Differential Neural Activity during Retrieval of Specific and General Autobiographical Memories derived from Musical Cues

Jaclyn Hennessey

A thesis submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Master of Arts in the Department of Psychology.

Chapel Hill

2009

Approved by:

Kelly Giovanello

Joseph Hopfinger

Neil Mulligan

ABSTRACT

JACLYN HENNESSEY: Differential Neural Activity during Retrieval of Specific and General Autobiographical Memories derived from Musical Cues

(Under the direction of Dr. Kelly Giovanello)

In the current studies, musical cues were used to elicit memories from multiple levels of specificity. Musical cues allowed for construction of emotional memories that had low levels of prior retrieval. Owing largely to the use of music, memories from varying levels of specificity were retrieved, allowing for comparison of the characteristics and neural correlates of retrieval. Subjects rated vividness, intensity, and re-experiencing greater for specific compared to general memories (Experiments 1 & 2). Additionally, these memories were associated with increased activation in regions within the autobiographical memory network, such as the hippocampus and sensory regions (Experiment 2). Other regions within the network, such as the medial prefrontal cortex, were activated during all autobiographical conditions. These results suggest that regions in the autobiographical network may be involved in different processes during retrieval, some being engaged during all autobiographical construction conditions and others being preferentially engaged during construction of event-specific memories.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Kelly Giovanello, for her guidance and invaluable assistance during the course of this project. I would also like to express my gratitude to the other members of my committee, Dr. Joseph Hopfinger and Dr. Neil Mulligan, for their assistance and suggestions.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

When one refers to a "memory," he or she is typically referring to a form of memory known as autobiographical memory (AM). This form of memory includes a summation of all self-relevant knowledge from previous personal experience. Within this collection of information, one can retrieve information regarding a single event, such as a first date. During retrieval of this event, an individual might select specific information about the location, the time of day, and emotional reactions one may have had during the date. These memories are often more vivid and emotional than traditional episodic memory tasks (e.g. memory for a word list or a set of pictures). The increase in vividness and overall sense of reliving leads to an enhancement of recollection typically absent from memories for events that occur in the lab (Cabeza & St. Jacques, 2007).

The study of autobiographical memory is important to the general field of memory because it enables us to better understand retrieval of remote, emotional, detailed, and self-relevant memories. Autobiographical memories, by definition, include memories as remote as an individual's very first memory. By tapping into memories that are over a decade old, autobiographical memory researchers are able to examine how the passage of time may influence the nature of a memory. The emotional and detailed nature of autobiographical memories also allows researchers to measure the recollective qualities of different types of events. Finally, autobiographical memories involve an

interesting re-constructive retrieval process that is not easily measured using simpler memory tests.

Despite the importance to the general memory literature, autobiographical memory remains relatively understudied due to the complications involved in designing controlled research studies. Autobiographical memory encoding typically occurs naturally and out of the control of the experimenter. Additionally, a vast majority of autobiographical memory research focuses on only one type of retrieval. Retrieval of autobiographical information in the real world can occur when an individual is instructed to retrieve a memory for a cue ("try to remember the last time you went bowling"), but may also occur spontaneously when an individual happens to encounter a salient cue (driving past the bowling alley) (Conway & Williams, 2008; Haque and Conway, 2001). Most autobiographical memory research, including the current study, focuses on intentional and deliberate memory retrieval following an explicit instruction.

The Nature of Autobiographical Memories

Autobiographical memory of an event often combines vivid imagery of specific details and abstract knowledge about the self (Conway & Williams, 2008; Conway, Pleydell-Pearce, & Whitecross, 2001; Levine, Turner, Tisserand, Hevenor, Graham, & McIntosh, 2004). The relative contribution of each type of autobiographical knowledge depends on several key features. First, autobiographical memories generally become more generalized over time and over multiple retrievals of the event details. Participating in an event multiple times (e.g., going to your grandmother's each Saturday) may also lead to a semanticized script for the event. Finally, memory narratives from certain

populations (older adults, amnesic patients, etc.) tend to include more autobiographical facts than specific details (Cabeza & St. Jacques, 2007).

Conway and colleagues (Conway, Turk, Miller, Logan, Nebes, Meltzer, & Becker, 1999; Conway et al. 2001; Conway, Singer, & Tagini, 2004; Conway & Williams, 2008) proposed three levels of autobiographical knowledge in their Self Memory System. The first two levels, *lifetime period knowledge* and *general event knowledge*, are occasionally combined and described as our overall "long-term knowledge" (Conway, 2005; Haque & Conway, 2001). The third level, *event specific knowledge*, contains specific details, including vivid imagery, mental time travel, and autonoetic consciousness (Levine et al. 2004; Cabeza & St. Jacques, 2007).

Lifetime period knowledge refers to memory for a time period in one's life, often with a clear starting and ending point. For example, one may have a memory for the time when he or she lived with a particular significant other. Lifetime period knowledge would include very general information pertaining to that time in the person's life: when the period was, information about the significant other, pets they may have had, etc. This level of abstraction is often described as autobiographical knowledge, as it relates only to facts and not episodes (Conway et al. 1999; Conway & Pleydell-Pearce, 2000; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). The information in this level provides a context for more specific information in the other two levels of memory (Conway et al. 1999).

General event knowledge includes memory for clusters of events. Similar to lifetime period knowledge, this information is routed in knowledge of the self. However, this level focuses on memory for actual events (Conway et al. 1999). A cluster can

include some category of events (e.g, going to the park with your mother) or a single, prolonged event (e.g., a trip to France in December) (Conway et al. 1999; Conway & Pleydell-Pearce, 2000). Importantly, general event knowledge contains no specific details from a particular event (Conway et al. 1999; Conway & Williams, 2008).

Finally, Conway and colleagues proposed a level of knowledge known as event specific knowledge, or ESK (Conway et al. 2001; Conway et al. 1999; Conway, 2005; Conway et al. 2004). ESK involves sensory knowledge and mental time travel related to a particular autobiographical event (Conway et al. 1999). The specific details that make up ESK provide the substantive content for most autobiographical memories, with autobiographical knowledge providing the foundation for the details (Conway et al. 1999).

Retrieval of Autobiographical Memories

AM retrieval can occur intentionally following explicit instruction or spontaneously following exposure to a salient cue (Haque and Conway, 2001). *Generative* autobiographical memory retrieval is often described as a constructive (or *re*constructive) process that involves a complex search through an underlying knowledge base (Conway et al. 2001; Conway et al. 1999; Conway et al. 2004; Haque & Conway, 2001; Conway & Pleydell-Pearce, 2000; Conway, 2005). This process involves a search through autobiographical knowledge, starting with abstract personal knowledge and ending with a specific memory representation consisting of event-specific details (Conway et al. 2001; Conway et al. 1999). The activated information is monitored for suitability, and either selected for recall or rejected. Unlike retrieval for most laboratory memories, the monitoring of information in autobiographical memory retrieval is an

intuitive and unconscious process (Conway et al. 2001). This process of *searching* through and *monitoring* self-relevant knowledge repeats iteratively until an appropriate memory has been retrieved (Conway et al. 2001).

This complex retrieval process is directed by a subset of working memory that Conway and colleagues have termed the *working self* (Conway et al. 1999; Conway et al. 2004; Haque & Conway, 2001; Conway & Pleydell-Pearce, 2000; Conway, 2005). Conway and colleagues explicitly link the working self to Baddeley's concept of a central processing system that coordinates the functions of other systems (Conway & Pleydell-Pearce, 2000; Conway, 1992). The working self operates the iterative process of searching through abstract and specific knowledge systems to retrieve an appropriate autobiographical memory (Conway, 1992).

The process of searching for a specific autobiographical memory takes several seconds, as more abstract personal knowledge is referenced and monitored. During this process, initial autobiographical knowledge is retrieved more quickly than subsequent details. Therefore, interrupting retrieval at different points during retrieval results in the recall of different types of autobiographical information (Haque and Conway, 2001). Interrupting retrieval after two or five seconds results in the retrieval of a greater proportion of autobiographical knowledge (lifetime period and general event knowledge) than when retrieval was interrupted after 30s. These results provide empirical evidence for Conway's suggestion that generative retrieval is a complex, iterative process of repeated search and retrieval (Haque & Conway, 2001; Conway et al. 2001).

Once an autobiographical memory has been retrieved, it can be maintained in mind and elaborated on (Daselaar et al. 2008). During this phase, the autobiographical

memory is held in mind and additional details are retrieved. *Elaboration* generally involves the retrieval of additional specific details that further develop the memory. However, it is possible that elaboration may lead to retrieval of autobiographical knowledge of a time period or particular people.

Not all autobiographical memory retrieval occurs as a generative process. Many studies of autobiographical memory retrieval include presentation of retrieval cues that are exceptionally salient and specific. In these studies, *direct* autobiographical memory retrieval occurs in place of a generative retrieval process (Conway et al. 2001; Conway et al. 1999; Conway & Pleydell-Pearce, 2000; Conway, 2005). Direct retrieval occurs when a cue is so salient that it does not require abstract knowledge to facilitate retrieval of a specific event. Rather, the event information is cued directly, activating the representation in memory (Conway et al. 2001; Conway et al. 1999; Conway & Pleydell-Pearce, 2000; Conway, 2005). When direct retrieval occurs, event specific autobiographical memories come to mind spontaneously, without any iterative search processes through abstract information.

Although the working self is not active in the search of a memory representation during direct retrieval, it is involved in the monitoring of information. The working self examines autobiographical information that has been activated via direct retrieval for relevance to current goals (Conway & Pleydell-Pearce, 2000; Conway et al. 2001). Relevant memories are selected so individuals can consciously recall the activated information. Information that is irrelevant is often inhibited and not recalled by the individual, who is never aware that the information was ever activated (Conway & Pleydell-Pearce, 2000). Occasionally, an irrelevant memory will bypass the working self,

often when the working self is distracted, and will be recalled as an involuntary memory. Without the role of the working self in inhibiting irrelevant autobiographical memories, individuals would constantly retrieve involuntary memories through this direct retrieval process (Conway & Pleydell-Pearce, 2000; Conway et al. 2001). Additionally, *elaboration* of memories that are retrieved directly occurs exactly as in memories that have gone through an iterative search. Through elaboration, details and knowledge can be retrieved to supplement the information that was activated initially.

Findings from Special Populations

Autobiographical memory retrieval does not function perfectly in all populations. Two recent articles (Addis, Wong, & Schacter, 2008; Levine et al. 2002) compared autobiographical memory retrieval in young adults and healthy older adults. In both studies, both young and older adults were asked to retrieve a specific autobiographical memory across several time periods. In both studies, healthy older adults produced fewer specific memory details and more general information than younger adults. Addis and colleagues also found this pattern of results when younger and older adults were asked to imagine an event in the future (Addis et al. 2008). These results suggest an enhanced retrieval of autobiographical knowledge and an impairment in retrieval of autobiographical details in older adults.

Research investigating neuropsychological populations can provide evidence as to which regions in the brain are associated with autobiographical memory retrieval. Importantly, some groups show selective impairment to specific autobiographical memory retrieval with relatively intact autobiographical knowledge (Conway & Fthenaki, 2000; Gilboa, Winocur, Rosenbaum, Poreh, Gao, Black, Westmacott, & Moscovitch,

2006; Steinvorth, Levine, & Corkin, 2005). Additionally, research including individuals with distinctive patterns of neural damage suggests that certain regions of the brain are connected to autobiographical knowledge (and not specific memory) impairment (Gilboa, Ramirez, Kohler, Westmacott, Black, & Moscovitch, 2005).

Patients with brain lesions can reveal many interesting patterns of autobiographical memory loss. Individuals suffering from semantic dementia (SD) typically exhibit severe retrieval impairments for autobiographical knowledge, but can perform well in tasks of specific AM retrieval (Ivanoiu, Cooper, Shanks, & Venneri, 2006). These patients, with damage to inferior and anterior temporal lobes, generally have trouble remembering names of significant others or facts from their past. Memory for appointments and everyday events can remain entirely normal in mild SD, but will start to decline in more severe stages.

The opposite pattern of memory loss (impairment to specifc AM retrieval with intact autobiographical knowledge) is more common in the neuropsychological literature. In a review of patients with severe autobiographical memory impairments, Conway and Fthenaki (2000) identified patients with damage to left frontal, temporofrontal, and parietal regions. In addition to a difficulty retrieving specific information, these patients also had mild autobiographical knowledge impairments. Conway and Fthenaki propose that lesions to these regions interfere with the generative retrieval process required to select an autobiographical memory for retrieval. In other words, the search process is interrupted after successful retrieval of personal semantic knowledge, but before retrieval of episodic details. This pattern allows for relatively normal performance on semantic tests and severely impaired performance on episodic tests.

Retrieval of specific autobiographical memories can also be impaired following lesions to the medial temporal lobe (MTL). Damage to this region can make retrieval of an episodic autobiographical memory difficult, particularly when damage is extensive (Gilboa et al. 2006). Although patients with MTL lesions can demonstrate intact retrieval of basic autobiographical knowledge, they have difficulty retrieving specific details for autobiographical events (Steinvorth et al. 2005). These results suggest that the MTL is involved in the retrieval of specific autobiographical events to a greater extent than the retrieval of abstract personal knowledge.

Additionally, memory for autobiographical events can be impaired after individuals suffer damage to the occipital lobes (Conway & Fthenaki, 2000). One patient with a lesion to the occipital lobes revealed relatively intact knowledge of lifetime periods and general events. However, memory for specific autobiographical events was severely impaired. It is likely that this patient was able to retrieve the information related to the specific memory, but could not engage the vivid visual imagery that often accompanies (and may be required by) episodic mental time travel (Conway & Fthenaki, 2000).

Finally, individuals diagnosed with Alzheimer's disease may demonstrate varying levels of autobiographical memory impairment, driven by different patterns of tissue loss. To examine how tissue loss may be associated with retrieval deficits, researchers have correlated neural volume with memory performance in a sample of Alzheimer's patients (Gilboa et al. 2005). In this study, reduced volume in the anterior lateral temporal and medial temporal lobe structures was associated with impaired memory for autobiographical events. Impaired memory for personal facts (names, dates, locations,

etc) was associated with reduced volume in bilateral anterior and posterior lateral temporal cortex.

Functional Neuroimaging Research

A more complete understanding of the neural correlates of autobiographical memory has been enhanced using studies of functional neuroimaging. During the last fifteen years, positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies focuding on autobiographical memory retrieval have allowed researchers to identify the brain regions particularly involved in retrieval of these personal memories (Addis et al. 2004b; Fink, Markowitsch, Reinkemeier, Bruckbauer, Kessler, & Heiss, 1996; Botzung, Denkova, Ciuciu, Scheiber, & Manning, 2008; Burianova & Grady, 2007; Cabeza, Prince, Daselaar, Greenberg, Budde, Dolcos, LaBar, & Rubin, 2004; Conway et al. 1999; Daselaar, Rice, Greenberg, Cabeza, LaBar, & Rubin, 2008; Denkova, Botzung, Scheiber, & Manning, 2006a; Denkova, Botzung, Scheiber, & Manning, 2006b; Levine et al. 2004; Maquire & Mummery, 1999). Autobiographical memories are highly detailed, emotional, and self-relevant, leading to a large network of regions involved in their retrieval. Studies have shown that memory detail is associated with regions of the MTL, mainly the hippocampus and parahippocampal cortex (Botzung et al. 2008; Daselaar et al. 2008; Addis et al. 2004b; Cabeza et al. 2004; Maquire & Mummery, 1999). Details are also associated with sensory cortices, primarily the visual cortex, due to the role of visual imagery in autobiographical memory (Cabeza et al. 2004; Daselaar et al. 2008). Emotion, in all forms of memory retrieval, is associated with activity in the amygdala (Cabeza et al. 2004; Conway et al 2001; Daselaar et al. 2008; Denkova et al. 2006a). Retrieval of autobiographical

information is also associated with brain regions involved in self-reference, most notably the medial prefrontal cortex (mPFC) (Botzung et al. 2008; Cabeza & St. Jacques, 2007; Maquire & Mummery, 1999). One study also connected neural activity in the posterior cingulate to reference to the self during retrieval (Botzung et al. 2008).

