

EXAMINING THE INFLUENCE OF TIME AND REPETITION ON RECENT AND  
REMOTE AUTOBIOGRAPHICAL MEMORY RETRIEVAL USING fMRI

by

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## DEDICATION

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## ABSTRACT

Repetition and the passage of time influence the consolidation of long-term episodic memories. The experiments presented here have explored the influence of repetition on recent and remote autobiographical memories both behaviorally with regard to qualitative and quantitative measures of content, and neuroanatomically, focusing on changes within the hippocampus and adjacent structures.

The first experiment tested the prediction made by MTT that hippocampal memory traces expand and strengthen as a function of repeated memory retrievals. An fMRI paradigm was used to compare the effect of memory retrieval versus the mere passage of time on hippocampal activation. Participants retrieved remote autobiographical memories that had been previously retrieved either one month earlier, two days earlier, or multiple times during the preceding month. Behavioral analyses revealed that the number and consistency of memory details retrieved increased with multiple retrievals but not with the passage of time. Hippocampal activation did not change as a function of either multiple retrievals or the passage of time.

The second behavioral investigation was a follow-up to the first experiment, examining the retrieval of those same memories one year later in order to determine whether the level of detail remained stable or whether the memories returned to their original state. Participants reported even more details than they had recalled at least one year earlier, including new details. This finding was consistent across both multiple and single retrieval conditions. These findings together with those of the first study suggest that both repetition and the passage of time are important factors that may result in an

increase in recall.

The third and final experiment explored the behavioral and neural influences of repeated reactivation of both recent and remote autobiographical memories. Participants were interviewed a total of five times throughout one month and retrieved 20 significant life event memories, from either within the past several months or more than five years ago. Additionally, two fMRI scan sessions were collected, which enabled a direct comparison of the same 20 memories before and after a series of repetitions. Activation increased with repetition in several brain regions including bilateral posterior cingulate and precuneus. Behaviorally, repetition resulted in increased accessibility as suggested by decreased reaction times between the initial and final retrieval sessions, and a general maintenance of the level of recall resulted with repetition.

## I.

## INTRODUCTION

## **Background**

Although the concept of memory consolidation was first introduced over one hundred years ago by Muller and Pilzecker (1890; as cited in McGaugh, 2000), the neural underpinnings of this process, especially the role of the hippocampus, have been the source of much debate for over a decade in the field of memory research. Two prominent theories of long-term memory consolidation have emerged with somewhat different ideas regarding the role of the hippocampus. The standard theory of consolidation posits that the role of the hippocampus is time-limited for both components of explicit memory, namely episodic memory and semantic memory. On the other hand, multiple trace theory (MTT) states that the role of the hippocampus is time-invariant and always necessary as regards episodic memory. Evidence supporting each theory, considerable variation in methods, the use of different types of memories/stimuli, and discrepancies in the length of the consolidation period have contributed to the uncertainty surrounding the role of the hippocampus through time.

The debate has ignited a large body of research regarding what happens to episodic memories with the passage of time and as memories are repeatedly retrieved throughout the lifespan. Based on evidence from patient HM, Scoville and Milner (1957) first postulated that the role of the hippocampus was temporary, as their patient exhibited retrograde amnesia with spared remote memory, impaired recent memory, and loss of the ability to form new memories. This evidence gave way to what was eventually dubbed the standard theory of memory consolidation (Squire, Cohen & Nadel, 1984; Squire & Alvarez, 1995; McClelland, McNaughton & O'Reilly, 1996). Some evidence in support

of this theory suggests that the hippocampus is only necessary as a retrieval index for several years (Graham & Hodges, 1997; Schmidtke & Vollmer, 1997) and other data have suggested the hippocampus may be important for memory retrieval for up to ten years (Rempel-Clower, et al., 1996; Reed & Squire, 1998).

Evidence suggesting that remote memories of amnesic patients were in fact not as well preserved as initially thought (Steinvorth et al., 2005) and the variability in the length of the consolidation period led Nadel and Moscovitch (1997, 1998) to formulate an alternate view of long-term memory consolidation in which the hippocampus is always necessary for episodic memory retrieval regardless of memory age. This theory was called the multiple trace theory (MTT) and stated that each time a memory is retrieved it is also reconsolidated in such a way that a new or embellished neural trace represents that memory. In this way, the theory explains the temporal gradient (Ribot 1881) that typically accompanies brain trauma to the hippocampus and surrounding structures; the more extensive the damage to the medial temporal structures, the more extensive the subsequent memory loss.

