UNIVERSITY OF CALIFORNIA

Santa Barbara

The Parietal Cortex and Recognition Memory: Activity is Modulated by Changes in Task Demands

A dissertation submitted in partial satisfaction of the requirements

for the degree Doctor of Philosophy in Psychology

by

Amy Lee Frithsen

Committee in charge:

Professor Michael B. Miller, Chair

Professor F. Gregory Ashby

Professor Barry Giesbrecht

Professor Jonathan Schooler

March 2015

The dissertation of Amy L. Frithsen is approved.

_____

F. Gregory Ashby

_____

Barry Giesbrecht

_____

Jonathan Schooler

_____

Michael B. Miller, Committee Chair

January 2015

Acknowledgments

I would like to give an enormous thanks to my advisor, Dr. Michael B. Miller for his continued advise, guidance, and overall support throughout my graduate career. I never would have made it to this point without him and am truly thankful to have had him as an advisor. I would also like to thank the other members of my dissertation committee: Dr. Jonathan Schooler, Dr. Barry Giesbrecht, and Dr. F. Gregory Ashby for their important input and feedback on the interpretation of these results. Immeasurable thanks are also due to several Miller lab members for their help in this work in one way or another including: Danielle King, Craig Bennett, Brian Lopez, Benjamin Turner, Misty Schubert, and countless research assistants. Most importantly, I would like to thank my mother Joy Toro, stepfather Robert Toro, and father Thomas Frithsen for their unconditional love and support. Finally, thank you to all of my friends and family who have helped me make it to where I am today. I could never have done it without all of you!

Curriculum Vitae

Amy L. Frithsen

University of California
Santa Barbara, CA 93106-9660
(978) 235-2209
frithsen@psych.ucsb.edu

Education

University of Massachusetts at Amherst, B.A. in Psychology, September 2006.
Thesis: *"The Effects of Television on Children's Play Development"* (advisor: Dr. Daniel Anderson).

University of California at Santa Barbara, Pursuing Ph.D. in Psychological and Brain Sciences (Expected Completion in February 2015).
Thesis: *"The Posterior Parietal Cortex and Recognition Memory: Activity is Modulated by Changes in Task Demands"* (advisor: Dr. Michael B. Miller).

Research Experience

2007 – Present: Graduate Student Researcher, University of California at Santa Barbara

- Laboratory of Dr. Michael B. Miller. Conducted and analyzed neuroimaging (fMRI) experiments focusing on the neural correlates of recollection and familiarity within the posterior parietal cortex. Also conducted and analyzed several behavioral experiments investigating changes in response criterion during recognition memory.

2004 – 2006: Undergraduate Research Assistant, University of Massachusetts at Amherst

- Laboratory of Dr. Caren Rotello. Conducted behavioral experiments in order to model response time data during tests of recognition memory.
- Laboratory of Dr. Daniel Anderson. Collected and analyzed behavioral data investigating the effect of television on young children's play development.

Publications

Frithsen, A., & Miller, M.B. (2014). The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity. *Neuropsychologia, 61*, 31 -44.

Frithsen, A., Kantner, J., & Miller, M.B. (in preparation). The generalizability of switching criterion: A comparison between recognition memory and perceptual tasks.

Aminoff, E.; Clewett, D.; Freeman, S.; **Frithsen, A.**; Tipper, C.; Johnson, A.; Grafton, S.T.; Miller, M.B. (2014). Maintaining a cautious state of mind during a recognition test: A large-scale fMRI study. *Neuropsychologia, 67*, 132-147.

Hermundstad, A.M.; Brown, K.S., Bassett, D.S.; Aminoff, E.; **Frithsen, A**.; Johnson, A.; Tipper, C.M.; Miller, M.B.; Grafton, S.T.; Carlson, J.M. (2014). Structurally-constrained relationships between cognitive states in the human brain. *PLOS Computational Biology, 10*(5), 1-9.

Hermundstad, A.M.; Bassett, D.S.; Brown, K.S.; Aminoff, E.M.; Clewett, D., Freeman, S.; **Frithsen, A**.; Johnson, A., Tipper, C.M., Miller, M.B.; Grafton, S.T.; Carlson, J.M. (2013). Structural foundations of resting-state and task-based functional connectivity in the human brain. *Proceedings of the National Academy of Sciences, 110*(15), 6169-6174.

Aminoff, E.; Clewett, D.; Freeman, S.; **Frithsen, A.**; Tipper, C.; Johnson, A.; Grafton, S.T.; Miller, M.B. (2012). Individual differences in shifting decision criterion: A recognition memory study. *Memory & Cognition, 40*(7), 1016-1030.

Conference Presentations

Frithsen, A. (2014). Retrieval-related activity within the posterior parietal cortex is modulated by changes in task demands, Bay Area Memory Meeting, Palo Alto.

Frithsen, A. & Miller, M.B. (2014). Differences in criterion placement and the ventral parietal cortex. Cognitive Neuroscience Society, Boston.

Frithsen, A., Miller, M.B., & Marinsek, N. (2013). Differences in functional connectivity patterns in the lateral parietal cortex during a resting-state scan. Cognitive Neuroscience Society, San Francisco.

Frithsen, A. & Miller, M.B. (2013). The lateral parietal cortex: Neural correlates of recollection and familiarity depend on how they are defined. New Horizons in Human Brain Imaging, Kahuku.

Frithsen, A.; Kanter, J.; Lopez, B.; Santander, T.; Aminoff, E.; Vettel, J.; Tipper, C.; Grafton, S.; & Miller, M. (2012). Behavioral and neural components of flexible and optimal decision-making. Institute for Collaborative Biotechnologies, Santa Barbara.

Frithsen, A. & Miller, M.B. (2012). Separating recollection and familiarity. Remember-know and source memory tests. Cognitive Neuroscience Society, Chicago.

Frithsen, A. & Miller, M.B. (2012). Successful subsequent memory is associated with deactivation of the right hemisphere during encoding. Bay Area Memory Meeting, San Francisco.

Frithsen, A. & Miller, M.B. (2011). Dissociating recollection and familiarity in the brain. Society for Neuroscience, Washington, D.C.

Frithsen, A. & Miller, M.B. (2011). Neural correlates of recollection and familiarity as defined by the remember-know and source memory tests. Bay Area Memory Meeting, Berkeley.

Teaching Experience

2012: Teaching Associate, University of California at Santa Barbara

- Cognitive Neuroscience (Summer 2012). Created lecture materials, delivered lectures three days a week, created and graded exams.

2008- Present: Teaching Assistant, University of California at Santa Barbara

- Biological Basis of Psychology (Spring 2014). Delivered two lectures to entire class (approximately 350 students), graded exams.
- Introduction to Experimental Psychology (Summer 2013). Graded students' work, helped create exam questions, graded exams.
- Introduction to Statistics (Winter 2014, Spring 2012). Conducted a discussion section each week, graded students' weekly assignments and exams.
- Research Methods Laboratory (Fall 2011, Summer 2011, Spring 2011, Fall 2012). Conducted a laboratory section each week, graded students' work including research papers, assisted in students' projects.

- Cognitive Neuroscience (Spring 2009). Performed administrative duties such as making photocopies, attended lecture, graded exams.
- Introduction to Psychology (Winter 2008, Summer 2013). Conducted three section lectures per week, graded students' work, conducted review sessions for exams.
- Evolutionary Psychology (Summer 2008). Graded students' weekly assignments and exams.
- Cognitive Psychology (Summer 2008) Graded students' work and exams, conducted review sessions for exams, delivered one lecture to entire class.

2004 – 2006: Teaching Assistant, University of Massachusetts at Amherst

- Introduction to Psychology (Spring 2006). Graded students' weekly assignments, held review sessions for exams.
- Logical Reasoning (Spring 2004). Graded students' work throughout semester, delivered one lecture to entire class.

Academic Awards

- Nominated for 2014 GSA Excellence in Teaching Award.

Membership in Professional Organizations

- Society for Neuroscience. Member since January 2011.
- Cognitive Neuroscience Society. Member since March 2007.

ABSTRACT

The Parietal Cortex and Recognition Memory: Activity is Modulated by Changes in Task Demands

by

Amy Lee Frithsen

Recently there has been an increased interest in the lateral parietal cortex's role in successful memory retrieval. Several theories have been put forth to explain this phenomenon including the idea that this region plays a direct role in memory retrieval, temporarily storing episodic content until a decision can be made. Other explanations report a more indirect role of the parietal cortex during memory retrieval. Some of these theories include modulations of attentional systems that may guide memory retrieval or representations of subjective awareness of one's memories. According to these theories, parietal activations may *assist* successful memory retrieval, but are not *necessary* for it to occur. Although this region is consistently found to be active when memories are successfully retrieved, these results were initially difficult to reconcile with reports from neuropsychology, which show a lack of severe memory impairment when damage to this region occurs. These findings are specifically difficult for theories that assume this region is directly related to memory retrieval (i.e. the episodic buffer account), which assume this activity is necessary for successful retrieval to occur. The purpose of the experiments described in this

dissertation is to test whether parietal activations are modulated by task demands that should not affect the amount of episodic content retrieved. These task demands include modifying the way retrieval states are operationalized and varying the base rates of studied items presented at test. Although these procedural changes should affect extra-mnemonic cognitive processes, there is no reason to assume they should affect the amount of mnemonic information retrieved. Results from these studies in fact do show a modulation of both dorsal and ventral lateral parietal activations based on these procedural manipulations. These results are difficult to explain with an episodic buffer account of parietal activity. Instead, the results point to a more indirect role of parietal involvement in memory retrieval and are the most in line with the idea of this area representing the subjective awareness that can accompany successful retrieval, particularly during recollection. When these results are compared to results from neuropsychology, an extra-mnemonic role for the parietal cortex, particularly one associated with the subjective experience of retrieved content, appears to be the most parsimonious explanation. However, a subjective awareness account of parietal activity cannot adequately explain all of the findings from the literature, and most likely is only part of the story. The parietal cortex is an extremely heterogeneous area, both in structural and functional connectivity. The full story of the parietal cortex's role in memory retrieval will most likely be explained with a variety of theories. Increased levels of spatial segregation of the parietal cortex into distinct functional sub-regions will most likely reveal a myriad of functional roles that this region is playing during the complex cognitive process that is memory retrieval.

Table of Contents

Chapter 1: Background and Introduction

Recollection and Familiarity:

In a standard recognition memory test, subjects are presented with a set of stimuli and must decide whether or not they have encountered each stimulus before. There are numerous techniques one can employ in order to accomplish this task, and in fact, a great deal of individual variability has been shown to exist (Kirchoff, 2009; Kirchoff & Buckner, 2006; Miller, Donovan, Van Horn, German, Sokol-Hessner, & Wolford, 2009). Although there are a myriad of strategies one can utilize, the type of recognition generally falls under one of two categories (or both). A subject can recognize the item using familiarity and/or use recollection to inform their memory decision. Familiarity has been described as an undifferentiated, strength-like memory signal (Mandler, 1980). This type of recognition is devoid of specific contextual information from the encoding event. As a result, these memories are often weak in comparison to items recognized via recollection. Recollection refers to memories that are often contextually rich and vivid, containing details about what was occurring during the encoding episode. According to some, the defining feature of recollection is the experience of mentally traveling back in time to 're-experience' the original event. Tulving (2002) has argued in fact, that this ability to mental travel through time (which he refers to as autonoetic consciousness) is uniquely human. This ability has been thought to rely on a deeper understanding of a sense of self, without which there would be no 'traveler'. Despite whether this ability to mentally travel through

time is uniquely human or not, there is a wealth of empirical evidence indicating that these two types of memory retrieval are distinct.

The idea that there are two unique modes of retrieval can be illustrated with a relatively common experience often referred to as the 'butcher-on-the-bus' phenomenon (Mandler, 1980). The classic story is as follows: imagine you are riding on a public bus and you see a fellow passenger whom you *know* that you have encountered previously. This recognition is usually followed by a search process intending to answer the question, 'Where do I know this man from?'. You may ask yourself if you know him from work, from church, or from a variety of places you may often frequent. If you're lucky, the search may end with the insight, 'That's the butcher from the supermarket!'. The initial sense of knowing that you've seen the man previously is context-free – that is, you cannot recall the environment in which this previous encounter has occurred. This acontextual recognition is an example of familiarity-driven recognition. The realization that the man works at the supermarket is supposed to illustrate recollection. Most likely, when you come to this realization, you are able to envision a time that you had been at the supermarket and can in a sense 're-live' an experience you may have had with this particular man.

Although the 'butcher-on-the-bus' phenomenon is one that is familiar to many of us, if the past has taught us anything, introspection can often lead scientists astray. This begs the question, what does the evidence reveal? Surely if memories can be accurately described by one type of retrieval process instead of two then, according to Occam's Razor, this should be the preferred explanation. However, decades worth of

results from cognitive, neuropsychological, and neuroimaging studies of human memory strongly indicate that recognition memory performance reflects two distinct memory processes, i.e. familiarity and recollection.

Behavioral Results

Behavioral studies investigating encoding manipulations provide evidence of the distinction between recollection and familiarity. For example, studies that have manipulated processing speed have shown that subjects are able to make accurate discriminations that can be based on familiarity relatively quickly, such as distinguishing between items that were recently studied and items that were not studied (item recognition). In fact, in studies in which the speeded conditions required subjects to respond within approximately 1 second after the stimulus was presented, familiarity was not greatly affected by responses deadline. On the contrary, discriminations that require subjects to use recollection to retrieve specific contextual information about the study event, such as what list or modality an item was presented in, tend to take significantly longer and are significantly disrupted when short response deadlines are imposed (Hintzman & Caulton, 1997; Gronlund, Edwards, & Ohrt, 1997; Hintzman, Caulton, & Levin, 1998).

A number of related studies have shown that as the time allowed to make a response is increased, the probability of incorrectly accepting a new item (i.e. making a false alarm) that is either similar to a studied item, or is from an inappropriate study list, first increases then decreases, producing biphasic accuracy/response-time functions (Dosher, 1984; Gronlund & Ratcliff, 1989; Hintzman & Curran, 1994;

Jacoby, 1999; McElree, Dolan, & Jacoby, 1999; Rotello & Heit, 2000). These results indicate that a fast familiarity process leads to false alarms to critical lures and only with additional retrieval time are subjects able to recollect the information that allows them to reject those items. Collectively, it appears that a familiarity assessment can be completed relatively quickly, while recollection requires additional retrieval time. One exception to the finding that familiarity is faster than recollection comes from studies employing the remember/know paradigm, where know responses (which represent familiarity) are generally found to be slower than remember response (which represent recollection) (Dewhurst & Conway, 1994; Trott, Friedman, Ritter, & Fabiani, 1999). However, these effects likely reflect the fact that the instructions in remember/know tests require subjects to respond 'know' only if the item is 'familiar and not recollected.' As a result, subjects are essentially instructed to wait until both processes are complete before making a 'know' response. Therefore the fact that familiarity-driven responses are slow in this paradigm is not inconsistent with the idea that familiarity is generally a fast process.

Another encoding manipulation that differently affects familiarity and recollection has been highlighted by studies that manipulate the level of processing. Deeper encoding, which usually involves processing the meaning of a stimulus (e.g. is the word abstract or concrete?) compared to shallow encoding, which usually involves processing the perceptual aspects of a stimulus (e.g. is the word in upper or lower case?) leads to an increase in recollection and a smaller but consistent increase in familiarity (Gardiner, 1988; Gardiner, Java & Richardson-Klavehn, 1996; Gardiner,

Ramponi, & Richardson-Klavehn, 1999; Gregg & Gardiner, 1994; Java, Gregg, & Gardiner, 1997; Khoe, Kroll, Yonelinas, Dobbins, & Knight, 2000; Komatsu, Graf, &Uttl, 1994; Perfect, Williams, & Anderton-Brown, 1995; Rajaram, 1993; Toth, 1996; Wagner, Gabrieli, & Verfaellie, 1997; Wagner, Stebbins, Masciari, Fleischman, & Gabrieli, 1998; Yonelinas, 2001; Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998). The same general result has been found depending on whether or not subjects are required to engage in deeper encoding by generating a word at the time of study (e.g. solving the anagram "ocuch" for the word "couch"), compared to simply reading the word. Combined, these results suggest that both recollection and familiarity are sensitive to changes in levels of processing at study, but that recollection may be more sensitive to this influence than familiarity.

Another study manipulation that differently affects recollection and familiarity rates is the amount of attention devoted to the stimulus at the time of encoding. When subjects are required to complete a concurrent task during encoding (i.e. divide their attention), this tends to have larger negative effect on rates of subsequent recollection compared to subsequent familiarity, suggesting that encoding that leads to recollection is more attention-demanding than encoding that leads to familiarity (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996). Some research has even suggested that familiarity may not be reduced at all by dividing attention under certain conditions (Jacoby & Kelley, 1992).

Not only does dividing attention during encoding affect subsequent recollection rates, but there also seems to be a similar effect when subjects are forced to divide

their attention at the time of retrieval. Like that during encoding, this additional processing at the time of retrieval seems to disrupt recollection but does not appear to affect familiarity (Gruppuso, Lindsay, & Kelley, 1997; Dodson & Johnson, 1996). For example, in one experiment subjects were required to complete a memory test while simultaneously performing an auditory number-detection task. This additional task effectively lowered recollection estimates while having no effect on estimates of familiarity (Gruppuso, Lindsay, & Kelley, 1997). These results suggest that recollection is more cognitively demanding and thus is more sensitive than familiarity to the effects of dividing attention during the test phase.

Manipulations designed to increase the processing fluency of test items has been found to lead to an increase in familiarity-based responses (both for studied and non-studied items), while leaving recollection-based responses relatively unaffected. A myriad of manipulations have been used to increase processing fluency of test items including briefly flashing a word just prior to presenting it in a recognition test (Jacoby & Whitehouse, 1989), visually presenting a word more clearly than other words at test (Whittlesea, Jacoby, & Girad, 1990), and presenting a word in a conceptually related compared to an unrelated context. These manipulations have been shown to increase processing fluency and specifically to increase familiarity rates while not effectively changing the rates of recollection. On a related note, changing the perceptual characteristics of a word between study and test (e.g. changing the presentation modality between visual and auditory modalities) leads to a decrease in familiarity, but not in recollection (Gregg & Gardiner, 1994).

Additionally, manipulations of response criterion (e.g. the amount of memory evidence required to make an 'old' response) during a recognition test seem to largely affect the probability that items will be accepted based on familiarity but tend to have little to no effect on recollection responses. Specifically, relaxing the response criterion (i.e. requiring less evidence to make an 'old' response) generally leads to increases in the hit and false alarms rates of familiarity responses, whereas hit and false alarm rates of recollection remain relatively unchanged. This pattern of results is seen when response criterion varies as a function of response confidence (Yonelinas,Dobbins, Szymanski, Dhaliwal, & King , 1996; Yonelinas, 2001), changes in the reported proportion of target items in the test list (Strack & Forster, 1995), and changes in the proportion of test items that subjects are required to accept as old (Strack & Forster, 1995). Although most studies have shown no effect of criterion on rates of recollection, there have been some challenges to this finding. Specifically, some studies have reported small, but statistically significant changes in recollection rates (mostly driven by an increase in hit rates) when a laxed criterion is used to make memory decisions (Postma, 1999; Hirshman & Henzler, 1998).

Another illustration of the distinction between familiarity and recollection is accomplished by recording receiver operating characteristics (ROCs) data. Typically this information is collected by requiring subjects to rate the confidence of their yes/no recognition decisions at the time of the recognition test. Then one plots the hit rates against false alarm rates as a function of response confidence. By examining the effect of varying response confidence on hit and false alarm rates, it is possible to

estimate the contribution of recollection and familiarity on recognition performance (Yonelinas, 1994). The goal is to derive an equation that describes how hits and false alarms should be related if indeed performance reflects a combination of recollection and familiarity. The equation is then fit to the observed empirical ROC in a manner similar to that used during linear regression. However, in this case, the function is not linear and the two parameters that are estimated reflect familiarity and recollection rather than the slope and intercept respectively. When this is done, the observed empirical functions are curvilinear and their shapes change across conditions, such that they require no less than two functionally independent memory parameters to describe them (Kelley & Wixted, 2001; Yonelinas, 1994, 1999; Yonelinas, et al., 1996). This indicates that at least two separate memory components are needed to account for recognition performance. There is a general consensus in the field that familiarity is easily represented by signal detection measures, with familiarity strength varying along a continuum. On the other hand, many in the field would argue that this is *not* the case with recollection, and that instead recollection is better represented as a threshold process where it either occurs in full or not at all (Yonelinas, 1999). Although this threshold version of recollection is the more popular model, there have been some strong criticisms against this interpretation. Specifically, it has been argued that recollection, like familiarity, can also be described as varying along a memory strength continuum (albeit at the higher end of the continuum) and that in fact it can be experienced in a graded fashion. Proponents of this idea argue that recollection simply reflects a stricter decision criterion used by

the subject and that the apparent dual process results that come from ROC data can instead be explained by differences in unequal variances between old and new item distributions (Wixted & Stretch, 2004**;** Donaldson, 1996; Dunn, 2004).

Results from Special Populations

In addition to experiments focused on normal, young, healthy subjects, numerous studies have been conducted focusing on special populations. For example, several studies have investigated the effects of aging on familiarity-and-recollection-based retrieval. Since older adults tend to be less impaired in tests of item recognition than for the recovery of source or contextual information (see Spencer & Raz, 1995 for a review), it is generally believed that age-related memory loss is primarily observed for recollection (Cabeza, Anderson, Locantore, & McIntosh, 2002; Davidson & Glisky, 2002; Duarte, Ranganath, Winward, Hayward, & Knight, 2004) while familiarity is generally spared (Daselaar et al., 2006; Howard, Bessette-Symons, Zhang, & Hoyer 2006**;** Jacoby, 1999**;** Jennings & Jacoby, 1993; Rybash & Hoyer, 1996; Spencer & Raz, 1995**;** Titov & Knight, 1997; Yonelinas, 2001). It has been suggested that a decline in the attentional resources allocated during encoding and retrieval, perhaps due to frontal lobe changes associated with normal aging, maybe responsible for the decrease in recollection in this group (Anderson, Craik, & Naveh-Benjamin, 1998; Buckner, 2004; Park, Smith, Dudley, & Lafronza 1989; Salthouse, 1994; Whiting & Smith, 1997). Nonetheless, results from some studies suggest that, for some adults, both recollection and familiarity may be impaired (Davidson &

Glisky, 2002). However most studies that have examined aging effects on memory have not considered intersubject variability, leaving open the possibility that different subgroups of elderly individuals might exhibit different patterns of memory changes. One study by Duarte and colleagues (Duarte, Ranganath, Truhillo, & Knight, 2006) separated elderly subjects into groups based on their overall memory performance. Those who were 'high functioning' older adults showed normal rates of familiarity but decreased recollection rates, while 'low functioning' older adults showed reduced rates of both types of retrieval. These results suggest that the underlying processes related to recollection and familiarity are dependent upon individual memory performance and may be related to the degree of underlying neural dysfunction suffered by the individual.

Like healthy aging subjects, brain-damaged patients tend to show higher rates of impairment with recollection than with familiarity. Specifically, damage that includes the hippocampus and surrounding temporal lobe areas have been found to disrupt both recollection and familiarity, but generally has a larger disruptive effect on recollection. In contrast, relatively selective hippocampal damage appears to disrupt recollection, but not familiarity (Vann, Tsivillis, Denby, Quamme, Yonelinas, Aggleton, Montaldi, & Mayes, 2009). While impaired recollection seems to be the case in the majority of amnesia studies, the apparent non-effects on familiarity have been challenged. Specifically, one study using the remember/know procedure showed that familiarity as well as recollection was severely disrupted (Knowlton & Squire, 1995), and another has provided evidence that familiarity was actually

enhanced in amnesia patients (Schacter, Verfaellie, & Pradere, 1996). However this discrepancy may be due to the somewhat messy nature of neuropsychology and the specific impairments that patients present may depend on how much of the medial temporal lobe outside of the hippocampus proper is damaged. Beyond amnesia patients, a similar specific impairment on recollection has been reported for patients exhibiting the negative symptoms of schizophrenia (Thoma, Zoppelt, Wiebel, Daum, 2006) as well as those suffering from Alzheimer's disease (Tendolkar, Schoenfeld, Golz, Fernandez, Kuhl, Ferszt, Heinze, 1999).

Neuroimaging Results

In addition to the numerous behavioral studies, neuroimaging studies also provide evidence for the distinction between recollection and familiarity. Beginning in the early 1980s, numerous studies have reported that ERPs elicited in recognition memory tasks demonstrate old/new effects. These effects take the form of more positive-going waveforms for recognized old items (hits) than for correctly rejected new items (correct rejections) (Johnson, 1995; Curran & Cleary, 2003; Vilberg, Moosavi, & Rugg, 2006). These general 'old/new' effects seem to be dissociable into a familiarity and recollection signal. A 300-500 ms familiarity-related effect, which has been called the FN400 old/new effect is frontally distributed. A later 400-800 ms recollection-related ERP effect has been localized within the parietal lobe and has been aptly named the parietal old/new effect. The evidence for relating the parietal old/new effect to recollection is particularly strong. First, the parietal old/new effect

is associated with the recollection of specific information such as study modality and temporal source (Wilding & Rugg, 1996). That is, the parietal old/new effect is primarily observed when such details are correctly recollected, but not when recognition occurs without such recollections. Second, the parietal old/new effect is sensitive to the variables previously mentioned (e.g. depth of processing) that are thought to affect recollection more than familiarity. Finally, when the remember/know paradigm is used to segregate items retrieved with recollection from those retrieved via familiarity, it is the recollected trials that are found to be associated with the parietal old/new effect (Smith, 1993).

More recent studies have begun to establish a correspondence between the FN400 old/new effect and familiarity. Several studies have tested recognition memory with semantically similar lures. Assuming that the familiarity of studied and similar items is comparable, yet greater than for new items, the finding that the FN400 differentiated new from studied/similar words (new>similar=studied) was consistent with the hypothesis that it reflects familiarity.

Although studies using ERPs are crucial in determining temporal differences in the neural signals underlying recollection and familiarity, the spatial resolution offered by this technique is less than optimal. Luckily, studies using functional magnetic resonance imaging (fMRI) have also investigated this issue. Results from these studies show that across studies that vary widely in their designs, analysis methods, stimulus materials and test procedures, there is a consistent tendency for familiarity- and recollection-related effects to be localized to different neural regions. This effect

seems to be the most noticeable within the lateral parietal cortex. Whereas familiarity-related effects are concentrated around the intraparietal sulcus (IPS) with a center of mass located in BA 7, recollection-related effects are more likely to be localized to the posterior part of the inferior parietal cortex, with a center of mass located within BA 39. This dorsal/ventral distinction within the lateral parietal cortex will be discussed in more detail later.