It is important to note that studies have consistently found activity in autobiographical memory retrieval to be left lateralized, particularly in the PFC (Botzung et al. 2008; Conway et al. 1999; Daselaar et al. 2008; Denkova et al. 2006a; Denkova et al. 2006b; Levine et al. 2004; Maquire & Mummery, 1999). These studies have used both words (Conway et al. 1999; Levine et al. 2004; Maquire & Mummery, 1999) and photos (Denkova et al. 2006a; Botzung et al. 2008) as memory retrieval cues. However, a small number of studies show bilateral, or even right lateralized, activity in autobiographical memory retrieval (Conway et al. 2001; Denkova et al. 2006a). Some researchers suggest that this pattern (i.e., non-left lateralization) is associated with more emotional autobiographical memories (Conway et al. 2001). It is also possible that differences in methodology (generative v. direct retrieval, length of elaboration, etc) may produce lead to right lateralization (Conway et al. 2001). Interestingly, some neuropsychological studies also implicate the right frontal regions as essential for autobiographical memory retrieval (Daselaar et al. 2008). Such differences between neuropsychological and neuroimaging results are not uncommon as neuropsychological studies pinpoint what regions are critical for a process and neuroimaging research identify the full neural architecture involved in a process.

A recent fMRI study compared personal episodic, non-personal episodic, and non-personal semantic memory retrieval to determine similarities and differences across

these forms of memory (Burianova & Grady, 2007). The only regions to show common activity across all three types of retrieval were regions within the left MTL. Finding equivalent MTL activation in the semantic and episodic conditions lead researchers to believe that subjects were always retrieving some episodic information despite instructions to focus on semantic information. Episodic and autobiographical memory shared some brain activity not seen in semantic retrieval. Of particular interest were inferior parietal and left lateral parietal cortices. Common activity was expected in this study, as subjects were instructed to retrieve specific autobiographical events (Burianova & Grady, 2007). Autobiographical retrieval was associated with medial frontal and left parahippocampal activity above and beyond retrieval of both non-personal conditions.

Several studies have identified a number of regions as belonging to a "core network" that is activated during daydreaming, self-projection, theory of mind tasks, and, importantly, retrieval of autobiographical memories (Addis, Wong, & Schacter, 2007; Buckner, Andrews-Hanna, & Shacter, 2008; Buckner & Carroll, 2007; Hassabis & Maquire, 2007). This network has been described as including regions within the medial PFC, posterior cingulate cortex, inferior parietal lobe, lateral temporal cortex, and, frequently, the hippocampus and surrounding cortical regions (Buckner et al., 2008). These regions can be broken down further into an MTL subsystem responsible for memory of associations and a medial PFC subsystem responsible for self-reference (Buckner et al., 2008).

Of particular interest in the current study are differences between the levels of Conway's Self Memory System. Although no fMRI or PET studies have explicitly compared these three levels, several have directly compared memory of specific events to

memory for general events or autobiographical knowledge (Addis et al. 2004b; Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004a; Levine et al. 2004; Maquire & Mummery, 1999). One PET study compared retrieval of autobiographical events, public events, general (non-personal) knowledge, and autobiographical facts (Maquire & Mummery, 1999). Each item was presented as a "true/false" proposition, potentially reducing the extent to which subjects were actually retrieving the full memory. Researchers identified brain regions that had a differential response to forms of autobiographical knowledge: medial frontal, temporopolor, and temporoparietal junction. In addition, particular regions were more active in autobiographical events relative to facts: medial frontal cortex, hippocampus, and temporal pole. No regions were selectively active for facts over events (Maquire & Mummery, 1999).

Levine and colleagues (2004) used functional MRI to compare specific and general autobiographical memories to non-personal information. After presentation of the stimulus in the scanner, subjects in this study were given 60s to answer questions about the event. Both autobiographical conditions were associated with activity in left antereomedial PFC, but specific memories were associated with activity in this region to a greater extent. Specific autobiographical memories, relative to generalized autobiographical memories, were also association with greater activity in the medial temporal lobe, diencephalic regions, and the posterior cingulate (Levine et al. 2004).

Addis and colleagues (2004a) used a partial least squares (PLS) analysis to compare patterns of neural activity differentially involved in retrieval of semantic and episodic autobiographical memory. In a pre-scan interview, subjects retrieved events that occurred once (specific) or multiple times (general). Sentence titles were created from

these events and were presentd as stimuli were presented to subjects in the scanner for six seconds. Using the PLS approach, two different networks within the autobiographical network were identified at two different time courses. Specific event retrieval was associated with activity in regions believed to be involved in visual processing, the left precuneus, left superior parietal lobule, and right cuneus. Additionally, general AM retrieval was associated with activity in the right inferior temporal gyrus, right medial frontal cortex, and left thalamus.

Conway and colleagues (2001) have looked at the time course of memory retrieval using event related potentials (ERPs). ERPs are especially useful for measuring neural activity over time, allowing for an examination of how neural activity changes during the autobiographical retrieval process. Conway and colleagues found an early left frontal negativity that they associated with a complex generative retrieval process (Conway et al. 1999). It is also likely that autobiographical information accessed early in retrieval (abstract personal knowledge) is associated with this frontal activity (Cabeza & St. Jacques, 2007). A later temporal and occipital negativity was also associated with the formation and maintenance of episodic autobiographical memories (Conway et al. 2001).

These ERP findings suggest that the initial search process occurs in anterior regions of the brain in the first few seconds of generative autobiographical memory retrieval. Retrieval of a specific autobiographical memory is associated with more posterior regions of the brain, namely in the temporal and occipital lobes (Conway et al. 2001). An fMRI study has provided support for these results by mapping the time course of two regions, the dorsolateral PFC and MTL, during memory retrieval (Botzung et al.

2008). As predicted by Conway's ERP results, peak activity for PFC regions occurred 2.5 seconds before MTL regions.

Some studies have found an uncharacteristic right lateralization during autobiographical memory retrieval. One PET study showed highly right-lateralized activity in the prefrontal cortex during autobiographical memory retrieval (Fink et al. 1996). Conway and colleagues (Conway et al. 2001; Conway et al. 2004; Haque & Conway, 2001) suggest that this could be due to several factors. One possibility is that the stimuli used in this study were salient and emotional enough to *directly* access an episodic autobiographical event, bypassing the generative retrieval process. The right PFC has been associated with monitoring of autobiographical information, suggesting that the right lateralization of the prefrontal cortex in this case reflects skipping the *search* process in the left PFC and relying only on the *monitoring* process in the right PFC.

Testing Autobiographical Memories

Despite the increase in neuroimaging research on autobiographical memory during the last decade, the retrieval of autobiographical knowledge remains difficult to study in a controlled setting (Cabeza et al. 2004; Levine et al. 2004). In order to study autobiographical events, researchers lose control over the degree of prior rehearsal, level of personal significance, emotionality, and the difficulty of memory retrieval (Levine et al. 2004). Attempting to study the neural correlates of autobiographical memory retrieval in an MRI scanner compounds these problems (Cabeza & St. Jacques, 2007). There are currently several popular methods designed to handle some of these problems, but they all have flaws of their own.

The simplest method for studying autobiographical memory retrieval is the general cue method. In this method, subjects are presented with a novel verbal or auditory cue in the scanner. Although this cue allows for fresh retrieval of memories, memories are not necessarily emotional, significant, or from any given time period or category. Additionally, subjects require a much longer retrieval trial to successfully retrieve a memory; occasionally, no memory will be retrieved at all (Daselaar et al. 2008; Cabeza & St. Jacques, 2007).

There are several ways to exert experimental control over the memories subjects retrieve in the scanner. One common method involves asking subjects to participate in an interview before the scanning session. During the interview, subjects are presented with cues and are asked to retrieve specific autobiographical memories related to each cue. In the scanner, subjects view the self-generated titles for their pre-retrieved memories and retrieve them again (Botzung et al. 2008). Although this method allows for greater control over many aspects of the retrieved memory, it introduces a number of confounds by adding explicit rehearsal of the event. Creating a script of the event during the interview may make the representation more "semanticized". In addition, retrieval during the interview leads to a truncated version of a natural autobiographical memory search at test, eliminating the "retrieval" phase and leaving only the "elaboration" (Cabeza & St. Jacques, 2007). Most importantly, subjects may be retrieving the original remote autobiographical event at test, but may also be retrieving a recent autobiographical memory of the pre-scan interview. Specifically, this complication is controversial for studies attempting to examine neural activity during retrieval of memory for remote events. The problems with this method can be attenuated by using less specific cues or a

longer duration between interview and scan (Cabeza & St. Jacques, 2007; Botzung et al. 2008), but the issues cannot be eliminated.

Another popular method used to reduce variability in autobiographical memory retrieval is to exert control over the encoding of the event. In some studies, researchers have asked subjects to record daily events over several months (Levine et al. 2004), and then tested subjects on this recorded information in the scanner. This method allows researchers to test events for content, but does not allow for the analysis of memories any earlier than the beginning of the study. Some researchers also express concern in the role that recording a memory might play in its encoding. In other words, these memories may be encoded differently than typical autobiographical memories (Cabeza & St. Jacques, 2007). A recent study took this method a step further by creating a scenario where all subjects encoded the same autobiographical memory as part of the study (Cabeza et al. 2004). Subjects in this study took photographs of campus landmarks and viewed these photos in a scanner. Compared to photos taken by other students, a subject's own photos elicited memories containing personal recollective qualities. In addition to the problems previously discussed, this study's methodology also evoked memories that were less emotional and personally significant than typical autobiographical events.

A final method uses novel cues that have high levels of personal relevance to the subject. Researchers often collect cues (photos or stories) from friends and family to present to the subject in the scanner. Because these cues are more self-relevant, they have a much more potent emotional component. This method removes the pre-scan interview, but still raises the probability that subjects will retrieve a memory at test (Denkova et al. 2006a; Denkova et al. 2006b). The memories are also not selected by the subject,

suggesting that the memory may not be as over-rehearsed as those that the subject selects on his or her own. However, it is very time consuming to collect personally relevant cues for each subject, and there is no method to ensure that the cues are standardized across individuals. Additionally, specific memories of previously viewing photos may be retrieved instead of the emotional and self-relevant event intended by the researcher.

Because selecting personally relevant and emotional cues has been shown to simplify and speed up autobiographical memory retrieval without the controversial pre-scan interview, it would be beneficial to find a type of cue with these qualities but that can be used universally and efficiently across participants (Cady, Harris, & Knappenberger, 2008). To solve this problem, researchers have turned to a novel cuing method to examine the retrieval of autobiographical memories – musical cues (Cady et al. 2008; Janata, Tomic, & Rakowski, 2007). From an early age, individuals learn information through popular songs, chants, and advertising jingles. Our history with learning through music makes musical clips unique in their ability to cue personal memories (Cady et al. 2008). The emotional nature of familiar music clips leads to retrieval of autobiographical memories that are more emotional than those retrieved with general verbal cues (Schulkind et al. 1999; Mitterschiffthaler, Fu, Dalton, Ander, & Williams, 2007; Janata et al. 2007).

In addition, the saliency of musical cues has some therapeutic effects in patient populations. Music has been useful in improving retrieval of unrelated autobiographical material in individuals diagnosed with Alzheimer's disease (Irish, Cunningham, Walsh, Coakley, Lawlor, Robertson, & Coen, 2006; Foster & Valentine, 2001). When researchers played familiar classical music in the background during a standard

autobiographical memory task, patients showed a significant improvement in retrieval of information from childhood, young adulthood, and recent adulthood (Irish et al. 2006). In addition, one older adult in the severe stages of Alzheimer's disease (MMSE= 8/30) had equivalent performance to healthy older adults in tasks of music memory including tune recognition, familiarity judgments, and recall of lyrics (Cuddy & Duffin, 2005). This study suggests that memory for musical information is more resilient than other knowledge.

For years, researchers have used music to test subjects' memory for the characteristics of popular music pieces (name, year of popularity, lyrics, etc), but the personal memories evoked by these musical associations have not been thoroughly examined (Bartlett & Snelus, 1980; Schulkind, Hennis, & Rubin, 1999). Two recent behavioral studies have looked at the characteristics of autobiographical memories elicited by clips of popular music (Janata et al. 2007; Cady et al. 2008). Both studies discovered that popular music cues can often lead to retrieval of autobiographical memories, but the content of these memories was not examined.

The current study will utilize familiar musical cues due to their unique ability to evoke unrehearsed and emotional autobiographical knowledge from all three levels of Conway's SMS. Previous studies have explicitly asked subjects for memories from a specific time period (Addis, Wong, & Schacter, 2007; Levine et al. 2002) and have instructed subjects concerning which type of memory (specific or general) they should retrieve (Addis et al. 2004b). Music clips can cue time periods associated with the popularity of the particular song, creating a natural distribution across a subject's lifetime. One recent study suggests that music is able to elicit both specific

autobiographical memories and autobiographical knowledge naturally, making it a useful cue for examining the retrieval of memories from all levels (Janata et al. 2007).

A single neuroimaging study has utilized this musical cuing paradigm to examine neural activation during presentation of familiar and unfamiliar music cues (Janata, 2009). Importantly, the subjects in this study only reported autobiographical associations with 42% of presented songs. Additionally, subjects were not asked to retrieve any autobiographical information while in the scanner, but were only told to evaluate the song on its ability to evoke a memory in the future. As such, no conclusions could be drawn regarding neural correlates of autobiographical memory retrieval or elaboration. This study identified regions within the medial PFC that were activated when subjects heard music to which they had an autobiographical association. However, other neural regions typically implicated in autobiographical memory retrieval, such as the posterior cingulate, MTL, and thalamus, were not observed.

Current Study

The current study examines the cognitive structure and neural substrates of autobiographical memory retrieval using musical cues. The unique properties of music as a retrieval cue will allow subjects to retrieve both specific and general autobiographical knowledge without explicit retrieval instructions. The natural distribution of memories across the three levels of Conway's Self Memory System will allow for direct comparisons between memories retrieved from each. A neuroimaging study will then compare the neural underpinnings of episodic and semantic autobiographical memories retrieved using this paradigm.

Previous research provides some hypotheses for neural correlates of the three levels of autobiographical information. Conway, Pleydell-Pearce, and Whitecross (2001) propose that more abstract autobiographical knowledge is associated with frontal regions, while event specific knowledge is associated with the temporal and occipital lobes. Recent fMRI studies have compared single event memories to general event memories (Levine et al. 2004; Addis et al. 2004a). These studies demonstrate additional activity for specific relative to general autobiographical memories in several regions of the core network (i.e., PFC, parahippocampal gyrus, left superior gyrus, left precuneus, and posterior cingulate) and have implicated the lateral temporal lobes in autobiographical memory knowledge (Addis et al. 2004a). These studies both largely focused on the elaboration of autobiographical information due to the nature of their cuing paradigms.

The current project includes one behavioral study (Experiment 1) and one functional neuroimaging study (Experiment 2). The behavioral study was conducted to establish the utility of music cues to access different levels of AM. This study extended previous research examining differences between memories retrieved from the three levels of Conway's SMS (Conway, 2005; Haque and Conway, 2001). Additionally, Experiment 1 provided support for two recent behavioral studies that suggest that musical cues are particularly useful in evoking autobiographical memories (Janata et al. 2007; Cady et al. 2008). Based on the results of Experiment 1, a similar paradigm was used in an fMRI study designed to examine neural differences across memory levels. This study expanded on previous research revealing differences between specific and general autobiographical memories. Additionally, it serves as the first use of musical cues to evaluate retrieval of autobiographical memory content in the scanner.

CHAPTER 2: EXPERIMENT 1

The current study utilized a novel cuing paradigm using popular music clips as memory cues. This study was motivated by two recent behavioral experiments that demonstrated the ability of music cues to elicit AMs (Cady et al. 2008; Janata et al. 2007). Experiment 1 was performed to verify the utility of this methodology. Specifically, musical cues will be used to elicit retrieval of emotional, self-relevant, and unrehearsed autobiographical memories of varying specificity. Qualitative characteristics of memories were compared across levels of memory to examine the content and cognitive structure of memory.

Methods

Participants

14 healthy young adults (age range 18-26) volunteered for this study in exchange for partial class credit. Participants were all native English speakers without a history of psychiatric illness or neurological disorder. Before participating in the study, participants gave written informed consent in accord with the requirements of the Institutional Review Board at the University of North Carolina at Chapel Hill.

Materials

Musical clips for the experimental trials consisted of fifty 30-second clips from popular songs from the years 1998-2007. Songs were downloaded from the iTunes music

store and recorded using MacStim's sound recorder. Popular songs were selected so most subjects would have some level of familiarity with the stimuli. In addition, several previous musical memory studies have used this genre of music (Cady et al. 2008; Schulkind et al. 1999; Bartlett & Snelus, 1980; Janata et al. 2007). Initially, the top ten songs were selected from each of the ten years (n=100) using an Internet "top ten" website (i.e., Rock on the Net). A 30s clip was selected from each song to contain the chorus and other highly recognizable segments.

