A large region was identified in the bilateral insula that was not considered previously. Activity in this region was not significantly different from baseline but could be predicted by the trial condition. Past research has found a role for insula activity in retro-cue VSTM study designs. This area differentiated conditions that were cued ahead of the memory presentation or after the memory presentation (Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015). Insula activity may then be responsible for management of memory resources after initial encoding. Although cues were presented simultaneously with the memory display in the current task they may not have been utilized until the maintenance period to boost the signal of the prioritized item, similar to a retro-cue paradigm. Future studies may investigate the exact timing of insula involvement and contrast with a retro-cue paradigm.

**An evolutionary theory for VSTM.**

A large network is used to support VSTM ability: sensory areas in the occipital cortex, intra-parietal sulcus, and several frontal regions including the dlpFC, bilateral frontal gyrus, and bilateral insula. The characterization of VSTM resources limits the understanding of how the network supports an object in memory. A sticking point for the discrete resource model has been the apparent plateaus in neural activity at a fixed item limit. While evidence has cast doubt on the discrete resource model, there is not a satisfactory explanation for the apparent plateau in the continuous resource model. On the other hand, despite reliable measures of a plateau in neural activity there is not a strong
rational for why there would be a fixed item limit in VSTM at all. It is apparent that a model of VSTM will have to account for both continuous behavioral performance and neural patterns that appear to plateau – although the plateaus may be represented by a saturated exponential decay function (Ma et al., 2014). Using evolutionary theory, van den Berg & Ma, (2017) theorized that the limitation in working memory is the outcome of an optimal tradeoff between behavioral performance and the cost of neural firing. Their framework explains behavioural data from delayed-estimation, change detection, change localization, and visual search paradigms as well as motivated super-threshold performance (van den Berg & Ma, 2017). Their theory does not make direct claims about what neurological measures would look like when performing optimally except to minimize the cost of firing. This principal could explain stepwise increases in activity as shown in the CDA and IPS activity as less firing is needed to maintain fewer items but at higher loads it is more effective to reduce behavioural performance than to increase firing. The mechanism for memory maintenance is not localized to one region but a network of optimally performing regions. This network consists of multiple mechanisms in sensory areas, the IPS, and frontal regions that work together to optimize performance but minimize the ecological cost of neural firing.

The data presented can be interpreted within a framework of optimized behavior with minimized cost. Flexible allocation of memory resources is a behavior optimizing strategy that requires input from memory maintenance activity in the IPS, dIPFC and insula activity to assist in the maintaining all the items. Whole-brain cluster analysis revealed several regions that were greater in the FA condition than at load four. One-sample t-tests of some regions revealed this activity did not significantly differ from zero.
It could be possible that these regions are optimized to support VSTM in a way that differentiates memory load and attentional demands without differing from baseline activity. For instance, in low-load conditions the insula activity was below baseline levels, but at or above baseline levels in the high-load conditions. Similarly, MVPA analysis has demonstrated that patterns of activity can contain information about the content of memory in regions that are not increased above baseline levels (Emrich et al., 2013; Harrison & Tong, 2009). Activity that can support VSTM without great ecological costs of neural firing would be preferable to a system that was calibrated to minimize energy costs while maximizing behavioral performance.

**Conclusions**

The work presented here successfully replicated behavioral results demonstrating flexible allocation of memory resources in a delayed-estimation task and extended this finding to neurological data. Typical VSTM maintenance activity in the IPS was identified with increasing activity as memory load increased. Importantly, the FA condition activity was elevated along side the load-four activity suggesting that participants were holding four items in memory despite significantly different error reports between these two conditions. Further regions were identified that were associated with the flexible allocation of memory resources in the dIPFC, bilateral insula, and right middle frontal gyrus. Although the mechanism for these regions to interact with maintenance activity was not determined, it is predicted that these regions would provide support to optimize behaviour according to an evolutionary valid rational strategy (van den Berg & Ma, 2017).
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https://doi.org/10.1167/13.10.9


https://doi.org/10.1037/a0035234


https://doi.org/10.1038/nature04262


https://doi.org/10.1038/nature06860
Appendix A – Table of study conditions

Memory load is equal to the total number of items that could have been probed in each condition. Proportion of resources are predicted by $1/(\text{number of cued items})$, or the validity of the cue in the case of the FA condition. $1/\text{proportion of resources}$ is calculated for the purpose of plotting data so that load and resource plots are in a consistent direction.