The examples just described indicate that recognition tests that can be based on familiarity are functionally distinct and rely on partially separate neural substrates than those that require subjects to recollect information about the study event. Such dissociations are expected if recognition performance relies on two distinct memory processes. In contrast, if all recognition memory judgments were based on the assessment of a single form of memory, then these types of dissociations should not have been observed.

Operationalizing Recollection and Familiarity:

Both recollection and familiarity can be used to guide memory decisions during a standard recognition memory test (Mandler, 1980). Therefore, in order to isolate the neural regions uniquely associated with recollection and familiarity, one must be able to differentiate which items were retrieved via recollection and which relied on familiarity.

By far, the two most common strategies for operationalizing recollection and familiarity during neuroimaging studies are the remember/know test and tests probing

source memory. During a remember/know test, the subject is asked to identify what retrieval state (recollection or familiarity) was experienced on a trial-to-trial basis (Tulving, 1985). When subjects believe they are using familiarity to make their recognition decision, they are asked to make a 'know' response, indicating that they know that they have seen the test item before. However, when recollection occurs (i.e. when contextual information about the study episode is retrieved) subjects are asked to make a 'remember' response, indicating that recollection occurred. Source tests take a much more objective approach, operationalizing the retrieval state according to whether or not recognition was accompanied by the recovery of a specific piece of contextual information (Johnson, Hashtroudi, & Lindsay, 1993). For instance, if words are the stimuli being used, the font color of the word may vary during the encoding phase. At test, subjects may be required to recollect what font color the word was presented in. Only if this specific piece of contextual information (i.e. font color) is correctly retrieved is recollection considered to have occurred.

Both methods have been heavily criticized in the literature. First off, the remember/know test has shown to be very sensitive to variations in instructions (Geraci, McCabe, & Guillory, 2009). Prior to testing, the experimenter must explain to the subject when it is appropriate to make a know response vs. a remember response. The nuance between the two modes of retrieval can be difficult even for some memory researchers to grasp, let alone your every-day subjects that participate in a psychology experiment. Unfortunately, changes in this instruction process only exacerbates this problem and leads to unconstrained differences between experiments.

Therefore, the remember/know test has been criticized for its subjective nature and exclusive reliance on the subject's ability to correctly classify their retrieval state (Rotello, Macmillan, Reeder, & Wong, 2005; Donaldson, 1996; Dunn 2004; Dunn, 2008; Wixted, 2007; Wais, Mickes, & Wixted, 2008). On the other hand, the source test is criticized for being too restrictive on what qualifies as a recollected response (i.e. the 'non-criterial problem') (Yonelinas & Jacoby, 1996). Specifically, some have argued that recollection may in fact be occurring even if the specific contextual information chosen by the experimenter is not retrieved. For example, a subject may be accurately retrieving visual imagery or associations created during the encoding phase even if the font color of the word is not also retrieved. During a source memory test, this would not be considered recollection because the only contextual information that counts as recollection (in this example) is font color.

Despite these differences in procedural methodology, there seems to be a general assumption that these methods are essentially functionally equivalent, and as a result are often used interchangeably to separate familiarity and recollection. Some researchers have gone so far as to claim that results from the remember/know and source tests are "neurally and functionally equivalent" (Rugg, Schloerscheidt, & Mark., 1998, p.47), and are "indistinguishable" (Mark & Rugg, 1998, p.861) from and "near identical to" (Yonelinas & Jacoby, 1995, p.637) each other. This ostensible equivalence has been described both at the behavioral level (Yonelinas & Jacoby, 1995) and at the neural level using evidence from event-related potentials (ERP) (Rugg, et al., 1998; Mark & Rugg, 1998). In regards to the parietal lobe, both

methods have found recollection to be associated with the so-called 'parietal old/new effect' ERP component (Vilberg & Rugg, 2006; Curran, 2004; Wilding, 2000). Results from functional magnetic resonance imaging (fMRI) studies have also shown a general convergence between these two approaches as to what brain regions within the left posterior parietal cortex (PPC) are sensitive to recollection and familiarity. Specifically, both methods have shown a dorsal/ventral dissociation within this area, with familiarity activating more dorsal regions centered around the intraparietal sulcus (IPS) and extending dorsally into the superior parietal lobule (SPL), and recollection activating more ventral regions within the inferior parietal lobule (IPL) (for reviews see: Ciaramelli, Grady, & Moscovitch, 2008; Hutchinson, Uncapher, & Wagner, 2009; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). This apparent convergence is informative because it suggests that the neural representations of familiarity and recollection are the same regardless of the methodology used to index them.

Parietal Activity During Memory Retrieval:

It has long been known that episodic memory – the act of consciously encoding and retrieving information – depends on brain regions within the medial temporal lobe (MTL) and prefrontal cortex. The MTL memory system comprises multiple structures, including the hippocampal formation and surrounding parahippocampal, perirhinal, and entorhinal cortices. Decades worth of neuropsychological and neuroimaging studies of human MTL have indicated this region during the encoding,

consolidation, and retrieval of memories (Squire & Zola, 1991; Scoville & Milner, 1957; Ranganath & Knight, 2003; Preston & Wagner, 2007; Squire & Zola, 1998). Prefrontal regions have been indicated during the encoding of information, as well as pre-and-post monitoring during retrieval of memories (Wagner, 2002; Ranganath, Johnson, D'Esposito 2003; Dobbins & Wagner, 2005; Kohler et al., 2004).

The advent of functional neuroimaging, first with PET and then with fMRI has led to a heightened appreciation of the extent of cortical involvement in long-term memory encoding and retrieval. Among the regions identified most consistently in early studies of memory retrieval were medial and lateral posterior parietal cortex (Fletcher, Frith, & Rugg, 1997; Konishi, Wheeler, Donaldson, & Buckner 2000; Rugg, 1995). The blocked designs employed in early PET and fMRI studies present serious difficulties in the interpretation of retrieval-related neural activity. These arise from the inability to characterize item-related activity according to the study history of the item or the response made by the subject. With the development of event-related fMRI it became possible to directly contrast the activity elicited by different classes of recognition memory test item, and it soon became evident that both lateral and medial parietal cortex demonstrate 'retrieval success' effects (also referred to as 'old/new' effects). The effects take the form of greater activity for recognized studied items than for correctly rejected new items (e.g. Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Konishi, et al., 2000). These 'old/new' effects have consistently been found to be lateralized to the left hemisphere, despite changes in stimuli (Guerin & Miller, 2009; for a review see Vilberg & Rugg, 2008; but see

Klostermann, Loui, & Shimamura, 2009). Beyond simply identifying neural regions that demonstrate old/new effects, neuroimaging studies have suggested a range of distinct memory-related influences on parietal activation. These include differences in activity based on recollection vs. familiarity, weak vs. strong memories, memories made with high vs. low confidence, the perception that the item is old, the frequency with which the target appears, and the expectancy of the subject (for a review see Ciaramelli, 2008). Each of these influences will be discussed in the following subsection.

Recollection vs. Familiarity

Vilberg and Rugg (2008) conducted a review of published event-related fMRI studies where contrasts were employed that allowed retrieval-related activity associated with recollection-and-familiarity-driven recognition judgments to be separately identified. This was mostly done through the use of the 'remember-know' paradigm (Henson et al., 1999, Vilberg & Rugg, 2007, Wheeler & Buckner, 2004), source memory tests (Cansino et al., 2002, Kahn et al., 2004), or parametric tests involving confidence responses (Yonelinas, et al. 2005; Daeselaar et al., 2006). Two studies (Henson, Hornberger, & Rugg 2005; Iidaka, Matsumoto, Nogawa, Tamamoto, & Sadato, 2006) were included where probability of recollection was modulated by a 'depth of processing' manipulation during study (under the assumption that the benefit to recognition accruing from deep as opposed to shallow study is predominantly due to increased probability of recollection).

Although the data collected varied widely in their designs, analysis methods, stimulus materials and test procedures, they found a consistent tendency for familiarity- and recollection-related effects to be localized to different regions of the left lateral posterior parietal cortex. Whereas familiarity-related effects were concentrated in more dorsal/superior parietal regions (centered around the IPS), recollection-related effects were more localized to the ventral/inferior parietal regions (centered around the angular gyrus).

Memory Strength/Confidence

Dorsal and ventral parietal regions have also been shown to dissociate based on the strength/confidence of the memory being retrieved (for a review, see Ciaramelli, 2008). Stronger, more confident memories tend to activate ventral regions of parietal cortex, whereas weaker, less confident memories have been shown to activate more dorsal regions. For example, a recent fMRI study (Kim & Cabeza, 2007) compared brain activity for high-confidence vs. low-confidence "old" responses to studied words (hits). The results yielded a clear dissociation between DPC and VPC regions: whereas DPC showed greater activity for low-than high-confidence hits, VPC showed greater activity for high- than low-confidence hits.

A study by Moritz and colleagues (2006) found similar results. Items that received high vs. low confidence judgments, irrespective of accuracy, were characterized by higher activity in left inferior parietal lobule. Unexpectedly, items that were recognized with low confidence showed increased activity in the right

superior parietal lobule. Similar results were obtained by Fleck et al. (2006) who demonstrated that a region in the right superior parietal lobule signaled low confidence with memory decisions.

There have also been a number of studies where the investigator has manipulated the study conditions in order to indirectly test for memory strength/confidence at the time of retrieval. For instance, Henson et al. (2005) manipulated depth of processing during the study session. Words were pre-cued for either a semantic decision ('deep processing') or orthographic decision ('shallow processing'). At test, subjects were asked to distinguish the studied words form other words that were not studied. Given the evidence that deeper semantic encoding increases the likelihood that the memory will be subsequently remembered, hits given to words that received deeper encoding were thought to reflect stronger memories than those that received the shallow task at the time of encoding. Results of this manipulation showed that the stronger memories (those associated with the deep encoding task) activated left inferior parietal regions, whereas weaker memories (those afforded the shallow encoding task) activated more superior parietal regions centered around the intraparietal sulcus.

Perception of Oldness

Although a lot of focus has been on activity that occurs during correct responses (i.e. hits and correct rejections), examining memory errors can provide important insight as to how this region is contributing to memory retrieval. Two fMRI studies (at least that I am aware of) have addressed this important issue, measuring parietal

activation not only during accurate responses but also during memory errors (Wheeler & Buckner, 2003; Kahn et al., 2004). Results showed that regions within the parietal lobe, in or around the inferior parietal cortex, were activated not only by hits but also by false alarms. That is, this region was activated by the perception that the item was old, not by its actual mnemonic status.

Retrieval Mode

A study by Dobbins et al. (2003) manipulated the retrieval mode a subject experienced on a trial-by-trial basis. Subjects were either asked to report on the recency of the word or to attempt to retrieve its source at encoding. Results showed that areas within the left lateral parietal cortex (particularly within the superior parietal subregions) were greater during attempts at source retrieval than recency retrieval, even when these attempts were unsuccessful (i.e. when an incorrect source attribution was made). These results suggest that regions within the parietal cortex may have more to do with an attempt at retrieval rather than the actual output (i.e. memory representation) of the retrieval attempt.

Target Frequency

The activity in the superior parietal cortex has been shown to be modulated by the frequency of targets during recognition memory tests (Vilberg & Rugg, 2009; Herron et al., 2004; Aminoff et al., 2014). These experiments involved varying the relative probability of old and new test items and examining the effect on the neural correlates of recognition memory. When old items were relatively infrequent (25:75 ratio)

robust old/new effects were evident in left superior parietal regions. These effects were absent however, and in some cases even showed a non-significant tendency to reverse direction, when the old/new ratio was reversed (Herron et al., 2004). The study by Aminoff and colleagues (2014) showed that activity within the superior parietal cortex was positively correlated with the subjects' criterion value, indicating a relationship between response monitoring and parietal activity. Furthermore, when subjects were divided into groups based on how much they shifted criterion between the low and high probability conditions, it was clear that the 'old/new effect' seen at the group level in the superior parietal regions was driven by the group that shifted criterion between conditions. A study by Vilberg & Rugg (2009) investigated the effect probability manipulations would have specifically on familiarity-and-recollection-driven responses using a source memory task to dissociate recollection from familiarity. General retrieval success effects (regardless of source information) were found in superior parietal areas. Specifically, a region in the anterior portion of the IPS and another region in the posterior superior parietal cortex were found to be modulated by changes in probability – with greater old/new effects exhibited in the low old (25%) probability condition. Somewhat surprisingly and in contrast to previous results, the old/new effect within the middle portion of the IPS was not found to be modulated by the manipulation of probability. Finally a region in ventral parietal cortex (specifically the angular gyrus) was found to be sensitive to recollection as operationalized by the source task and, like the middle IPS, was also not modulated by the probability condition. Regardless of whether the targets were

infrequent or frequent, this ventral region showed maximal activity to hits compared to correct rejections. The authors argued that these probability-insensitive regions were likely candidates for supporting processes directly related to memory retrieval and that the angular gyrus in particular may be recruited for recollection-related retrieval.

Expectancy Violations

Only a few studies have investigated how subjects' expectancies can modulate activity in the parietal cortex. O'Connor et al. (2010) used a novel memory analog of attentional cueing in order to manipulate the correspondence between anticipated and actual recognition evidence by presenting valid or invalid anticipatory cues (e.g.,"likely old") before recognition judgments. Although a superior parietal region demonstrated the retrieval success pattern, a larger inferior parietal lobule region tracked the validity of the memory cueing (invalid cueing > valid cueing) and no retrieval success-sensitive lateral parietal region was insensitive to cueing. Jaeger and colleagues (2013) used a similar cueing paradigm and found that the lateral parietal cortex could actually be segregated into three distinct areas depending on the effects the cueing manipulation had on differential activations. An anterior angular region was found to exhibit an unexpected familiarity signal, showing greater activity for hits compared to correct rejections, but only when cued with the 'likely new' cue. In contrast, a posterior angular region was found to be more activated for correct rejections compared to hits, but this was only evident when cued with the 'likely old'

cue. A region in the middle of these two areas, located around middle IPS was found to be maximally activated by whatever stimulus was unexpected (i.e. a hit cued by the 'likely new' condition or a correct rejection cued by the 'likely old' condition). The authors interpreted this finding as this region displaying a memory orienting pattern – with differential activity depending on subjects' expectations of the item history of the upcoming stimulus. Importantly, the authors argued that this region is most likely not reflecting memory content per se, but instead re-directing attention towards an unexpected familiarity (anterior angular gyrus) or an unexpected novelty (posterior angular gyurs) signal. Using a different memory paradigm, Ciaramelli and colleagues (2010) also found increased activity in posterior parietal cortex (particularly in ventral regions) when memory items were successfully retrieved after being invalidly cued. Instead of cueing subjects with 'likely old' or 'likely new', the authors used intact or recombined word pairs to modulate subjects' expectations as to the item history of the upcoming stimulus. Retrieval success effects were found to be maximal when subjects expected a new item to appear, but instead correctly recognized an old item (i.e. when their expectations contrasted with reality). Additionally, patients with lesions in the ventral parietal cortex that participated in this study were found to have problems recognizing unexpected (invalidly cued) targets. The authors argued that their results showed evidence of the ventral parietal cortex playing a role in detecting relevant yet unexpected memory content. They likened this process to the everyday experience of having a memory spontaneously pop into mind, and while doing so, interrupting pre-existing mental process (e.g. whatever the person was currently

thinking about). For instance, using the classic butcher-on-the-bus story, this would be akin to unexpectedly coming across someone who is familiar on a bus. Your bottom-up attention system acts to disrupt your current train of thought and instead focuses your attention towards this familiar man.

Results from Neuropsychology

The striking consistency of parietal activation during memory retrieval has perplexed a lot of memory researchers. This is mostly because lesions in this area do not typically yield severe episodic memory deficits, such as the ones associated with medial temporal lobe damage. Results from initial studies seemed to support this paradoxical relationship between neuroimaging data and neuropsychological data, with parietal lobe patients performing as well as controls on tests of source memory (Ally et al., 2008; Simons et al., 2008, 2010). Simons and colleagues (2008) tested participants with unilateral parietal damage in areas that overlap with fMRI brain activations observed during source memory tasks. At encoding, subjects were shown words or pictures and for each item had to decide whether the item was either pleasant/unpleasant or from entertainment/politics. At test, subjects had to recall which judgment had been made for each stimulus. The patients performed as well as controls on the source memory test. Later, Simons et al. (2010) extended these findings to bilateral parietal patients. In this study, subjects heard sentences presented in a male or female voice. At test, they indicated whether the sentence was old or new, rated their confidence on the old/new decision, judged whether the original voice had been male or female and finally rated their confidence on their source

decision. Although the bilateral parietal patients had normal source memory compared to controls, their confidence ratings for these decisions was significantly lower. A follow-up experiment using visual stimuli found the same pattern of results, with normal source memory accuracy, but attenuated confidence associated with those decisions. A study by Davidson et al. (2008) had parietal lobe patients encode words with definitions in a visual or auditory format and later asked them to retrieve the sensory domain at encoding and to make remember or know responses. While the patients performed accurately when performing the source memory judgment, they made significantly fewer remember responses. In three experiments performed by Berryhill and colleagues (2007), patients with bilateral parietal lobe lesions performed as well as matched healthy controls in recollecting the context in which previous events were experienced. Their source recollection ability held firm despite variations in task requirements across experiments. These results provide evidence that recollection confidence declines after posterior parietal lobe damage, despite leaving the actual memory content unaffected. Further evidence of reduced confidence in posterior parietal patients' memories comes from a variety of paradigms (Hunkin et al., 1995; Ally et al., 2008; Davidson et al., 2008; Berryhill et al., 2009; Drowos et al., 2010; Simons et al., 2010; for a review see Berryhill, 2012). The dissociation between intact source recollection and reduced recollection confidence indicates that the bilateral patients retained the ability to recollect contextual information accurately, but that their experience of recollection may have been deficient in the rich episodic detail typical of healthy participants, resulting in

lower ratings of confidence (Lyle and Johnson 2006, 2007). Reduced subjective recollection is consistent with anecdotal observations by Davidson et al. (2008), also noted in other studies (Ally et al. 2008; Simons et al. 2008), of parietal patients reporting diminished confidence in their memory abilities when faced with an episodic recollection task, and remarking that their recollection of events lacks richness or vividness. A role for the parietal lobe in supporting subjective aspects of recollection is also consistent with data from functional neuroimaging studies. Although parietal activity has been observed in studies that have used subjective recollection tasks, such as remember/know judgments (e.g., Henson et al. 1999), and more objective measures of recollection, such as source memory (e.g., Simons et al. 2008), studies that have examined both subjective and objective memory within participants have indicated that parietal cortex may be particularly important for subjective memory. For example, Chua, Schacter, Rand-Giovannetti, & Sperling (2006) demonstrated that parietal activity was greater when participants made subjective memory confidence assessments than when they made objective recognition memory decisions. Moreover, Duarte et al. (2008) linked parietal cortex activity to subjective ‘‘remember’’ responses but not objective source judgments in young and high functioning older adults, and showed that this parietal activity was significantly reduced in low-functioning older adults who were impaired at the subjective remember/know task. Similarly, Drowos and colleagues (2010) recently found that patients with bilateral parietal damage express an unusually low number of remember responses, but a normal number of know responses, on a false memory

task. Interesting, patient S.M. reported by Davidson and colleagues (2008) reported that she could recall events of her life but that her memories did not seem to be accompanied by a sense of having experienced the event herself. Thus, patients with parietal lesions appear to have deficits in the assessment and monitoring processes that contribute to subjective aspects of recollection, resulting in low confidence, diminished detail in spontaneous autobiographical narratives and in reported mnemonic vividness and richness (Berryhill et al. 2007; Davidson et al. 2008; Simons et al. 2008), as well as reduced ‘‘remember’’ responses (Davidson et al. 2008; Drowos et al. 2009). The subjective memory processes described above may contribute towards objective measures of recollection such as source memory, as evidenced by parietal activity during source memory in healthy volunteers (e.g., Simons et al. 2008), but they appear in many instances not to be necessary for accurate objective recollection to occur, as demonstrated by the intact source recollection observed in the present study and in previous reports (Davidson et al. 2008; Simons et al. 2008).

Theories of Parietal Activity During Memory Retrieval:

There is no shortage of theories meant to explain parietal activity observed during memory retrieval. I will discuss the four most popular explanations in the following section: 1. the dual attentional processes hypothesis, 2. the episodic output buffer hypothesis, 3. the mnemonic accumulator hypothesis, and 4. the subjective experience hypothesis. In order to determine exactly how these parietal regions may be contributing to memory processes, many researchers first turned to the more

classical cognitive functions that are usually associated with parietal cortex activity. The one that has gained the most support is the role that this region plays in attention. However, before the role of attention in memory can be addressed, its well-known role in perception must first be explained.

According to Corbetta and Shulman (2002), the human attentional system is comprised of two partially segregated networks of brain areas that carry out different attentional functions. One system, which includes dorsal regions of the parietal cortex and superior regions within the frontal cortex, is involved in preparing and applying goal-directed (top-down) selection for stimuli and responses. People are better at detecting an object in a visual scene when they know in advance something about its features, such as its location, motion, or color. This facilitation depends on the ability to represent this advanced information, and to use it to bias the processing of incoming visual information. Corbetta and Shulman (2002) reviewed evidence of this top-down allocation of attention and found it to be associated with activity within the dorsal parietal cortex – particularly in the superior parietal lobule (SPL) and around the intraparietal sulcus (IPS). In a simple detection study, Corbetta et al. (2000) presented a cue in the form of an arrow indicating the most likely location of a subsequent visual target. They found these regions to be maximally active during the cue period, i.e. when attention was oriented toward a relevant location. Furthermore, when the delay after the cue offset was extended, forcing subjects to maintain attention at the cued location for longer, these regions were the only ones that showed a sustained response. Activation in these dorsal parietal regions is not apparently

restricted to shifts in visuo-spatial attention alone. This region has been activated by shifts between two different features of an object (Liu, Slotnick, Serences, & Yantis, 2003) and shifts between two different sensory modalities (Shomstein & Yantis, 2003). Additionally, recent fMRI studies have shown these regions to be activated by voluntary orienting to nonperceptual properties of the stimuli, such as their semantic category (Cristescu, Devlin, & Nobre, 2006).

The other attentional system, which includes more ventral regions of parietal cortex and inferior regions within the frontal cortex, is specialized for the detection of behaviorally relevant stimuli, particularly when they are salient or unexpected. This ventral frontoparietal networks works as a 'circuit breaker' for the dorsal system, directing attention to the salient events. A number of fMRI studies have documented that regions in the ventral parietal cortex including the temporo-parietal junction (TPJ), supramarginal gyrus, and angular gyrus are activated by the bottom-up attentional capture by stimuli that are potentially important for the individual. In the experiment by Corbetta et al. (2000) mentioned above, activity in the ventral parietal cortex (centered around the right TPJ) was specifically engaged during the detection of the target, whereas it showed little if any response to the orienting cue. When the targets occurred at an unexpected location, the activity in this region was further enhanced. The authors concluded that activation of this region may mediate automatic attention toward relevant, yet unattended, stimuli. Additionally, this region is selectively activated when subjects are presented with infrequent targets, such as auditory or visual oddball stimuli.

Patients with lesions in the right ventral parietal cortex often show signs of unilateral neglect, a deficit in detecting contralesional stimuli across diverse sensory modalities. Consistent with the idea that these regions mediate bottom-up attention, these patients often have a deficit in detecting stimuli that are unattended and outside the focus of processing but they can voluntarily direct attention to the contralesional side (Corbetta & Shulman, 2002).

Corbetta and Shulman (2002) do not describe the difference between the attentional functions of the dorsal and ventral parietal cortices as a sharp dichotomy but as a more graded difference. First, they note that the dorsal parietal cortex (DPC) shows some sensitivity to the presentation of infrequent events, which suggest it is also affected by bottom-up attentional processes. Second, although ventral parietal cortex (VPC) activity is driven by incoming information, activity in this region is also modulated by task relevancy. For instance, this region will show greater activity to salient, infrequent stimuli in the modality being attended, but not in a different modality. Also, an fMRI study found that during search for a red target, right VPC was activated by red distractors, which apparently captured attention bottom-up, but not by distractors in other salient colors, which did not capture attention (Serences et al., 2005; for a review see Corbetta, Patel, & Shulman, 2008). Thus, in order to activate the VPC, it is not enough that a stimulus is salient; it must also be relevant to the goals of the current task (which are maintained by the DPC). Conversely, the detection of unexpected events in VPC can enhance or attenuate sustained goal-

driven processes in DPC. It is in this kind of fluid dynamic that ventral and dorsal parietal regions interact with and influence each other.

The Dual Attentional Process Hypothesis

As discussed above, research in the attentional domain has shown that dorsal parietal regions are implicated in the voluntary orienting of attention to relevant aspects of the environment, whereas ventral parietal regions mediate the automatic allocation of attention to task-relevant information (Corbeta & Shulman, 2002). According to the Dual Attentional Processes (DAP) hypothesis, the dorsal and ventral regions of the parietal lobe play conceptually similar roles in episodic memory retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, et al., 2008; Ciaramelli, et al., 2010). It is proposed that the dorsal parietal cortex is associated with the allocation of attentional resources to memory retrieval according to the strategic goals of the rememberer (top-down attention), particularly engaged when sought-after memories are difficult/effortful to retrieve. On the other hand, the ventral parietal cortex is believed to be associated with the capture of attentional resources by relevant memory cues and/or recovered memories (bottom-up attention). This region is maximally active when strong memories spontaneously 'pop' into a subject's memory and internal attention is redirected towards this surprised recovery of mnemonic information. Just as in the attention model provided by Corbetta & Shulman (2002), these dorsal and ventral regions of parietal cortex should not be thought of as a strict dichotomy, but rather as an interacting system. Some evidence

for this theory comes from the patient literature. Specifically, Berryhill and colleagues (2007) showed that patients with ventral parietal damage (ostensibly affecting their bottom-up attention system) were unable to freely recall autobiographical memories. These same patients however, were able to answer specific questions about their memories when probed. The authors argued that the patients' intact dorsal parietal cortex (ostensibly reflecting top-down attention) allowed them to access these memories even though an impaired bottom-up attention system failed to retrieve them automatically. They likened this impairment to visual neglect patients who have difficulty freely attending to certain areas in space although these same patients are able to do so when provided with the proper visual cues. Similar evidence comes from a study performed by Ciaramelli and colleagues (2010) who directly manipulated top-down and bottom-up attention in an fMRI experiment with controls and parietal lobe patients. Results showed that control subjects engaged the left dorsal parietal cortex when provided with memory cues and the ventral parietal regions were maximally engaged when items were invalidly cued. Although valid cueing offered control subjects a behavioral advantage, dorsal parietal cortex patients did not benefit from this additional information (which most likely involves top-down attention). On the other hand, ventral parietal patients had difficulty recognizing invalidly cued memory items, suggesting that these patients had deficits recognizing unexpected mnemonic information (i.e. when the bottom-up attention network is likely engaged).