All 100 songs were tested in a pilot study where undergraduate volunteers listened to 30s clips and reported memories associated with each song. The results of this pilot study allowed for the selection of 50 songs that consistently elicited autobiographical memories across all subjects. The five songs from each year with the highest ratings of familiarity and memory detail were selected for the current study's memory cues.

For the control task, subjects performed a semantic memory task (described below) during ten 30s classical music clips. The selections were taken from a list of classical pieces rated as "neutral" in a recent fMRI study examining classical music's effect on mood (Mitterschiffthaler et al. 2007). Of the 60 musical pieces that were tested, these ten pieces were rated as the most neutral. Using neutral pieces for the control trials allows researchers to examine the emotional content of experimental trials more directly.

Finally, subjects recorded memories on a digital voice recorder with triple microphones. Specifically, the post-retrieval interview was recorded using a Sony Memory Stick Digital Voice Recorder. Following each subject's participation, interviews were downloaded and saved to audio CDs.

Procedure

Before beginning the experiment, subjects engaged in 30-minute instructional session on the components of autobiographical memory. Specifically, subjects learned the three levels of abstraction (lifetime period knowledge, general event knowledge, and event specific knowledge) described by Conway and colleagues (Conway et al. 1999; Conway & Pleydell-Pearce, 2000; Conway, 2005; Haque & Conway, 2001). Subjects were also carefully instructed on the ten rating scales they would use during the study. The instructions for the rating scales are included in the appendix. In brief, the subjects rated familiarity, song preference, genre preference, emotion, intensity, vividness, relivingness, prior rehearsal, relation to previous memory, and recency of memory.

The instruction period was intended to educate participants on the purpose of the study and to establish that they could effectively rate the qualities and level of each memory. When subjects completed the instructions and felt comfortable with this knowledge, they were able to begin the study. Each subject participated in three consecutive sessions of autobiographical memory retrieval followed by a brief post-retrieval interview. Each session consisted of ten experimental trials and three or four control trials.

Experimental Trials

Before each trial, subjects were presented with a single tone (1-3s) as a warning to prepare for the upcoming stimulus. For experimental trials, subjects were asked to listen to 30s clips of popular songs and to retrieve any autobiographical memory that came to mind. Retrieval of any memory level was acceptable and subjects were asked to focus on any memory the song elicited, in as much detail as possible. Subjects were informed that

they could elaborate on any memory that came to mind, even if it did not seem to directly relate to the song. If a song reminded them of a person or place, or even another song, they should elaborate on it and report this information later. During retrieval, subjects identified the level of abstraction that best fit their memory (1=lifetime period knowledge, 2=general event knowledge, and 3=event specific knowledge) by pressing the appropriate button. Subjects were asked to focus on the first memory that came to mind, but were told that the memory may become more or less specific over time. If this change should occur, subjects indicated the change by selecting the corresponding button. As such, some trials were associated with multiple button responses, while others were only associated with one. Since visual imagery is a key component of autobiographical memories, subjects were asked to keep their eyes closed during the entire task. Additionally, to best simulate the subject's performance in the scanner, subjects remained still and did not speak during memory retrieval. Therefore, all memories were retrieved covertly.

Following the musical cue, subjects rated two aspects of the memory or song. The two aspects were randomly selected out of the ten possible rating scales (i.e., familiarity, song preference, genre preference, emotion, intensity, vividness, relivingness, prior rehearsal, relation to previous memory, and recency of memory). Subjects had six seconds to listen to the rating category and select their response with a button press. The ratings provided during the memory trials were compared to responses acquired during the post-retrieval interview. This comparison has been used in previous autobiographical memory studies (Addis et al. 2004b) to provide evidence for consistency between

retrievals. After the ratings, subjects were presented with a new warning tone and were asked to clear their minds of the previous memory and song.

Control Trials

Control trials also consisted of a 1-3s warning tone followed by a 30s music clip. For these trials, clips of classical music pieces were selected for their neutrality[1]. During the 30-second clip, subjects were asked to select an adjective that described the piece and to define the adjective in any way they like. After each decision, the subject was asked to hit the appropriate button (1 after selecting an adjective and 2 after supplying a definition). Although it is possible that a classical piece could elicit personal memories for some subjects, classical pieces are generally less well known than popular pieces in college students, reducing the likelihood of an intruding autobiographical memory. Additionally, participants were explicitly warned to avoid retrieval of personal memories during the control task. To confirm the unfamiliarity of these songs, subjects rated the song for preference and familiarity. These ratings allowed researchers to predict the likelihood of personal memory intrusions from the selected classical pieces, and will control for the act of making a rating during the experimental trials.

Post-Retrieval Interview

After all three sessions, subjects listened to musical clips a second time and reported memories orally for each music cue. During this interview, subjects were instructed to remember the memory they retrieved during the earlier memory and to report it exactly as it had been remembered previously. This re-retrieval was recorded

[1] Because classical pieces were used, high levels familiarity with classical music may lead to autobiographical remembering in the control condition. As such, subjects were screened for exposure to classical music..

using the digital recorder and was later used to analyze and code the different types of memory. After each retrieval, subjects rated the memory on all ten characteristics.

Ratings

To analyze the content of retrieved autobiographical memories, different rating systems were used. First, two methods were used to categorize memories into the three levels of Conway's SMS. All memories were categorized based on the initial level (1, 2, or 3) reported by the subject during retrieval ("SubLevel" method). Additionally, a written transcript of each memory was read and rated by researchers as a lifetime period memory, general event memory, or event-specific memory ("RALevel" method). Each researcher was provided with the following definitions:

> 0- No information/memory
> 1 (lifetime period knowledge)- Knowledge that is specific to a period in the subject's life (10th grade, middle school, etc.) but not to any event. No event or series of events is described.
> 2 (general event knowledge)- Clear reference to an event or set of events that does not include details specific to time and place. This could include clusters of events as well as repeated events.
> 3 (event-specific knowledge)- Evidence of highly detailed knowledge of an event that is isolated in time and place (i.e. specific details about a specific event)

Each memory was rated by two independent researchers with an initial interrater reliability of 78.3%. As is typical in coding procedures, all conflicting responses were resolved with discussion (Haque & Conway, 2001). Other studies using similar methods report interrater reliabilities as low as 88% before discussion (Haque & Conway, 2001; Levine et al, 2002).

To obtain distinct episodic and semantic classifications for memories, another coding system was used. Brian Levine and colleagues have developed a coding system as a component of their Autobiographical Interview (Levine et al. 2002) that calculates the

number of episodic and semantic details in a narrative. In addition to categorizing memories into three levels, all memories were categorized based on the relative proportion of each type of detail calculated using this coding system. The post-retrieval description of each memory was scored for the number of episodic and semantic details in the narrative (RA episodic/semantic). Details (location, people, actions) that relate directly to a specific event were coded as episodic (internal) details. Basic knowledge, repetition of information, and details that relate to irrelevant events were coded as semantic (external) details. Each memory detail was coded by two independent raters, with an initial interrater reliability of 87.2% (discussed to 100%).

Results and Discussion

The results reported are based on the subject's own categorization of memories. That is, each memory was categorized based on the initial memory level reported by subjects. One subject was excluded from these analyses due to missing level data. Overall, 13 subjects reported 376 memories (out of 390 total trials): 149 began with lifetime period knowledge, 102 began with general event knowledge, and 125 began with event specific knowledge. Across participants, the average number of memories retrieved from each level did not differ significantly ($F(2, 24)=1.33$; $p=.284$; see figure 2). These results support the notion that musical cues are able to naturally and directly elicit memories from all levels of specificity. However, the variability across subjects in the number of memories per level was larger than would be expected (4-18 lifetime period knowledge, 3-18 general event memories, and 3-23 event specific memories). Therefore, some subjects were almost exclusively retrieving one type of autobiographical memory during retrieval sessions.

Qualitative characteristics of memories were compared across the three levels. Consistent with previous results (Addis et al. 2004), recollective qualities (emotional intensity, relivingness, and vividness) increased across levels ($F(2,370)=37.58$, $p < .001$; $F(2,371)=41.2$, $p < .001$; $F(3, 372)= 33.33$, $p < .001$, respectively; see figure 3). In other words, event specific memories involved a greater degree of detail and mental time travel compared to more abstract lifetime period and general event memories. In addition, these recollective qualities appear to be more prominent in recent relative to remote memories. The more recently an event occurred, the larger the ratings for all three memory qualities ($F(3, 410)=6.404$, $p < .001$; $F(3, 411)=9.240$, $p < .001$; $F(3, 412)=7.962$, $p < .001$, respectively; see figure 4).

To examine the emotional quality of retrieved memories, highly emotional events were compared across the three memory levels. Ratings of “Highly Positive” were more common in event specific memories than in general event or lifetime period knowledge (see figure 5a). Interestingly, of the three memory levels, a vast majority of memories rated as “Highly Negative” were retrieved at the lifetime period knowledge level (figure 5b). Research in clinical depression has repeatedly shown that depressed and anxious populations retrieve over-generalized memories (memories lacking in event details) (Conway, 2005). Conway has proposed that the over–generalization of memories in these populations is a result of avoidance of specific memory for highly negative events. According to this hypothesis, the working self halts retrieval of negative events at an early stage (the lifetime period knowledge phase) in order to prevent additional negative feelings. The current data support this hypothesis by showing an increase in abstract knowledge (relative to specific details) for highly negative events.

Additionally, it is possible that memories that begin at different levels are retrieved differently. Memories that began at the most specific level were identified faster than those that began at more abstract levels of knowledge ($F(2, 373)=7.315$, $p=.001$; figure 6). Haque and Conway have suggested that event specific memories that are retrieved without first searching through lifetime period knowledge are a product of *direct* autobiographical memory retrievals. Direct autobiographical memories do not require a search and are more automatic (and, therefore, more rapidly retrieved) than generatively retrieved memories. Memories that begin with more abstract knowledge, on the other hand, are likely a product of a more deliberate generative retrieval. Because the process is less automatic, retrieving the first piece of autobiographical information with generative retrieval should be more time consuming.

The analyses just described were also performed using the two other coding systems (RALevel and RA episodic/semantic). Results of the RALevel method were equivalent to the reported results for the SubLevel method. Results based on the RA episodic/semantic method generally replicated those found using the first categorization method. The only pattern of results that did not replicate across coding systems was the retrieval time difference (see figure 6). When memories were categorized based on the proportion of episodic (relative to semantic) details, no retrieval time difference was found between the two levels ($F(1, 418)= .09$, $p= .764$). The retrieval time difference across memory levels has been explained as being caused by differential contributions of direct and generative retrieval processes. Because the proportion categorization does not take into account what information is retrieved *first*, it cannot distinguish between retrieval processes. Therefore, no difference in retrieval time would be expected.

Because the differences across levels were largely consistent using all three coding systems, we believe that subjects are reliably rating the specificity level of their own memories. Additionally, the ratings of subjects were significantly correlated with those of the experimenters (rho=.461; $p < .001$). These data also verify that subjects are consistently reporting the same information during the interview that they retrieved during the initial phase. The between phase consistency is also supported by a high correlation between ratings provided during retrieval and those given during the post-retrieval interview (67%).

In addition to examining the qualities of different levels of memory, the current study was intended to identify benefits of the musical memory paradigm. The benefit of directly eliciting memory from all levels of memory has already been discussed. In addition, we have hypothesized that salient and self-referential musical cues will lead to retrieval of unrehearsed autobiographical memories. In fact, 63.6% of memories were rated as having being rehearsed "almost never" in the past. Another 22.9% of memories were rated as having been rehearsed only rarely in the past. Only 2.1% of memories received the very highest rating of prior rehearsal (frequently rehearsed and retold), suggesting that subjects were not relying on these favorite stories in their retrieval of event information. Of the more remote memories (over 10yrs old and 5-10 years old), no memories were rated as frequently rehearsed, and only 1.8% of events that occurred 1-5yrs ago had been frequently rehearsed. Musical cues appear to successfully access memories that have not undergone multiple retrievals and reconstructions in the past.

One possible concern with using music as a memory cue is the danger of having a song from a previous trial carry over into a current trial. Due to the naturally associative

nature of memory, particularly autobiographical memory, it is always a concern that a memory retrieved for one cue is actually an elaboration from a previous memory. This concern was even greater for the current study as musical cues can become "stuck" in memory even after presentation has ended. To check for possible connections between adjacent memories, ratings of memory relatedness were obtained following each memory. Overall, subjects rated 84.6% of memories as not related or only marginally related to their previous retrieval. Only 2.8% of memories were rated as highly related to the previous memory, suggesting that musical cues did not cause subjects to retrieve similar memories repeatedly across trials.

Finally, familiarity ratings were collected for the classical pieces used during control trials. Familiarity ratings were obtained to determine the likelihood of a personal involuntary memory intruding during the semantic control task. Overall, subjects rated the classical pieces as completely unfamiliar 58.1% of the time and as somewhat unfamiliar an additional 27.2% of the time. Of the 140 possible cases (10 control trials for 14 subjects) only two cases (1.5% of all possible cases) received ratings of highly familiar. Additionally, in an informal debriefing that followed the post-retrieval interview, a majority of subjects indicated that they had no problem preventing personal intrusions during the control task.

The current study provided support for previous studies that revealed musical pieces as reliable cues for autobiographical memories (Cady et al., 2008; Janata et al., 2007). Additionally, this study demonstrated that musical cues may be used to evoke memories from all three levels of Conway's SMS without explicit instruction. This ability was particularly important for the current study, as it allowed for an analysis of the

qualitative characteristics of each individual level. In Experiment 2, this musical memory paradigm will be used in the scanner in order to identify the neural underpinnings of these three memory levels. Currently, no research has compared all three levels to determine which regions show common activation across groups (regions involved in all autobiographical memory activation) and which regions are preferentially involved in memories that are more specific v. more general.

CHAPTER 3: EXPERIMENT 2

Experiment 1 supported the use of musical clips in eliciting autobiographical memories naturally. In addition, clear behavioral differences were identified between the three levels of autobiographical knowledge. With this evidence, the musical memory paradigm was used to elicit autobiographical memory retrieval in a functional neuroimaging study. The current imaging study compared neural activity associated with autobiographical memories retrieved using the same memory paradigm.

Methods

Participants

16 healthy young adult volunteers (eight female; age range 18-23) participated in the current fMRI study and were financially compensated for their participation[2]. Subjects were all right-handed native English speakers without a history of psychiatric illness, neurological disorder, or hearing impairment. Before participating in the study,

[2] Six additional subjects were recruited and screened for the study but could not be analyzed. Two subjects (two female, ages 20 and 21) were not comfortable in the scanner environment and asked to terminate the study early. One subject (male, age 19) participated fully, but an equipment malfunction in the scanner lead to unusable data. Finally, three subjects' (two female, one male; ages 20-22) behavioral data suggests that they did not understand the instructions for the experimental and control tasks.

participants gave written informed consent in accord with the requirements of the Institutional Review Board at the University of North Carolina at Chapel Hill.

Materials

The majority of the materials that were used in the behavioral companion were used in the neuroimaging study. Although no new songs were required for the experimental condition, new songs were selected were for the control task. In Experiment 2, "B-side" pop music was used in place of classical musical in the semantic control task. These songs were selected to match experimental stimuli in all respects except predicted familiarity to participants.

Selection of new control stimuli involved identifying a number of songs from 1998-2007 that matched the experimental stimuli in message, rhythm, and genre. In fact, a majority of the control stimuli were selected from albums that experimental stimuli were selected from. Selections were then piloted to test for subject familiarity; all songs that were familiar to even one pilot subject were eliminated from control stimuli. Matching stimuli for the two conditions ensured that differences that arose could not be attributed to characteristics of the stimuli.

Behavioral Procedure

The behavioral procedure for Experiment 2 study was nearly identical to that described previously, with only a few changes. Due to the variability in memory level ratings observed in Experiment 1, only eight of the thirteen subjects would have been eligible for fMRI analysis. In order to increase the number of subjects reaching an acceptable number of memories, the current study included five, instead of three, test lists. These added lists increased the number of memories per condition across subjects,

increasing power and the number of eligible subjects. Additionally, a four second tone (two 2-second TRs) was added at the beginning of each run to allow for scanner equilibrium.

The control task procedure was identical to that in Experiment 1, but the stimuli now matched the experimental stimuli in all ways except predicted familiarity for the subject. Accordingly, subjects were instructed prior to each trial which task they should participate in during stimuli presentation. A single instruction (either "personal" or "adjective") was presented in place of the "warning tone" presented in Experiment 1. This sound clip varied between 2-4s in Experiment 2 (as opposed to 1-3s in Experiment 1) due to the 2s TR.