The concept of reconsolidation has been recently studied in both animal (Nader, et al. 2001) and human models (Hupbach, et al. 2007). During recall, memories enter a labile state and must be reconsolidated. It has been well documented that other species including crabs, chicks, honeybees, Medaka fish, *Lymnaea*, humans, and rodents reconsolidate information as well (Tronson & Taylor, 2007). The process of reconsolidation may serve as a means to update information, to reinforce that the memory is still relevant, or to strengthen the memory for continued use. Results from both animal

and human investigations suggest that reconsolidation occurs in conjunction with the incorporation of new information (Rodriguez-Ortiz et al., 2005; Hupbach et al., 2007, 2008), and some animal work suggests that memories are strengthened after retrieval (Frenkel et al., 2005).

The ongoing debate between these two theories has ignited a large body of research addressing the fundamental question of what happens to episodic memories with the passage of time and as memories are repeatedly retrieved: ‘What is the role of the hippocampus throughout the lifespan?’ A variety of techniques have been used to gain insight including patient case studies (e.g. Steinvorth et al., 2005; Noulhiane et al., 2007), human neuroimaging methods (e.g. Ryan et al., 2001; Rekkas & Constable, 2005), and animal models (for review see Dudai, 2004). Another variation among human models has been the type of memory assessed ranging from public event memories, such as famous faces/names (Haist et al., 2001; Woodard et al., 2007), to autobiographical memory (Gilboa et al., 2004; Steinvorth et al., 2006). The two theories of long-term memory consolidation are in agreement that semantic memories are over time consolidated within areas of neocortex and are no longer dependent upon the hippocampus for retrieval, though multiple trace theory suggests that retrieval of semantic information frequently calls on episodic memory (Ryan et al., 2008), as Barsalou and colleagues (1998) suggested some time ago. The two theories disagree about whether the hippocampus is always important in the retrieval of spatial, contextually-rich episodic memories.

Due to its contextual and emotional complexity compounded with the ability to gather a large number of remote memories, autobiographical memory is often used to

assess memories through time. Contextually-rich, emotional, autobiographical memories separate from personal semantic and/or generic memories have been shown to engage the hippocampus and surrounding medial temporal lobe structures during retrieval (e.g. for review see Cabeza & St. Jacques, 2007). Autobiographical memory may be thought of as a special case of episodic memory as it includes auto-noetic consciousness and the ability to mentally time travel (Tulving, 1985; Kopelman et al, 1989; Conway, 2001).

Researchers have emphasized several functions of autobiographical memory, including its importance as a social tool, maintaining a consistent self through time, and using prior experience to shape future behavior (Hyman & Faries, 1992; Rubin, 1995; Conway & Pleydell-Pearce, 2000; Bluck, Alea, & Habermas, 2005). The use of actual past event memories versus those created in the laboratory is most like examining everyday memory in its real world context; the stimulus sets used throughout the studies described below are comprised of autobiographical memories.

Neuroimaging has proven an incredibly resourceful tool in examining long-term memory consolidation in normal subjects. Several techniques have been used to acquire autobiographical memories from participants, as reviewed by Cabeza & St. Jacques (2007), including the use of generic cues as prompts in the scanner (Conway et al. 1999; Graham et al. 2003), a pre-scan interview (Fink et al. 1996; Maguire et al. 2001; Greenberg et al. 2005), interviewing independent sources such as a spouse or close friend (Ryan et al. 2001; Gilboa et al. 2004; Steinworth et al. 2006), and the prospective method involving the encoding of new information (Levine et al. 2004; Cabeza et al. 2004). Each method offers several advantages and disadvantages; however, use of the pre-scan

interview enables sufficient control of the content, age, emotionality, and vividness of the memories that are selected for use in the scanner. As a result, the series of studies presented here have adopted the pre-scan interview method.

A network of brain regions, including the medial and ventrolateral prefrontal cortex, medial/lateral/superior temporal, medial and lateral parietal, anterior and posterior cingulate cortices, temporoparietal junction, and amygdala is consistently activated in response to autobiographical memory retrieval (Vandekerckhove et al., 2005; Svoboda, McKinnon, & Levine, 2006; Spreng, Mar, & Kim, 2008). In order to elucidate the role of the hippocampus through time many imaging investigations contrast recent and remote memories. Many of these studies have demonstrated support for MTT and a perpetual role of the hippocampus (e.g. Maguire, et al., 2001; Ryan et al., 2001; Gilboa et al., 2004; Rekkas & Constable, 2005; Steinworth et al., 2006; Viard et al., 2007; Piolino et al., 2008; Svoboda & Levine, 2009), yet others stand in opposition to these findings, supporting a time-limited role of the hippocampus (Haist et al., 2001; Niki & Luo, 2002; Piefke et al., 2003).