Episodic Output Buffer Hypothesis

The episodic output buffer hypothesis suggests that this region actually represents or holds retrieved information in a form accessible to decision-making processes, analogous to Baddeley's proposed working memory buffer (Baddely, 1998). Although long-term memories are not stored in neuronal firing patterns, in order to influence decision-making, such memories must be expressed in active neuronal response patterns. The lateral parietal cortex could act as the buffer into which stored information is transferred. Specifically, the lateral parietal cortex could be an episodic memory output buffer that temporarily stores recovered long-term representations in a form rapidly accessible to decision making. Under this framework, raw memory representations are assumed inaccessible or too distributed for decision making systems to act upon and instead require an intermediate term store or buffer for conscious access during choice or reasoning (Baddeley, 2000). Thus the lateral parietal cortex would act as a temporary buffer similar to those proposed to operate in verbal or visual working memory in order to make retrieved episodic memory contents rapidly available for ongoing reasoning or executive operations. Some evidence that supports this theory comes from a study conducted by Vilberg and Rugg (2007) where they manipulated the amount of information recollected at the time of retrieval. Their results showed that the more information that was successfully recollected, the more active the parietal cortex (specifically the ventral portion) became.

Mnemonic Accumulator Hypothesis

According to this hypothesis, regions in posterior parietal cortex would play a role in accumulating, or temporally integrating, neural signals related to the target and store information about it until a criterion is reached that leads to the memory decision required by the task at hand. In other words, parietal activity reflects the accumulation of an "oldness" signal until a response is finally made. The portions of lateral parietal cortex connected to the MTL, for example, could integrate its retrieval activity over time, triggering a judgment of recognition when information levels reached a decision bound. Such a function is conceptually similar to other proposed forms of information accumulation in posterior parietal cortex neurons. The strongest support for this theory comes studies that have shown that parietal regions become active even when new items are falsely recognized as old (Wheeler & Buckner, 2003; Kahn et al., 2004). This is in line with an accumulator explanation because an oldness signal would lead to an 'old' response regardless of the accuracy of the decision. Additionally, some parietal regions have been shown to modulate activity in a linear fashion, with the least activity to correct rejections, slightly more for misses, greater activity for false alarms, and the most activity to hits (Wheeler & Buckner, 2003). This linear modulation is in line with an accumulator model of parietal activity.

Subjective Experience Hypothesis

This view puts forth the idea that the lateral parietal cortex signals the experience

of retrieving a remembered event. In essence, this distinguishes between something vividly retrieved versus something vaguely recalled. Proponents suggest that damage to this processing explains findings of reduced confidence in parietal patients' memories across various paradigms (Hunkin et al., 1995; Ally et al., 2008; Davidson et al., 2008; Berryhill et al., 2009; Drowos et al., 2010; Simons et al., 2010). This theory also involves processing personal ownership of retrieved memories. When recollected memories are re-experienced, they are done so through the eyes of an 'experiencer'. According to Endel Tulving (2002), this sense of self is critical to episodic memories. Without this self, there is no time traveler to go back in time to re-live the original event (i.e. autonoetic consciousness). When a specific personal event is retrieved from memory, it is not just factual information that is retrieved, but instead it is an entire experience that the person remembering is reliving. According to this theory, it is this part of the brain that creates this egocentric point of view, a sense of personal ownership, that is associated with recollected memories. This may explain why Davidson's patient S.M. who had bilateral parietal damage was able to accurately describe memories from her past but described them as not belonging to her (Davidson et al., 2008).

Multiple Explanations

It is important to note that none of these theories are mutually exclusive. Especially given the large expanse of cortical space the lateral parietal cortex encompasses and its exceptional extent of structural and functional heterogeneity, it is

quite possible that several or even all of these theories may be correct. For example, a recent view has been to create a hybrid of two existing proposals: the subjective experience and dual attention hypothesis (Berryhill et al., 2009; Drowos et al., 2010). The advantage for this merger is that it includes a role for the lateral parietal cortex in strategically accessing and attending to the full set of details associated with a particular event. It also includes the function of assessing the vivid richness of memories to account for the deficits in memory confidence. In other words, when the lateral parietal cortex is damaged, patients may not be able to fully reactivate the full assembly of stored details to revivify the event. This would lead to impoverished recollections and a reduced sense of re-experiencing a past event. Furthermore, it is also very much possible that both the dual attentional processes hypothesis and episodic output buffer hypothesis are valid descriptions of parietal involvement in memory retrieval. It just may be that different subregions of this heterogeneous region are responsible for various functions that all must occur simultaneously for accurate memory retrieval to happen.

Overview of Experiments

This dissertation will report two experiments that aim to test whether parietal activations will be modulated by changes in task demands. Specifically, experiment 1 will compare the two main methodologies for segregating familiarity and recollection (i.e. the remember/know paradigm and a source memory test). Experiment 2 will manipulate the base rates of old and new items presented at test using the

remember/know paradigm. These task demands should affect extra-mnemonic processes that guide memory decisions, but should not be associated with changes in the *amount* of memory content retrieved. Any parietal differences observed based on these procedural manipulations would be difficult for an episodic buffer theory to explain. Instead, such modulations would be in agreement with theories that suggest an extra-mnemonic role for the parietal cortex during memory retrieval, such as changes in attentional demands or changes in the subjective experience associated with retrieved memory content.

Chapter 2: Experiment 1. The Posterior Parietal Cortex: Comparing remember/know and source memory tests of recollection and familiarity

Introduction

As previously described, there is a general agreement across neuroimaging studies indicating more dorsal/superior lateral parietal regions in familiarity-driven recognition, with more ventral/inferior regions associated with recollection (for a review see Vilberg & Rugg, 2008). This general dissociation has been found regardless of whether a remember/know test or a source memory test is used to separate responses according to familiarity and recollection. While this convergence is somewhat reassuring, the fMRI literature is lacking a direct and adequate comparison of the neural correlates of recollection and familiarity between these two methods. Without this, there remains a possibility that this apparent convergence is merely an illusory finding. If results of such a comparison concluded that different lateral parietal regions were active depending on the test used, this would suggest that these two methods are not as equivalent at measuring recollection and familiarity as is currently assumed. In particular, it would suggest that these divergent brain regions may be representing either a difference in retrieved memory content or a difference in the cognitive demands associated with retrieval depending on what method was used to operationalize recollection and familiarity. Specifically, it could be the case that recollected memories from the source task may be more constrained than memories retrieved via the remember/know task. Additionally, it may be relatively effortful to search for the specific contextual information required by the source test. This

increased search effort may engage the top-down attentional system to a greater degree than during the remember/know test. Regardless of what theory is used to explain any differences that might be found, this result would be informative to the field since the standard view is to treat remember/know and source memory tests as equivalent measures of recollection and familiarity.

While some fMRI comparisons have been made between the two methods, the vast majority have been conducted between experiments (Ciaramelli et al., 2008; Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). Thus, comparisons have been made across a wide range of stimuli, variations in experimental design, differences in analysis technique, and perhaps most detrimentally, between different subjects. Without controlling for these confounding variables, neural differences between remember/know and source memory tests may be difficult, if not impossible to detect. In other words, even if specific sub-regions of the parietal cortex were more sensitive to one test than the other, co-varying differences in experimental designs may attenuate or even completely mask this effect. Take for instance, the type of stimulus used during testing. Variations in the specific location of neural activity have been found within the left ventral parietal depending on the stimulus type that was used to invoke the activity (Elman & Shimamura, 2013; Klosterman, et al., 2009). Research investigating individual differences during recognition memory tests has shown extensive yet reliable differences in brain activity patterns between individuals (Miller, Van Horn, Wolford, Hnady, Valsangkar-Smyth, Inati, Grafton, & Gazzaniga, 2002; Miller, et al., 2009).

If variables such as these are free to vary during comparisons of the remember/know and source memory tests, one could imagine how any true differences in neural activity between the two methods may go undetected.

Although most fMRI comparisons have been conducted with this between-experiment approach, there have been a few comparisons utilizing a within-subjects design (Duarte, et al., 2008; Vilberg & Rugg, 2007; Yu, Johnson, & Rugg, 2012). The goal of these studies, however, was not to directly compare the two methodologies, but instead to focus on how the amount of recollected information modulates activity within the lateral parietal cortex. While successful in tackling their specific goal, the designs of these studies were not optimal for a direct comparison between remember/know and source tests. First of all, none of these studies directly compared the neural correlates of familiarity between these two methods. Instead, they focused exclusively on recollection-related comparisons. While lately much focus has been made to elucidate the neural correlates of recollection, familiarity-related activity is still far from understood. Therefore, when comparing parietal activations between remember/know and source tests, it is just as important to investigate familiarity-related activity as it is activity related to recollection. Furthermore, none of these studies used the traditional testing methodologies, but instead used variants of the remember/know paradigm to find brain regions that were active during the remember/know task and were additionally modulated by the source task. Therefore, when identifying regions that were sensitive to source recollection, analysis was constrained to regions that were

additionally active during recollection in the remember/know task. As a result, no independent measure of objective recollection was/could be reported. Although helpful in highlighting brain regions that are modulated by the *amount* of information recollected (Vilberg & Rugg, 2007; Yu et al., 2012), without an independent measure of source recollection they cannot speak to the apparent convergence between remember/know and source memory tests.

In an effort to avoid the limitations of between-subject designs, the same group of subjects will participate in both a remember/know test and a source memory test. Additionally, the same stimuli (words), scanner protocol, and analysis parameters will be used for both tests. To obtain independent measures of subjective and objective recollection and familiarity, the remember/know test and source test will be taken independent of each other (as opposed to a combined procedure where subjects make a remember/know and/or a source judgment on each trial). The results from these two tests will be directly compared so that potential differences in neural activation may be found, with specific focus on activation within the left lateral parietal cortex.

The results of this direct comparison may reveal something important about the assumed equivalence of the remember/know and source memory tests at indexing recollection and familiarity. If neural differences are found between testing methods, then the generally-held assumption that these methods are tapping into functionally equivalent memory processes would need to be readdressed. Additionally, attempts to attribute any particular functional role to parietal activity during memory retrieval

would need to take these differences into account which would be particularly problematic for the episodic buffer theory.

Methods

Subjects

Twenty-five healthy subjects (7 female) took part in this study. Subjects ranged in age from 19 – 35 years old (M = 24.8, SD = 4.6). Data from eight additional subjects were not included in any reported analyses (one due to a failure to complete the experiment in its entirety, two due to an insufficient number of trials of interest <20, and five for excessive movement). All subjects were native English speakers and all except one reported their right hand to be dominant. All subjects gave informed consent as approved by the UCSB Institutional Review Board and were paid for their participation.

Stimuli

Stimuli consisted of 608 nouns selected using the MRC Psycholinguistic Database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). For counterbalancing purposes, words were pseudorandomly divided into two lists of 304 words each. These lists were matched (as closely as possible) on ratings of concreteness, familiarity, imagability, Kucera Francis written frequency, number of letters and number of syllables. Words were back projected onto a screen at the head of the scanner bore and were visible to the subject by a mirror mounted on the head coil. Words were

presented in the center of the screen in black 85-point Times New Roman font against a white background. Stimulus presentation was controlled by a MacBook Pro laptop running Matlab R2008a version 7.6.0 (The Mathworks Inc., USA), using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Procedure

Before entering the scanner, subjects engaged in a short practice session that mimicked what they would experience in the scanner. During this practice session, subjects took a source memory test and a remember/know test. Just prior to the remember/know test, subjects were given explicit instructions and examples of when to make a 'remember' and a 'know' response. These instructions were modified versions from those previously used in the literature (Rajaram, 1993) (see Appendix for a copy of the test instructions). In an attempt to ensure that these instructions were understood, after completing the practice remember/know test, subjects were asked what specific details were recalled for the items that were given 'remember' responses. Subjects were not allowed to continue with the procedure until the experimenter was convinced that a proper understanding of when to make a 'remember' vs. a 'know' response was achieved.

Once in the scanner, the task consisted of four study runs and four test runs. Subjects underwent all four study runs followed shortly by four test runs. During each study run, 76 words were presented one at a time on the screen for 2.5 seconds

followed by a blank screen for .7 seconds. During two of the study runs, subjects were asked to make a 'Pleasant/Unpleasant' decision about each word, for the other study runs subjects made an 'Abstract/Concrete' decision about each word. Subjects alternated between 'Pleasant/Unpleasant' and 'Abstract/Concrete' runs, with the order pseudo-randomized between subjects. After the fourth study run, an anatomical scan (approximately 9 minutes long) was collected, during which the subject was allowed to rest. Following this, the subjects began the first of four test runs. Each test run consisted of 152 words (76 old, 76 new), for a total of 608 test words. Each word was displayed on the screen for 2.7 seconds followed by a blank screen for .5 seconds. For two test runs, memory was tested using a source memory paradigm. Subjects indicated whether each word had been studied during one of the 'Pleasant/Unpleasant' study runs, during one of the 'Abstract/Concrete' study runs, whether the item was recognized as being part of the study session but the subject did not recall which run the word was presented in ('Don't Know' response), or whether the word was new. For the remaining test runs, subjects engaged in a remember/know paradigm, where subjects made a 'remember' response when recollection occurred, a 'know' response when familiarity was used to make their decision, or a 'new' response. Subjects alternated between 'Remember/Know' and 'Source Memory' runs, with the order pseudo-randomized between subjects. To minimize fatigue, subjects were given a one-minute break in the middle of each 12-minute test scan. During both the study runs and the test runs, a response scale appeared on the screen below the word to help subjects remember which button mapped onto which response option.

Assignment of words to test paradigm and to old/new status was pseudo-randomized between subjects. All responses were made using an MRI-compatible button box held in their right hand. To enable event-related analysis, 41 fixation trials were added to each study run and 79 fixation trials were added to each test run. The order of stimulus events during study and test runs was pre-determined by a genetic algorithm that optimized the design efficiency for the old/new contrast (Wager and Nichols, 2003).

Although one could argue that a more effective way to compare the two testing methods would be to integrate remember/know and source decisions within the same run instead of segregating into different runs, we had a specific rationale for avoiding this methodology. Basically, we wanted to replicate how these testing procedures are most commonly used. If we were to introduce a requirement to switch between making remember/know decisions and source decisions on a trial-to-trial basis, then this may involve additional processing that is not normally required during these recognition tests. Particularly since the dorsal parietal area has been shown to be involved with top-down attention (Corbetta & Shulman, 2002), requiring this additional processing of task-switching may modulate the PPC activity, not because of differences between the two tasks, but instead because of this additional procedural step. Therefore, we decided to segregate remember/know and source tests into different runs.

MRI Data Acquisition

A 3T Siemens TIM Trio scanner with a standard 12-channel head coil located at the UCSB Brain Imaging Center was used to scan all subjects. Earplugs were provided to minimize noise disturbance and cushions were placed around the subjects' head to minimize movement. A high-resolution anatomical image was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE) with TR = 2.3s, TE = 2.98ms, and FA = 9°. Each volume was collected with 3-D acquisition and consisted of 160 sagittal slices that were each 1.1 mm thick with 1 mm x 1 mm in-plane resolution. The eight functional runs consisted of a T2*-weighted single shot gradient-echo, echo planar image (EPI) sequence sensitive to the BOLD contrast with TR = 1.6s, TE = 30ms, and FA = 90°. Volumes were acquired parallel to the AC-PC plane in an interleaved pattern using generalized autocalibrating partially parallel acquisitions (GRAPPA). Each volume consisted of 30 slices that were each 3mm thick with a .5 mm gap and a 3 mm x 3 mm in-plane resolution. The first four volumes of each functional scan were discarded to allow equilibration of tissue magnetization. Although functional images were collected during the study sessions, these results are beyond the scope of this paper and are not discussed further.

Preprocessing of MRI Data

SPM8 (Wellcome Department of Imaging Neuroscience) was used to perform standard spatial preprocessing of the MRI data. All functional images were realigned

to the first volume of the first functional scan using a least squares approach and a 6 parameter (rigid body) spatial transformation. During realignment, images were unwarped in order to minimize variance caused by the susceptibility-by-movement interaction (Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The functional images were then coregistered to the anatomical image using the mean functional image generated during realignment. Next, using standard segmentation procedures, the anatomical T1 image was segmented into images of grey matter, white matter, and cerebral spinal fluid. These images were then spatially normalized to the ICBM Tissue Probabilistic Atlases that come standard in SPM8. The parameters of this transformation were then applied to the functional images, which were re-sampled to 3 mm isotropic voxels. Finally, the normalized images were spatially smoothed using an isotropic Gaussian kernel with an FWHM = 8 mm.

Analysis of Functional Data

SPM8 (Wellcome Department of Imaging Neuroscience) was used for further data analysis. Neural activity at stimulus onset was modeled using a delta (stick) function that was convolved with the canonical hemodynamic response function (HRF). To account for differences in response time (see Results), reaction time was entered into the model as a parametric modulator of the HRF using a first-order linear transform of the delta function. Data across the four functional runs was concatenated, and session-specific regressors were added into the model. Eleven event-types were modeled in total. Five for the remember/know test: correct rejections, remember hits,

know hits, false alarms, and misses and five for the source test: correct rejections, source hits, no source hits, false alarms and misses. 'Source hits' refers to trials in which the item was correctly recognized and was given the correct source attribution. 'No source hits' refers to trials in which the item was correctly recognized but was either given the wrong source attribution or received a 'Don't Know' response. There was an additional event-type of no interest, which was comprised of trials with omitted or multiple responses and trials when instructional information was presented on the screen. The data was high-pass filtered at 128s and an AR(1) model was used to estimate and correct for non-sphericity of the error covariance (Friston, Glaser, Henson, Kiebel, Phillips, & Ashburner, 2002). The general linear model (GLM) was used to obtain parameter estimates of events of interest and subsequent contrast *t*-maps were created for each subject. These contrast maps were then passed on to a second-level random-effects analysis that consisted of testing the contrast against zero using a one-sample *t*- test independently at each voxel across the brain.

Regions of Interest (ROI) Analysis

Marsbar (Brett, Anton, Valabreque, & Poline, 2002) was used to create and analyze BOLD activation from a priori chosen regions of interest (ROIs). Structural ROIs were determined according to the AAL atlas that is included with the Marsbar software package. These regions were the left superior parietal lobule (BA 7) and the left angular gyrus (BA 39). For these ROIs, the mean percent signal change from baseline within that region was calculated for each event type. Values representing

recollection and familiarity (as defined by each test) were then calculated for each subject by subtracting the percent signal change from the appropriate events (e.g. subtracting the percent signal change to know hits from the percent signal change to remember hits for remember/know recollection). These values were then averaged across subjects to obtain a mean percent signal change value for each contrast of interest.

Results

Behavioral results

We calculated overall d' (memory accuracy) and c (decision criterion) collapsed across recollection and familiarity responses using signal detection analysis. We used a series of paired-samples *t*-tests to compare results between the remember/know test and source memory test,. Results revealed no significant difference in d', $t(24) = .976$, $p = .339$, nor in c, $t(24) = .409$, $p = .686$ between the tests. There was, however, a significant difference in reaction time with remember hits ($M = 1.29$ s, $SD = .15$ s) being made significantly faster than source hits ($M = 1.69$ s, $SD = .17$ s), $t(24) = -14.61$, $p < .001$ and know hits ($M = 1.58$ s, $SD = .20$ s) being made significantly faster than no source hits ($M = 1.74$ s, $SD = .18$ s), $t(29) = -5.20$, $p < .001$. To ensure that this difference in reaction time was not driving any neural differences that we might find, we added reaction time into our model as a parametric modulator of the delta function used to model the neural activity (See Methods section 2.6). There was also a significant difference in the amount of recollected trials between the

remember/know and source memory tests with a significantly higher number of remember hits (M = 76.8, SD = 24.0) than source hits (M = 64.0, SD = 24.6), $t(24)$ = 2.27, p = .032. There was no significant difference between the number of know hits and the number of no source hits, $t(24)$ = -1.648, p = .112. For a summary of the behavioral results, see Table 1.

Table 1

	d'	c	**Rec rt*** **	**Fam rt*** **	**# of Rec Trials***	# of Fam Trials
Remember/ Know	2.11 (.69)	-.07 (.34)	**1.29 (.15)**	**1.58 (.20)**	**76.80 (24.05)**	51.12 (19.95)
Source	2.03 (.81)	-.09 (.37)	**1.69 (.17)**	**1.74 (.18)**	**64.00 (24.62)**	59.88 (17.93)

TABLE 1: Overall memory accuracy (d') and response bias (c) are shown. 'Rec' refers to recollection (either remember hits or source hits) and 'Fam' refers to familiarity (either know hits or no source hits), while 'rt' refers to reaction time. Mean values are shown with their associated standard deviations in parentheses. Significant differences between the tests are shown in bold font and the significance value is indicated with the associated star(s) ($p < .05$ = *, $p < .001$ = ***).

fMRI results

Although some minor activation was found in the right hemisphere for the contrasts of interest, the following analyses focus mostly on the activation in the left hemisphere. The activity within the left hemisphere was significantly stronger and more consistent than that in the right hemisphere. Additionally, it is activity within

the left hemisphere that is consistently reported in the memory retrieval literature. Recollection was operationalized for the remember/know test as the 'Remember hits > Know hits' contrast, and for the source test as the 'Source hits > No Source hits' contrast. Familiarity was operationalized as the 'Know hits > Correct rejections' contrast for the remember/know test and as the 'No Source hits > Correct rejections' contrast for the source test. 'Correct rejections' included only those responses from that test (e.g. correct rejections in the source contrast only included correct rejections from the source test). Unless otherwise specified, voxels were tested at a False Discovery Rate (FDR) adjusted p value of $< .05$ with a voxel extent of 10.

Brain regions activated by both tests

Despite which testing method was used, recollection activated relatively ventral PPC regions, while familiarity activated more dorsal PPC regions. Specifically, recollection activated the left angular gyrus (BA 39). Outside of the PPC, regions in the left dorsolateral prefrontal cortex (BA 9 & 46), left ventrolateral prefrontal cortex (BA 45 & 47), regions within the left lateral temporal cortex (BA 22), as well as the posterior cingulate gyrus (BA 23 & 31) were also activated by both tests for recollection. Defined by either test, familiarity activated the area around the intraparietal sulcus (IPS). This activation extended dorsally into the superior parietal lobule (BA 7) and also into the more superior areas of the angular gyrus (BA) 39 and the supramarginal gyrus (BA 40). Extensive familiarity-related activation was also found during both tests in the left dorsolateral prefrontal cortex (BA 9 & 46), left

ventrolateral prefrontal cortex (BA 44, 45, & 47), the precuneus (BA 7), and posterior cingulate gyrus (BA 23). See Figure 1 for a visualization of these common activations. See Table 2 for a list of peak voxel activations associated with these results.

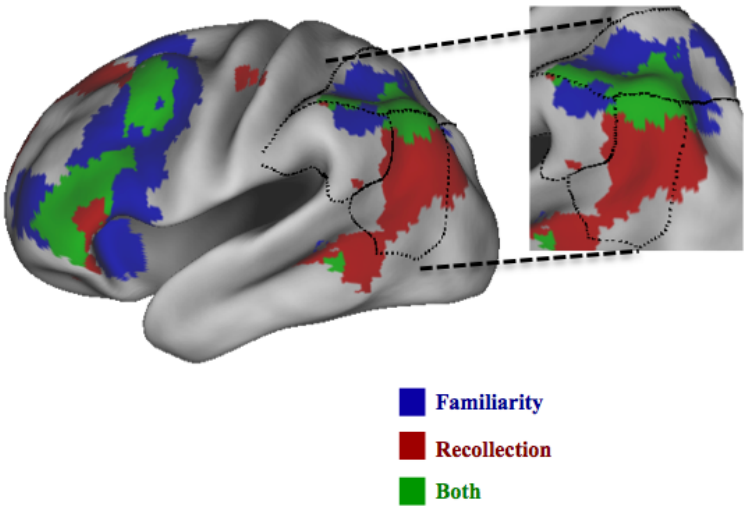


Figure 1: Brain regions identified by both tests at the group level. Blue indicates regions that were active for familiarity, red for recollection, and green represents regions that were active for both familiarity and recollection. For visualization purpose, results were transformed to the PALS atlas and rendered onto 3D inflated brains using CARET software (Van Essen, Dickson, Harwell, Hanlon, Anderson, & Drury, 2001). Brodmann areas 7, 39, and 40 are indicated with the dotted line (defined by the BA list that comes with the CARET software).