The post-retrieval interview took place after the subjects have been removed from the scanner. In addition to the interview used in Experiment 1, a debriefing was added to document any personal memories that may be retrieved during control trials. Following the post-retrieval interview, subjects were presented with all control stimuli and asked whether they inadvertently retrieved any autobiographical knowledge during the control task. Finally, all analyses were performed using subjects' level assignments, removing the middle step of using researcher ratings.

Data Acquisition

Magnetic resonance images were acquired using a Siemens Trio 3-T scanner. Subjects' heads were held in place using cushions and a headrest. An initial localizing scan was followed by a high resolution T1 weighted structural scan for anatomical visualization (160 1mm slices, TR=1750ms, TE=4.38ms). The structural scan was followed by functional scans collected during memory retrieval and elaboration. Whole

brain, gradient-echo, echo planar images (35 5mm slices, TR=2s, TE=23ms, Flip angle=90) were acquired at an angle perpendicular to the long axis of the hippocampus, identified during the T1 scan.

To present the stimuli in the scanner, magnet-safe headphones were selected that minimized distortion of the auditory signal. Specifically, we pilot tested a set of STAX SR-003 headphones to ensure that all stimuli could be successfully recognized in the scanner. To decrease the amplitude of noise associated with a running scanner, scanner safe noise-reducing earmuffs were used to diminish sound by at least 25 decibels. All data was collected using a magnet-safe button response box.

Data Analysis

Images were preprocessed and analyzed using SPM8 software implemented in MATLAB (Wellcome Department of Cognitive Neurology, London, UK). Images were co-registered, slice-time corrected, realigned, normalized and smoothed using a Gaussian 8mm kernel. Only experimental trials for which the subjects successfully retrieved AMs were preprocessed and analyzed.

Due to the complexity and length of retrieval, autobiographical memory retrieval typically varies by trial and by individual, resulting in a natural jitter (Addis et al. 2007). Because retrieval times vary across subjects and across trials, each trial was modeled individually using the subject's response. Each trial was split into memory phases based on the button response. Similar to modeling in previous research (Daselaar et al. 2008; Addis et al. 2007), memory *retrieval* was modeled as the period between trial onset and 1000ms before the button press. Control trials were modeled similarly, with the word acquisition identified as CTLRet and the definition phase identified as CTLElab.

For trials where participants identified only one level of memory, the remainder of the trial (until the first rating) was modeled as memory *elaboration*. When participants retrieved memories that included multiple level of memory specificity, more phases had to be taken into account. The time between cue onset and 1000ms prior to the first response was still modeled as retrieval, and the period between 1000ms prior to the final response and the final ratings was modeled as elaboration of that final level. However, the phase between button presses was considered a complex mix of elaboration and retrieval. Because the two processes could not be separated in this phase, it was not modeled (see Figure X).

The analysis was performed as a 2 X 3 factorial ANOVA with phase (retrieval and elaboration) as one factor and level (lifetime period, general event, and event-specific knowledge) as a second. This design resulted in six experimental conditions of interest. At the fixed-effects level for each subject, six contrasts were performed to compare each condition greater than the control condition (e.g. LTPRet > CTLRet).

These fixed-effects contrasts were entered into a flexible factorial ANOVA at the random-effects level. In order to identify regions involved in retrieval and elaboration, across memory levels, conjunctions were conducted within the ANOVA to detect regions commonly activated by all retrieval conditions greater than control and all elaboration conditions greater than control. Conjunction analyses were also designed to compare all retrieval to all elaboration conditions in order to isolate regions preferentially activated during the two phases.

Of particular interest in this study were regions that were modulated by the specificity of memory retrieval and elaboration. As such, contrasts were created that

examined regions that were preferentially activated by event specific > general event > lifetime period retrieval and lifetime period > general event > event specific retrieval. The same contrasts were created for activation during elaboration of the three levels. Once these contrasts were generated, individual planned contrasts further investigated the relationships.

Results and Discussion

Behavioral Results

The behavioral results in Experiment 2 largely replicated those in Experiment 1. The behavioral results of interest identified the differences in retrieval and phenomenological characteristics across levels. These results suggest that the memories retrieved at Conway's three levels are different types of memories, supporting earlier behavioral research on the self-memory system (Conway, 2005; Haque and Conway, 2001).

Distribution and Retrieval Times

As in Experiment 1, we had an equal number of "pure" memory trials (i.e. only one level of autobiographical memory knowledge) across the three memory levels with $F(2,30)= .712$, $p =.499$. Additionally, although the total number of retrievals in the three memory levels was equal across subjects ($F(2,30)=.898$; $p=.418$), the total number of memory elaborations was larger in the more specific memory levels ($F(2,30)=3.553$; $p< .05$). This finding suggests that more memories reach the specific than the general event or lifetime period levels during elaboration. However, of interest in the current study was only each subject had enough general event and lifetime period elaborations to analyze in the fMRI analysis.

Of particular interest was the average time taken to retrieve autobiographical memories in this study. Memories identified as lifetime period and general event took an average of 12.34s and 12.03s to retrieve. These RTs are similar to the average retrieval time reported in a recent fMRI study that utilized auditory word cues for autobiographical memory retrieval (12.25 s; Daselaar et al,, 2007). However, memories identified as event-specific were significantly faster than the other two levels ($t(14)=5.369$, $p<.001$ and $t(14)=2.861$, $p<.05$ for general event and lifetime period, respectively) at 10.03s. In addition, the retrieval time for the control task (at 11.33s; see Figure 7) was not significantly different from any of the experimental conditions, suggesting that it may be well-matched in difficulty to the experimental task.

Level Differences

Memories were divided into three groups based on their elaboration phase level in order to compare ratings. As in Experiment 1, the results of Experiment 2 suggest that the characteristics of autobiographical memories are different across levels of Conway's SMS. In particular, specific memories are more emotionally intense, vivid, and can be "relived" to a greater extent ($F(2,28)=5.79$, $p<.01$; $F(2,28)=14.22$, $p<.001$; and $F(2,28)=13.43$, $p<.001$, respectively). Additionally, more specific memories are more positive than more general memories at $F(2,28)=6.397.16$, $p = .005$ (See Figure 8). Of particular interest, the recency of memories did not differ across memory levels ($F(2,28)=.977$, $p=.389$).

Manipulation Checks

To evaluate our musical cuing paradigm, several manipulation checks were performed. Of primary interest was the familiarity of the songs presented for the

experimental condition and the control condition. Average familiarity was very high in experimental conditions (3.18/4, 3.46/4, and 3.59/4 for lifetime period, general event, and event-specific, respectively) and did not differ significantly across levels ($F(2,28)= 2.7$, p=.084). Song familiarity for the control stimuli was significantly lower than familiarity for all three memory levels ($t(14)= 11.74$, $p <.001$: $t(14)= 16.25$, $p <.001$: and $t(14)= 18.188$, $p <.001$ for lifetime period, general event, and event specific, respectively; see Figure 9) at an average of 1.24 out of 4.

One possible concern with using such familiar songs as memory cues was the potential for "carry-over" of one song into the next trial. This type of contamination could lead to very highly related memories that were retrieved outside of the "retrieval" phase. To check for this contamination, we asked subjects for a measure of relation between each memory and the memory immediately preceding it. Across all three memory levels, the average relation rating was very low (1.43, 1.59, and 1.50 for lifetime period, general event, and event specific).

It was predicted that musical cues would evoke memories that had not been retrieved many times previously. To check for this finding, we asked subjects for a "prior rehearsal" rating that measured the degree of previous retrieval for each memory. For all three memory levels, this level was very low (1.53, 1.50, and 1.53 out of 4 for lifetime period, general event, and event specific).

Imaging Results

Common Activations in Retrieval and Elaboration across levels

To examine regions activated by autobiographical memory retrieval processes, we performed a conjunction analysis that included each retrieval condition (i.e. LTP

Retrieval, GE Retrieval, and ESK Retrieval) greater than control. Therefore, the conjunction included regions that were activated in all three retrieval conditions greater than the control retrieval condition. A number of regions that have been identified as belonging to the core autobiographical memory network were identified at $p < .001$, suggesting that all three memory levels contained true autobiographical memories. The regions of significant activation in this conjunction include bilateral regions of the lateral temporal lobes, posterior cingulate, and medial prefrontal cortex. Additionally, we identified left lateralized activity in the precuneus (see Table 1 and Figure 10).

A similar conjunction was performed to examine activation during elaboration across all memory levels. This conjunction included regions that were activated during all three elaboration conditions greater than the control elaboration condition. At a threshold of $p < .001$, elaboration of autobiographical memories of all levels activated regions within the core network. Interestingly, the activation at elaboration of all three levels highly resembled the activation at retrieval. Specifically, we identified activity in regions of the bilateral posterior cingulate and medial prefrontal cortex, left precuneus and superior occipital gyrus, and right lateral temporal lobe and anterior cingulate (see Table 2 and Figure 11). These two findings highlight the overlap in neural activation that has been shown to exist within autobiographical memory retrieval and elaboration (Addis et al., 2007).

Differential Activations across Memory Phases

Both retrieval and elaboration of all three memory levels activated a number of regions in the autobiographical memory network. In order to identify neural regions that were differentially activated during autobiographical memory retrieval and elaboration,

two conjunction analyses were carried out. In the first analysis, a single conjunction included regions that were significantly more active in the retrieval phase compared to the elaboration phase in *all three memory levels.* In other words, we created a conjunction that included the retrieval greater than elaboration contrast for each condition (i.e. LTP Ret > Elab AND GE Ret > Elab AND ESK Ret > Elab). Across all three memory levels, retrieval preferentially activated regions in the bilateral lateral temporal lobes, the right lingual gyrus, and the right thalamus at $p < .001$ (see Table 3 and Figure 12). These results may suggest that retrieval, to a greater extent than elaboration, involves the processing of sensory information

To examine regions that were activated more by elaboration of autobiographical information than retrieval, we combined the "Elab > Ret" contrast across all three memory levels (i.e. LTP, GE, and ESK). This conjunction identified the regions that were significantly more active in the elaboration phase compared to the retrieval phase in *all three* memory levels. At $p< .001$, no voxels reached significance. To identify any trends in activation, we examined this same conjunction at $p < .005$, but there were still no significant voxels. These results suggest that the autobiographical memory core network is involved in both retrieval and elaboration of all three memory levels, but the retrieval phase has a slightly larger network of activity.

Differential Activations in Retrieval across Memory Levels

The conjunction of all retrieval conditions greater than the control condition revealed activation of the core autobiographical memory network. The retrieval > elaboration contrast additionally suggested that some of these regions are preferentially involved in retrieval of autobiographical memories. To investigate what type of retrieval

drives the activation of the core network, we performed contrasts to identify regions that are modulated by the specificity of the memory being retrieved. First, we generated a contrast to isolate regions that were preferentially activated during retrieval of more *general* autobiographical information. This contrast identified regions that were more active in life time period compared to general event retrieval AND more active in general event than in event specific retrieval (i.e. LTP > GE > ESK Retrieval). No regions were identified in this contrast at either $p < .001$ or $p < .005$. It is likely that no regions were identified because all activity retrieved in the general autobiographical memory condition is also included in retrieval of specific autobiographical memory retrieval.

To isolate regions that were preferentially activated during retrieval of more *specific* autobiographical information, we generated the reverse contrast (i.e. ESK > GE > LTP Retrieval). At $p < .001$, several regions, including some within the core network were activated (of interest, the bilateral dorsolateral prefrontal cortex, bilateral thalamus, and left premotor cortex see Table 4). Due to extensive core network activity in the conjunction analysis and prior literature on core network activation in the retrieval of autobiographical memories, we lowered our threshold to $p < .005$. At this more liberal threshold, a number of regions showed preferential activation during retrieval of specific, compared to general, memory retrieval. Of interest was bilateral activation in the dorsolateral PFC, inferior PFC, lateral temporal lobes, and anterior cingulate. We also identified left lateralized activity in the thalamus, posterior cingulate, parahippocampal gyrus, and hippocampus (see Table 5 and Figure 13).

To further investigate which regions were modulated by specificity of retrieval information, we performed four planned contrasts. The LTP > GE > ESK retrieval

contrast did not reveal any significant regions of activation. However, we further examined the neural correlates of *general* retrieval by testing for regions that showed statistically greater activation for LTP greater than GE separately from a test for regions that showed statistically greater activation for GE greater than ESK. Regions in the right middle occipital gyrus, inferior gyrus, and lingual gyrus were preferentially activated in the most general retrieval condition (lifetime period) relative to the general event level at $p < .001$ (See Table 6). No regions exceeded this threshold in the contrast comparing general event greater than event specific retrieval.

The contrast examining the neural correlates of *specific* AM retrieval implicated regions within the autobiographical memory core network as being modulated by the specificity of memory retrieval, with the core network being more activated with more specific retrieval. The planned contrast comparing event specific memory retrieval (ESK) greater than general event (GE) retrieval activated many regions at $p < .001$. Of interest, this contrast revealed bilateral activation in the dorsolateral PFC, orbitofronal PFC, lateral temporal lobes, parahippocampal gyrus, occipital lobes, posterior cingulate, and anterior cingulate. Left lateralized activations were also seen in the thalamus and hippocampus (See Table 7). Many of the same regions were revealed in the contrast comparing general event and lifetime period retrieval. In this contrast, significant regions of activation included bilateral lateral temporal, parahippocampal gyrus, premotor cortex, dorsolateral cortex, and posterior cingulate. As in the ESK > GE contrast, left lateralized activity was present in the thalamus (See Table 8).

Differential Activations in Elaboration across Memory Levels

As with retrieval, contrasts were generated within elaboration to identify regions that were modulated by specificity of the memory being elaborated on. Once again, one contrast was created to isolate regions involved in elaboration of *general* information (i.e. LTP > GE > ESK Elaboration) and another was created to identify those involved in elaboration of *specific* information (i.e. ESK > GE > LTP Elaboration). Neither contrast resulted in any significant activations at $p < .001$ or $p < .005$. These results suggest that elaboration of different types of autobiographical information recruits the same mnemonic processes. This finding is consistent with previous research (Addis et al., 2008) comparing retrieval of past information and projection into the future tat also showed significant differences in the construction phase, but not in the elaboration phase.

The results of these contrasts suggest that there were no neural differences during elaboration of the three levels of memory. However, the behavioral results indicate that the content of these memories may be different. Further planned contrasts were performed to examine neural correlates of these differences. Two contrasts were employed to interrogate elaboration of *general* autobiographical information (LTP>GE and GE >ESK) and two investigated regions associated with elaboration of *specific* information (ESK>GE and GE>LTP).

A distributed network of regions was activated more during elaboration of lifetime periods more than general events at $p < .001$. Included in this network was the right parahippocampal gyrus, right medial prefrontal cortex, left anterior cingulate, and bilateral lateral temporal gyrus (See Table 9). The only region to exceed the $p < .001$ threshold in the general event greater than event specific elaboration contrast was a region in the left lingual gyrus (See Table 10).

Activity in the event specific > general event elaboration contrast at $p < .001$ was largely left lateralized, with activity in regions of the posterior cingulate, parahippocampal gyrus, and prefrontal lobe (See Table 11). The general event > lifetime period contrast was also left lateralized, with activity in the inferior frontal gyrus, superior frontal gyrus, and somatosensory association cortex.

CHAPTER 4: GENERAL DISCUSSION

The current studies examined the characteristic and neural differences across the levels of Conway's Self Memory System. Conway and colleagues have described memory retrieval as an iterative process that begins at abstract personal knowledge (general event or lifetime period) and moves toward more specific memories (Conway and Pleydell-Pearce, 2001). The current study examines the process of memory construction by directly comparing memories from each level of the self memory system.

In order to obtain memories from each level of autobiographical memory, a novel method of musical cuing was used. Previous research has suggested that musical cues can access general and specific autobiographical knowledge naturally, without explicit instruction, making this method uniquely suited for our interests (Janata et al., 2007). Experiments 1 and 2 used these musical cues in an experimental design that collected information from the subject about which level of memory each musical cue evoked. As such, comparisons could be made across the three levels in regards to both qualitative characteristics (Experiment 1 and 2) and neural activation (Experiment 2).