Table 1. Summary of study conditions.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Memory Load</th>
<th>Proportion Resource</th>
<th>$1/\text{Proportion Resource}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1.000</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0.500</td>
<td>2</td>
</tr>
<tr>
<td>FA-cued</td>
<td>1</td>
<td>0.500</td>
<td>2</td>
</tr>
<tr>
<td>FA-uncued</td>
<td>4</td>
<td>0.167</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>0.250</td>
<td>4</td>
</tr>
</tbody>
</table>
Appendix B – ROI and Cluster Coordinates

Table 2.
Summary of ROI MNI coordinates and cluster maxima for planned contrasts and whole brain cluster analysis.

<table>
<thead>
<tr>
<th>Region</th>
<th># Voxels</th>
<th>MNI Coordinates</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right IPS</td>
<td>90</td>
<td>22, -63, 49</td>
<td>Todd &amp; Marois (2004)</td>
</tr>
<tr>
<td>Left IPS</td>
<td>90</td>
<td>-22, -69, 46</td>
<td></td>
</tr>
<tr>
<td>Right Mid. Frontal</td>
<td>81</td>
<td>48, -10, 44</td>
<td>McNab &amp; Klingberg (2008)</td>
</tr>
<tr>
<td>Left Mid. Frontal</td>
<td>81</td>
<td>-40, -12, 50</td>
<td></td>
</tr>
<tr>
<td>Right dIPFC</td>
<td>500</td>
<td>52, 34, 32</td>
<td>Edin et al. (2009)</td>
</tr>
</tbody>
</table>

Cluster Analysis

<table>
<thead>
<tr>
<th>Region</th>
<th># Voxels</th>
<th>MNI Coordinates</th>
<th>FWE-corrected p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right Insula</td>
<td>1029</td>
<td>32, 22, -6</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>Left Insula</td>
<td>256</td>
<td>-30, 24, -4</td>
<td>p = 0.001</td>
</tr>
<tr>
<td>Cingulate Gyrus</td>
<td>379</td>
<td>0, 22, 42</td>
<td>p = 0.002</td>
</tr>
<tr>
<td>Right dIPFC</td>
<td>233</td>
<td>52, 34, 22</td>
<td>p = 0.028</td>
</tr>
<tr>
<td>Right Mid. Frontal</td>
<td>230</td>
<td>50, 10, 50</td>
<td>p = 0.023</td>
</tr>
<tr>
<td>Right LOC</td>
<td>198</td>
<td>46, -54, 60</td>
<td>p = 0.017</td>
</tr>
<tr>
<td>Left LOC</td>
<td>90</td>
<td>-8, -76, 50</td>
<td>p = 0.011</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>-10, -70, 36</td>
<td>p = 0.034</td>
</tr>
<tr>
<td>Right Mid. Temp.</td>
<td>97</td>
<td>68, -34, -6</td>
<td>p = 0.026</td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>48, -24, -8</td>
<td>p = 0.035</td>
</tr>
<tr>
<td>Right Supramarginal</td>
<td>159</td>
<td>62, -42, 55</td>
<td>p = 0.023</td>
</tr>
</tbody>
</table>
Appendix C – Summary of linear multilevel output of behavioral data

Table 3. Summary of linear multilevel model for absolute error.

<table>
<thead>
<tr>
<th>Model</th>
<th>Chi-squared</th>
<th>p-value</th>
<th>AIC</th>
<th>SSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear-Load</td>
<td>$\chi^2(1)$ = 53.19</td>
<td>$p&lt;0.0001$</td>
<td>524.77</td>
<td>7725.18</td>
</tr>
<tr>
<td>Linear-Resource</td>
<td>$\chi^2(1)$ = 82.67</td>
<td>$p&lt;0.0001$</td>
<td>489.63</td>
<td>785.88</td>
</tr>
<tr>
<td>Log-Resource</td>
<td>$\chi^2(1)$ = 94.66</td>
<td>$p&lt;0.0001$</td>
<td>-77.70</td>
<td>0.41 **</td>
</tr>
</tbody>
</table>

**Indicates best model fit by SSR in for each model parameter
Appendix D – Plot of residuals versus actual value from behavioral data models

Residual plots show how closely the predicted values of the power-law model are to the actual values with data approximating a line $y = x$.

A.

B.

C.