Table 2

a. Recollection-related activity

X Y Z Coordinates (MNI)	Hemi – sphere	Brain Region	BA	t value	Cluster size (voxels)
-9 -43 34	Left	Posterior Cingulate / Precuneus	31	5.76	672

-3 -58 10	Left	Posterior Cingulate	29	5.10	*
-6 -58 28	Left	Precuneus / Posterior Cingulate	31	4.91	*
-33 14 52	Left	Middle / Superior Frontal Gyrus	8	5.48	254
-15 59 22	Left	Superior Frontal Gyrus	10	5.38	*
-6 50 31	Left	Superior Frontal Gyrus	9	5.14	*
-42 -67 46	Left	Precuneus / Angular Gyrus	39	5.39	475
-42 -73 31	Left	Lateral Occipital Cortex / Angular Gyrus	39	5.32	*
-42 -49 37	Left	Angular Gyrus	39	3.86	*
-36 32 -11	Left	Inferior Frontal Gyrus	47	5.25	198
-24 32 -11	Left	Inferior Frontal Gyrus	11	5.18	*
-45 35 7	Left	Inferior Frontal Gyrus	45	5.02	*
-12 -73 -11	Left	Lingual Gyrus	18	4.83	61
-30 -37 -14	Left	Parahippocampal Gyrus	36/37	4.70	51
-18 -43 -11	Left	Lingual Gyrus / Cerebellum		4.56	*
-60 -37 -8	Left	Middle Temporal Gyrus	21	4.16	34
-57 -52 -8	Left	Middle Temporal Gyrus	21	4.10	*
24 -37 -11	Right	Lingual Gyrus / Parahippocampal Gyrus	36	4.08	22
18 -88 31	Right	Lateral Occipital Cortex / Cuneus	19	3.82	21
18 8 -11	Right	Putamen		3.62	22
12 11 -5	Right	Caudate / Putamen		3.53	*

b. Familiarity-related activity

X Y Z Coordinates (MNI)	Hemi - sphere	Brain Region	BA	t value	Cluster size (voxels)
-45 -49 46	Left	Supramarginal Gyrus / Angular Gyrus / Superior Parietal Lobule	40/7	6.23	882
-33 -70 52	Left	Superior Parietal Lobule	7	6.19	*
-9 -70 43	Left	Precuneus	7	4.61	*
-48 17 37	Left	Middle Frontal Gyrus	9	5.94	1842
-39 50 10	Left	Middle Frontal Gyrus	10	5.61	*
-6 23 49	Left	Superior Frontal Gyrus	8	5.56	*
-12 11 1	Left	Caudate		5.59	65
-12 11 10	Left	Caudate		5.21	*
-6 -28 25	Left	Posterior Cingulate	23	5.19	140
12 11 1	Right	Caudate		4.53	62
36 20 -2	Right	Insular Cortex	47	4.20	101
39 8 58	Right	Middle Frontal Gyrus	6	3.90	40
45 -58 52	Right	Lateral Occipital Cortex / Angular Gyrus / Superior Parietal Lobule	39/7	3.88	69
-3 -25 -2	Left	Thalamus		3.56	10
-3 -25 -11	Left	Brainstem		3.35	*
48 29 37	Right	Middle Frontal Gyrus	9	3.49	14

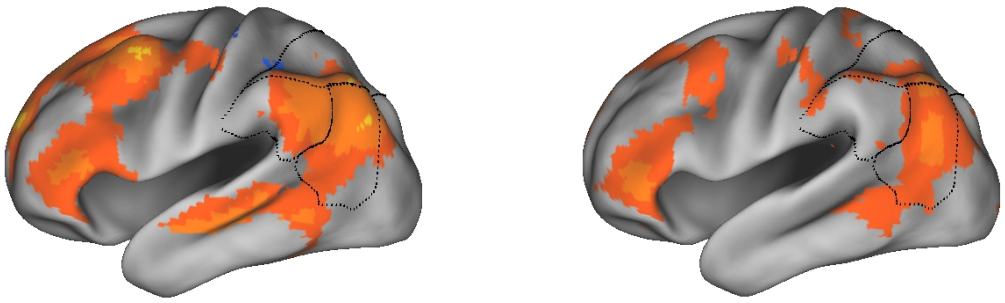
TABLE 2: Information from peak voxels found by inclusively masking the 'Remember Hits > Know Hits' and 'Source Hits > No Source Hits' contrasts to represent recollection[a], and the 'Know Hits > Correct Rejections' and 'No Source > Correct Rejections' contrasts to represent familiarity[b]. Closest Brodmann areas (BA) labels are provided when possible. * denotes that the peak voxel is part of the cluster in the row(s) directly above it.

Results from each test

In addition to the brain regions that were common to both tasks, some brain regions were uniquely identified depending on what test was used to operationalize recollection and familiarity. Of specific interest to this study, recollection-related activity was only seen in the supramarginal gyrus (BA 40) when it was operationalized by the remember/know test. Familiarity, on the other hand, appeared to activate a larger portion of the superior parietal lobule (BA7) when operationalized by the source test. See Figure 2 for the results of the second level of analysis independently for the remember/know test and for the source test. See Table 3 for a list of peak voxel activations associated with these results.

Remember Know Test **Source Test**

a. b.



Recollection

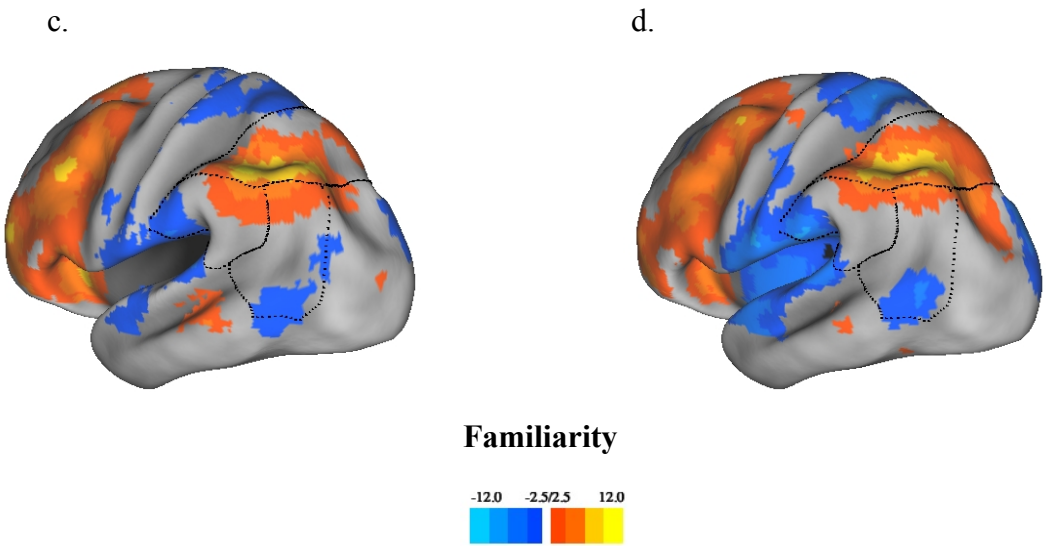


FIGURE 2: Group-level results of Remember Hits > Know Hits[a], Source Hits > No Source Hits [b], Know Hits > Correct Rejections [c], and No Source Hits > Correct Rejections [d] For optimal visualization recollection is presented on a lateral view of the brain and familiarity is presented at a slightly more dorsal view.

Table 3

a. Remember Hits > Know Hits

X Y Z Coordinates (MNI)	Hemi - sphere	Brain Region	BA	t value	Cluster size (voxels)
-9 -43 34	Left	Posterior Cingulate Gyrus	31	8.61	21030
-30 -34 -14	Left	Parahippocampal Gyrus	36	6.73	*
-18 59 22	Left	Superior Frontal Gyrus	9/46	7.94	20830
-36 8 52	Left	Middle Frontal Gyrus	6	7.93	*
-42 -67 46	Left	Lateral Occipital Cortex/ Angular Gyrus	19/39	7.64	11170
-54 -61 37	Left	Supramarginal Gyrus/ Angular Gyrus	40/39	6.95	*
-36 32 -11	Left	Inferior Frontal Gyrus	47	7.29	344
-57 -28 -8	Left	Middle Temporal Gyrus	21	7.28	434

30 -43 -8	Right	Parahippocampal Gyrus	36	6.64	147
51 -70 22	Right	Angular Gyrus/Lateral Occipital Cortex	39/19	5.63	57
69 -25 4	Right	Superior Temporal Gyrus	22	5.32	164
54 35 4	Right	Inferior Frontal Gyrus	45/46	5.20	59
24 -82 40	Right	Precuneus/Cuneus/ Lateral Occipital Cortex	19	4.79	79
21 -88 31	Right	Cuneus	18/19	4.55	*
-45 -16 49	Left	Postcentral Gyrus	3	4.49	24

b. Source Hits > No Source Hits

X Y Z Coordinates (MNI)	**Hemi - sphere**	**Brain Region**	**BA**	**t value**	**Cluster size (voxels)**
-6 -58 28	Left	Posterior Cingulate Gyrus/ Precuneus	31	9.08	958
-45 -67 19	Left	Middle Temporal Gyrus/ Lateral Occipital Cortex	37/19	5.98	490
-39 -67 46	Left	Lateral Occipital Cortex/ Angular Gyrus	19/39	5.84	*
-45 44 7	Left	Middle Frontal Gyrus/ Inferior Frontal Gyrus	10/46	5.97	292
-9 56 34	Left	Superior Frontal Gyrus	9	5.35	238
36 -31 -11	Right	Parahippocampal Gyrus/ Hippocampus	37	5.02	86
3 -1 31	Right	Anterior Cingulate Gyrus	24	4.80	27
21 -1 -11	Right	Amygdala		3.75	33

-24 -37 -17	Left	Fusiform Cortex	20	4.53	47
-18 -40 -8	Left	Parahippocampal Gyrus	36	4.12	*
39 - 79 1	Right	Lateral Occipital Cortex	19	4.44	51
18 - 49 40	Right	Precuneus	31	4.37	11
36 -31 52	Right	Postcentral Gyrus	3	4.28	18
-12 -79 -2	Left	Lingual Gyrus	18	4.25	56

c. Know Hits > Correct Rejections

X Y Z Coordinates (MNI)	**Hemi - sphere**	**Brain Region**	**BA**	**t value**	**Cluster size (voxels)**
-45 -49 46	Left	Superior Parietal Lobule/ Supramarginal Gyrus	7/40	10.04	933
-9 -70 43	Left	Precuneus	7	5.92	*
-48 17 37	Left	Middle Frontal Gyrus	8/9	9.12	26220
-39 50 10	Left	Middle Frontal Gyrus	10	8.20	*
-6 23 49	Left	Superior Frontal Gyrus	8	8.05	*
-3 -16 31	Left	Anterior Cingulate Gyrus	23	6.16	250
-60 -43 -5	Left	Middle Temporal Gyrus	20/21	5.25	73
36 20 -2	Right	Insula	47/13	5.17	141
42 47 16	Right	Middle Frontal Gyrus	10	4.77	59
45 -58 52	Right	Superior Parietal Lobule/ Angular Gyrus	7/39	4.63	117
48 -49 43	Right	Angular Gyrus/ Supramarginal Gyrus	39/40	4.56	*

d. No Source Hits > Correct Rejections

X Y Z Coordinates (MNI)	Hemi - sphere	Brain Region	BA	t value	Cluster size (voxels)
36 -73 40	Right	Precuneus	19	9.86	18730
-30 -67 49	Left	Precuneus/Lateral Occipital Cortex	19	8.88	*
-45 -49 46	Left	Angular Gyrus/ Supramarginal Gyrus/ Superior Parietal Lobule	39/40/7	8.86	*
-48 11 37	Left	Middle Frontal Gyrus	9	7.74	21140
36 5 61	Right	Middle Frontal Gyrus	6	6.79	186
-3 -28 31	Left	Posterior Cingulate Gyrus	23	6.78	151
30 23 -5	Right	Insula	13	5.73	121
-18 -79 -11	Left	Fusiform Gyrus	18/19	5.06	64
51 32 28	Right	Middle Frontal Gyrus	9	4.82	70

TABLE 3: Information from peak voxels for Remember Hits > Know Hits[a], Source Hits > No Source Hits[b], Know Hits > Correct Rejections[c], and No Source Hits > Correct Rejections[d] contrasts from the group analysis. Closest Brodmann areas (BA) labels are provided when possible. * denotes that the peak voxel is part of the cluster in the row(s) directly above it.

Direct comparisons between tests

To specifically compare the results of the two methods, the contrasts that were used to define recollection and familiarity at the first level of analysis for each test were statistically compared. Specifically, activation resulting from each subject's 'Source Hits > No Source Hits' contrast (source recollection) was subtracted from their 'Remember Hits > Know Hits' contrast (remember/know recollection).

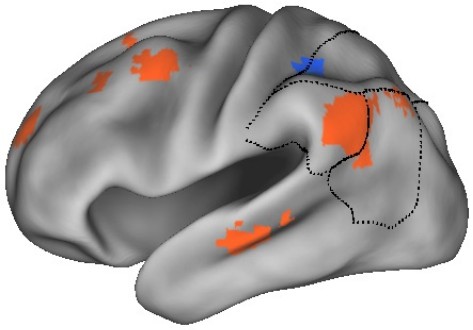
Similarly, for familiarity, activation resulting from each subject's 'No Source Hits > Correct Rejections' contrast (source familiarity) was subtracted from their 'Know Hits > Correct Rejections' contrast (remember/know familiarity). The resulting difference *t*-maps (with positive values indicating brain regions that were more active during the remember/know test compared to the source test) were then brought up to the second-level of analysis and compared against zero using a one-sample *t*-test at each voxel across the brain. These results are described below and are shown in Figure 3[ab].

Since recollection is defined by subtracting out activity to familiarity hits, we wanted to ensure that any neural difference observed between recollection was truly due to differences in recollected hits, and not to differences to familiarity hits. Therefore, at the first-level of analysis, a 'Remember Hits > Source Hits' contrast was generated for each subject. The same argument holds for familiarity. To ensure that the neural differences observed were not due to differences to correct rejections, a 'Know Hits > No Source Hits' contrast was generated for each subject. The resulting *t*-maps were brought up to the second level of analysis and compared against zero using a one-sample *t*-test at each voxel across the brain. These results are described below and are shown in Figure 3[cd].

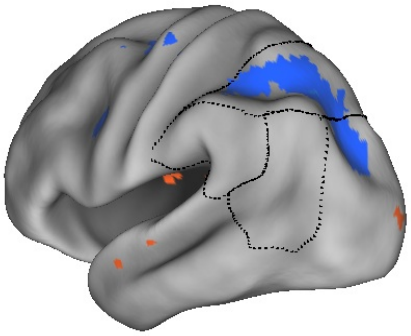
Results from both of these analyses show that the ventral region of the left PPC (specifically the supramarginal gyrus) was significantly more active when recollection was indexed by the remember/know test compared to when it was indexed by the source test. Conversely, the dorsal PPC region was significantly more

active when familiarity was indexed by the source test compared to when it was indexed by the remember/know test.

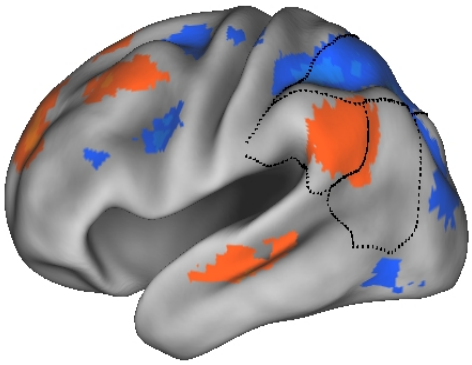
a. Recollection: RK > Source



b. Familiarity: RK > Source



c. Recollection: R hits > Source hits



d. Familiarity: K hits >No Source hits

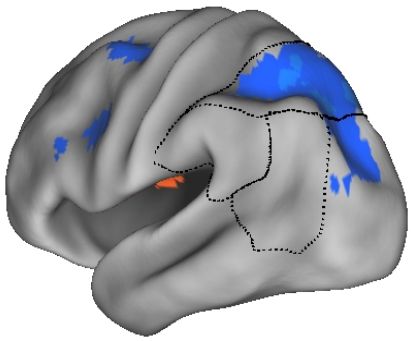


FIGURE 3 Group-results ($p < .001$, voxel extent = 10) for Recollection[ac] and Familiarity[bd]. Contrasts show the difference between the remember/know and source tasks for recollection[a] and familiarity[b]. Also shown are the contrasts between 'remember hits > source hits'[c] and 'know hits > no source hits'[d].

Regions of Interest (ROI) Analysis

Percent signal change from (implicit) baseline was calculated for each event type

for each subject. To calculate the percent signal change associated with recollection and familiarity, the following subtractions were performed: 'Remember hits – Know hits', 'Source hits – No Source hits', 'Know hits – Correct Rejections', and 'No Source hits – Correct Rejections'. These differences represent the percent signal change for remember/know recollection, source recollection, remember/know familiarity, and source familiarity respectively. Figure 4 shows the mean (across subjects) percent signal change for these events calculated within the left angular gyrus (BA 39) and left superior parietal lobule (BA 7) for recollection and familiarity respectively. Although the left angular gyrus was active for recollection during both tests, results from a paired samples *t*-test revealed a significant difference in the mean percent signal change between recollection indexed by the remember/know test (M = .18, SD = .12) and recollection indexed by the source test (M = .09, SD = .08), $t(24) = 3.88$, $p < .001$, with the remember/know test significantly activating this region more than the source test. Similarly, while both tests activated the superior parietal lobule during familiarity, a paired samples *t*-test revealed a significant difference between familiarity as defined by the remember/know test (M = .05, SD = .10) and by the source test (M = .13, SD = .14), $t(24) = -3.01$, $p = .006$, with the source test significantly activating this region more than the remember/know test.

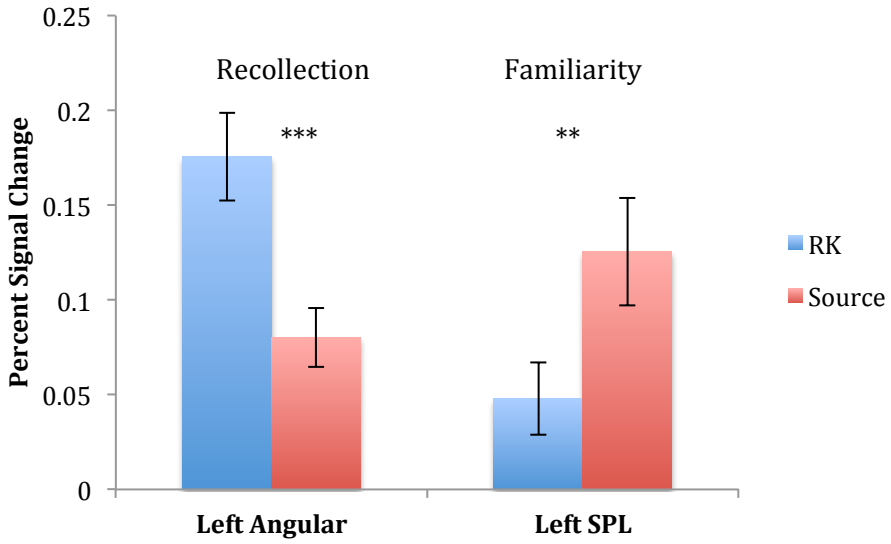


FIGURE 4: Mean (across subjects) percent signal change for recollection and familiarity. On the left is the change in signal in the left angular gyrus (BA 39) for remember hits (blue) and for source hits (red). On the right is the change in signal in the left superior parietal lobule (BA 7) for know hits (blue) and no source hits (red). Error bars represent the standard error of the mean. Significance values are indicated with the associated number of stars ($p < .01$ = **, $p < .001$ = ***).

Discussion

Summary of current findings

The current design allowed for the direct comparison of the neural correlates of recollection and familiarity as operationalized by the remember/know and source memory procedures. Results revealed large areas of convergence, namely familiarity-related activity within the superior parietal lobule and recollection-related activity within the angular gyrus. In addition to this overlap, striking divergent activations were also observed between the testing methods. Within the left PPC, the magnitude of activation significantly differed between testing method. Although both tests revealed familiarity-related activity within the SPL, this activity was greater when

familiarity was indexed by the source test compared to when it was indexed by the remember/know test. While both tests showed recollection-related activity within the left IPL, specifically in the left angular gyrus, this activation was significantly greater when recollection was probed by the remember/know test compared to the source test (as evidenced in the ROI analysis).

Beyond differences in magnitude, the extent of activity also varied between testing procedure. When familiarity was assessed using the source test, activation spread more dorsally, covering a greater extent of the left SPL. When the remember/know paradigm was used, familiarity-related activation spread slightly more ventrally into the superior regions of the left supramarginal and angular gyri. Turning to activity related to recollection, the most striking regional differences were observed. While source memory recollection was confined to the more posterior portion of the IPL, namely the angular gyrus, remember/know recollection extended well into the supramarginal gyrus and into the temporo-parietal junction (TPJ).

Relation to previous findings

Previous research has found a similar difference in the magnitude of recollection and familiarity-related activations between the remember/know and source test procedures. In a meta-analysis, Ciaramelli et al. (2008) compared the results from nine experiments using the remember/know paradigm with 11 experiments using a source memory test. Results showed that the left SPL was associated with higher levels of activity when using source memory compared to the remember/know procedure. Conversely, regions within the left IPL were more strongly activated by

experiments that used the remember/know test compared to those using tests of source memory. The current experiment replicated these findings within the same group of subjects. This finding is important because it shows that this differential activation is still present even when confounding variables such as differences in stimuli, analysis technique, scanner protocols, specific subjects tested, etc. are held constant. Thus, this difference is most likely truly attributable to differences in task demands and not to differences in extraneous variables that were previously free to vary between testing procedure.

Turning to differences in the extent of activity, this difference was most noteworthy in the activity associated with recollection. While both tests activated the angular gyrus, only the remember/know test additionally activated the supramarginal gyrus. In these analyses, a more lenient threshold of uncorrected $p < .001$ was used in these direct comparisons because the analyses were testing the significant difference between differences. Although a more liberal threshold was used, the specific lateral parietal area of significant activity (the left supramarginal gyrus) was precisely the area predicted by the previous analyses that used a more conservative threshold. In addition to this, the extent of activity was relatively large (257 voxels). Therefore we feel confident that the result of this analysis is not merely a reflection of spurious activity. Although it is unclear why only subjective measures of recollection activated this anterior region of the IPL, there is some literature that supports this finding. Using the combined remember/know & source memory paradigm, Yu et al. (2012) found that the angular gyrus was active for recollection using either testing

method, but a cluster within the supramarginal gyrus/TPJ was active for recollection only as indexed by the remember/know test. The results of the current experiment replicate these findings and more importantly show that these results can be found when using the traditional remember/know and source memory testing procedures, which allow recollection and familiarity to be operationalized independently by both testing methods.

General Conclusions

While the ubiquitous dorsal/ventral dissociation between familiarity and recollection was found using both the remember/know test and the source memory procedure, further distinctions were found within the left parietal cortex when these two methods were directly compared. In the dorsal parietal regions, where activity is most likely reflecting a cognitive process related to memory retrieval, there was a significant difference in the magnitude of familiarity-related activity between the two tests. This difference is most likely explained in terms of differences in task demands such as top-down attention or retrieval monitoring, between the source and remember/know tests. In the ventral parietal regions, where there is less of a consensus in the literature, a difference not only in the magnitude of recollection-related activity but also in the extent of this activity was observed between the two tests. If we do not look at this study in isolation, but instead combine results from other experimental techniques (structural and functional connectivity studies, patient data, etc.) it seems more likely that this differential activity is representing some difference in cognitive demands (i.e. bottom-up attention or self-referential

processing) between the tasks. Furthermore, if an episodic buffer theory is used to explain the differential ventral parietal activations, then one must assume that recollection is a graded, as opposed to a threshold (all-or-none) process, which is in debate in the literature (Mandler, 1980; Yonelinas, 1997; Yonelinas, 2001; but see Wixted, 2007; Mickes, Wais, & Wixted, 2009). For these reasons, we assume the most parsimonious explanation of the differential ventral parietal activation observed in the current study is a reflection of a difference in some cognitive process(es) associated with each task. Regardless of what theory is used to explain the differences observed, the fact that these differences exist between the tasks is enough to challenge the widely held belief that these two methods are functionally equivalent at separating the neural correlates of recollection and familiarity. With such a heated debate in the memory literature as to what functional role(s) (if any) the parietal cortex is playing during memory retrieval, activation differences due simply to the procedure used to probe recollection and familiarity must be considered.

Chapter 3: Experiments 2. Modulations of Posterior Parietal Cortex Due to Changes in Base Rate Information

Introduction

During a recognition memory test subjects are required to make a decision as to whether or not they have encountered each stimulus previously. Clearly, these decisions rely upon the amount of mnemonic information available for each stimulus. Somewhat less obvious, is how these decisions involve quantifying how much mnemonic information is enough to conclude that a prior experience has occurred (i.e. that the stimulus is old). This value, known as a subject's *criterion* according to signal detection theory (Macmillan & Creelman,1990) has been shown to be influenced by several factors including: instructional motivation (Egan, 1958**;** Verfaellie, Giovanello, & Keane, 2001; Postma, 1999), payoff manipulations that preferentially reward correct 'old' or 'new' responses (Healy & Kubovy, 1978; Van Zandt, 2000), and manipulations of the (alleged or true) base rates of studied and new trials (Strack & Forster, 1996; Aminoff et al. 2014; Van Zandt, 2000, Verfaellie et al.; Hirshman & Henzler, 1998). For instance, if subjects are told that the base rate of studied (old) to non-studied (new) trials is 70% to 30% respectively, a shift in criterion is often observed, with subjects lowering their criterion to a more liberal setting, thus requiring less mnemonic evidence to make an 'old' response (Aminoff et al., 2012; Aminoff et al., 2014).

While several studies have investigated the influence of payoff manipulations on standard 'old/new' recognition responses, only a limited number have explored its

effect on 'remember/know' responses. The results of which have been mixed, which has led to debate in the field as to the true nature of the dichotomy between these responses and if they truly reflect qualitatively different cognitive states. As initially described, recollection (ostensibly represented by 'remember' responses) is typically thought of as a threshold process, in which it either occurs in full or does not occur at all (Mandler, 1980; Yonelinas, 1997, 2001). As such, it is not usually thought of as being influenced by manipulations of a decision criterion. Familiarity (ostensibly represented by 'know' responses) on the other hand, is usually described as varying in degree along a continuum of mnemonic evidence (Mandler, 1980). This type of retrieval fits nicely with signal detection theory in which items that are associated with an amount of evidence (i.e. familiarity) that is above the criterion are classified as 'old' and those below are classified as 'new'. Therefore, when experimental manipulations affect criterion placement, they also affect familiarity responding.

Initial studies using the remember/know procedure supported this distinction between remember and know responses, finding that only know responses were affected by manipulations of criterion (Strack & Forster, 1996). However, additional studies have challenged this idea and have shown that under the right conditions, even remember responses can be affected by these manipulations (Hirshman & Henzler, 1998). To further complicate matters, some studies have shown that when 'guess' responses are given as an additional option at test, neither remember nor know response are affected by criterion manipulation (Gardiner, Richardson-Klavehn, & Ramponi, 1997). As if that were not complicated enough, a major drawback to all of

these studies is their between-subjects design. Extensive individual differences in the effectiveness of criterion manipulations have been shown to exist (Aminoff et al., 2012; 2014). Therefore, when comparing across individuals, it is impossible to determine how much of the difference between criterion levels is due to the experimental manipulation and how much is due to naturally-existing individual differences.