Conway's Self Memory System

The current studies expand on previous investigations of the self memory system by allowing for natural retrieval of autobiographical memories. It has been proposed that during generative retrieval, individuals begin searching for a specific memory using abstract autobiographical knowledge (typically general event, but occasionally lifetime period) and perform an effortful search to identify event-specific knowledge that applies to the cue. Until now, most autobiographical memory studies have attempted to evaluate this retrieval process by explicitly requesting that subjects retrieve a single specific event memory. By allowing subjects to retrieve whichever level of autobiographical knowledge the cue evoked, we were able to examine autobiographical information from all three levels of the self memory system.

In Experiments 1 and 2, memories identified as lifetime period, general event, and event specific were associated with increasing levels of emotional intensity, vividness, relivingness, and emotional positivity. These results are consistent with descriptions of the hierarchy of Conway's Self Memory System from which autobiographical memories can be retrieved (Conway, 2005; Conway & Pleydell-Pearce, 2000; Conway, Turk, Miller, Logan, Nebes, Meltzer, & Becker, 1999; Conway et al. 2001; Conway, Singer, & Tagini, 2004; Conway & Williams, 2008; Haque & Conway, 2001). Within this system, autobiographical information is stratified based on the level of specificity the information contains, with lifetime period knowledge consisting of very abstract personal knowledge, general event knowledge consisting of scripted knowledge of grouped events, and event specific knowledge consisting of individual details from a event isolated in place and time.

In addition to qualitative differences, retrieval of the three levels of autobiographical knowledge may be associated with different retrieval strategies. In the current studies, response times responses to event specific knowledge were significantly faster than those for the other (more abstract) memory levels. It is likely that this result is due to a difference in retrieval strategies, with memories that began at more abstract levels of knowledge (lifetime period or general event) utilizing a strategic generative process and memories that began at event specific knowledge utilizing a more direct automatic process. This difference has been described by Conway and colleagues (Conway & Pleydell-Pearce, 2000; Haque & Conway, 2001), but future research is still required to determine if this difference in response times is actually driven by retrieval strategies.

Neural Activation in the Three Levels of Autobiographical Knowledge

Neural activity associated with the three levels of autobiographical knowledge was of particular interest in the current project. The behavioral evidence in Experiments 1 and 2 identified many ways in which the three levels were different (such as vividness and emotional intensity) and some ways in which they were the same (such as memory recency and prior rehearsal). In Experiment 2, we extended this research and identified the regions of neural activation for which the three levels overlapped and those for which they diverged.

During retrieval and elaboration of all three memory levels (greater than the control condition), regions within the autobiographical memory core network were activated. Of particular interest, we identified activity in bilateral regions of the medial PFC, reflecting the involvement of self referential processing. The only regions that

showed preferential activation during retrieval compared to elaboration were the thalamus and sensory cortices. These results are consistent with results from a recent study that asked subjects to retrieve memories of personal events and imagine possible future events (Addis et al., 2007). In this study, construction of events preferentially engaged a number of regions implicated in visual processing, including superior, middle, and inferior occipital gyrus, fusiform gyrus, and cuneus.

When examining neural activity for elaboration greater than that for retrieval, no significant activations were identified. However, Addis and colleagues (2007) identified a number of left frontal regions in this same contrast. In their study, subjects always constructed and elaborated on *specific* events, whereas our contrast included memories from all three levels of specificity. It is possible that the frontal regions identified by Addis et al. (2007) are only preferentially involved in elaboration of specific memories.

The more natural retrieval of all three levels of autobiographical knowledge allowed for comparisons across levels of retrieval and elaboration. The current imaging study is the first to compare the three levels of knowledge during both phases of memory, providing a unique look at their similarities and differences. Retrieval of specific memories was associated with greater activation in a number of regions within the core network. Of interest, we identified activity in the dorsolateral PFC, associated with search and retrieval of autobiographical information, and left lateralized activity in the MTL, associated with construction of episodic memories. Interestingly, specific memories were not associated with greater activation in any regions at elaboration. Therefore, it is unlikely that an increase in emotional or contextual content itself can account for the activity seen in the retrieval contrast.

No neural regions were found to be more active in general knowledge retrieval and elaboration when compared with specific retrieval and elaboration (LTP>GE>ESK ret or LTP>GE>ESK elab) initially suggesting that more specific memories may include all of the information available in an abstract memory. However, the results from the individual planned contrasts in Experiment 2 suggest that the regions in the lifetime period>general event contrast do not overlap with those in the general event>event specific contrast. These contrasts suggest that the three levels of autobiographical knowledge are not necessarily ordinal, but rather three distinct types of memory content.

Although Experiment 2 is the first imaging study to compare all three levels of autobiographical knowledge, several have compared memory for specific event to autobiographical facts (Maquire & Mummery, 1999) or to general events (Addis et al., 2004b; Levine & Turner, 2004). It is difficult to compare the results of these studies to those in the current fMRI study due to large differences in methodology. All three studies collected memories from subjects prior to the scanning session and re-presented the information to subjects with instructions to answer questions about the event (Levine & Turner, 2004; Maquire & Mummery, 1999) or re-retrieve the event (Addis et al, 2004b). As such, these studies did not differentiate between retrieval (or initial construction) and elaboration (or development) of autobiographical knowledge.

Music and Autobiographical Memory

A secondary goal of the current experiments was to evaluate the utility of music as a cue in autobiographical memory studies. Music has been proposed as an emotional and self-relevant memory cue that can be used universally across subjects of the same cohort (Cady et al., 2008; Janata et al., 2007). Unlike the songs used in previous studies,

the materials used in Experiments 1 and 2 were all highly familiar to participants, yielding a high number of successfully retrieved memories. Additionally, the current studies took advantage of the ability of music to cue different memory levels to compare across Conway's SMS.

Using musical cues also allowed subjects to retrieve a wide range of memories that had not been retrieved many times previously. Accessing relatively under-rehearsed memories gives this study an advantage over neuroimaging studies that have employed a pre-scan interview (e.g. Addis et al., 2004b) or prospective collection of memories (e.g. Levin & Turner, 2004). Importantly, the level of prior rehearsal was consistently low across all levels and did not differ based on the age of the memory. This consistency allowed for a better comparison of characteristic qualities and neural activation across levels.

Retrieval of autobiographical memories to musical cues activated multiple regions within the core network, including medial PFC, posterior cingulate, precuneus, and medial temporal lobe. In the only other imaging study to use musical cues (Janata, 2009), many of these regions were not identified. This difference likely occurred because subjects in the previous study were not explicitly asked to retrieve any memories. Instead, subjects in their study were asked to rate the song on the ability to identify an autobiographical memory at a later point (Janata, 2009). Activity was observed in regions within the medial prefrontal cortex for both studies, suggesting that they both require self-referential processing. However, because subjects in Janata's imaging study were not asked to recall their memory, they may have not engaged other regions typically observed in core network activation.

Core Network

The current results may provide substantial steps toward understanding the purpose of core network activation. Currently, the reason for widespread network activation during daydreaming, theory of mind, autobiographical memory, and many other tasks remains unclear. Possible explanations that have been proposed have been scene construction (Hassabis & Maguire, 2007), self-projection (Buckner & Carroll, 2007; Buckner et al., 2008), and a "watchfulness" or monitoring of the external environment (Buckner et al., 2008). Only the first two proposed explanations (scene construction and self-projection) can account for the involvement of the core network in autobiographical remembering.

In the current study, the core network was activated in all memory conditions (both retrieval and elaboration) greater than control. By definition, memories from our first level of memory (lifetime period memories) are not isolated in a particular location, but rather include abstract knowledge about all locations from a time in one's life. Although it's possible that some subjects envisioned a scene as a background for their abstract knowledge, it is unlikely that this memory would involve the complex scene construction described by Hassabis and Maquire (2007). However, all autobiographical knowledge would involve projection of the self into the recalled lifetime period, consistent with the self-projection explanation posed by Buckner and Carroll (2007).

In addition to finding core network activity in all three memory levels at retrieval and elaboration, we found that the specificity of memory modulated network activity at retrieval. Regions that were preferentially engaged included the left MTL and regions involved in visual processing. Interestingly, the medial prefrontal cortex was not

observed in this contrast, suggesting that it may be equally involved in the retrieval of all three levels of autobiographical knowledge. Because specific memories in this study were more vivid, emotionally intense, emotionally positive, and subject to reliving, it is possible that any of these characteristics could have driven the increased activity in the core network. As such, these findings are consistent with both the scene-construction hypothesis and the self-projection hypothesis. It is possible that one subsystem of the core network may be driven by scene-construction, while the other is driven by self-projection. Future research will be required to directly compare the effects of each of these characteristics, individually, on activation within the core network.

The core network is engaged by default in most subjects, but can be disturbed in a number of populations. Of interest in the current research is how activity in the core network might be affected by depressive symptoms, post-traumatic stress disorder (PTSD), and Alzheimer's disease. Although disruption in the core network in depression and PTSD are currently not fully understood, a number of structural and functional studies have explored how Alzheimer's disease might affect the core network (Buckner, Snyder, Shannon, LaRossa, Sachs, Fotenos, Sheline, Klunk, Mathis, Morris, & Mintun, 2005) . In particular, early stages of the disease are associated with accelerated atrophy in regions of the posterior cingulate and MTL, but medial frontal structures remain relatively intact (Buckner et al. 2008; Buckner et al. 2005).

Future Directions

The current studies demonstrated that subjects rate specific memories as more vivid, emotional, and subject to reliving. Although it is clear that the core network is preferentially engaged by retrieval of specific memory retrieval, it is currently unclear as

to which quality drives this activation. Future research will be required to examine how each quality may individually modulate regions within the core autobiographical memory network. Specifically, it will be important to identify how activation in regions within the MTL may vary depending on the qualitative memory ratings. A future study, utilizing the methods of Experiment 2, could use parametric modulation to specifically target regions within the MTL that are activated to a greater extent with higher ratings on these three qualities.

A series of studies may also be performed to better understand the increase in emotional positivity in specific autobiographical memories. In Experiments 1 and 2, highly positive memories were preferentially retrieved at the most specific level of autobiographical knowledge. Of greater interest, highly negative memories were preferentially retrieved at the most general level of autobiographical knowledge. This pattern is consistent with a large field of research that has demonstrated that individuals diagnosed with depression (or show depressive symptoms) consistently retrieve overly general autobiographical memories (e.g. Williams & Broadbent, 1986).

It has been proposed that overgeneralization in depressed individuals is a result of affect-regulation processes during retrieval (Hermans, de Decker, de Peuter, Raes, Eelen, & Williams, 2008). This research suggests that retrieving negative memories in a less specific way may help prevent painful emotions. Specifically, cognitive control processes, such as those measured by executive control or basic working memory tasks, may assist individuals in preventing specific retrieval of negative information (Dalgleish, Williams, Golden, Perkins, Barrett, Barnard, Yeung, Murphy, Elward, Tchanturia, & Watkins, 2007; Schmeichel, Volokhov, & Demaree, 2008). In order to better understand

the overgeneralization of highly negative memories in the current studies, a behavioral study could be conducted that included a measure of cognitive control in addition to the methods of the current studies. An increased overgeneralization of negative memories in individuals with high scores on cognitive control scales would provide added support for the affect-regulation model.

Additionally, the current autobiographical memory tasks should be implemented in populations who demonstrate distinctive patterns of memory retrieval. Specifically, healthy older adults have shown both a positivity effect (Comblain, D'Argembeau, & Van der Linden, 2005) and an overgeneralization effect (Addis et al. 2008; Levine et al. 2002) in autobiographical memory retrieval. Therefore, it would be unlikely for them to show the same increase in positivity across memory levels. Instead, it is probable that an older adult population would retrieve an increased number of highly positive memories at a lifetime period level. A future study that used the current methodology in a population of healthy older adults may help explain the overgeneralization of memory retrieval that is typically seen. Importantly, this future study may be able to separate the effects of emotional valence and emotional intensity of memory retrieval in this older population.

Finally, it would of great interest to use music cues in an autobiographical memory study looking at older adults who suffer from the early stages of Alzheimer's disease (AD). At least one previous study has shown that simply playing music in the background during autobiographical memory tasks facilitates retrieval in patients (Irish et al. 2006). It has recently been suggested that processing familiar music activates the same neural regions that are involved in self reference, above and beyond the activation from the memory task (Janata, 2009). It is possible that this activation may help engage the

entire autobiographical memory network by employing core network regions that remain relatively intact (medial PFC) to compensate for accelerated atrophy in the MTL and posterior cingulate. If retrieval of autobiographical memories to musical cues reveals an increase in medial PFC activation, this might suggest a role of music in therapy for individuals in the early stages of AD.

Summary

The current studies use natural retrieval of autobiographical memories to identify characteristic and neural activation differences between the three levels of autobiographical knowledge as proposed by Conway and colleagues (Conway, 2005; Conway & Pleydell-Pearce, 2000; Conway, Turk, Miller, Logan, Nebes, Meltzer, & Becker, 1999; Conway et al. 2001; Conway, Singer, & Tagini, 2004; Conway & Williams, 2008; Haque & Conway, 2001). Experiments 1 and 2 revealed that subjects rated specific memories as the most vivid, emotional, and subject to reliving. Additionally, these memories were associated with increased activation in several regions within the core network, such as the MTL, thalamus, and visual processing regions. However, other regions within the core network, such as the medial PFC and posterior cingulate, were activated during all autobiographical memory tasks.

The results of these studies also support recent research studies that propose musical stimuli as ideal cues for autobiographical memory tasks (Cady et al, 2008; Janata, 2009; Janata et al, 2007). Musical cues allowed subjects in the current study to retrieve all three levels of autobiographical memory naturally, without explicit instruction. Additionally, the memories retrieved were often highly emotional (both negative and positive) and had not been repeatedly retrieved by the subject previously.

These findings support the use of musical cues in future memory studies, particularly those in populations with distinctive retrieval patterns (e.g. depressed individuals, older adults, and Alzheimer's patients).

APPENDIX:

INSTRUCTIONS FOR MEMORY RATINGS

Familiarity: How familiar are you with the song? 1= not at all, 4= know it almost perfectly

Song Preference: How much do you like the song? 1= not at all, 4= one of your favorites

Genre Preference: How much do you like songs like the one you just listened to? 1= not at all, 4= one of your favorites

Emotion/Affect: How negative or positive was the memory? 1= highly negative, 4= highly positive

Intensity: How intense (emotionally) was this memory? 1= not at all, 4= very

Vividness: How many details can you retrieve about this memory? How clear are these details? 1= very vague memory, 4= very clear and distinct

Reliving: Can you put yourself back into the memory? 1= almost like watching the events unfold like a home movie, 4= a feeling of re-experiencing the event

Prior Retrieval: When was the last time you retrieved (remembered) this event? 1= haven't really thought about the event since it happened, 4= I have retrieved this event very recently

Relation: How strongly is the memory you retrieved for this song related to the memory you retrieved for the previous song. 1= not related at all, 4= very highly related *For example, if one song evoked a memory of going running, then the next song evoked another memory of running, that second memory would have a high relation rating (4).

However, if the second song evoked a memory of driving in your car, it would be less related (1 or 2)

Recency: How long ago did this event occur? 1=more than 10 years ago, 2= 5-10 years ago, 3=1-5 years ago, 4= less than a year ago

References

Addis, D.R., McIntosh, A.R., Moscovitch, M., Crawley, A.P., & McAndrews, M.P. (2004a). Characterizing spatial and temporal features of autobiographical memory retrieval networks: A partial least squares approach. *NeuroImage, 23,* 1460-1471.

Addis, D.R., Moscovitch, M., Crawley, A.P., & McAndrews, M.P. (2004b). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus, 14,* 752-762.

Addis, D.R., Wong, A.T., & Schacter, D.L. (2007) Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia, 45,* 1363-1377.

Addis, D.R., Wong, A.T., & Schacter, D.L. (2008). Age-related changes in the episodic simulation of future events. *Psychological Science, 19(1),* 33-41.

Bartlett, J.C. & Snelus, P. (1980). Lifespan memory for popular songs. *American Journal of Psychology, 93,* 551-560.

Botzung, A., Denkova, E., Ciuciu, P., Scheiber, C., & Manning, L. (2008). The neural bases of the constructive nature of autobiographical memories studied with a self-paced fMRI design. *Memory, 16,* 351-363.

Buckner, R.L., Andrews-Hanna, J.R., & Schacter D.L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences, 1124,* 1-38.

Buckner, R.L. & Carroll, D.C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11(2),* 49-57.

Buckner, R.L., Snyder, A.Z., Shannon, B.J., LaRossa, G., Sachs, R., Fotenos, A.F., Sheline, Y.I., Klunk, W.E., Mathis, C.A., Morris, J.C., & Mintun, M.A. (2005). Molecular, structural, and functional characterization of Alzheimer's Disease: Evidence for a relationship between default activity, amyloid, and memory. *The Journal of Neuroscience, 25,* 7709-7717.