The length of the consolidation period has been a source of much debate as well as which criteria should be used to distinguish recent and remote memory. Some evidence in support of the standard theory suggests that the hippocampus is only necessary as a retrieval index for several years (Graham & Hodges, 1997; Schmidtke & Vollmer, 1997) and other data has suggested the hippocampus may be important for memory retrieval for up to ten years (Rempel-Clower, et al., 1996; Reed & Squire, 1998). Since the time frame of systems consolidation is uncertain, the designation of recent and



remote varies widely across studies. Some approaches separate memories into four (Maguire et al., 2000; Maguire & Frith, 2003) or five (Viard et al., 2007; Piolino et al., 2008) time bins throughout the lifespan. Most studies consider recent to be within the past several years (Ryan et al., 2001; Niki & Luo, 2002; Piefke et al., 2003; Gilboa et al., 2004), with only one study examining memories as new as 2.5 days on average (Rekkas & Constable, 2005). Remote distinctions vary from 20+ years ago (Ryan et al., 2001), up to ten years of age (Piefke et al., 2003), and anything occurring more than several years ago (Niki & Luo, 2002; Rekkas & Constable, 2005; Nadel et al., 2007). Not only does this variability pose a challenge to the standard theory, it may also account for the variability of results seen throughout the literature.

Episodic memories can be retold and recounted many times throughout our lives in many contexts. Each time a memory is recalled, possibly as a result of reconsolidation, it may be changed from its original representation. Some information may be altered and some forgotten but what remains is assumed by the individual to be an accurate, veridical recollection. Neisser referred to this type of memory as “reepisodic” memory (1981). In addition to understanding more about the neural contributions to memories through time with the use of fMRI, the design of the studies described here also enable the behavioral exploration of the effect of time and repetition on new and old memories. As mentioned above, MTT alludes to the lability of memories through time and with repetition, as a reconsolidated trace may incorporate some or all aspects of the current retrieval context.

Increased accessibility of memories over time with repeated reactivation is another prediction made by MTT; in support of this idea, some evidence suggests that

recall facilitates future recall. Erdelyi and Becker (1974) demonstrated that recall for pictures increased over the course of three memory tests with delays, and coined the term hypermnesia to refer to the phenomenon of increased recollection as a function of retrieval practice. Other studies of hypermnesia have resulted in a similar outcome where participants' recall improved for both verbal and visual materials over repeated test sessions (Klein et al., 1989; Payne & Roediger, 1987; Roediger & Thorpe, 1978). Bluck et al. (1999) also reported a significant increase in autobiographical memory details across three closely spaced retrievals. Still other studies have shown a decrease in detail results over very long delays (Barrick et al., 2008). Differing behavioral results emerge depending on time after encoding and the type of information being consolidated.

## **Overview of the Dissertation Experiments**

The main research question this dissertation addresses is ‘what is the role of the hippocampus throughout the life of an episodic memory?’ This puzzle piece has been the crux of an ongoing debate in the field of memory and the key distinction between the two prominent theories of long-term memory consolidation. I have investigated the influence of the passage of time and repetition on both recent and remote autobiographical memory retrieval using fMRI. Behavioral analyses were also simultaneously conducted exploring the qualitative and quantitative changes that occur to memories through time and after a series of repetitions. Three experiments comprise this dissertation, each examining changes in memory through time and with repeated reactivation. The first experiment used fMRI to simultaneously explore the influence of repetition and the passage of time on remote autobiographical memories. This study was published in 2007 and is included in Appendix A, and a brief summary is provided below. Two additional studies followed, one a behavioral follow-up study of the original and the other an fMRI study addressing both recent and remote memory retrieval with repetition. Brief synopses of these are provided below as well.

### **Autobiographical Memory Retrieval and Hippocampal Activation as a Function of Repetition and the Passage of Time**

Two things undoubtedly occur as memories become remote: time moves forward and memories may be repeatedly reactivated, via online active retrieval and offline processes, often during sleep. The first experiment, Autobiographical Memory Retrieval

and Hippocampal Activation as a Function of Repetition and the Passage of Time, seeks to examine the influence of the passage of time and the effect of repeated retrieval on remote memory and how the hippocampus contributes to the neural processes that underlie remote memory maintenance. Current data are equivocal: results supporting each of the theories discussed earlier have been obtained and the role of the hippocampus through time remains uncertain.