Turning to neuroimaging studies, there are even fewer experiments that have investigated the effects of criterion manipulations. These effects could be especially telling for areas within the posterior parietal cortex, whose function is still greatly debated in the field. If this region is directly related to the temporary storage of mnemonic information (i.e. the episodic buffer theory), then its activity should not vary according to differences in base rates. This is because there is no reason to believe that such a manipulation would have any effect on the amount of retrieved memory content itself, but instead, would have effects on extra-mnemonic functions such as target detection, adjustment of expectancies, an overriding of prepotent response tendencies, etc. Therefore, if activity within this region were found to be modulated by base rate information, it would provide evidence that it is not acting as an episodic buffer, but is instead functioning in some other cognitive process that aids memory retrieval but is not necessary for it to occur (i.e. allocating attention, subject awareness, etc.).

Some early electrophysiological studies have investigated the manipulation of base rate information on the ERP correlates of recognition memory. As previously

described, there is the 'parietal old/new' ERP component that has been associated with successful retrieval (specifically with recollection) that presents itself as a positive-going waveform that is greater for hits than correct rejections. Studies that varied the ratio of old and new items at test have found that the parietal old/new ERP component is invariant to this manipulation (Friedman, 1990; Herron et al., 2004; Smith & Guster, 1993) and as a result some have suggested that this component is a likely neural correlate of episodic recollection and not of extra-mnemonic processes that co-occur with retrieval (Friedman & Johnson, 2000; Rugg & Allan, 2000).

While informative, the spatial resolution offered by such ERP studies leaves a lot to be desired. Fortunately, a handful of studies have followed up on these results using fMRI techniques in order to capitalize on its superior spatial resolution. Specifically, Herron, Henson, and Rugg (2004) varied the probability of old and new test items across three study-test cycles. The ratio of old to new words differed in each test phase, and was either 25:75, 50:50, or 75:25. Results of this manipulation depended upon what sub-region of the posterior parietal cortex was observed. Within the superior parietal cortex (BA 7), there was a significant interaction with old/new ratio, where retrieval success effects varied according to whether old or new items were the rarer stimulus class, with the more infrequent items eliciting greater activity. Following the logic outlined above, the authors argued that these regions are unlikely to directly support the recovery or representation of stored mnemonic information. In direct contrast to this finding, regions within the inferior parietal cortex (BA 39) that were sensitive to the 'hits > correct rejections' contrast were found not to be sensitive

to the probability manipulation. The authors took this to as evidence that this region was directly related to memory processes per se and not to extra-mnemonic processes occurring during retrieval.

However, a major limitation of this study was the lack of a behavioral shift in response patterns between the test phases. There was no effective change in criterion placement across the different probability conditions. Without a behavioral shift in performance, it is difficult to interpret the null effect that was found. There could have been no modulation in parietal activity because this region is directly related to memory representations (as argued by the authors), but could just as easily be explained by a lack of statistical power. Perhaps the criterion manipulation was not strong enough to induce a neural modulation. In fact, the authors admit that this failure to find a probability effect on response bias was inconsistent with some previous reports (e.g. Ratcliff, Sheu, & Gronlund, 1992). It was suggested by Herron et al. (2004) that a possible reason for this disparity may be because subjects in this study were not explicitly informed about the ratio changes in each block (i.e. what the probabilities would be) but instead were only made aware that changes would occur across blocks. An even more crucial and obvious instructional difference is the fact that the experimenters instructed their subjects to try not to allow the change in base rates to 'influence their recognition judgments' (Herron et al., 2004, page 3).

Fortunately, a more recent study by Aminoff et al. (2014) was able to replicate the results found within the superior parietal cortex. This study was much larger (N = 95) and had subjects participate in two recognition memory tests (one using words as

stimuli, the other using faces) while their neural activity was collected via fMRI. Again, base rate information was manipulated across testing blocks such that some blocks contained 70% old items and some contained only 30% old items. Unlikely the Herron study, subjects were explicitly made aware of the changes in base rates between blocks. Maybe as a result of this, subjects did shift their criterion appropriately (although less than optimally) between the high and low probability conditions, adopting a more lenient criterion in the high probability condition where items were more likely to be old. As with the Herron study, regions within the superior parietal cortex (BA 7) were found to be modulated by probability manipulation. Although a full cross-over effect was not found (i.e. correct rejections were not found to elicit more activity than hits in the high probability condition), the old/new effect was almost completely eliminated during the high probability condition. Furthermore, when the data were split into two groups of subjects based on whether they shifted their criterion between blocks or not, the parietal old/new effect was robust for the group that shifted and essentially non-existent for the group who did not. Additionally, regions of interest (ROI) analyses in this study showed a strong correlation between subjects' criterion placement and amount of dorsal parietal activity during the 'hits > correct rejections' contrast. This converging evidence strongly suggests that the superior parietal activity seen during successful retrieval is at least partially related to non-mnemonic processes that occur during recognition.

Although very informative, one major limitation of both of these studies, was that responses were not separated according to whether they were recognized by

recollection or familiarity. Subjects performed a standard recognition memory task and simply responded 'old' or 'new' to each item. Additionally, recognition accuracy (as measured by d') was admittedly low in the study by Aminoff and colleagues. This was intentionally done so that subjects would be more inclined to use the probability manipulation to guide their memory responses. Although successful in their goal of getting subjects to shift criterion between probability blocks, this low memory performance most likely limited retrieval to familiarity-based responses with very little, if any, recollection occurring. As a result, these studies cannot speak to the distinct effect criterion manipulations may have on the neural correlates of recollection and familiarity.

An fMRI study conducted by Vilberg and Rugg (2009) sought to expand these initial findings from the Herron study. Like the Herron study, old/new ratios were varied between testing conditions, with 25% of items being old in one block and 75% old in another block. Additionally, they investigated the effects of varying old/new ratio on the neural correlates of successful versus unsuccessful source memory. As previously described, source memory, like the remember/know paradigm, is a common way of segregating items recognized with familiarity from those recognized with recollection. The authors first looked at generic retrieval success effects (regardless of source information) and found two regions within the more superior parietal areas (specifically an anterior and a posterior region along the intraparietal sulcus) to be modulated by the probability condition. These old/new effects were robust in the low probability condition (25% old) but greatly attenuated during the

high probability condition (75% old). Somewhat surprisingly, a larger region within the middle intraparietal sulcus was found *not* to be modulated by the probability change. Turning to regions that demonstrated recollection-related effects (as operationalized by correct source retrieval), this involved more inferior parietal areas, specifically a region within the posterior angular gyrus. This region, like the middle intraparietal sulcus was not shown to be sensitive to the change in probability. Regardless of the ratio of old to new items, this region showed maximal activity to hits compared to correct rejections, particularly to hits that were associated with the correct source attribution. The authors argued that these probability-insensitive regions were likely candidates for supporting processes directly related to memory retrieval and that the angular gyrus in particular may be recruited for recollection-related retrieval.

While successful in segregating familiarity and recollection related responses, this study was unsuccessful in inducing a behavioral change in response bias between the testing conditions. Like the Herron et al. (2004) study, the subjects in this study were not made explicitly aware of the change in base rates between conditions and were instructed not to let any apparent change in base rate affect their recognition decisions. Additionally, in this experiment subjects were told to make a new response either when they were sure the item was new or when they were uncertain if it was old. They were instructed only to respond old if they were confident in their recognition. Such instructions have been shown to increase subjects' criterion level, requiring a relatively higher amount of mnemonic information in order to respond old (Postma,

1999). This instruction was the same across testing condition, and therefore may have induced a relatively strict criterion across both testing conditions, leaving little opportunity for the base rate information to have an effect on their response patterns. Therefore, it is once again difficult to interpret the null effect of probability manipulation on the neural correlates of recognition responses. Another potential limitation in this study was the use of the source test as a means of operationalizing recollection and familiarity. As has been shown in a review paper by Ciaramelli et al. (2008) and in the first experiment outlined in this dissertation, much more ventral parietal activity is found when using the remember/know approach, compared to the source task paradigm, to operationalize recollection. This may explain why the ventral parietal activity in this experiment was relatively dorsal (located just inferior to the intraparietal sulcus) and posterior (restricted to the angular gyrus) compared to previous reports of recollection-related retrieval.

The current experiment intends to expand upon these previous findings by manipulating old/new ratios during a remember/know memory test. Subjects will participate in eight memory test sessions, some of which will contain 70% old items and some will contain only 30% old items. Subjects will be made explicitly aware of these probability manipulations in the hopes that they will use this information to guide their memory decisions. In order to separate responses made via familiarity from those made by recollection, subjects will make either a 'know' or a 'remember' respectively. Recognition performance will aim to be higher than the previous experiment by Aminoff et al. (2014) so that recollection-related retrieval will be more

likely to occur, but low enough that subjects will use the probability information to guide their memory decisions when they are unsure of their response. It is predicted that 'know' responses will activate relatively dorsal parietal regions and that these responses and the associated neural activity will be modulated by the changes in base rate information. Specifically, it is predicted that the dorsal parietal regions will be more active during the unlikely (30% old) condition. 'Remember' responses are predicted to activate relatively ventral parietal sub-regions. However, due to the mixed results of behavioral experiments and to the lack of a behavioral effect in the Vilberg & Rugg study, it is not clear at this point whether this probability manipulation will at all affect remember responses or its associated parietal activity. If activity in this ventral region *is* found to be modulated by this manipulation, then this would be evidence that this region, like the more dorsal parietal area, is reflecting some extra-mnemonic cognitive process that is associated with memory retrieval as opposed to directly reflecting the retrieved memory content itself.

Methods

Subjects

Twenty-four healthy subjects (15 female) took part in this study. Subjects ranged in age from 19 – 34 years old (M = 24.4, SD = 4.7). Data from three additional subjects were not included in any reported analyses (one due to a failure to complete all functional runs, one due to a technical failure, and one subject did not make any remember responses). All subjects were native English speakers and right-handed.

All subjects gave informed consent as approved by the UCSB Institutional Review Board and were paid for their participation.

Stimuli

Stimuli consisted of 640 nouns selected using the MRC Psycholinguistic Database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). For counterbalancing purposes, words were pseudorandomly divided into two lists of 320 words each. These lists were matched (as closely as possible) on ratings of concreteness, familiarity, imagability, Kucera Francis written frequency, number of letters and number of syllables. Words were back projected onto a screen at the head of the scanner bore and were visible to the subject by a mirror mounted on the head coil. Words were presented in the center of the screen in black 85-point Times New Roman font against a white background. Stimulus presentation was controlled by a MacBook Pro laptop running Matlab R2008a version 7.6.0 (The Mathworks Inc., USA), using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, et al., 2007; Pelli, 1997).

Procedure

Before entering the scanner, subjects engaged in a short practice session that mimicked what they would experience in the scanner. During this practice session, subjects studied a series of words and then participated in two practice test sessions where they completed two remember/know tests, one 'likely' and one 'unlikely'. Just prior to the remember/know test, subjects were given explicit instructions and examples of when to make a 'remember' and a 'know' response. These instructions

were modified versions from those previously used in the literature (Rajaram, 1993) (see Appendix for a copy of the test instructions). In an attempt to ensure that these instructions were understood, after completing the practice remember/know test, subjects were asked what specific details were recalled for the items that were given 'remember' responses. Subjects were not allowed to continue with the procedure until the experimenter was convinced that a proper understanding of when to make a 'remember' vs. a 'know' response was achieved.

Once the practice session was successfully completed, the task consisted of four study runs and eight test runs. The study sessions took place outside of the scanner, while the test sessions were conducted inside of the scanner. During each study run, 72 words (for a total of 288 words) were presented one at a time on the screen for 2 seconds followed by a blank screen for .5 seconds. During each of the study runs, subjects were asked to make an 'Abstract/Concrete' decision about each word via a button press. After the fourth and final study run subjects were placed in the scanner and three anatomical scans were collected that collectively lasted approximately 10 minutes. Following this, subjects began the first of eight test runs. Each test run consisted of 80 words, for a total of 640 test words. For three of the test runs, subjects were correctly told that 70% (56 words) would be from the study session, and for five of the test runs only 30% (24 words) would be from the test session. These test runs were described as 'Likely' and 'Unlikely' respectively and the word 'Likely' or 'Unlikely' remained on the top of the screen throughout the test phase. The reason for the unmatched number of likely and unlikely runs was done in attempt to increase

the number of hits during the unlikely condition. By definition, the unlikely runs have a lower number of old items and this number is further decreased by the segregation of hits into remember and know responses. In order to ensure that enough trials of each type (<15) were made, the number of unlikely runs was increased from three to five.

Each word was displayed on the screen for 2.7 seconds followed by a blank screen for .5 seconds. Subjects were instructed to make a 'remember', a 'know', or a 'new' response for each word. Specifically, a 'remember' response was to be made when recollection occurred, a 'know' response when familiarity was used to make their decision, or a 'new' response if they believed the word was not seen during the study session. a response scale appeared on the screen below the word to help subjects remember which button mapped onto which response option. Subjects alternated between 'Likely' and 'Unlikely' runs, with the order pseudo-randomized between subjects.

After a preliminary analysis of the first 16 subjects, activity within the ventral parietal cortex (associated with remember responses) seemed markedly attenuated from the results observed in the first experiment of this dissertation. We were not sure what was causing this attenuation, but believed it may have been due to the addition of probability information to the design of the experiment. As a result, we had 6 of the subjects come back for an additional day where they performed the exact same task except the old/new ratio was 50/50 for each test run. For the remaining subjects that we had yet to scan, we also had them complete this additional day of

scanning with a neutral (50/50) old/new ratio condition. In total, 13 subjects completed this neutral condition, however three were not included in the final analysis (two due to a technical failure and one subject did not make any remember responses), leaving 10 subjects included in the analyses.

Assignment of words to test condition and to old/new status was pseudo-randomized between subjects. All responses were made using an MRI-compatible button box held in their right hand. To enable event-related analysis, 44 fixation trials were added to each test run. The order of stimulus events during study and test runs was pre-determined by a genetic algorithm that optimized the design efficiency for the old/new contrast (Wager and Nichols, 2003).

MRI Data Acquisition

A 3T Siemens TIM Trio scanner with a standard 12-channel head coil located at the UCSB Brain Imaging Center was used to scan all subjects. Earplugs were provided to minimize noise disturbance and cushions were placed around the subjects' head to minimize movement. A high-resolution anatomical image was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE) with TR = 2.3s, TE = 2.98ms, and FA = 9°. Each volume was collected with 3-D acquisition and consisted of 160 sagittal slices that were each 1.1 mm thick with 1 mm x 1 mm in-plane resolution. The eight functional runs consisted of a T2*-weighted single shot gradient-echo, echo planar image (EPI) sequence sensitive to the BOLD contrast with TR = 1.6s, TE = 30ms, and FA = 90°. Volumes were acquired

parallel to the AC-PC plane in an interleaved pattern using generalized autocalibrating partially parallel acquisitions (GRAPPA). Each volume consisted of 30 slices that were each 3mm thick with a .5 mm gap and a 3 mm x 3 mm in-plane resolution. The first four volumes of each functional scan were discarded to allow equilibration of tissue magnetization.

Preprocessing of MRI Data

SPM8 (Wellcome Department of Imaging Neuroscience) was used to perform standard spatial preprocessing of the MRI data. All functional images were realigned to the first volume of the first functional scan using a least squares approach and a 6 parameter (rigid body) spatial transformation. During realignment, images were unwarped in order to minimize variance caused by the susceptibility-by-movement interaction (Andersson, et al., 2001). The functional images were then coregistered to the anatomical image using the mean functional image generated during realignment. Next, using standard segmentation procedures, the anatomical T1 image was segmented into images of grey matter, white matter, and cerebral spinal fluid. These images were then spatially normalized to the ICBM Tissue Probabilistic Atlases that come standard in SPM8. The parameters of this transformation were then applied to the functional images, which were re-sampled to 3 mm isotropic voxels. Finally, the normalized images were spatially smoothed using an isotropic Gaussian kernel with an FWHM = 8 mm.

Analysis of Functional Data

SPM8 (Wellcome Department of Imaging Neuroscience) was used for further data analysis. Neural activity at stimulus onset was modeled using a delta (stick) function that was convolved with the canonical hemodynamic response function (HRF). To account for differences in response time reaction time was entered into the model as a parametric modulator of the HRF using a first-order linear transform of the delta function. Data across the eight functional runs was concatenated, and session-specific regressors were added into the model. Thirteen event-types were modeled in total. Remember Hits, Know Hits, Correct Rejections, Misses, Know False Alarms, and Remember False Alarms were modeled separately for the Likely and Unlikely runs and there was an additional event-type of No Interest, which was comprised of trials with omitted or multiple responses. The data was high-pass filtered at 128s and an AR(1) model was used to estimate and correct for non-sphericity of the error covariance (Friston, et al., 2002). The general linear model (GLM) was used to obtain parameter estimates of events of interest and subsequent contrast *t*-maps were created for each subject. These contrast maps were then passed on to a second-level random-effects analysis that consisted of testing the contrast against zero using a one-sample *t*- test independently at each voxel across the brain.

Regions of Interest (ROI) Analysis

Marsbar (Brett, Anton, Valabreque, & Poline, 2002) was used to create and analyze BOLD activation from regions of interest (ROIs). Structural ROIs were

determined according to the AAL atlas that is included with the Marsbar software package. Two functional ROIs were created, one to test the familiarity-related activity within the dorsal parietal regions and another to test the recollection-related activity within the ventral parietal regions. The familiarity-related ROI was taken from the Aminoff et al. (2014) experiment mentioned previously in which peak activation was found during the 'hits > correct rejections' contrast. The ROI was 10mm in diameter and centered on the point x = -32, y = -50, z = 44. For the recollection-related ROI, whole-brain fMRI results were collapsed across all eight runs (across likely and unlikely conditions) and the peak voxel of activity from the 'remember hits > know hits' contrast was used as the center of the ROI. The center fell on the point x = -42, y = -55, z = 25 and was 10mm in diameter. For these ROIs, the mean percent signal change from baseline within that region was calculated for each event type. Values representing recollection and familiarity were then calculated for each subject by subtracting the percent signal change from the appropriate events (e.g. subtracting the percent signal change to know hits from the percent signal change to remember hits for remember/know recollection). These values were then averaged across subjects to obtain a mean percent signal change value for each contrast of interest.

Results

Behavioral Results

Subjects' memory accuracy and decision criterion were measured by d' and c

respectively using signal detection theory. For both measures three values were calculated: one for overall recognition (collapsed across remember and know responses), one for recollection (remember responses), and one for familiarity (know responses). A series of paired samples *t*-tests were conducted to compare the results between likely and unlikely conditions. Results revealed no significant difference in overall d', $t(23) = -9.54$, $p = .350$, nor in recollection d', $t(23) = -.242$, $p = .811$. There was however, a significant difference in familiarity d', with the unlikely condition ($M = .35$, $SD = .52$) being significantly higher than the likely condition ($M = .21$, $SD = .58$), $t(23) = -2.70$, $p = .01$. Follow-up analyses revealed that this difference was due to a change in know responses to new items (i.e. false alarms) between conditions, with significantly more false alarms during the likely condition ($M = .24$, $SD = .14$) than during the unlikely condition ($M = .17$, $SD = .09$), $t(23) = 4.124$, $p < .001$. Although there was also a significant difference in know hits between conditions, the magnitude of this difference was much less (likely $M = .30$ vs. unlikely $M = .26$) and thus the difference in memory performance emerged. In addition to hit and false alarm rates, the rate of correct rejections was also compared between probability conditions. Results revealed a significant difference, with a higher correct rejection rate during the unlikely condition ($M = .78$, $SD = .11$) compared to the likely condition ($M = .70$, $SD = .16$), $t(23) = -4.245$, $p < .001$.

Importantly, a significant difference was found between overall criterion (c values) between the two probability conditions, with subjects adopting a more liberal criterion ($M = -.18$, $SD = .40$) during the likely condition compared to the unlikely

condition (M = .03, SD = .37), t(23) = -4.030, p = .001. When looked at separately, this difference was also significant for familiarity criterion (likely M = .68 vs. unlikely M = .85), t(23) = -3.661, p = .001, but no significant difference was found for recollection criterion, t(23) = -1.482, p = .152. For reaction time, the only significant differences between probability conditions were for remember hits and for correct rejections. Remember hits were made significantly faster during the likely condition (M = 1.23, SD = .23) compared to the unlikely condition (M = 1.26, SD = .23), t(23) = -4.126, p < .001. On the other hand, correct rejections were made significantly faster during the unlikely condition (M = 1.33, SD = .19) compared to the likely condition (M = 1.37, SD = .20), t(23) = 2.142, p = .043. Refer to table 4 for a summary of these results.

Table 4

	d'			**c**		
	overall	*rec*	*fam*	*overall*	*rec*	*fam*
Likely	1.53 (.48)	1.80 (.61)	**.21 (.58)***	**-.18 (.40)****	.89 (.47)	**.68 (.40)****
Unlikely	1.58 (.55)	1.82 (.50)	**.35 (.52)***	**.03 (.37)****	.94 (.51)	**.85 (.30)****

TABLE 4: Memory accuracy (d') and response bias (c) are shown. 'Overall' refers to recognition collapsed across remember and know responses, 'rec' refers to recollection (remember responses) and 'fam' refers to familiarity (know responses). Significant differences between the likely and unlikely conditions are shown in bold font and the significance value is indicated with the associated star(s) (p = .01 = *, p = .001 = **).

fMRI Results

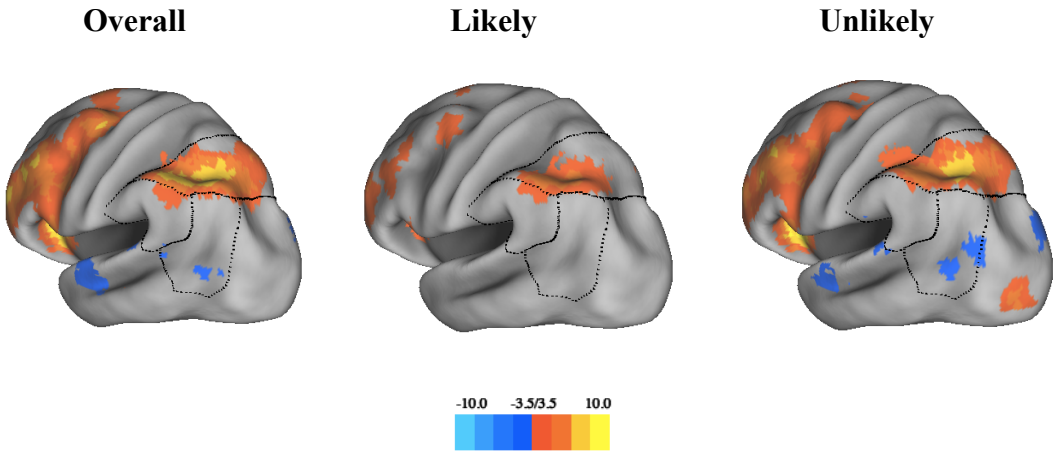
Familiarity was operationalized as the 'know hits > correct rejections' contrast and recollection as the 'remember hits > know hits' contrast. This was done separately for the likely and unlikely conditions. As with experiment 1 in this dissertation, the following analyses focus mostly on the activation in the left hemisphere. The activity within the left hemisphere was significantly stronger and more consistent than that in the right hemisphere. Additionally, it is activity within the left hemisphere that is consistently reported in the memory retrieval literature. Although a subset of subjects participated in a 'neutral condition' (50/50 old/new ratio), no significant neural difference was found within the parietal regions when results from this condition were compared to the likely and unlikely probability conditions. Therefore, all results reported are restricted to data collected during the likely and unlikely conditions. Unless otherwise specified, voxels were tested at a value of $p < .001$ with a voxel extent of 10.

Familiarity & Recollection

During both the likely and unlikely conditions, familiarity (know hits > correct rejections) activated regions within the left prefrontal cortex and areas within the left superior parietal lobule, specifically BA 7. However, the magnitude of this activity as well as its spatial extent was greater during the unlikely condition. During the unlikely condition, familiarity-related activity extended more superiorly and posteriorly into the superior parietal lobule. Recollection-related activity (remember hits > know hits) was confined to more ventral regions of the lateral parietal cortex.

While this contrast revealed relatively robust activity within the supramarginal gyrus (BA 40) and angular gyrus (BA 39) in the likely condition, this activity was greatly attenuated in the unlikely condition. Since the behavioral results revealed a significant difference in correct rejection rate between conditions, we decided to additionally operationalize recollection as the 'remember hits > correct rejections' contrast within each condition. Within the lateral parietal cortex, activity extended both superiorly and inferiorly from the intraparietal sulcus, reaching areas within BA 7, BA 39, and BA 40 for both conditions. Results from this contrast mirror what was found in the previous contrasts, with more dorsal activity during the unlikely condition and more ventral activity observed during the likely condition. For a complete list of peak voxel activations associated with these results, see Table 5.

A. Familiarity Activity



B. Recollection Activity

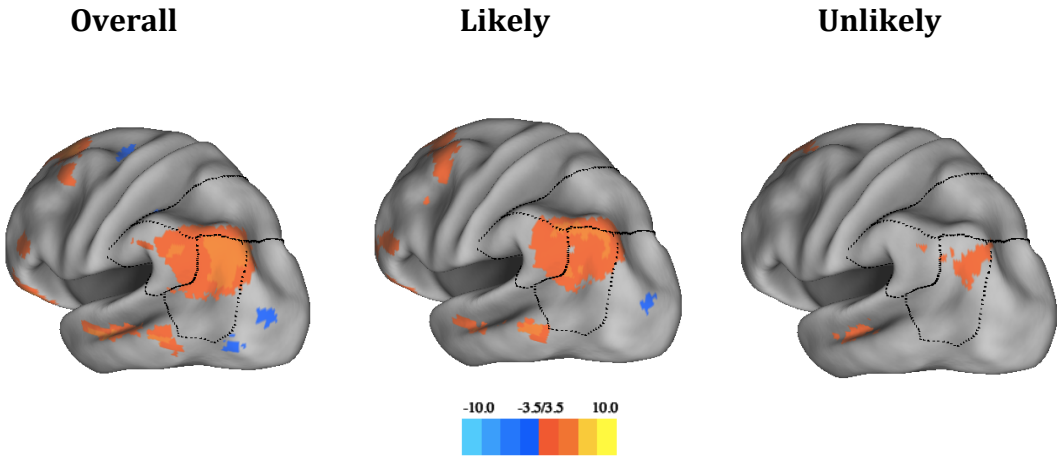


FIGURE 5: Group-results ($p < .001$, voxel extent = 10) for Familiarity[A] and Recollection[B]. Familiarity was defined by the 'Know hits > Correct rejections' contrast while recollection was defined by the 'Remember hits > Know hits' contrast. Results are shown for all eight runs collapsed across likely and unlikely conditions (overall), as well as separately for likely and unlikely runs.