Burianova, H., & Grady, C. L. (2007). Common and unique neural activations in autobiographical, episodic, and semantic retrieval. *Journal of Cognitive Neuroscience, 19(9),* 1520-1534.

Cabeza, R., Prince, S.E., Daselaar, S.M., Greenberg, D.L., Budde, M., Dolcos, F., LaBar, K.S., & Rubin, D.C. (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience, 16,* 1583-1594.

Cabeza, R. & St. Jacques. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences,* 11(5), 219-227.

Cady, E.T., Harris, R.J., & Knappenberger, J.B. (2008). Using music to cue autobiographical memories of different lifetime periods. *Psychology of Music, 36,* 157-177.

Comblain, C., D'Argembeau, A., & Van der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research, 31,* 173-189.

Conway, M.A. (1992). A structural model of autobiographical memory. In M.A. Conway, D.C. Rubin, H. Spinnler, & W.A. Wagenaar (Eds.), *Theoretical Percpectives on Autobiographical Memory* (pp. 167-193). Dordrecht, the Netherlands: Kluwer Academic.

Conway, M.A. (2005). Memory and the self. *Journal of Memory and Lanugage, 53,* 594-628.

Conway, M. A., & Fthenaki, A. (2000). Disruption and loss of autobiographical memory. In L. Cermak (Ed.), *Handbook of neuropsychology: Memory and its disorders* (2nd ed., pp. 281-312). Amsterdam: Elsevier.

Conway, M.A. & Pleydell-Pearce, C.W. (2000). The construction of autobiographical memories in the self-memory system. *Psychological Review, 107,* 261-288.

Conway, M.A., Pleydell-Pearce, C.W., & Whitecross, S.E. (2001). The neuroanatomy of autobiographical memory: A slow cortical potential study of autobiographical memory retrieval. *Journal of Memory and Language,* 45, 493-524.

Conway, M.A., Singer, J.A., & Tagini, A. (2004). The self and autobiographical memory: Correspondence and coherence. *Social Cognition,22,*491-529.

Conway, M.A., Turk, D.J., Miller, S.L., Logan, J., Nebes, R.D., Meltzer, C.C., & Becker, J.T. (1999). A positron emission tomography (PET) study of autobiographical memory retrieval. *Memory, 7,* 679-702.

Conway, M.A. & Williams, H.L. (2008). Autobiographical Memory. In H.L. Roediger III (Ed.), *Learning and Memory: A Comprehensive Reference, Vol. 2: Cognitive Psychology of Memory* (pp.893-910). New York: Elsevier.

Cuddy, L.L. & Duffin, J. (2005). Music, memory and Alzheimer's disease: Is music recognition spared in dementia, and how can it be assessed? *Medical Hypotheses, 64,* 2299-235.

Dalgleish, T., Williams, J.M.G., Golden, A-M. J., Perkins, N., Barrett, L.F., Barnard, P.J., Yeung, C.A., Murphy, V., Elward, R., Tchanturia, K.,& Watkins, E. (2007). Reduced specificity of autobiographical memory and depression: The role of executive control. *Journal of Experimental Psychology: General, 136,* 23-42.

Daselaar, S.M., Rice, H.J., Greenberg, D.L., Cabeza, R., LaBar, K.S., & Rubin, D.C. (2008). The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex, 18,* 217-229.

Denkova, E., Botzung, A., Scheiber, C., & Manning, L. (2006a). Material-independent cerebral network of re-experiencing personal events: Evidence from two parallel fMRI experiments. *Neuroscience Letters, 407,* 32-36.

Denkova, E., Botzung, A., Scheiber, C., & Manning, L. (2006b). Implicit emotion during recollection of past events: A nonverbal fMRI study. *Brain Research, 1078,* 143-250.

Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. (1996). Cerebral respresentation of one's own past: Neural networks involved in autobiographical memory. *The Journal of Neuroscience, 16,* 4275-4282.

Foster, N.A. & Valentine, E.R. (2001). The effect of auditory stimulation on autobiographical recall in dementia. *Experimental Aging Research, 27,* 215-228.

Gilboa, A., Ramirez, J., Kohler, S., Westmacott, R., Black, S.E., & Moscovitch, M. (2005). Retrieval of autobiographical memory in Alzheimer's Disease: Relation to volumes of medial temporal lobe and other structures. *Hippocampus, 15,* 535-550.

Gilboa, A., Winocur, G., Rosenbaum, R.S., Poreh, A., Gao, F., Black, S.E., Westmacott, F., & Moscovitch. (2006). Hippocampal contributions to recollection in retrograde and anterograde amnesia. *Hippocampus, 16,* 966-980.

Graham, K.S., Lee, A.C.H., Brett, M., & Patterson, K. (2003). The neural basis of autobiographical and semantic memory: New evidence from three PET studies. *Cognitive, Affective, & Behavioral Neuroscience, 3,* 234-254.

Haque, S. & Conway, M.A. (2001). Sampling the process of autobiographical memory construction. *European Journal of Cognitive Psychology, 13,* 529-547.

Hassabis, D. & Maguire, E.A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Science, 11(2),* 299-306.

Hermans, D., de Decker, A., de Peuter, S., Raes, F., Eelen, P., & Williams, J.M.G. (2008). Autobiographical memory specificity and affect regulation: Coping with a negative life event. *Depression and Anxiety, 25,* 787-792.

Irish, M., Cunningham, C.J., Walsh, J.B., Coakley, D., Lawlor, B.A., Robertson, I.H., & Coen, R.F. (2006). Investigating the enhancing effect of music on autobiographical memory in mild Alzheimer's disease. *Dementia and Geriatric Cognitive Disorders, 22,* 108-120.

Ivanoiu, A., Cooper, J.M., Shanks, M.F., & Venneri, A. (2006). Patterns of impairment in autobiographical memory in the degenerative dementias constrain models of memory. *Neuropsychologia, 44,* 1936-1955.

Janata, P. The neural architecture of music-evoked autobiographical memories. *Cerebral Cortex,* Advance Access published February 24, 2009, doi:10.1093/cercor/bhp008.

Janata, P., Tomic, S.T., & Rakowski, S.K. (2007). Characterization of music-evoked autobiographical memories. *Memory, 15(8),* 845-860.

Levine, B., Svoboda, E., Hay, J.F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology and aging, 17(4),* 677-689.

Levine, B., Turner, G.R., Tisserand, D., Hevenor, S.J., Graham, S.J., & McIntosh, A.R. (2004). The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. *Journal of Cognitive Neuroscience, 16,* 1633-1646.

Maguire, E.A. & Mummery, C.J. (1999). Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus, 9,* 54-61.

Mitterschiffthaler, M.T., Fu, C.H.Y., Dalton, J.A., Andrew, C.M. & Williams, S.C.R. (2007). A functional MRI study of happy and sad affective states induced by classical music. *Human Brain Mapping, 28,* 1150-1162.

Rock on the Net. 1997-2008. http://www.rockonthenet.com/archive/index.htm.

Rubin, D.C. & Greenberg, D.L. (1998). Visual memory-deficit amnesia: A distinct amnesic presentation and etiology. *PNAS, 95,* 5413-5416.

Schmeichel, B.J., Volokhov, R.N., & Demaree, H.A. (2008). Working memory capacity and the self-regulation of emotional expression and experience. *Journal of Personality and Social Psychology, 95,* 1526-1540.

Schulkind, M.D., Hennis, L.K., & Rubin, D.C. (1999). Music, emotion, and autobiographical memory: They're playing your song. *Memory & Cognition, 27,* 948-955.

Steinvorth, S., Levine, B., & Corkin, S. (2005). Medial temporal lobe structures are needed to re-experience remote autobiographical memories: Evidence from H.M. and W.R. *Neuropsychologia* 43, 479-496.

Thompson-Schill, S.L. (2003). Neuroimaging studies of semantic memory: Inferring "how" from "where". Neuropsychologia, 41, 280-292.

Williams, J.M.G. & Broadbent, K. (1986). Autobiographical memory in suicide attempters. *Journal of Abnormal Psychology, 95,* 144-149.

Table 1. Common Regions of Significant Activation during Construction of All Three Memory Levels

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Superior Temporal Gyrus	L	22	-60	-18	2	7.78
			-64	-26	2	7.19
	R		62	-10	-2	5.91
Anterior Temporal Lobe	L	38	-54	12	-24	4.04
	R		56	2	-10	5.53
			46	20	-34	3.21
Precuneus	L	31	-10	-60	24	6.98
Posterior Cingulate	R	29	8	-50	6	6.76
		23	8	-58	14	6.66
	L	31	-16	-50	20	3.21
Middle Temporal Gyrus	R	21	60	-2	-4	5.87
Orbitofrontal Cortex	L	11	-16	44	-12	4.78
	R		34	34	-10	3.55
Medial Prefrontal Cortex	L	11	-6	54	-12	4.25
	R	10	2	54	-10	3.92
Caudate Body	R		16	-4	28	3.52
	L		-18	-18	30	3.32
Caudate Tail	R		22	-32	26	3.47
Inferior Temporal Gyrus	R	20	34	-12	-28	3.35
Premotor Cortex	R	6	58	-2	46	3.28

Regions significant at uncorrected threshold of $p<.001$
BA= approximate Brodmann Area

Table 2. Common Regions of Significant Activation during Elaboration of All Three Memory Levels

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Posterior Cingulate	R	23	8	-60	18	7.25
		29	8	-50	6	6.21
	L	31	-8	-58	20	6.87
			0	-36	38	3.53
Angular Gyrus	R	39	46	-72	34	5.53
Supramarginal Gyrus	R	40	46	-68	48	3.73
Precuneus	L	19	-30	-84	36	5.14
			-38	-80	36	5.08
		7	-12	-78	52	4.12
			-16	-84	46	3.34
			-18	-84	42	3.23
Superior Occipital Gyrus	L	19	-42	-82	28	4.72
Superior Frontal Gyrus	R	8	24	34	48	4.86
		10	14	56	-2	3.50
	L	8	-26	24	44	3.45
			-28	22	46	3.33
Medial Prefrontal Cortex	L	10	0	58	-6	4.80
			-14	42	-12	3.94
	R		2	66	2	3.49
Somatosensory Association Cortex	L	7	-8	-74	60	3.75
Fusiform Gyrus	L	37	-28	-40	-16	4.07
Middle Frontal Gyrus	L	10	-38	58	-2	3.59
Anterior Cingulate	R	25	2	10	-6	3.36
Anterior temporal lobe	R	38	50	14	-32	3.25

Regions significant at uncorrected threshold of $p<.001$

BA= approximate Brodmann Area

Table 3. Regions of Significant Activation Construction > Elaboration
All Memory Levels

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	Peak t
Superior Temporal Gyrus	L	22	-58	-20	0	4.22
			-60	-32	2	2.95
		41	-44	-30	2	3.43
	R	22	50	-18	-4	3.55
			50	-8	-8	3.35
Premotor Cortex	L	6	-48	-6	58	3.44
Thalamus	R		4	-10	4	3.44
Superior Frontal Gyrus	L	6	-10	-4	78	3.37
Lingual Gyrus	R	19	32	-62	0	3.33
Hypothalamus	L		-6	-4	-10	3.24

Regions significant at uncorrected threshold of $p<.001$
BA= approximate Brodmann Area

Table 4. Regions of Significant Activation during Construction
ESK > GE > LTP

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Superior Frontal Gyrus	L	8	0	26	58	4.05
Premotor Cortex	L	6	-40	-4	50	3.89
			-2	2	60	3.58
Dorsolateral Prefrontal Cortex	L	9	-46	4	30	3.57
			-54	10	34	3.57
			-52	8	40	3.22
		46	-40	30	20	3.40
	R	9	54	20	36	3.48
Inferior Frontral Gyrus	L	47	-52	18	2	3.37
	R	9	42	8	32	3.32
Thalamus	L		-6	-10	10	3.26
	R		4	-18	-18	3.26

Regions significant at uncorrected threshold of p<.001
BA= approximate Brodmann Area
ESK = Event Specific Knowledge; GE = General Event; LTP = Lifetime Period

Table 5. Regions of Significant Activation during Construction
ESK > GE > LTP

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Superior Frontal Gyrus	L	8	0	26	58	4.05
			-26	26	50	2.66
	R		52	14	44	2.91
Premotor Cortex	L	6	-2	2	60	3.58
			-40	-4	50	3.89
			-18	30	60	2.8
			-30	-16	56	2.84
	R	6	10	18	56	3.13
			38	4	58	3.03
Dorsolateral Prefrontal Cortex	L	9	-46	4	30	3.57
			-54	10	34	3.57
			-50	26	34	2.86
			-14	50	38	2.71
		46	-40	30	20	3.4
			-8	-24	-4	2.72
			-44	46	10	2.8
			-52	26	26	2.72
			-50	30	22	2.71
			-42	14	20	2.65
	R	9	54	20	36	3.48
			56	14	28	2.66
		46	54	38	16	2.94
		9	42	8	32	3.32
Inferior Frontal Gyrus	L	47	-52	18	2	3.37
			-50	24	-4	2.89
			-30	16	-22	2.78
			-10	-62	-40	2.78
		45	-56	24	12	2.77
		44	-44	8	22	2.67
	R	45	56	22	24	2.79
Thalamus	L		-6	-10	10	3.26
			-10	-4	6	2.93
			0	-14	4	2.88
			-4	-28	0	3.14
Somatosensory Association Cortex	L	7	-28	-64	44	3.09
			-28	-68	54	3.08
			-28	-54	42	3.05
Middle Temporal Gyrus	L	21	-66	-44	-4	3.08
			-64	-52	0	2.71

	R	21	54	6	-18	2.96
		22	68	-44	0	2.77
Posterior Cingulate	L	29	-2	-42	6	3.01
			-4	-48	14	2.64
Precuneus	L	19	-44	-78	38	2.97
Anterior Cingulate	L	32	-6	12	46	2.69
	R	32	8	20	30	2.91
Fusiform Gyrus	R	20	46	-8	-26	2.84
Hippocampus	L		-30	-10	-18	2.8
Putamen	L		-30	-16	-4	2.71
	R		18	2	16	2.76
			16	2	10	2.74
Primary Somatosensory Cortex	L	3	-40	-28	56	2.73
			-40	-26	60	2.66
Parahippocampal Gyrus	L	28	-22	-18	-8	2.71
		36	-24	-4	-36	2.7
Insula	L	13	-40	8	22	2.7

Regions significant at uncorrected threshold of $p<.005$

BA= approximate Brodmann Area

ESK = Event Specific Knowledge; GE = General Event; LTP = Life-time Period

Table 6. Regions of Significant Activation during Construction
LTP > GE

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Middle Occipital Gyrus	R	19	28	-90	14	5.3
			38	-76	0	4.17
Inferior Occipital Gyrus	R	19	40	-82	-6	3.6
Lingual Gyrus	R	19	30	-62	-6	4.39

Regions significant at uncorrected threshold of $p<.001$; extent= 5 voxels.
BA= approximate Brodmann Area;
GE = General Event; LTP = Life-time Period

Table 7. Regions of Significant Activation during Construction
ESK > GE

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Dorsolateral Prefrontal Cortex	L	9	-8	50	26	5.58
			-28	42	32	3.98
			-46	4	38	3.49
		46	-40	28	18	3.41
	R	46	52	22	30	4.45
		9	16	44	28	3.45
Orbitofrontal Cortex	R	11	20	52	-10	5.06
			40	34	-12	4.16
	L		-18	42	-12	4.12
			-10	54	-20	3.66
Premotor Cortex	L	6	-6	30	60	4.93
			-42	-10	48	4.83
			-50	2	30	4.06
	R		44	-2	40	4.15
			40	12	58	4.08
			34	2	46	3.41
Parahippocampal Gyrus	L	28	-20	-16	-28	5.55
	R	36	26	-6	-38	4.78
			30	-18	-28	4.61
Inferior Temporal Gyrus	L	20	-38	-16	-36	5.53
			-58	-30	-18	3.94
			-32	-6	-48	3.83
			-30	4	-50	3.42
			-36	2	-50	3.42
	R		38	-20	-26	4.12
			38	-10	-36	4.5
			46	-6	-26	3.92
Hippocampus	L		-28	-16	-20	5.13
Primary Motor Cortex	L	4	-34	-30	68	5.34
Somatosensory Association Cortex	L	5	-32	-44	62	4.4
		7	-20	-68	58	4.49
			-32	-62	60	4.05
			-28	-60	44	3.92
			-8	-52	50	3.82
			-18	-72	32	3.78
			-10	-56	70	3.69
			0	-50	60	3.32
	R	5	40	-50	60	3.84