Table 5

A. Familiarity-Related Activity

X Y Z Coordinates (MNI)	Hemi - sphere	Brain Region	BA	t value	Cluster size (voxels)
-9 26 43	Left	Superior Frontal Gyrus	32	7.07	365
-9 17 52	Left	Superior Frontal Gyrus	6	6.56	*
15 17 64	Right	Superior Frontal Gyrus	6	4.53	*
-48 -46 55	Left	Superior Parietal Lobule	7	6.60	397
-45 -55 49	Left	Superior Parietal Lobule	7	6.21	*
-30 -58 40	Left	Superior Parietal Lobule	7/19	5.46	*
-42 53 10	Left	Middle Frontal Gyrus	46	5.53	425

-45	50	1	Left	Middle Frontal Gyrus	46	5.38	*
-48	32	31	Left	Middle Frontal Gyrus	9	4.61	*
-9	-67	40	Left	Precuneus	7	5.33	90
-36	5	52	Left	Middle Frontal Gyrus	6	4.69	67
-33	11	40	Left	Middle Frontal Gyrus		3.90	*
-3	-22	28	Left	Posterior Cingulate Gyrus	23	4.60	26
12	29	28	Right	Anterior Cingular Gyrus	32	4.37	18
12	14	10	Right	Caudate		4.16	17
39	-58	43	Right	Superior Parietal Lobule/Lateral Occipital Cortex	7/19	4.11	14
36	23	4	Right	Insular Cortex		3.82	20
27	26	-2	Right	Insular Cortex		3.61	*

B. Recollection-Related Activity

X Y Z Coordinates (MNI)			**Hemi - sphere**	**Brain Region**	**BA**	**t value**	**Cluster size (voxels)**
-15	44	49	Left	Superior Frontal Gyrus	8	6.13	74
-21	32	49	Left	Superior Frontal Gyrus	8	5.40	*
-6	47	10	Left	Medial Frontal Gyrus	9	5.82	384
-9	59	22	Left	Superior Frontal Gyrus	9	5.62	*
-9	62	10	Left	Medial Frontal Gyrus	10	5.35	*
-39	-73	40	Left	Angular Gyrus / Lateral Occipital Cortex	39/19	5.27	101

-54	-61	25	Left	Angular Gyrus	39	5.04	*
-45	-67	40	Left	Angular Gyrus	39	4.76	*
-57	-19	-14	Left	Middle Temporal Gyrus	21	5.14	19
-57	-43	-5	Left	Middle Temporal Gyrus	21	4.58	12
-9	-58	16	Left	Precuneus / Posterior Cingulate Cortex	30	4.05	12

TABLE 5: Information from peak voxels for Know Hits > Correct Rejections[A] and Remember Hits > Know Hits[B], contrasts from the group analysis across all eight test runs (collapsed across likely and unlikely conditions). Closest Brodmann areas (BA) labels are provided when possible. * denotes that the peak voxel is part of the cluster in the row(s) directly above it.

Direct Comparisons

To directly compare the neural activity between the likely and unlikely conditions, a series of paired-samples *t*-tests were conducted. No significant activations were found when familiarity-related activity was compared between conditions. Similarly, when recollection was operationalized as the 'remember hits > know hits' contrast, no differences in active voxels were revealed. However, when recollection was operationalized as the 'remember hits > correct rejections' contrast, a region within the left ventral parietal cortex, specifically within the angular gyrus, was revealed to be more active during the likely condition compared to the unlikely condition.

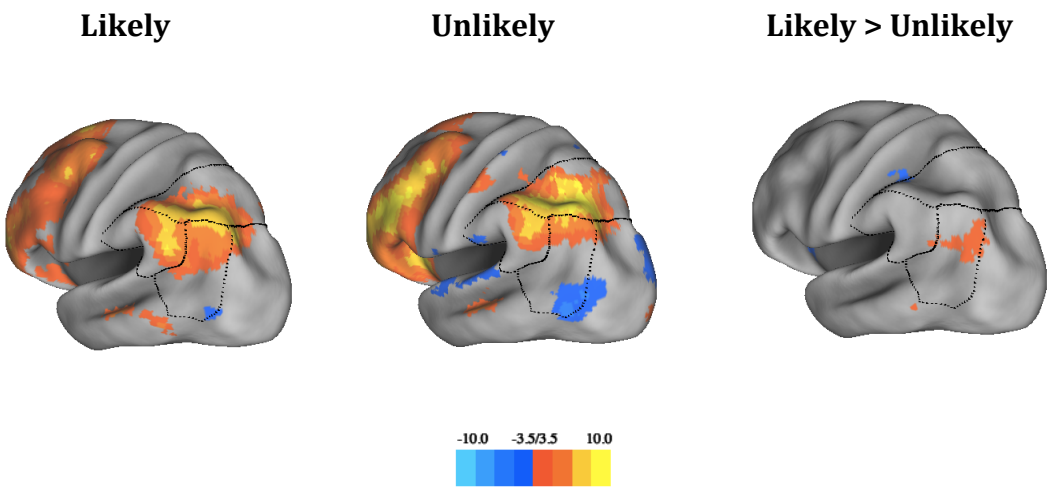


FIGURE 6: Group-results ($p < .001$, voxel extent = 10) for Recollection as defined by the 'Remember hits > Correct rejections' contrast. Results are shown separately for likely and unlikely conditions as well as the direct contrast for Likely > Unlikely runs.

Table 6

Recollection (Remember Hits > Correct Rejections): Likely > Unlikely

X Y Z Coordinates (MNI)	Hemi - sphere	Brain Region	BA	t value	Cluster size (voxels)
-15 -10 40	Left	Cingulate Gyrus	24	5.32	28
66 -43 19	Right	Supramarginal Gyrus	40/22	4.82	13
-45 -76 31	Left	Angular Gyrus	39	4.60	95
-39 -55 22	Left	Angular Gyrus	39	4.16	*
-51 -61 25	Left	Angular Gyrus	39	3.90	*
-3 44 -8	Left	Anterior Cingulate Gyrus	32	4.56	83
-9 32 -8	Left	Anterior Cingulate Gyrus	24	4.44	*
-3 56 -5	Left	Medial Frontal Gyrus	10	4.24	*

-6	-52	28	Left	Posterior Cingulate Gyrus	31	4.09	41
-9	-52	16	Left	Posterior Cingulate Gyrus / Precuneus	30	4.01	*

TABLE 6: Information from peak voxels for likely recollection > unlikely recollection. Recollection was defined as the 'Remember hits > Correct rejections' contrast. Closest Brodmann areas (BA) labels are provided when possible. * denotes that the peak voxel is part of the cluster in the row(s) directly above it.

Results Based on Criterion-Shifting

Although there was no significant difference in remember criterion between probability conditions across all subjects, there was a great deal of individual variability. To further investigate this, we divided subjects into different groups based on how much they shifted their criterion between conditions. We took the top ten subjects who appropriately (i.e. in the right direction) shifted their remember criterion between conditions and considered them the 'high shift group'. Likewise, we took the bottom ten subjects who did not shift at all or shifted in the opposite direction between conditions and considered them the 'low shift group'. Behaviorally speaking, what separated these two groups of subjects from each other was not a difference in remember hit rate, but instead a difference in remember false alarm rate. The same analysis as above was performed on these groups separately. When recollection was operationalized as the 'remember hits > know hits' contrast, no lateral parietal regions survived the relatively high threshold ($t = 4.3$ with N = 10). However, when recollection was operationalized as the 'remember hits > correct rejections' contrast, a striking difference was observed between the 'high switch group' and 'low switch group', specifically within the likely old (70%) condition.

Within the 'high switch group', lateral parietal activity was relatively robust and crossed well below the intraparietal sulcus into areas within the supramarginal gyrus (BA 40) and the angular gyrus (BA 39). For the 'low switch group', hardly any lateral parietal cortex activity was observed at all, with the relatively small activations that were present occurring above the intraparietal sulcus within the superior parietal lobule (BA 7).

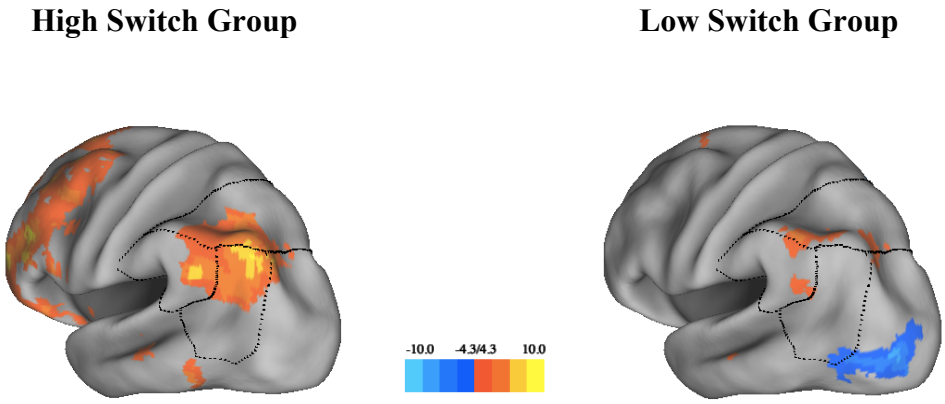


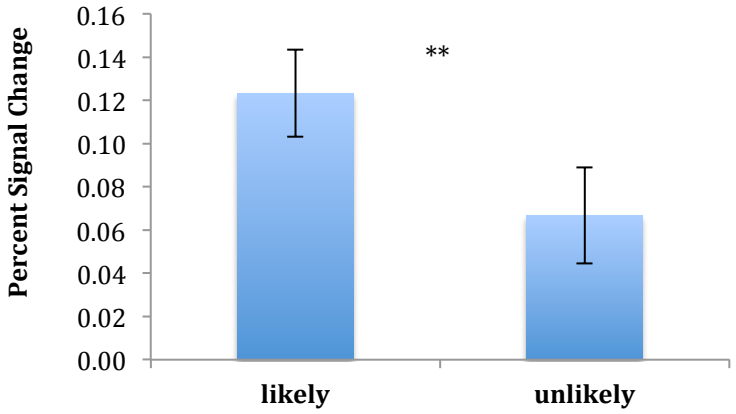
FIGURE 7: Group-results ($p < .001$, voxel extent = 10) for Recollection as defined by the 'Remember hits > Correct rejections' contrast. Results are shown separately for subjects who switched recollection-related criterion (high switch group) and for subjects who did not switch their recollection-related criterion (low switch group).

Regions of Interest (ROI) Analysis

Percent signal change from (implicit) baseline was calculated for each event type for each subject. To calculate the percent signal change associated with recollection and familiarity, the following subtractions were performed: 'Remember hits – Know hits' and 'Know hits – Correct Rejections', respectively. Figure 8 shows the mean (across subjects) percent signal change for these events calculated within the dorsal

parietal ROI (for familiarity) and ventral parietal ROI (for recollection). Familiarity and recollection-related activity between the likely and unlikely conditions was then compared. Although there was a numerical difference for familiarity-related activity within the dorsal ROI (with higher activity during the unlikely condition), results from a paired samples *t*-test showed that this result was not significant, $t(23) = -.70$, $p = .491$. Similarly, although there was a numerical difference for recollection-related activity within the ventral ROI (with higher activity during the likely condition), results from a paired samples *t*-test revealed that this result was not significant, $t(23) = .69$, $p = .497$. When recollection was operationalized by the 'Remember hits – Correct Rejections' contrast, a paired samples *t*-test revealed a significant difference, with more activity during the likely condition ($M = .12$, $SD = .10$) compared to the unlikely condition ($M = .07$, $SD = .11$), $t(23) = 3.41$, $p = .002$. Further investigation into this result revealed no significant difference between the activity to remember hits, $t(23) = .969$, $p = .343$. It seems that the result was driven by a significant difference in activation to correct rejections, with more activity during the unlikely condition ($M = -.16$, $SD = .10$) compared to the likely condition ($M = -.12$, $SD = .07$), $t(23) = -.253$, $p = .019$.

A. Recollection-Related Activity



B. Correct Rejection-Related Activity

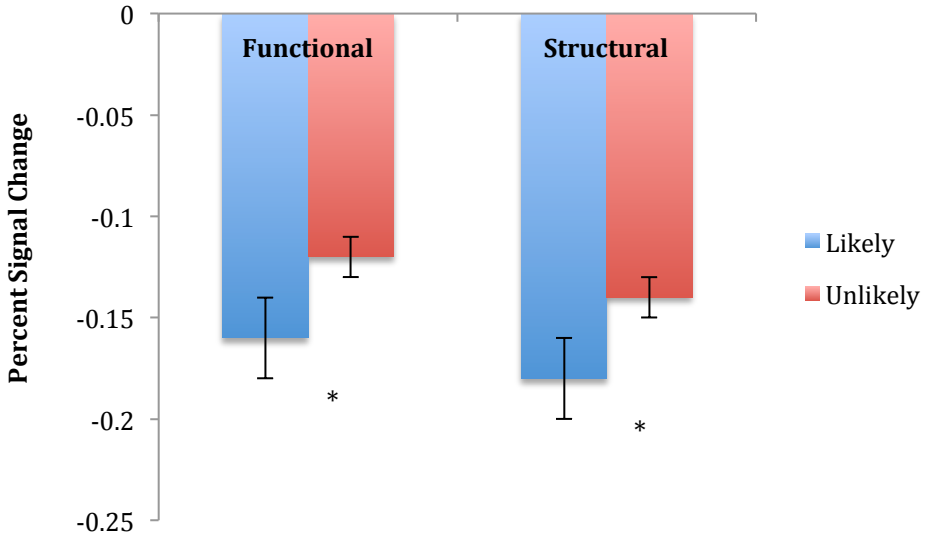
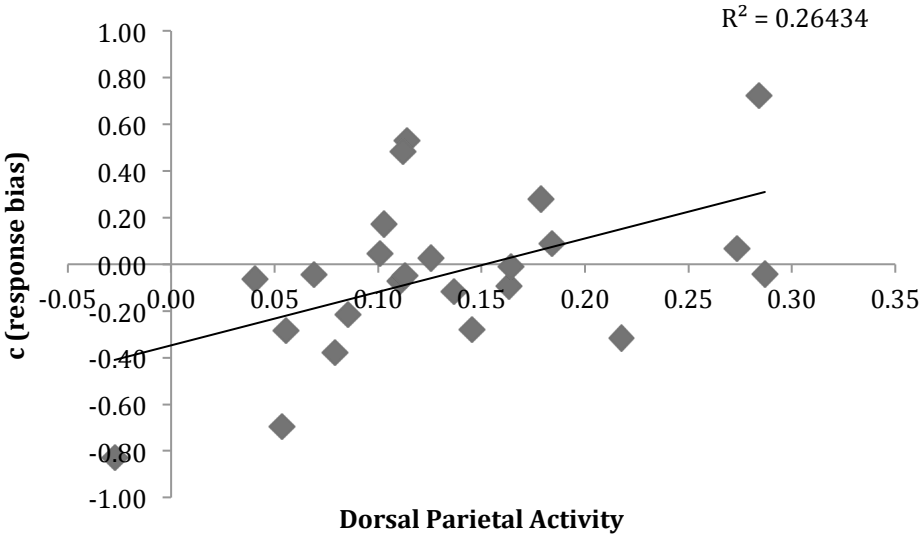


FIGURE 8: Mean (across subjects) percent signal change for recollection[A] and correct rejections[B]. Recollection is operationalized as the 'remember hits > correct rejections' contrast and is shown for likely and unlikely conditions separately within the functionally-defined ROI. Activity to correct rejections versus baseline is shown for likely and unlikely blocks for both the functionally-defined and structurally-defined ROI. Error bars represent the standard error of the mean. Significance values are indicated with the associated number of stars ($p < .05$ = *, $p < .01$ = **).

Individual Differences Analysis

Particularly because there was a relatively large degree of variability between subjects in terms of their memory accuracy (d') and their criterion setting (c), we wanted to see how these behavioral differences related to changes in parietal activity. We correlated activity (using the 'hits > correct rejections' contrast) within the dorsal and ventral parietal ROIs with each subjects' overall criterion value as well as with their overall d' value. Results revealed a significant positive correlation between dorsal parietal activity and criterion, $r(22) = .50$, $p = .012$. No significant relationship was found between dorsal parietal activity and d', $r(22) = .15$, $p = .50$. For the ventral parietal ROI, the reverse pattern was observed. Results revealed a significant positive correlation between ventral parietal activity and d', $r(22) = .628$, $p = .001$, while no relationship was found with criterion, $r(22) = -.137$, $p = .522$.

A. Familiarity-Related Activity



B. Recollection-Related Activity

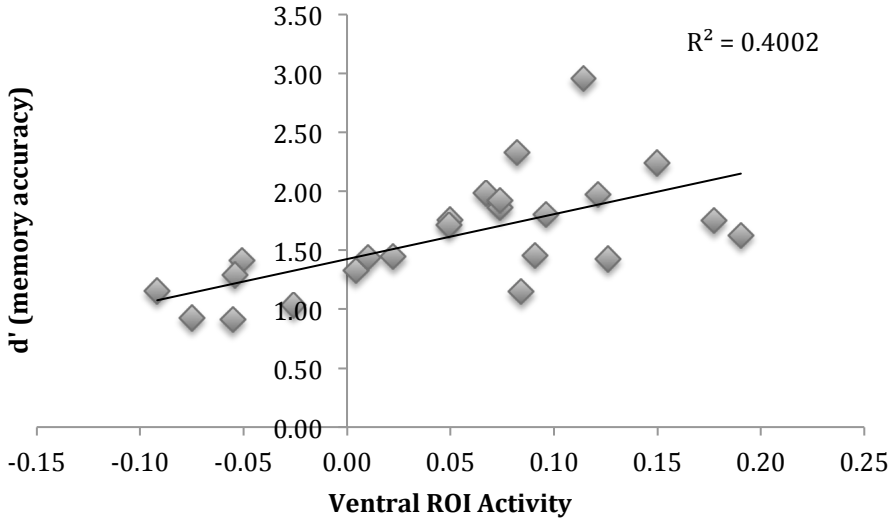


FIGURE 9: Relationship between the activity in dorsal parietal activity during familiarity (know hits > correct rejections) and subjects' criterion[A] and the relationship between activity within the ventral parietal activity during recollection (remember hits > know hits) and subjects d'[B].

Discussion

In the current experiment, subjects performed a remember/know test under two different probability conditions. In one condition (the likely condition) there was a high probability (70%) that items were old, in the other (the unlikely condition) there was a low probability (30%) that items were old. In agreement with previous literature (Strack & Forster, 1996; Aminoff et al., 2012, 2014; Van Zandt, 2000, Verfaellie et al., 2001; Hirshman & Henzler, 1998), this manipulation had the intended effect of changing subjects' criterion between conditions. Generally speaking, in the likely condition subjects adopted a more liberal criterion setting, essentially requiring less mnemonic information in order to endorse an item as old. Although this adjustment of criterion was found when collapsed across both recognition types and also for familiarity, no significant difference in criterion setting was found for responses associated with recollection. This result is in line with the idea that recollection is a threshold process, i.e. one that either occurs fully or not at all, and as a result should not be affected by changes in criterion (Mandler, 1980; Yonelinas, 1997, 2001). On the other hand, familiarity is often described by signal detection theory as existing as a continuum, one which can be influenced by changes in response strategies, including changes in criterion setting (Wixted, 2007; Mickes, et al., 2009).

However, in the current experiment there was a significant degree of individual variability in rates of recollection-related criterion changes between conditions. Although most subjects did not vary their recollection response strategies (i.e.

criterion) between probability conditions, there were those who did. For those subjects, the difference in response pattern was mostly driven by a change in recollected false alarm rates. Those who shifted their recollection criterion falsely endorsed more new items as 'remembered' during the likely condition than during the unlikely condition. Therefore there is some evidence that at least for some individuals even recollection can be affected by manipulations of probability. This individual variability may explain why there is a disagreement in the literature upon whether recollection is or is not affected by manipulations of criterion setting, with some results reporting shifts in recollection rates (Strack & Forster, 1995) and others not (Postma, 1999; Hirshman & Henzler, 1998).

Turning to the neural results reveals a general dorsal/ventral dissociation within the lateral parietal cortex for responses associated with familiarity and recollection respectively. Specifically, familiarity-related responses activated the area around the intraparietal sulcus and extended dorsally into the superior parietal lobule. Recollection-related responses activated areas inferior to the intraparietal sulcus, extending into the angular gyrus and supramarginal gyrus. This general dissociation is in line with the first experiment of this dissertation and also with a wealth of evidence from the literature (for reviews see Ciaramelli et al., 2008 or Vilberg & Rugg, 2008).

Although familiarity activated the superior parietal lobule during both the likely and unlikely conditions, this activity was stronger and covered a larger cortical area during the unlikely compared to the likely condition. This difference, although not

statistically significant, is at least in general agreement with the findings of Aminoff et al. (2014) who found more dorsal parietal activity during unlikely compared to likely trials. A highly possible reason for the lack of significance in the current study may be due to the smaller behavioral effect. In the current experiment, the average criterion shift for familiarity responses was .18, compared to the whopping .62 reported in the Aminoff et al. (2004) experiment. As previously explained, we aimed for a higher d' value in the current study in order to obtain a satisfactory number of recollection-related responses. As a result of an increased d', subjects relied less on the probability information to make their decisions, and therefore shifted their criterion to a lesser degree. With such a low shift amount, it is not surprising that the neural results were not statistically significant between conditions in the current experiment. Nevertheless, the fact that there was generally more activity in the dorsal parietal areas during the unlikely condition is in agreement with the previous finding from Aminoff and colleagues. Another finding from the current study that is in agreement with results from the Aminoff et al. (2014) study is the fact that activity within the dorsal parietal cortex was strongly positively correlated with subjects' criterion setting. This finding suggests that this parietal sub-region may be modulated by cognitive processes that are related to top-down attention which may be recruited when more stringent monitoring of potential memory content is required (i.e. during a time when old items are unlikely).

Results associated with recollection-related retrieval showed an opposite pattern of results from those associated with familiarity. The ventral activity observed for the

'remember hits > know hits' contrast seemed to be greatly driven by the results from the likely condition. When examined separately, a relatively large extent of the angular gyrus and supramarginal gyrus was active during recollection in the likely condition. This ventral parietal activity was greatly attenuated when examining results from the unlikely condition. However these results, like those in the dorsal areas, did not turn out to be statistically significant and are therefore difficult to interpret. At the very least, there seems to be a general trend that more activity was observed in the ventral parietal regions during the likely compared to the unlikely condition. The lack of a significant finding (at least when recollection was operationalized by the 'remember hits > know hits' contrast) may have to due with the low remember criterion shift amount between conditions. On average, subjects shifted their remember criterion a dismal amount of .06 between conditions. Perhaps if a stronger behavioral effect had been observed, a stronger neural result would have also been found. This idea is strengthened by the fact that those who did shift their remember criterion (high shift group) had an augmented neural difference between conditions, with relatively robust ventral parietal activity during the likely condition, while those who did not shift exhibited hardly any activity within this region.

Probably the most interesting and unexpected result from this study is the fact that activity was the most varied between conditions for responses that were associated with correct rejections. Using both functionally-defined and structurally-defined ROIs, results revealed significantly more activity within the ventral parietal areas (particularly the angular gyrus) for correct rejections made during the unlikely

compared to the likely condition. These results are consistent with previous reports of modified ventral parietal activity to correct rejections based on subjects' expectancies (O'Connor et al., 2010), subjects' confidence (Cabeza, 2008) with one report even showing a reverse old/new effect (greater activity to correct rejections than to hits) when new items were relatively infrequent (Jaeger et al., 2013).

Collectively these findings are difficult to reconcile with an episodic buffer account of parietal activity during memory retrieval. According to this theory, no difference in parietal activity should have been observed between the likely and unlikely probability conditions. Since modulations *were* found between conditions, this provides evidence against an episodic buffer account and suggests instead that these parietal activations most likely reflect some extra-mnemonic cognitive process(es) that occur during memory retrieval.

Chapter 4: Overall Discussion and Conclusions

Summary of Results

The purpose of experiment 1 was to directly compare the two most popular methods of separating items that are retrieved with familiarity from those recognized with recollection. Those two methods are the remember/know paradigm and tests involving source memory. These methods have been used somewhat interchangeably in the literature and have even been described as equivalent methods of separating recollection and familiarity during a recognition test (Mark & Rugg, 1998; Rugg et al., 1998; Yonelinas & Jacoby, 1995). This claim has been made despite the vast differences in task demands associated with each methodology. For instance, the remember/know task is much more subjective and inclusive in what is considered evidence for recollection, while the source task is comparably objective and exclusive in operationalizing recollection. Despite this, no experiment has adequately and directly compared the neural correlates of recollection and familiarity as operationalized by each method.

Experiment 1 served as this direct comparison and had the same group of subjects complete a remember/know test and a source memory test while their brain activations were recorded with fMRI. Results from both tests showed the ubiquitous dorsal/ventral parietal dissociation between familiarity and recollection, respectively. Activation relating to familiarity occurred around the left intraparietal sulcus (IPS) and extended well into the superior parietal lobule (SPL) during both the remember/know and source memory tests. Similarly, regardless of what test was used,

recollection-related activity occurred within the ventral parietal regions, activating the inferior parietal lobule (IPL), with overlap within the angular gyrus. Although both tests revealed this general dissociation, the extent and magnitude of this activation varied significantly between testing methodologies. Specifically, the source task activated the dorsal parietal areas to a larger magnitude and extent during familiarity-related recognition compared to that seen during the remember/know test. Conversely, the ventral parietal regions were more activate during recollection as operationalized by the remember/know test compared to the source test. While the angular gyrus was active for both tests of recollection, it was significantly more active during the remember/know test. Additionally, the supramarginal gyrus was only found to be active when recollection was identified by the remember/know test, with activation failing to reach significance during source recollection.