		7	30	-70	54	3.84
			2	-78	34	3.23
			16	-58	66	3.47
Angular Gyrus	R	39	52	-74	24	5.04
			44	-64	26	3.42
Inferior Frontal Gyrus	L	45	-60	14	2	4.64
			-60	20	14	4.01
		47	-56	20	-4	4.21
	R	45	52	32	6	3.64
		47	38	30	-20	4.53
			50	40	-14	4.24
			28	12	-16	3.47
			56	26	0	3.39
Posterior Cingulate	R	31	24	-46	40	4.48
			22	-36	40	3.61
			16	-68	14	4.25
			4	-48	34	3.79
			4	-78	26	3.63
		23	6	-24	34	3.32
	L	31	-6	-46	32	3.82
Anterior Cingulate	R	33	8	16	26	4.25
	L	24	-14	-16	42	4.07
			-6	-16	40	3.59
Superior Frontal Gyrus	R	8	26	18	50	4
	L	8	-52	10	46	3.97
		10	-38	52	20	4.07
Middle Temporal Gyrus	R	21	52	-4	-18	3.63
			54	4	-16	3.47
Insula	R	13	38	-38	26	3.91
			32	20	10	3.51
Thalamus	L		-8	-34	0	3.84
Supramarginal Gyrus	R	40	46	-40	46	3.42
	L		-46	-66	50	3.41
Premotor Cortex	L	6	-4	0	62	3.83
Fusiform Gyrus	L	37	-40	-48	-16	3.83
Superior Temporal Gyrus	R	41	44	-34	2	3.78
	L	22	-52	4	8	3.48
Middle Occipital Gyrus	R	19	46	-82	2	3.59
Lingual Gyrus	L	18	-12	-100	-10	3.48

Regions significant at uncorrected threshold of $p<.001$ with an extent= 5 voxels.
BA= approximate Brodmann Area;
ESK = Event Specific Knowledge; GE = General Event

Table 8. Regions of Significant Activation during Construction
GE > LTP

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Premotor Cortex	L	6	0	6	54	5.1
			-30	0	68	3.63
			-26	-16	58	3.58
	R		8	10	56	4.01
			34	0	56	4.78
Superior Frontal Gyrus	L	8	0	26	58	4.05
			-34	22	50	3.35
			-20	46	48	3.34
Inferior Frontal Gyrus	L	45	-42	22	6	4.9
		47	-32	34	-18	3.37
			-50	34	-14	3.52
Insula	L	13	-30	24	2	4.51
Dorsolateral Prefrontal Cortex	L	46	-36	34	10	4.45
	R	9	42	10	34	4.38
			54	16	40	4.01
Posterior Cingulate	L	30	-10	-52	14	4.21
	R	29	12	-52	16	3.74
		29	6	-56	10	3.63
Angular Gyrus	L	39	-54	-72	26	4.15
Middle Temporal Gyrus	L	19	-58	-66	16	3.88
	L	21	-62	-60	4	3.87
			-66	-46	-4	3.55
Precuneus	L	19	-28	-82	42	3.71
Parahippocampal Gyrus	R	28	18	-16	-14	4.1
	L	30	-22	-48	6	3.76
Thalamus	L		-6	-24	0	3.6
Superior Temporal Gyrus	L	22	-52	-40	-2	3.42
	R	39	48	-50	10	3.4
		22	66	-48	2	3.35
			58	-50	2	3.29

Regions significant at uncorrected threshold of $p<.001$ with an extent = 5 voxels.
BA= approximate Brodmann Area
GE = General Event; LTP = Life time Period

Table 9. Regions of Significant Activation during Elaboration
LTP > GE

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Precuneus	L	7	-16	-52	58	4.28
			-22	-52	50	3.37
	R		14	-48	48	3.58
Precentral Gyrus	R	44	46	12	14	4.18
		4	44	-16	42	3.46
Parahippocampal Gyrus	R	36	30	-2	-38	3.92
Somatosensory Association Cortex	R	5	10	-34	50	3.75
Medial Prefrontal Cortex	R	6	6	-26	52	3.57
Anterior Cingulate	L	24	-14	-6	46	3.7
Premotor Cortex	R	6	30	6	50	3.68
Primary Auditory Association Cortex	L	42	-60	-16	10	3.68
Superior Temporal Gyrus	L	42	-64	-26	8	3.34
		22	-60	10	2	3.39
	R	22	60	-4	0	3.56
Insula	R	13	32	22	10	3.61
Inferior Frontal Gyrus	R	47	36	28	4	3.49
	L	44	-58	14	12	3.52
Lingual Gyrus	L	19	-16	-62	-4	3.53
Cuneus	R	18	20	-80	18	3.44
Middle Temporal Gyrus	R	37	44	-70	6	3.4

Regions significant at uncorrected threshold of $p<.001$ with an extent= 5 voxels.
BA= approximate Brodmann Area
GE = General Event; LTP = Life time Period

Table 10. Regions of Significant Activation during Elaboration
GE > ESK

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Lingual Gyrus	L	19	-32	-66	0	3.9

Regions significant at uncorrected threshold of p<.001 with an extent= 5 voxels.
BA= approximate Brodmann Area
GE = General Event; ESK = Event Specific Knowledge

Table 11. Regions of Significant Activation during Elaboration
ESK > GE

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	Peak t
Premotor Cortex	R	6	4	6	76	3.94
	L		-50	-4	38	3.4
Middle Temporal Gyrus	L	21	-56	0	-30	3.8
Posterior cingulate	L	31	-6	-44	38	3.63
			-12	-38	42	3.51
Parahippocampal Gyrus	L	28	-22	-18	-30	3.59
Superior Frontal Gyrus	L	8	-2	40	52	3.56
		10	-18	56	4	3.47
Insula	L	13	-40	10	10	3.41

Regions significant at uncorrected threshold of $p<.001$ with an extent= 5 voxels.
BA= approximate Brodmann Area
GE = General Event; ESK = Event Specific Knowledge

Table 12. Regions of Significant Activation during Elaboration
GE > LTP

			MNI Coordinates			
Region of Interest	Hemisphere	BA	x	y	z	t-value
Inferior Frontal Gyrus	L	47	-28	18	-26	3.78
Superior Frontal Gyrus	L	10	-8	64	-4	3.75
Somatosensory Association Cortex	L	7	-16	-70	64	3.52
			-38	-70	54	3.44

Regions significant at uncorrected threshold of $p<.001$ with an extent= 5 voxels.
BA= approximate Brodmann Area
GE = General Event; LTP = Life time Period

Figure 1

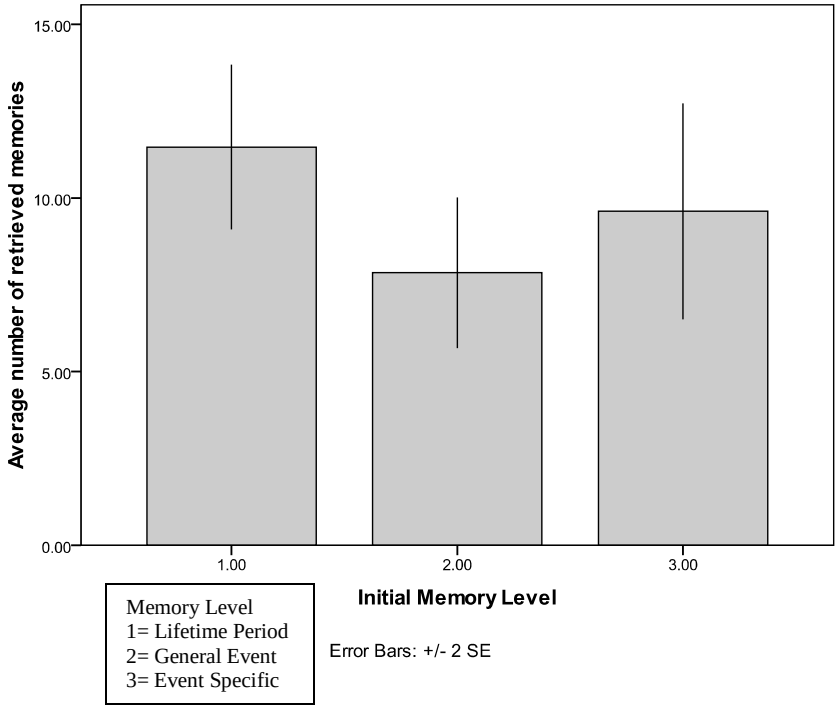
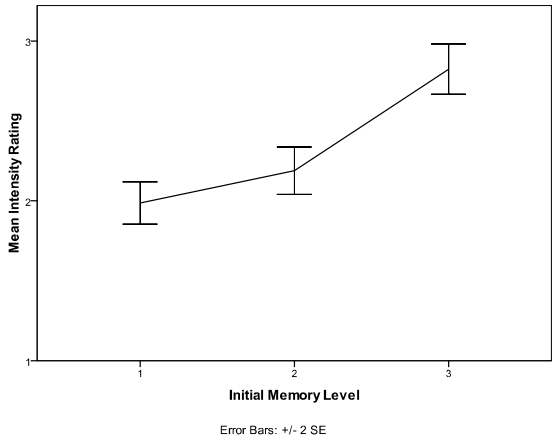
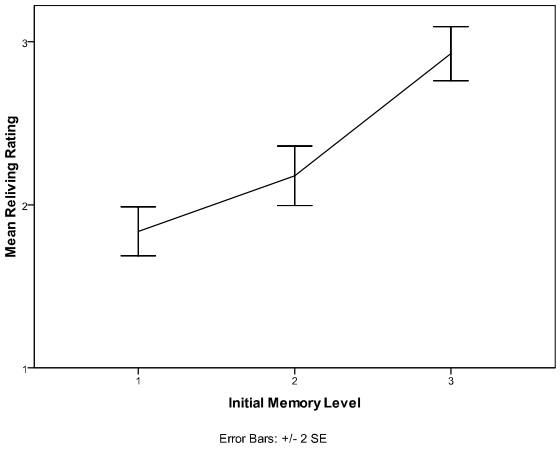

15.00
10.00
5.00
0.00
Average number of retrieved memories
1.00
2.00
3.00
Initial Memory Level
Memory Level
1= Lifetime Period
2= General Event
3= Event Specific
Error Bars: +/- 2 SE

Figure 2

INTENSITY



RELIVING



VIVIDNESS

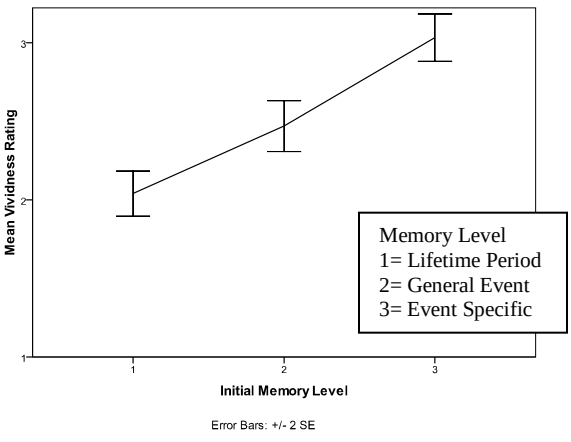
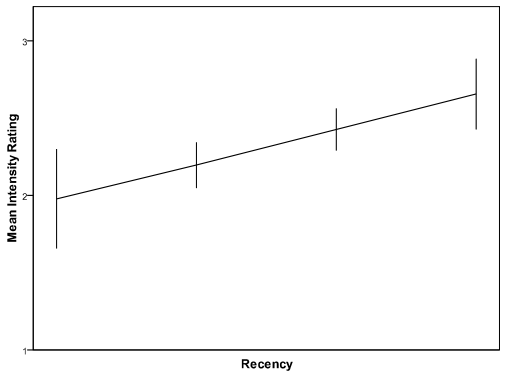


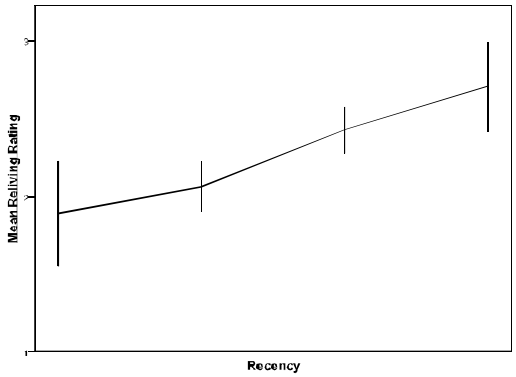
Figure 3

INTENSITY



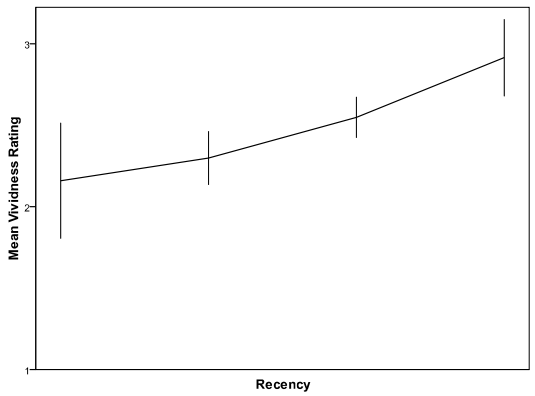
>10 yrs 5-10 yrs 1-5 yrs <1 yr

RELIVING



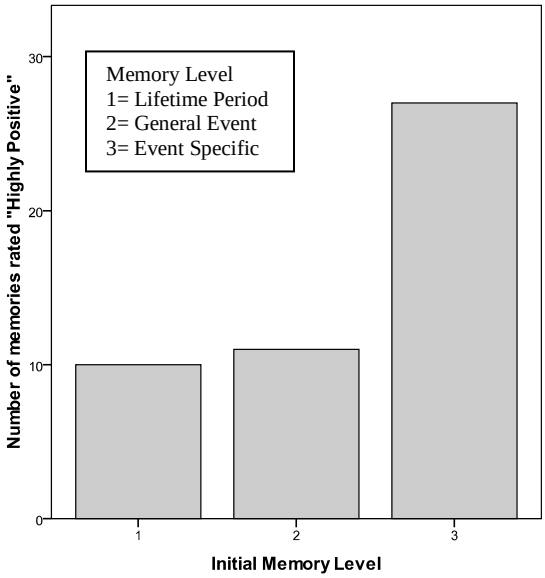
>10 yrs 5-10 yrs 1-5 yrs <1 yr

VIVIDNESS



>10 yrs 5-10 yrs 1-5 yrs <1 yr

Figure 4


Memory Level
1= Lifetime Period
2= General Event
3= Event Specific
Number of memories rated "Highly Positive"
30
20
10
0
1
2
3
Initial Memory Level