The goal of experiment 2 was to test whether ventral parietal regions, like dorsal parietal regions, are influenced by changes in criterion setting. Subjects performed a remember/know test under two different probability conditions. One condition was a likely scenario where 70% of the items were from the studied list. The other condition was an unlikely scenario where only 30% of test items were from the studied list. This is the first fMRI experiment to combine the use of a remember/know test with changes in the base rates of old and new items. Behavioral results showed that subjects did in fact modify their criterion between conditions (albeit a relatively small change), adopting a more liberal criterion during likely compared to unlikely trials. When responses were looked at separately for trials

associated with familiarity and recollection, it was evident that this criterion change was driven mostly by changes in familiarity-based criterion. That is, responses made with familiarity were the most sensitive to changes in the probability of the item being from the study list, with recollection-related responses left relatively unaffected. This difference in influence upon familiarity and recollection is in line with previous accounts of recollection being a threshold process, impervious to changes in response strategies (Mandler, 1980; Yonelinas, 1997, 2001), while familiarity is based on a continuum of mnemonic evidence that is heavily reliant on decision-based strategies the subject may employ (Wixted, 2007; Mickes, et al., 2009).

Neural activity within the lateral parietal cortex associated with recollection and familiarity were investigated separately. As in experiment 1, the ubiquitous dorsal/ventral parietal dissociation was found for items recovered with familiarity and recollection. Results from these contrasts were then compared between the likely and unlikely testing conditions. Although no statistically significant difference was found between the conditions, a general trend was that there was more familiarity-related activity in the dorsal parietal areas during the unlikely condition while there was more recollection-related activity in the ventral parietal areas during the likely condition. This ventral parietal difference was found to be significant when recollection was operationalized by comparing activity during hits made with a remember response to activity made when items were correctly rejected. Specifically, an area within the angular gyrus was found to be more active during recollection in the likely condition.

A somewhat unexpected result from this experiment was the modulation of ventral

parietal activity (particularly within the angular gyrus) when correct rejections were made. Correct rejections made during unlikely testing conditions activated this region to a larger magnitude than correct rejections made during likely conditions. This region is usually found to be active when memories are successfully retrieved, and it is thought to be involved with this retrieval process – either directly by temporarily storing the retrieved content (episodic buffer theory) or by contributing to some cognitive process (e.g. attention) that is engaged when content is retrieved. Since by definition, no memory content is being actively retrieved when correct rejections are made, it is somewhat surprising that this area was found to be modulated by whether or not new test items were likely to be encountered.

Finally, results from the ROI analysis showed significant relationships between activity within the parietal areas and behavioral performance on the memory test. How these relationships manifested depended on what part of the parietal cortex was measured. Specifically, dorsal parietal activity was found to be positively correlated with subjects' criterion setting, but no relationship was found for subjects' memory accuracy. On the other hand, ventral parietal activity was found to be positively correlated with subjects' memory accuracy with no correlation evident with criterion setting.

Relation to Theories of Parietal Theories

As outlined in the introduction of this dissertation, there exists a variety of theories to explain how lateral parietal activity relates to successful memory retrieval. The

biggest divide in the literature is whether this region is directly related to memory retrieval or whether it is involved with some extra-memory process that co-occurs with successful retrieval. The episodic buffer theory maintains that the parietal cortex is directly related to memory retrieval in that it acts as a temporary storage area for recovered episodic content (Wagner, 2005, Vilberg & Rugg, 2008). According to this account, this region acts much like the working memory buffers proposed within the prefrontal cortex by Baddeley (2000), storing information until a decision can be made. Others argue that the parietal cortex is not directly related to memory processes, but instead indirectly related by fostering some cognitive process that aids in successful memory retrieval, but is not necessary for it to occur. These theories include modulating top-down and bottom-up attention to retrieved memory content, accumulating mnemonic evidence of an 'old' response, and maintaining a sense of self-awareness and ownership of the contents of one's memories.

While the results of the current experiments cannot definitively explain what function the lateral parietal cortex is playing during memory retrieval, they seem to be the least consistent with the theory of an episodic buffer account. The results from the first experiment revealed a modulation of activation within both the dorsal and ventral parietal regions depending on what methodology was used to identify recollection and familiarity. This modulation is difficult for the episodic buffer theory to explain. While there is no reason to believe that these different methodologies should trigger a difference in the *amount* of information retrieved, they may have differed in the cognitive demands that were required for successful retrieval to occur.

Some of the processes suggested for the dorsal parietal area include: a modulation of top-down attention (Cabeza, 2008; Cabeza et al., 2008; Cabeza, Ciaramelli, & Moscovitch, 2012; Ciaramelli et al., 2008), retrieval orienting (Dobbins & Wagner, 2005; O'Connor, et al., 2010; Jaeger, et al., 2013), and the conservativeness of the subject's criterion (Aminoff et al., 2014). Although all three of these cognitive processes should occur during both the remember/know and source memory tests, one could argue that these processes may be in higher demand during the source memory test. While the results from this study cannot directly compare these competing theories, they go along with the general idea that source decisions as compared to remember/know decisions may result in additional cognitive processing. For instance, the very act of attempting to retrieve a specific contextual detail (as is required in the source test) has been shown to increase activity within the lateral parietal cortex. Specifically, simply orienting towards this type of source-related retrieval, even when it is not successful, has led to increased activity levels in the dorsal parietal regions, compared to when standard recognition is attempted (Dobbins & Wagner, 2005; Dobbins, Rice, Wagner, & Schacter, 2003). Additionally, source memory responses, as compared to remember/know decisions, may require an increase in top-down attention in order to navigate through the contents of memory to find that specific piece of contextual information. While remember responses can be made based on the retrieval of *any* contextual information, source responses are dependent upon the retrieval of *specific* contextual information. As described by Ciaramelli et al. (2008), this information may not be the first that pops into the subject's mind, and therefore,

may have to be strategically searched for. This often effortful search may require additional resources from ancillary cortical areas that may control functions such as top-down attention (Cabeza, 2008; Cabeza et al., 2008; Cabeza et al., 2012; Ciaramelli et al., 2008) or the orienting towards such types of associative retrieval (Dobbins & Wagner, 2005; O'Connor, et al., 2010; Jaeger, et al., 2013). This may be why some previous studies have shown additional activity in posterior parietal and prefrontal cortices when comparing source judgments to remember responses (Duarte, Ranganath, & Knight, 2005; Ciaramelli et al., 2008).

Numerous studies have shown that activity levels within the dorsal parietal cortex increases as the difficulty in memory search increases (Cabeza, 2008; Ciaramelli et al., 2008; Kim & Cabeza, 2007; Henson et al., 2005). In the current study, hits made during the source task took a significantly longer amount of time to make compared to hits made during the remember/know task (both for recollection and familiarity) suggesting that some additional cognitive processing was occurring during this test. Although we can't make claims as to what specific cognitive process(es) may be occurring during the source test, the fact that a greater level of activity was found in the dorsal parietal regions is consistent with the idea that *some* additional processing is occurring in this test that is not occurring during the remember/know test.

Some proponents of the episodic buffer theory have argued that this account only pertains to the more ventral sub-regions of the lateral parietal cortex. Even if this modification of the theory is applied, it is still hard to reconcile with the results from experiment 1. The modulation of parietal activity was not confined to areas within

the dorsal parietal areas, but extended well past the intraparietal sulcus into the more ventral sub-regions of this cortical region. In contrast to the dorsal modulation, ventral parietal regions were more active during recollection as operationalized by the remember/know task compared to the source task. Again, there is no reason why a difference in the amount of episodic content should vary between testing methodologies, so this result is difficult for the episodic buffer theory to explain. Even if one were to argue that there should be a difference in amount of retrieved episodic content, if anything, the results should have been the opposite in order to fit with a buffer account. As Vilberg and Rugg have previously argued (2006, 2007), there may be more episodic content retrieved with recollected memories identified by the source task compared to the remember/know task. Their rational is as follows: there is no reason to assume that source recollections do not have so called 'non-criterial' episodic content associated with them that would be relevant for the source task. In other words, if a subject is able to retrieve the specific piece of source information, they most likely are also able to retrieve additional contextual information from the study episode that is not relevant to the source task. On the other hand, one cannot assume that just because any piece of contextual information is retrieved (as recollection is operationalized by the remember/know task) that the specific source information is also retrieved. According to this logic, source recollections should contain *more* episodic content than remember/know recollection. If this is the case, then according to the episodic buffer theory, more not *less*, ventral parietal activity should have been revealed by the source test. The very same

argument could be used against a mnemonic accumulator theory of parietal activity. If anything, this theory should predict more activity during the source task because the more content that is retrieved, the more an 'oldness' signal there is to be accrued.

On the other hand, increased remember/know recollection-related activity is much more parsimonious with theories that suggest an indirect role of parietal involvement in memory retrieval. Of all the indirect theories, the one that best fits with these results is the subjective awareness account. As previously described, the remember/know test is much more subjective in its operationalization of recollection as compared to the source task. The retrieval of *any* contextual information is relevant for the remember/know task. Such information may include autobiographical memories (e.g. previous memories that the subject associated with the particular word) or self-referential processing (e.g. "*I* remember what *I* was thinking about when *I* saw that word on the study list") that would be sufficient to make a remember but not a source response. According to the subjective awareness account of parietal activity, this type of information should activate the parietal regions. Since this information is not relevant to source recollection, the fact that activity within this region was attenuated during the source task is in agreement with the general predictions of the subjective awareness explanation of parietal activity.

Results from experiment 2 are also difficult to reconcile with an episodic buffer account of parietal activity. Again, according to this theory, no difference in retrieval-related parietal activity should have been found between likely and unlikely conditions. Contrary to this, a general trend revealed higher activation levels within

the dorsal parietal cortex during familiarity-related retrieval in the unlikely condition, and higher activation within the ventral parietal cortex during recollection-related retrieval in the likely condition. If any difference in episodic content were to be expected, then one might be able to argue that more content should be retrieved during the unlikely condition. During this condition, subjects are not expecting to encounter many studied test items, and as a result, they behaviorally shifted their criterion to a more conservative level. Effectively this means that only memories with a higher level of episodic content will surpass this conservative criterion setting and be considered 'old'. If this were the case, then memories successfully identified as old during the unlikely condition should have a higher degree of episodic content than those endorsed as 'old' during the likely condition. The same rationale could be used for a mnemonic accumulator theory (e.g. stronger memories in the unlikely condition should lead to stronger 'oldness' signals). As previously described, the opposite pattern of results were found within the ventral parietal regions (the area suggested as an episodic buffer), suggesting something other than an episodic buffer explanation.

Furthermore, when subjects were split into groups based on whether they shifted their remember criterion or not, this difference in ventral parietal activity was augmented. Those who effectively switched their recollection criterion showed extensive ventral parietal activity, while those who did not, showed hardly any ventral activation at all. Behaviorally, these two groups differed in their recollection memory accuracy. Specifically, those who shifted had a significantly lower recollection d'

than those who did not. This difference was mostly due to an increase in the occurrence of incorrectly recollecting a non-studied item (i.e. false alarm). If an episodic buffer account is used to explain this activity, then the group with the higher d' should have shown *greater* parietal activity, not less.

Instead, the results from experiment 2 are more in line with those from experiment 1. The dorsal parietal regions were more active when subjects most likely had to engage more top-down attentional resources to monitor retrieved content when it should not have been expected (i.e. during the unlikely condition). When subjects increase their criterion setting, they are requiring more mnemonic evidence to override a prepotent 'new' response. In fact, activity within this dorsal parietal region was shown to be positively correlated with subjects' criterion level. The more carefully a subject was monitoring this unexpected memory information, the more the dorsal parietal cortex was recruited. This finding is in agreement with the previous study by Aminoff et al. (2014) showing a similar positive relationship between criterion setting and dorsal parietal activation levels.

The finding of increased ventral parietal activity during the likely condition is not only difficult to reconcile with an episodic buffer account, but it also conflicts with predictions made by a bottom-up attention account of ventral parietal activity. According to this theory, ventral parietal activity should have been maximal when mnemonic information was retrieved unexpectedly. Proponents of this theory have claimed that the bottom-up attentional system is maximally engaged when items are infrequent, much like during 'odd-ball' tasks in the perception literature (for a review

see Corbetta & Shulman, 2002). When memories are unexpectedly retrieved, the bottom-up attention system is supposed to act as a circuit-breaker, reorienting internal attention to the unexpected information (for a review see Cabeza et al., 2008). According to this theory then, the ventral parietal cortex should have been maximally active during the unlikely condition. As previously described, the opposite pattern of results was revealed, with relatively greater activity within the ventral parietal regions during the likely condition.

It is somewhat unclear to predict what results should have been revealed according to the subjective awareness account of ventral parietal activity. However, the reported results are not in conflict with this explanation. It wouldn't be too much of a stretch to imagine that subjects are less inquisitive of their mnemonic information during the likely condition. After all, they are expecting items to be from the studied list. Therefore, they may be more inclined to believe whatever mnemonic information is retrieved and to experience a subjective feeling of 'oldness' associated with these memories as a result. Subjects may be more cautious of items seen during the unlikely condition and may be more hesitant to trust any feelings of oldness that could be experienced. This cautiousness may inhibit subjects from entertaining subjective feelings of remembrance. Although no significant difference in the number of remember hits was found between conditions, subjects were significantly slower in making these responses during the unlikely condition. This provides some evidence that subjects were more hesitant in their recollection responses during the unlikely compared to the likely condition.

The finding of a modulation of activity between conditions for items that were correctly rejected is the most difficult to reconcile with an episodic buffer account. By definition, correct rejections have no episodic content, and therefore no difference should be found between probability conditions according to a buffer explanation. This finding is also difficult to reconcile with a bottom-up attention account of ventral activity. According to this theory, correct rejections should have activated this region to a larger degree during the likely condition since new items were more infrequent during this condition. In fact, the opposite pattern of results were observed, with greater activity to correct rejections within the angular gyrus during the unlikely condition.

Once again, it is difficult to predict what results would have been predicted to correct rejections according to the subjective awareness account of parietal activity. However, the subjective awareness account is less tied to memory content than the episodic buffer account. A feeling of subjective awareness and increased confidence can occur when subjects correctly reject items, especially when done so in a condition that encourages those responses. In fact, a previous study by Cabeza (2008) found that regions within the ventral parietal cortex were maximally activated not only when hits were made with high confidence, but also when correct rejections were made with high confidence. Although these results were interpreted in terms of a bottom-up attention account, they could just as easily be explained by a subjective awareness account. In the current study, the rate of correct rejections was not only higher in the unlikely condition, but these responses were made significantly faster

than correct rejections in the likely condition. Therefore, it is reasonable to believe that subjects were more confident in their correct rejections during the unlikely condition.

The ventral parietal activity to successful memory retrieval (operationalized as the 'hits > correct rejections' contrast) was found to be positively correlated with subjects' memory accuracy (measured as d'). This type of relationship is usually discussed as evidence of this region acting as an episodic buffer (Vilberg & Rugg, 2008). The rationale is that the stronger one's ability is to discriminate old items from new items, the more episodic content they should be retrieving to those items correctly identified as old. While this reasoning makes sense, episodic content is not the only phenomenon associated with strongly identified old items. A mnemonic accumulator account would suggest that those who have better discrimination rates would also have a higher accumulation of an 'oldness' signal. Likewise, one could argue that those who are better discriminators might have stronger memories that would be more salient and more successful at reorienting attentional systems to this retrieved content. Finally, if this region's activation were representing subjective awareness of the retrieved memory content, it would also make sense that this area would be maximally activated with stronger memories. Therefore, this finding cannot help us to distinguish which one of these theories (if any) of parietal activity is correct, but instead goes along with all of the accounts. In order to truly appreciate the results from these experiments, it is necessary to look to the patient literature and understand what memory retrieval is like for patients who have damaged this region of the brain.

Relation to Neuropsychology Results

The lack of a severe memory impairment of parietal lobe patients is the most difficult to reconcile with an episodic buffer account of parietal activations during memory retrieval. If this region were truly directly involved with memory retrieval and acting as a temporary storage site for retrieved episodic content, then these patients should exhibit more extreme memory impairments, perhaps resembling amnesic patients with medial temporal lobe damage. Instead, the deficits exhibited by parietal patients are much less extreme, with only subtle differences in performance being reported if at all (Hunkin et al., 1995; Ally et al., 2008; Davidson et al., 2008; Berryhill et al., 2009; Drowos et al., 2010; Simons et al., 2010; for a review see Berryhill, 2012). This type of subdued impairment is more consistent with the idea that this brain region is functioning as some extra-mnemonic process that guides memory processes but is not necessary for it to occur.

Probably the most popular theory of ventral parietal activation is the idea that this region is modulating changes in bottom-up attention (for a reviews see Cabeza et al., 2008; Cabeza, 2008). Results to support this claim come from a study by Berryhill and colleagues (2007). They described ventral parietal lobe patients who experienced recollections that lacked richness and specificity when they were asked to freely recall memories. Curiously, these same patients were able to access these memories when they were explicitly probed about them. This led the authors to explain their results in terms of the dual attentional processes hypothesis. Their reasoning is as follows: the damage in these patients was relatively limited to the ventral parietal

regions, thus according to the dual attentional processes hypothesis, only bottom-up attention should be affected with top-down allocation of attention left relatively intact. Since the patients were able to use explicit memory cues to retrieve memory content (ostensibly using top-down attention) but were unable to retrieve those same memories spontaneously via free recall (ostensibly using bottom-up attention), they believe their results were in line with this hypothesis. They likened this inability to use bottom-up attention to cue memory retrieval to a 'memory neglect syndrome', much like parietal patients who experience visual neglect and cannot use exogenous cues to orient attention towards visual stimuli (Bisiach & Luzzatti, 1978). Additional support of an attentional account of ventral parietal activity comes from a study by Ciaramelli et al. (2010). In this study, parietal patients were scanned while performing a recognition memory test. During the study sessions, words were presented in pairs and at test, pairs of words were shown one at a time. For most of the trials, the word was presented with the same word associate as during the study session. Therefore, this word served as a cue, initiating a search through one's memory storage to retrieve the associated word pair. Controls were able to use this information to enhance their memory performance, responding quicker than non-cued trials, and also showed increased dorsal parietal activation during this cued search phase. Dorsal parietal patients on the other hand, were not able to incorporate this information into their memory responses and showed no difference in response time between cued and uncued trials. On the other hand, some trials were paired with the wrong word associate. These trials were designed to engage the bottom-up attention

system by surprising the subject with an unexpected word. Control subjects showed increased ventral parietal activity during these trials while ventral parietal patients had difficulty recognizing these invalidly cued words. The authors argued that the distinct deficits occurring for dorsal vs. ventral parietal patients provided strong evidence in support of a dual-attentional account of parietal activity during memory retrieval.

The other theory that has been garnering more attention in the memory literature is the idea that parietal activations are representing the subjective experience associated with memories that are confidently retrieved. If all of the results from parietal patients are reviewed, the most common finding is that patients are less confident in their memories (Hunkin et al., 1995; Ally et al., 2008; Davidson et al., 2008; Berryhill et al., 2009; Drowos et al., 2010; Simons et al., 2010; for a review see Berryhill, 2012). Although patients can often report the content of their memories accurately, they are often experienced as less vivid, and devoid of rich contextual detail (Berryhill et al. 2007; Davidson et al. 2008; Simons et al. 2008). Additionally, parietal patients have shown diminished reports of remember/know recollection, while leaving source recollection relatively in tact (Drowos et al. 2010; Duarte et al., 2008). Interesting, patient S.M. reported by Davidson and colleagues (2008) reported that she could recall events of her life but that her memories did not seem to be accompanied by a sense of having experienced the event herself. All of these reports seem to point to a preserved ability to recall the c*ontents* of episodic memory, but with an impaired subjective *experience* of those same memories.

Concluding Remarks

While it is not yet clear what functional role (if any) the lateral parietal cortex is playing during successful memory retrieval, it seems unlikely that it is acting as an episodic buffer, temporarily storing retrieved episodic content. Not only is this account difficult to reconcile from the results presented in this dissertation, but it is also unable to explain the findings from neuropsychology. It appears much more likely that parietal activations during memory retrieval are representing some extra-mnemonic process that may help memory retrieval but is not necessary for it to occur. The theory that is the most parsimonious with the results from this dissertation and from neuropsychology is that activity within this brain region is somehow related to the subjective experience that is associated with particularly strong memories. However, this account cannot explain all of the neuroimaging and neuropsychology evidence and it is likely to not be the only explanation that is valid. Another favored theory is that this region is representing changes to top-down and bottom-up attention systems, much like it does during perceptual tasks. Given the extreme heterogeneity of the lateral parietal cortex it is likely that multiple theories may be needed to explain the activity within this area. In fact, several lines of recent research has suggested that more precise segregations of the parietal cortex may reveal different functional roles depending on where exactly the activity is located. This research includes results from diffusion tensor imaging (DTI) techniques (Caspers, Eickhoff, Rick, von Kapri, Kuhl, Huang, Shah, & Zilles., 2011), studies measuring functional-connectivity (Cohen, Fair, Dosenbach, Miezin, Dierker, Van Essen, Schlagger, &

Petersen, 2008; Daselaar, Huijbers, Eklund, Moscovitch, & Cabeza, 2013; Nelson, Cohen, Power, Wig, Miezin, Wheeler, Velanova, Donaldson, Phillips, Schlaggar, & Peterson, 2010), and meta-analyses of fMRI reports (Hutchinson et al., 2009). This idea that the parietal cortex may be playing various functional roles during memory retrieval is likely to explain the somewhat mixed results that have been reported thus far in the literature. Going forward, more specified sub-regions within both the dorsal and ventral lateral parietal areas should be targeted in order to better understand the complex workings of this cortical area.

References

Ally, B.A., Simons, J.S., McKeever, J.D., Peers, P.V., & Budson, A.E. (2008). Parietal contributions to recollection: Electrophysiological evidence from aging and patients with parietal lesions. *Neuropsychologia, 46,* 1800-1812.

Aminoff, E.; Clewett, D.; Freeman, S.; Frithsen, A.; Tipper, C.; Johnson, A.; Grafton, S.T.; Miller, M.B. (2012). Individual differences in shifting decision criterion: A recognition memory study. *Memory & Cognition, 40*(7), 1016-1030.

Aminoff, E.; Clewett, D.; Freeman, S.; Frithsen, A.; Tipper, C.; Johnson, A.; Grafton, S.T.; Miller, M.B. (2014). Maintaining a cautious state of mind during a recognition test: A large-scale fMRI study. *Neuropsychologia, 67*, 132-147.

Anderson, N.D., Craik, F.I.M., & Naveh-Benjamin, M. (1998). The attentional demands of encoding and retrieval in younger and adults: Evidence from divided attention costs. *Psychology and Aging, 13*(3), 405-423.

Andersson, J, Hutton, C., Ashburner, J, Turner, R., & Friston, K.J. (2001). Modelling geometric deformations in EPI time series. *NeuroImage, 13*(5), 903-919.

Baddeley, A. (1998). Recent developments in working memory. Curr. Opin. Neurobiol. 8, 234-238.

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4,* 417-423.

Berryhill, M.E., Phuong, L., Cabeza, R., & Olson, I.R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience, 27*(52), 14415-14423.

Berryhill, M.E. (2012). Insights from neuropsychology: Pinpointing the role of the posterior parietal cortex in episodic and working memory. *Frontiers in Integrative Neuroscience, 6*(31), 1-12.

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space.

Brainard, D.H. (1997). The psychophysics toolbox, *Spatial Vision, 10,* 433-436.

Brett, M., Anton J-L., Valabreque, R., & Poline, J.B. (2002). Region of interest analysis using SPM toolbox. Paper presented at 8th International Conference on Functional Mapping of the Human Brain, Sendai, Japan, June.

Buckner, R.L. (2004). Memory and executive function in aging and AD: Multiple factors that cause decline and reserve factors that compensate. *Neuron, 44*(1), 195-208.

Cabeza, R., Anderson, N.D., Locantore, J.K., & McIntosh, A.R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *Neuroimage, 17*, 1394-1402.

Cabeza, R. (2008). Role of parietal regions in episodic memory retrieval: The dual attentional process hypothesis. *Neuropsychologia, 46,* 1813-1827.

Cabeza, R., Ciaramelli, E., Oslon, I.R., & Moscovitch M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews: Neuroscience, 9,* 613-625.

Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences, 16*(6), 338-352.

Cansino, S., Maquet, P., Dolan, R.J., & Rugg, M.D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex, 12,* 1048-1056.

Caspers, S., Eickhoff, S.B., Rick, T., von Kapri, A., Kuhl, T., Huang, R., Shah, N.J., & Zilles, K. (2011). Probabilistic fibre tract analysis of cytoarchitectonically defined human inferior parietal lobule areas reveals similarities to macaques. *NeuroImage, 58*(2), 362-380.

Chua, E.F., Schacter, D.L., Rand-Giovannetti, E., & Sperling, R.A. (2006). Understanding metamemory: Neural correlates of the cognitive process and subjective level of confidence in recognition memory. *Neuroimage, 29*(4), 1150-1160.

Ciaramelli, E., Grady, C.L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia, 46,* 1828-1851.

Ciaramelli, E., Grady, C., Levine, B., Ween, J. & Moscovitch, M. (2010). Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: Neuroimaging and neuropsychological evidence. *The Journal of Neuroscience, 30*(14): 4943-4956.

Cohen, A.L, Fair, D.A., Dosenbach, N.U.F., Miezin, F.M., Dierker, D., Van Essen, D.C., Schlagger, B.L., & Petersen, S.E. (2008). Defining functional areas in individual human brains using resting functional connectivity MRI. *NeuroImage, 41*(1), 45-57.

Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P. & Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience, 3(3):* 292-297.

Corbetta, M. & Shulman G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201-215.

Corbetta, M., Patel, G., & Shulman, G.L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*(3), 306-324.

Craik, F.I.M., Govoni, R., Naveh-Benjamin, M., & Anderson, N.D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General, 125*(2), 159-180.

Cristescu, T.C., Devlin, J.T. & Nobre, A.C. (2006). Orienting attention to semantic categories. *Neuroimage, 33*, 1178-1187.

Curran (2004). Effects of attention and confidence on the hypothesized ERP correlates of recollection and familiarity. *Neuropsychologia, 42,* 1088-1106.

Curran, T., & Cleary, A.M. (2003). Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research, 15*, 191-205.

Daselaar, S.M., Fleck, M.S. & Cabeza, R.E. (2006). Triple dissociation in the medial temporal lobes: Recollection, familiarity, and novelty. *Journal of Neurophysiology, 96,* 1902-1911.

Daselaar, S.M., Huijbers, W., Eklund, K., Moscovitch, M., & Cabeza, R. (2013). Resting-state functional connectivity of ventral parietal regions associated with attention reorienting and episodic recollection. *Frontiers in Human Neuroscience, 7(38),* 1-9.