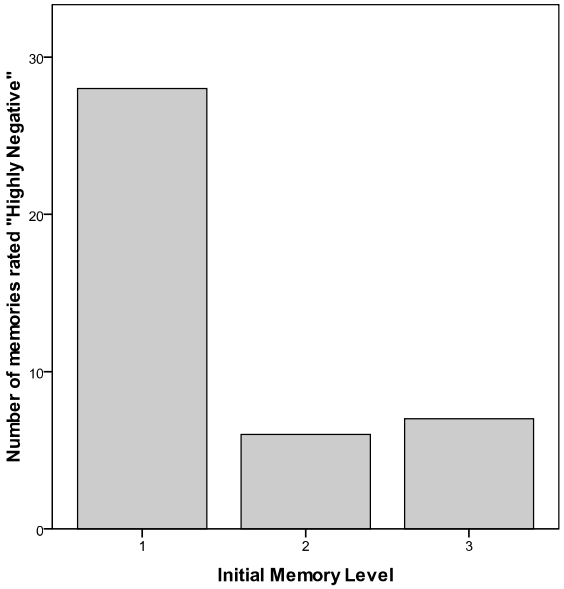

Number of memories rated "Highly Negative"
30
20
10
0
1
2
3
Initial Memory Level

Figure 5

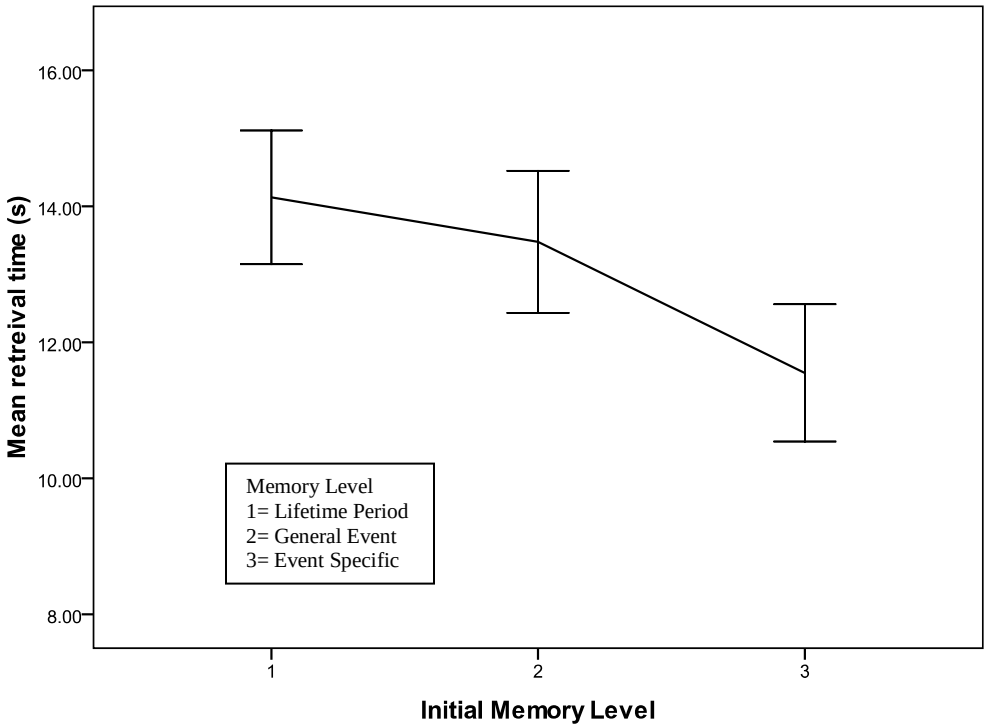

16.00
14.00
12.00
10.00
8.00
Mean retreival time (s)
Memory Level
1= Lifetime Period
2= General Event
3= Event Specific
1
2
3
Initial Memory Level
Error Bars: +/- 2 SE

Figure 6

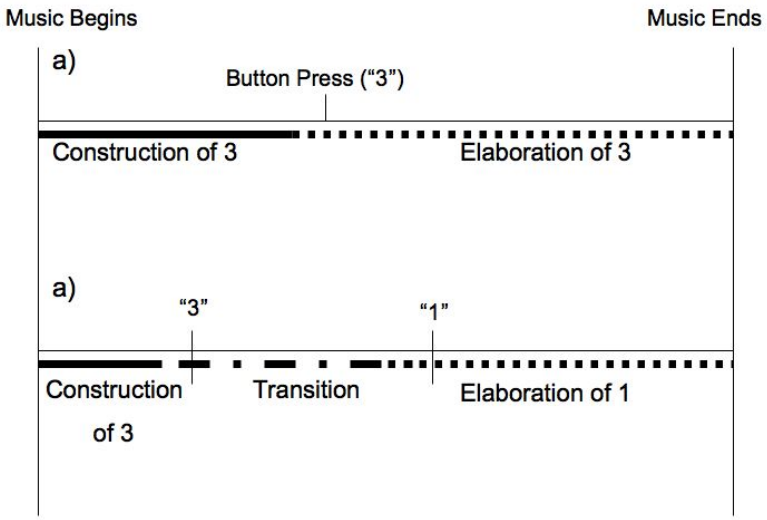

Music Begins
Music Ends
a)
Button Press ("3")
Construction of 3
Elaboration of 3
a)
"3"
"1"
Construction
of 3
Transition
Elaboration of 1

Figure 7

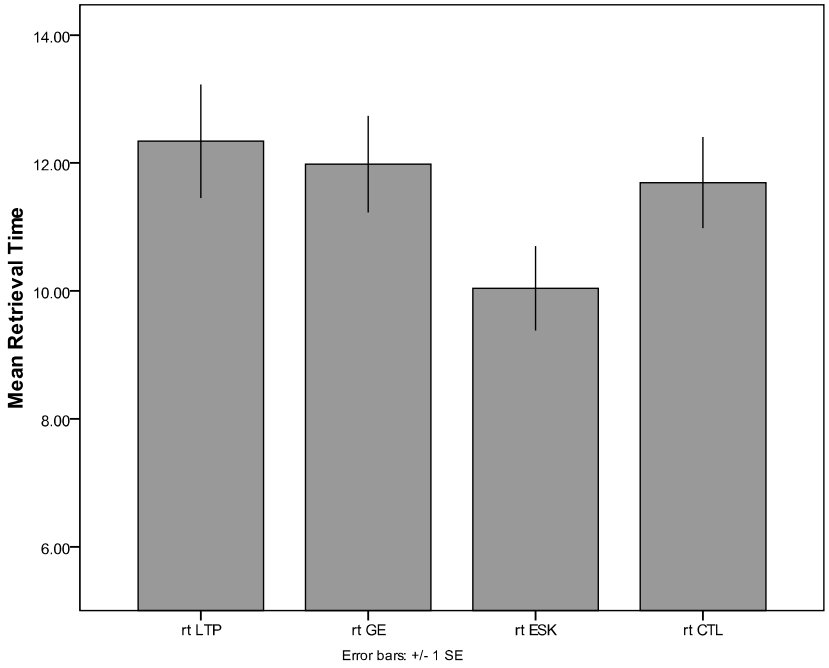

14.00
12.00
10.00
8.00
6.00
Mean Retrieval Time
rt LTP
rt GE
rt ESK
rt CTL
Error bars: +/- 1 SE

Figure 8

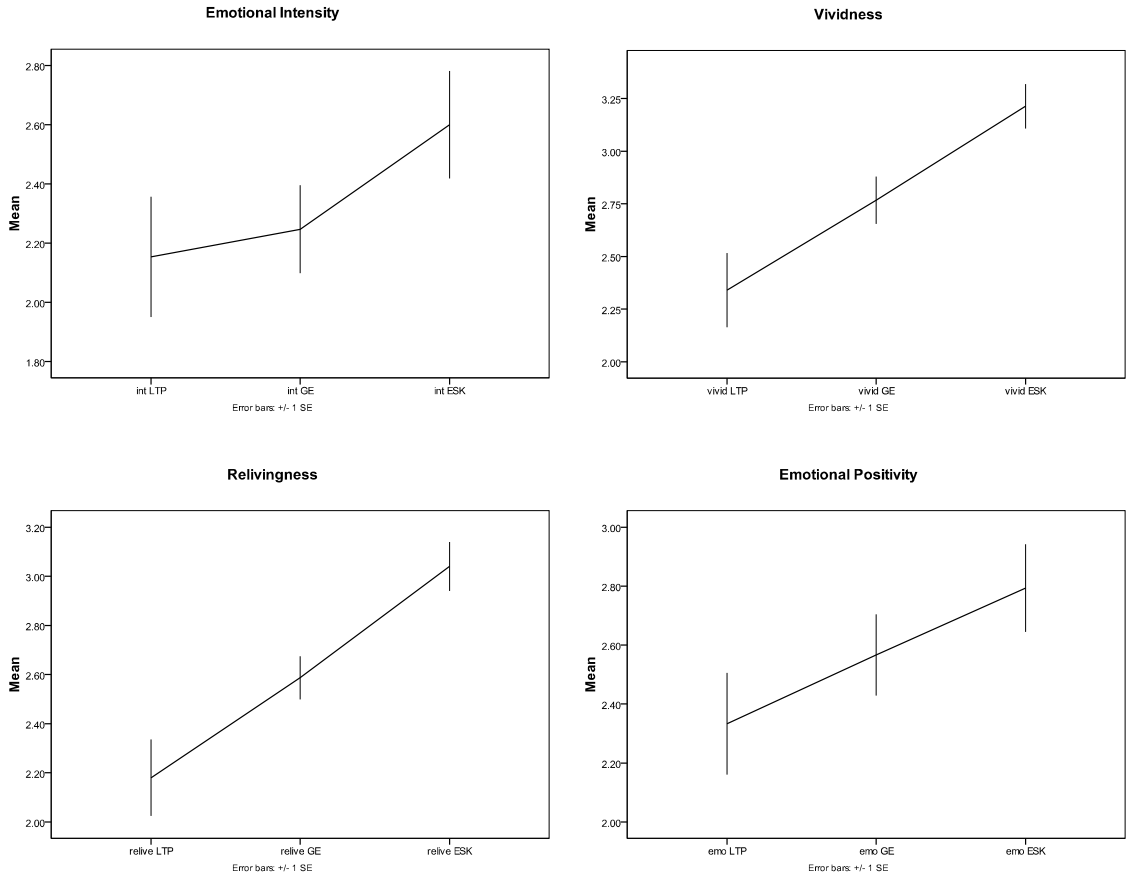

Emotional Intensity
Mean
2.80
2.60
2.40
2.20
2.00
1.80
int LTP
int GE
int ESK
Error bars: +/- 1 SE
Vividness
Mean
3.25
3.00
2.75
2.50
2.25
2.00
vivid LTP
vivid GE
vivid ESK
Error bars: +/- 1 SE
Relivingness
Mean
3.20
3.00
2.80
2.60
2.40
2.20
2.00
relive LTP
relive GE
relive ESK
Error bars: +/- 1 SE
Emotional Positivity
Mean
3.00
2.80
2.60
2.40
2.20
2.00
emo LTP
emo GE
emo ESK
Error bars: +/- 1 SE

Figure 9

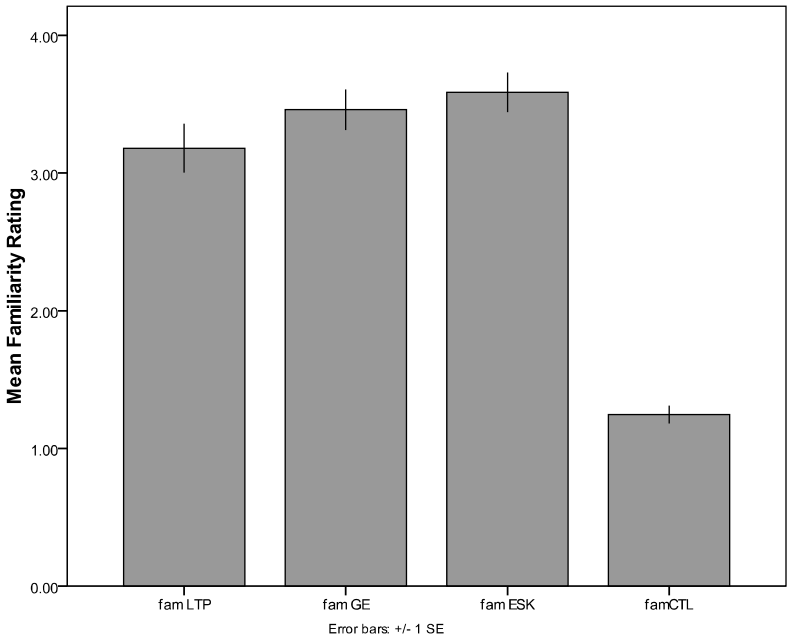

Mean Familiarity Rating
4.00
3.00
2.00
1.00
0.00
fam LTP
fam GE
fam ESK
famCTL
Error bars: +/- 1 SE

Figure 10

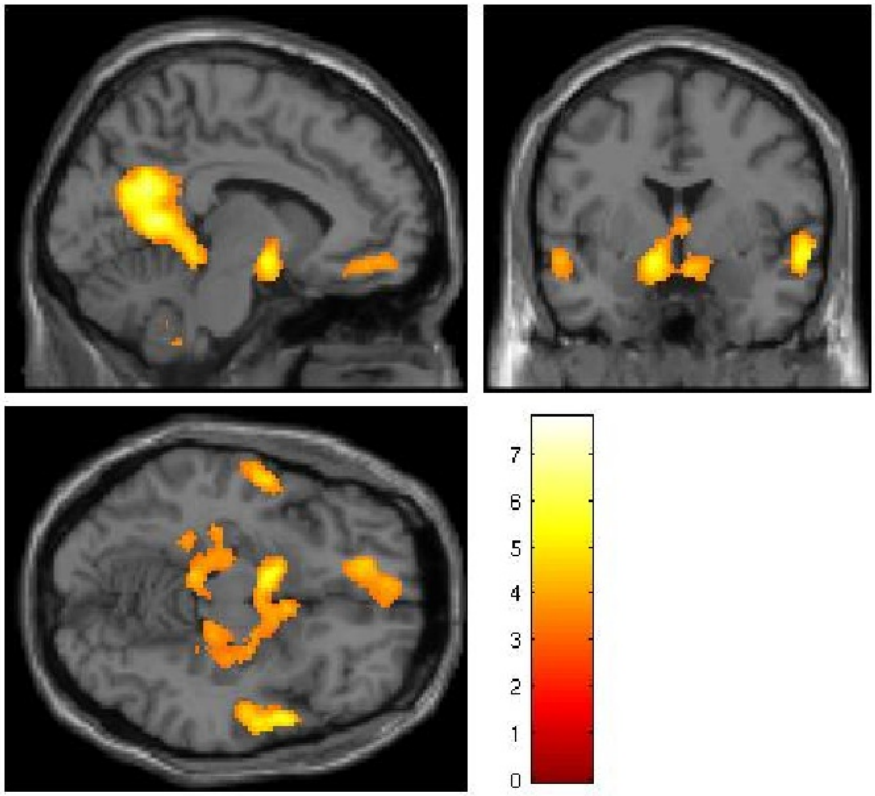


Figure 11

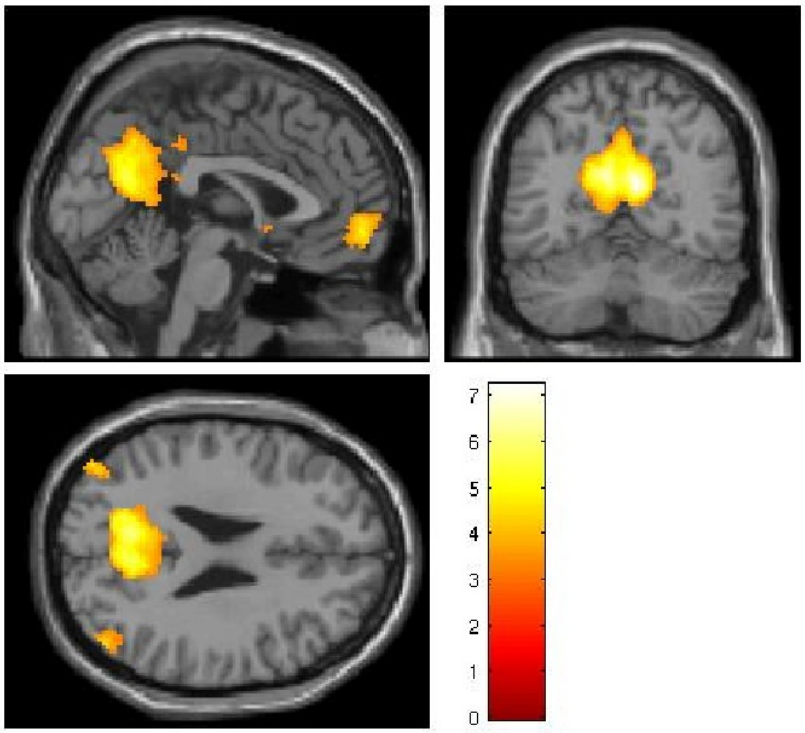


Figure 12

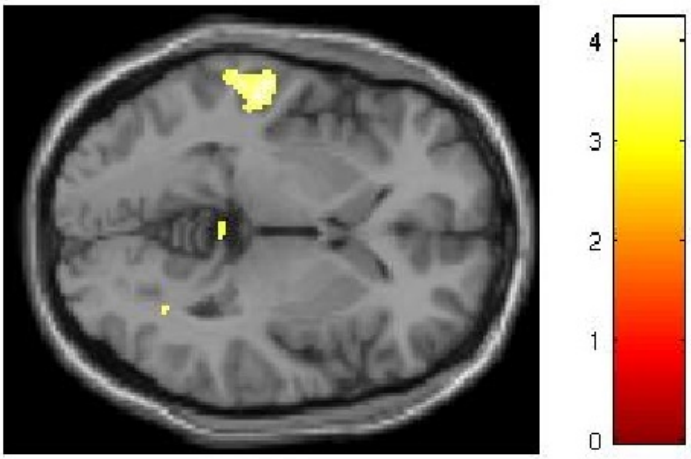


Figure 13