Davidson, P.S., & Glisky, E.L. (2002). Neuropsychological correlates of recollection and familiarity in normal aging. *Cognitive, Affective, & Behavioral Neuroscience, 2*, 174-186.

Davidson, P.S.R., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A.S.N., Murphy, K.J., Troyer, A.K., Moscovitch, M., & Levine, B. (2008). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia, 46,* 1743-1755.

Dewhurst, S.A., & Conway, M.A. (1994). Pictures, images, and recollective experience. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20*(5), 1088-1098.

Dobbins, I.G., Rice, H.J., Wagner, A.D., & Schacter, D.L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia, 41,* 318-333.

Dobbins, I.G. & Wagner, A.D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex, 15(11),* 1768-1778.

Dodson, C.S., & Johnson, M.K. (1996). Some problems with the process-dissociation approach to memory. *Journal of Experimental Psychology: General, 125*(2), 181-194.

Donaldson, W. (1996). The role of decision processes in remember and knowing. *Memory & Cognition, 24,* 523-533.

Dosher, B.A. (1984). Discriminating preexperimental (semantic) from learned (episodic) associations: A speed/accuracy study. *Cognitive Psychology, 16*(4), 519-555.

Drowos, D., Berryhill, M.E., Andre, J., & Olson, I.R. (2010). True memory, false memory and the subjective recollection deficits after focal bilateral parietal lobe lesions. *Neuropsychology, 24*(4)*,* 465-475.

Duarte, A., Ranganath, C., Winward, L., Hayward, D., & Knight, R.T. (2004). Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. *Brain Research, Cognitive Brain Research, 18*, 255-272.

Duarte, A., Ranganath, C., Trujillo, C., & Knight, R.T. (2006). Intact recollection memory in high-performing older adults: ERP and behavioral evidence. *Journal of Cognitive Neuroscience, 18*(1), 33-47.

Duarte, A., Ranganath, C., & Knight, R.T. (2005). Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *The Journal of Neuroscience, 25(36),* 8333-8337.

Duarte, A., Henson, R.N., & Graham, K.S. (2008). The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex, 18,* 2169-2180.

Dunn, J.C. (2004). Remember-know: A matter of confidence. *Psychological Review, 111*, 524-542.

Dunn, J.C. (2008). The dimensionality of the remember-know task: A state-trace analysis. *Psychological Review, 115,* 426-446.

Egan, J.P. (1958). Recognition memory and the operating characteristic. *USAF Operational Applications Laboratory Technical Note,* 58-51.

Elman, J.A., Cohn-Sheehy, B.L., & Shimamura, A.P. (2013). Dissociable parietal regions facilitate successful retrieval of recently learned and personally familiar information. *Neuropsychologia, 51*(4), 573-583.

Fleck, M.S., Daselaar, S.M., Dobbins, I.G., & Cabeza, R. (2006). Role of prefrontal and anterior cingulated regions in decision-making processes shared by memory and nonmemory tasks. *Cerebral Cortex, 16*(11): 1623-1630.

Fletcher, P.C., Frith, C.D., & Rugg, M.D. (1997). The functional neuroanatomy of episodic memory. *Trends in Neurosciences, 20*(5), 213-218.

Friedman, D. (1990). ERPs during continuous recognition memory for words. *Biological Psychology, 30*(1), 61-87.

Friedman, D. & Johnson Jr, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique, 51,* 6-28.

Friston, K.J., Glaser, D.E., Henson, R.N., Kiebel, S., Phillips, C., & Ashburner, J, (2002). Classical and Bayesian inference in neuroimaging: Applications. *NeuroImage, 16,* 484-512.

Gardiner, J.M. (1988). Functional aspects of recollective experience. *Memory & Cognition, 16*(4), 309-313.

Gardiner, J.M., Java, R.I., & Richardson-Klavehn, A. (1996). How level of processing really influences awareness in recognition memory. *Canadian Journal of Experimental Psychology, 50*(1), 114-122.

Gardiner, J.M., Ramponi, C., & Richardson-Klavehn, A. (1999). Response deadline and subjective awareness in recognition memory. *Consciousness and Cognition, 8*(4), 484-496.

Gardiner, J.M., Richardson-Klavehn, A., & Ramponi, C. (1997). On reporting recollective experiences and "direct access to memory systems'. *Psychological Science, 8*(5), 391-394.

Geraci, L., McCabe, D.P., & Guillory, J.J. (2009). On interpreting the relationship between remember-know judgments and confidence: The role of instructions. *Consciousness and Cognition, 18*(3), 701-709.

Gregg, V.H., & Gardiner, J.M. (1994). Recognition memory and awareness: A large effect of study-test modalities on "know" responses following a highly

perceptual orienting task. *European Journal of Cognitive Psychology, 6*(2), 131-147.

Gronlund, S.D., Edwards, M.B., & Ohrt, D.D. (1997). Comparison of the retrieval of item versus spatial position information. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23*(5), 1261-1274.

Gronlund, S.D., & Ratcliff, R. (1989). Time course of item and associative information: Implications for global memory models. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*(5), 846-858.

Gruppuso, V., Lindsay, D.S., & Kelley, C.M. (1997). The process-dissociation procedure and similarity: Defining and estimating recollection and familiarity in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23*(2), 259-278.

Guerin, S.A., & Miller, M.B. (2009). Lateralization of the parietal old/new effect: An event-related fMRI study comparing recognition memory for words and faces. *Neuroimage, 44*(1), 232-242.

Henson, R.N., Rugg, M.D., Shallice, T., Josephs, O., & Dolan, R.J. (1999). Recollection and familiarity in recognition memory: An fMRI study. *Journal of Cognitive Neuroscience, 17,* 1058-1073.

Henson, R.N.A., Hornberger, M., & Rugg, M.D. (2005). Further dissociating the processes involved in recognition memory: An fMRI study. *Journal of Cognitive Neuroscience, 17*(7), 1058-1073.

Herron, J.E., Henson, R.N.A., & Rugg, M.D. (2004). Probability effects on the neural correlates of retrieval success: An fMRI study. *Neuroimage, 21,* 302-310.

Hintzman, D.L. & Caulton, D.A. (1997). Recognition memory and modality judgments: A comparison of retrieval dynamics. *Journal of Memory and Language, 37*(1), 1-23.

Hintzman, D.L., Caulton, D.A., & Levitin, D.J. (1998). Retrieval dynamics in recognition and list discrimination: Further evidence of separate processes of familiarity and recall. *Memory and Cognition, 26*(3), 449-462.

Hintzman, D.L., & Curran, T. (1994). Retrieval dynamics of recognition and frequency judgments: Evidence for separate processes of familiarity and recall. *Journal of Memory and Language, 33*(1), 1-18.

Hirshman, E., & Henzler, A. (1998). The role of decision processes in conscious recollection. *Psychological Science, 9*(1), 61-65.

Howard, M.W., Bessette-Symons, B., Zhang, Y. & Hoyer, W.J. (2006). Aging selectively impairs recollection in recognition memory for pictures: Evidence from modeling and ROC curves. *Psychology and Aging, 21*(1), 95-106.

Hunkin, N.M., Parkin, A.J., Bradley, V.A., Burrows, E.H., Aldrich, F.K., Jansari, A., & Burdon-Cooper, C. (1995). Focal retrograde amnesia following closed head injury: A case study and theoretical account. *Neuropsycholgia, 33,* 509-523.

Hutchinson, J.B., Unchapher, M.R., & Wagner, A.D. (2009). Posterior parietal cortex and episodic retrieval: Convergent and divergent effects of attention and memory. *Learning & Memory, 16,* 343-356.

Iidaka, T., Matsumoto, A., Nogawa, J., Tamamoto, Y., & Sadato, N. (2006). Frontoparietal network involved in successful retrieval from episodic memory. Spatial and temporal analyses using fMRI and ERP. *Cerebral Cortex, 16,* 1349-1360.

Jacoby, L.L. (1999). Ironic effects of repetition: Measuring age-related differences in memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*(1), 3-22.

Jacoby, L.L., & Kelley, C.M. (1992). Unconscious influences of memory: Dissociations and automaticity. In E.A.D. Milner & E.M.D. Rugg (Eds.), *The neuropsychology of consciousness* (pp. 201-233). San Diego, CA: Academic Press.

Jacoby, L.L., & Whitehouse, K. (1989). An illusion of memory: False recognition influenced by unconscious perception. *Journal of Experimental Psychology: General, 118*(2), 126-135.

Jaeger, A., Konkel, A., & Dobbins, I.G. (2013). Unexpected novelty and familiarity orienting responses in lateral parietal cortex during recognition judgment. *Neuropsychologia, 51*(6), 1061-1076.

Java, R.I., Gregg, V.H., & Gardiner, J.M. (1997). What do people actually remember (and know) in "remember/know" experiments? *European Journal of Cognitive Psychology, 9*(2), 187-197.

Jennings, J.M. & Jacoby, L.L. (1993). Automatic versus intentional uses of memory: Aging, attention, and control. *Psychology and Aging, 8*(2), 283-293.

Johnson, M.K., Hashtroudi, S., & Lindsay, D.S. (1993). Source monitoring. *Psychological Bulletin, 114*(1), 3-28.

Johnson, R. (1995). Event-related potential insights into the neurobiology of memory systems. *Handbook of neuropsychology*, *10*, 135-135.

Kahn, I., Davachi, L., & Wagner, A.D. (2004). Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience, 24,* 4172-4180.

Kelley, R., & Wixted, J.T. (2001). On the nature of associative information in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27*(3), 701-722.

Khoe, W., Kroll, N.E.A., Yonelinas, A.P., Dobbins, I.G., & Knight, R.T. (2000). The contribution of recollection and familiarity to yes-no and forced-choice recognition tests in healthy subjects and amnesics. *Neuropsychologia, 38,* (10), 1333-1341.

Kim, H. & Cabeza, R. (2007). Common and specific brain regions in high-versus-low-confidence recognition memory. *Brain Research, 1282,* 103-113.

Kirchoff, B.A. (2009). Individual differences in episodic memory: The role of self-initiated encoding strategies. *The Neuroscientist, 15*(2), 166-179.

Kirchoff, B.A. & Buckner, R.L. (2006). Functional-anatomic correlates of individual difference in memory. *Neuron, 51,* 263-274.

Kleiner, M., Brainard, D., Pelli, D. (2007). "What's new in Psychtoolbox-3?". Perception 36 ECVP Abstract Supplement.

Klostermann, E.C., Loui, P., & Shimamura, A.P. (2009). Activation of right parietal cortex during memory retrieval of nonlinguistic auditory stimuli. *Cognitive, Affective, & Behavioral Neuroscience, 9*(3), 242-248.

Knowlton, B.J. & Squire, L.R. (1995). Remembering and knowing: Two different expressions of declarative memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*(3), 699-710.

Kohler, S., Paus, T., Buckner, R.L., & Milner B. (2004). Effects of left inferior prefrontal stimulation on episodic memory formation: A two-stage fMRI – rTMS study. *Journal of Cognitive Neuroscience, (16)2:* 178-188.

Komatsu, S., Graf, P., & Uttl, B. (1995). Process dissociation procedure: Core assumptions fail sometimes. *European Journal of Cognitive Psychology, 7*(1), 19-40.

Konishi, S., Wheeler, Donaldson, & Buckner, R.L. (2000). Neural correlates of episodic retrieval success. *Neuroimage 12,* 276-286.

Liu, T., Slotnick, S.D., Serences, J.T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex, 13,* 1334-1343.

Lyle, K. & Johnson, M. (2006). Importing perceived features into false memories. *Memory, 14*(2), 197-213.

Lyle K. & Johnson, M. (2007). Source misattributions may increase the accuracy of source judgments. *Memory & Cognition, 35*(5), 1024-1033.

Macmillan, N.A. & Creelman, C.D. (1990). Response bias: Characteristics of detection theory, threshold theory, and "nonparametric" indexes. *Psychological Bulletin, 107*(3), 401-413.

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review, 87*, 252-271.

Mark, R.E. & Rugg, M.D. (1998). Age effects on brain activity associated with episodic memory retrieval. An electrophysiological study. *Brain, 121*(5), 861-873.

McElree, B., Dolan, P.O., & Jacoby, L.L. (1999). Isolating the contributions of familiarity and source information to item recognition: A time course analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*(3), 563-582.

Mickes, L., Wais, P.E., Wixted, J.T. (2009). Recollection is a continuous process: Implications for dual-process theories of recognition. *Psychological Science, 20*(4), 509-515.

Miller, M.B., Van Horn, J.D., Wolford, G.L., Handy, T.C., Valsangkar-Smyth, M., Inati, S., Grafton, S., & Gazzaniga, M.S. (2002). Extensive individual differences in brain activations associated with episodic retrieval are reliable over time. *Journal of Cognitive Neuroscience 14*(8), 1200-1214.

Miller, M.B., Donovan, C.L., Van Horn, J.D., German, E., Sokol-Hessner, P., & Wolford, G.L. (2009). Unique and persistent individual patterns of brain activity across different memory retrieval tasks. *Neuroimage, 48*(3), 625-635.

Moritz, S., Glascher, J., Sommer, T., Buchel, C., & Braus, D.F. (2006). Neural correlates of memory confidence. *Neuroimage, 33*(4), 1188-1193.

Nelson, S.M., Cohen, A.L., Power, J.D., Wig, G.S., Miezin, F.M., Wheeler, M.E., Velanova, K., Donaldson, D.I., Phillips, J.S., Schlaggar, B.L., & Petersen, S.E. (2010). A parcellation scheme for human left lateral parietal cortex. *Neuron, 67,* 156-170.

O'Connor, A.R., Han, S., & Dobbins, I.G. (2010). The inferior parietal lobule and recognition memory: Expectancy violation or successful retrieval? *The Journal of Neuroscience, 30*(8), 2924-2934.

Park, D.C., Smith, A.D., Dudley, W.N., Lafronza, V.N. (1989). Effects of age and a divided attention task presented during encoding and retrieval on memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*(6), 1185-1191.

Pelli, D.G. (1997). The video toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437-442.

Perfect, T.J., Williams, R.B., & Anderton-Brown, C. (1995). Age differences in reported recollective experience are due to encoding effects, not response bias. *Memory, 3*(2), 169-186.

Preston, A.R. & Wagner, A.D. (2007). The medial temporal lobe and memory. *Neurobiology of Learning and Memory*, 2nd edition, pp. 305-337.

Postma, A. (1999). The influence of decision criteria upon remembering and knowing in recognition memory. *Acta Psychologia, 103*, 65-76.

Rajaram, S. (1993). Remember and knowing: Two means of access to the personal past. *Memory & Cognition, 21*(1), 89-102.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia, 41,* 378-389.

Ranganath, C., & Knight, R.T. (2003). Prefrontal cortex and episodic memory: Integrating findings from neuropsychoogy and event-related functional neuroimaging. Wilding, E., Bussey, T. (Eds), Memory encoding and retrieval: A cognitive neuroscience perspective. *Psychology Press*, New York, NY, pp. 83-99.

Ratcliff, R., Sheu, C.F., & Gronlund, S.D. (1992). Testing global memory models using ROC curves. *Psychological Review, 99,* 518-535.

Rotello, C.M. & Heit, E. (2000). Associative recognition: A case of recall-to-reject processing. *Memory & Cognition, 28*(6), 907-922.

Rotello, C.M., Macmillan, N.A., Reeder, J.A., & Wong, M. (2005). The remember response: Subject to bias, graded, and not a process-pure indicator of recollection. *Psychonomic Bulletin & Review, 12,* 865-873.

Rugg, M.D. (1995). Event-related potential studies of human memory. In *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 789-801, MIT Press.

Rugg. M.D., & Allan, K. (2000). Memory retrieval: An electrophysiological perspective, In: Gazzaniga, M.S. (Ed.), The New Cognitive Neurosciences, 2nd ed. The MIT Press, Cambridge, MA, pp. 805-816.

Rugg, M.D., Schloerscheidt, A.M., & Mark, R.E. (1998). An electrophysiological comparison of two indices of recollection. *Journal of Memory and Language, 39*(1), 47-69.

Rybash, J.M. & Hoyer, W.J. (1996). Process dissociation procedure reveals age differences in unconscious influences on memory for possible and impossible objects. *Aging, Neuropsychology, and Cognition: A Journal on Normal and Dysfunctional Development, 3*(4), 251-263.

Salthouse, T.A. (1994). Aging associations: Influence of speed on adult age differences in associative learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20*(6), 1486-1503.

Schacter, D.L., Verfaellie, M., & Pradere, D. (1995). The neuropsychology of memory illusions: False recall and recognition in amnesic patients. *Journal of Memory and Language, 35*(2), 319-334.

Scoville, W.B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal regions. *Journal of Neurology, Neurosurgery, and Psychiatry, 20*(1), 11-21.

Serences, J.T., Shomestein, S., Leber, A.B., Golay, X., Egeth, H.E., & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science, 16*(2), 114-122.

Shomstien, S., & Yantis, S. (2003). Control of attention shifts between vision and audition in human cortex. *Journal of Neuroscience, 24,* 10702-10706.

Simons, J.S., Peers, P.V., Hwang, D.Y., ally, B.A., Fletcher. P.C., & Budson, A.E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia, 46,* 1185-1191.

Simons, J.S., Peers, P.V., Mazuz, Y.S., Berryhill, M.E., & Olson, I.R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex, 20*(2), 479-485.

Smith, M.E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. *Journal of Cognitive Neuroscience, 5*1-13.

Smith, M.E. (1993). Decomposition of recognition memory event-related potentials yields target, repetition, and retrieval effects. *Electroencephalography and Clinical Neurophysiology, 86*(5), 335-343.

Spencer, W.D., & Raz, N. (1995). Differential effects of aging on memory for content and context: a meta-analysis. *Psychology and Aging, 10*(4), 527-539.

Strack, F., & Forster, J. (1995). Reporting recollective experiences: Direct access to memory systems? *Psychological Science, 6*(6), 352-358.

Squire, L.R. & Zola, S.M. (1991). The medial temporal lobe memory system. *Science, 253(5026):* 1380-1386.

Squire, L.R. & Zola, S.M. (1998). Episodic memory, semantic memory, and amnesia. *Hippocampus, 8,* 205-211.

Tendolkar, I., Schoenfeld, A., Golz, G., Fernandez, G., Kuhl, K.P., Ferszt, R., & Heinze, H.J. (1999). Neural correlates of recognition memory with and without recollection in patients with Alzheimer's disease and healthy controls. *Neuroscience Letters, 263*(1), 45-48.

Thoma, P., Zoppelt, D., Wiebel, B., & Daum, I. (2006). Recollection and familiarity in negative schizophrenia. *Neuropsychologia, 44*(3), 430-435.

Titov, N. & Knight, R.G. (1997). Adult age differences in controlled and automatic memory processing. *Psychology and Aging, 12*(4), 565-573.

Toth, J.P. (1996). Conceptual automaticity in recognition memory: Levels-of-processing effects on familiarity. *Canadian Journal of Experimental Psychology, 50*(1), 123-138.

Trott, C.T., Friedman, D., Ritter, W., & Fabiani, M. (1997). Item and source memory: Differential age effects revealed by event-related potentials. *NeuroReport, 8*(15), 3373-3378.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology, 26*(1), 1-12.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Reviews Psychology, 53,* 1-25.

Van Essen, D.C., Dickson, J., Harwell, J., Hanlon, D., Anderson, C.H., & Drury, H.A. (2001). An integrated software system for surface-based analyses of cerebral cortex. *Journal of American Medical Infomatics Association, 8*(5), 443-459.

Van Zandt, T. (2000). ROC curves and confidence judgments in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*(3), 582-600.

Vann, S.D., Tsivilis, D., Denby, C.E., Quamme, J.R., Yonelinas, A.P., Aggleton, J.P., Montaldi, D., & Mayes, A.R. (2009). Impaired recollection but spared familiarity in patients with extended hippocampal system damage revealed by 3 convergent methods. *Proceedings of the National Academy of Sciences of the United States of America, 106*(13), 5442-5447.

Verfaellie M., Giovanello, K.S., & Keane, M. (2001). Recognition memory in amnesia: Effects of relaxing response criteria. *Cognitive, Affective, & Behavioral Neuroscience, 1*(1), 3-9.

Vilberg, K.L. & Rugg, M.D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Research, 1122*, 161-170.

Vilberg, K.L. & Rugg, M.D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia,45,* 2216-2225.

Vilberg, K.L. & Rugg, M.D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia, 46,* 1787-1799.

Vilberg, K.L. & Rugg, M.D. (2009). An investigation of the effects of relative probability of old and new test items on the neural correlates of successful and unsuccessful source memory. *Neuroimage, 45,* 562-571.

Vilberg, K.L., Moosavi, R.F., & Rugg, M.D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Research, 1122*(1), 161-170.

Wager, T.D. & Nichols, T.E. (2003). Optimization of experimental design in fMRI: A general framework using a genetic algorithm. *NeuroImage, 18,* 293-309.

Wagner, A.D., Gabrieli, J.D.E., & Verfaellie, M. (1997). Dissociations between familiarity processes in explicit recognition and implicit perceptual memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23*(2).

Wagner, A.D., Stebbins, G.T., Masciari, F., Fleischman, D.A., & Gabrieli, J.D.E. (1998). Neuropsychological dissociation between recognition familiarity and perceptual priming in visual long-term memory. *Cortex, 34*(4).

Wagner, A.D. (2002). Cognitive control and episodic memory: Contributions form prefrontal cortex. *Neuropsychology of Memory,* 3rd edition, pp. 174-192.

Wagner, A. D., Shannon, B.J., Kahn, I., & Buckner, R.L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences, 9*(9*),* 445-453.

Wais, P.E., Mickes, L., Wixted, J. (2008). Remember/know judgments probe degrees of recollection. *Journal of Cognitive Neuroscience, 20,* 400-405.

Wheeler, M.E. & Buckner, R.L. (2003). Functional dissociations among components of remembering: Control, perceived oldness, and content. *Journal of Neuroscience, 23,* 3869-3880.

Wheeler, M.E., & Buckner, R.L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage, 21, 1337-1349.*

Whiting IV, W.L. & Smith, A.D. (1997). Differential age-related processing limitations in recall and recognition tasks. *Psychology and Aging, 12*(2), 216-224.

Whittlesea, B.W., Jacoby, L.L., & Girad, K. (1990). Illusions of immediate memory: Evidence of an attributional basis for feelings of familiarity and perceptual quality. *Journal of Memory and Language, 29*(6).

Wilding, E.L., & Rugg, M.D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain,* 889-905.

Wilding, E.L. (2000). In what way does the parietal ERP old/new effect index recollection? *International Journal of Psychophysiology, 35,* 81-87.

Wixted, J.T. (2007). Dual-process theory and signal detection theory of recognition memory. *Psychological Review, 114,* 152-176.

Wixted, J.T. & Stretch, V. (2004). In defense of the signal detection interpretation of remember/know judgments. *Psychonomic Bulletin & Review, 11*(4), 616-641.

Yonelinas, A.P. (1994). Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20*(6), 747-763.

Yonelinas, A.P. & Jacoby, L.L. (1995). The relationship between remembering and knowing as bases for recognition: Effects of size congruency. *Journal of Memory and Language, 34,* 622-643.

Yonelinas, A.P., Dobbins, I., Szymanski, M.D., Dhaliwal, H.S., & King, L. (1996). Signal-detection, threshold, and dual-process models of recognition memory: ROCs and conscious recollection. *Consciousness and Cognition, 5*(4), 418-441.

Yonelinas, A.P. & Jacoby, L.L. (1996). Noncriterial recollection: familiarity as automatic, irrelevant recollection. *Consciousness and Cognition, 5,* 131-141.

Yonelinas, A.P. (1997). Recognition memory ROCs for item and associative information: The contribution of recollection and familiarity. *Memory & Cognition, 25*(6), 747-763.

Yonelinas, A.P. (1999). The contribution of recollection and familiarity to recognition and source-memory judgments: A formal dual-process model analysis of receiver operating characteristics. *Journal of Experimental Psychology, 25(6)*, 1415-1434.

Yonelinas, A.P. (2001). Components of episodic memory: The contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society B, 356,* 1363-1374.

Yonelinas, A.P., Kroll, N.E.A., Dobbins, I., Lazzara, M., & Knight, R.T. (1998). Recollection and familiarity deficits in amnesia: Convergence of remember-know, process dissociation, and receiver operating characteristic data. *Neuropsychology, 12*(3), 323-339.

Yu, S.S., Johnson, J.D., & Rugg, M.D. (2012). Dissociation of recollection-related neural activity in ventral lateral parietal cortex. *Cognitive Neuroscience, 3(*3-4), 142-149.

Appendix

Remember/Know Instructions:

You will be presented with a series of words. Half of the words shown will be from the study list, the other half will be new words. By 'study list', I mean the four lists of words you initially saw, and made either an 'Abstract/Concrete' or 'Pleasant/Unpleasant' decision on.

For each word, please respond with either a "Remember", "Know", or "New" response. Each word will be on the screen for about 3 seconds.

A "Remember" response should be made when you recognize the word and can consciously recollect its prior occurrence in the study list. "Remember" is the ability to become consciously aware again of some aspect or aspects of what happened or what was experienced at the time the word was presented (e.g., aspects of the physical appearance of the word, or of something that happened in the room, or of what you were thinking and doing at the time). In other words, the "remembered" word should bring back to mind a particular association, image, or something more personal from the time of study, or something about its appearance or position (i.e., what came before or after that word). Please indicate a "remember" response by pressing button number 1 – the button all the way to the left under your index finger.

A "Know" response should be made when you recognize the word from the study list, but you cannot consciously recollect anything about its actual occurrence or what

happened or what was experienced at the time of its occurrence. In other words, respond with a "K" (for "know") when you are quite certain of recognizing the word, but the word fails to evoke a specific conscious recollection from the study list. Please indicate a "know" response by pressing button number 2 – the button under your middle finger.

I want to emphasize that the difference between a "Remember" response and a "Know" response is NOT merely a difference in confidence. In both cases, you are quite certain that the word was on the study list. The different responses reflect a different kind of memory EXPERIENCE. A "Remember" response should bring you back to the time you encountered the word during the study session – almost as if you are re-experiencing that event. A "Know" response does not have this kind of experience, but instead reflects a sense of familiarity in the absence of contextual details.

A "New" response means that you do not think that the word was on the study list. You have no awareness of the word being shown previously. Please indicate this response by pressing button number 3 with your ring finger.