In pursuit of resolving this discrepancy, a number of neuroimaging studies have explored the role of the hippocampus through time by contrasting the retrieval of recent and remote memories. The majority of studies have found that the hippocampus is activated by retrieval of both remote and recent memories (Maguire, et al., 2001; Ryan et al., 2001; Gilboa et al., 2004; Rekkas & Constable, 2005; Steinvorth et al., 2006; Viard et al., 2007; Piolino et al., 2008; Svoboda & Levine, 2009) but a few have found a decrease in hippocampal activation with age (Haist et al., 2001; Niki & Luo, 2002; Piefke et al., 2003). No study to our knowledge has addressed repetition manipulations of remote memories within the context of a single paradigm.

We designed the paradigm such that participants, a group of twelve middle-aged adults, recalled remote memories, which were considered any life event memory older than two years, during three separate retrieval conditions. Twelve salient autobiographical memories were recalled on Day 1 of the study and not again until scan Day 30, referred to as the remote retrieval condition. Another set of twelve memories were recalled five times throughout the course of one month spaced each a week apart and also in the scanner on Day 30, referred to as the multiple retrieval condition. Lastly,

an additional set of twelve memories were recalled initially on Day 28 and again during scanning on Day 30, the recent retrieval condition. The remote and recent retrieval conditions were included to control for any influence of recency, and the multiple retrieval condition was compared to both single retrieval conditions in order to determine if after a series of reactivations changes would be seen within the hippocampus.

Participants were given an explicit instruction set prior to each retrieval session and were urged to discuss all of the details that came to mind even if they had already mentioned them in past sessions and also to include any new details that they were able to recall. Each event memory was described in full detail during each retrieval session including any and all perceptual and emotional details. The initial retrieval session on Day 1 was conducted in our laboratory and all subsequent retrieval sessions were conducted over the phone, and all retrieval sessions were tape recorded. These recordings were transcribed and analyzed according to the methods of Levine et al. (2002) which distinguishes internal, external, and editorial details from each other (see Table 1). Internal details are those that pertain to the event itself, external details are those that “set the stage”, and editorial details are those that reflect uncertainty or any dialogue with the interviewer. Internal and external details were taken together as a total detail count, and a word count measure was also obtained. The interviewer was held constant throughout all retrieval sessions.

Table 1. Internal, external, and editorial detail types. A description and a specific example are provided for each. All details from each memory were coded in a specific format to distinguish each detail type. These details were then analyzed across interview sessions.

	Detail Type		
	<i>Internal</i>	<i>External</i>	<i>Editorial</i>
<i>Description</i>	specific event memory details including time, place, date, names of individuals, and actions	general information not unique to the event memory, or events that occurred outside of the time window of the event, or a judgment of the memory based on the past or future	statements reflecting uncertainty or dialogue with the interviewer, providing no information regarding the memory
<i>Example</i>	"This was during the summer before I turned sixteen."	"I had gone on train rides in the past, to the Grand Canyon and such."	"Now that I think about it, this had to have been...", or "You know the type, right?"

The existing literature on behavioral repetition effects are also mixed with some findings suggesting an increase in recall after repetition (Roediger & Karpicke, 2006). This effect is known as the practice or testing effect, and a similar effect known as hypermnesia resulting in an increase in recall has been described as well (Bluck et al., 1999). Other work has indicated that forgetting occurs with the passage of time (Bergman & Roediger, 1999; Bahrick et al., 2008), and in some cases retrieval has been shown to induce forgetting (Barnier et al., 2004).

There were two main hypotheses: 1. Repeatedly retrieved items, when compared to singly retrieved items may reveal less hippocampal activation because the memories for the former items have become more gist-like in nature, and hence dependent upon structures other than the hippocampus, or 2. Repeatedly retrieved items compared to singly retrieved items may elicit greater hippocampal activation as multiple traces contribute to their recall, and the increased strength of these memory traces will lead to greater accessibility, easier recall.

Behaviorally, for the multiple retrieval condition there was a significant increase

in word count and total detail count, internal and external details, across the first three retrieval sessions, and this increase was held constant throughout the final three retrieval sessions. Editorial details significantly decreased between the first and second retrieval sessions and stabilized at that low level. Detail count data over time were not available for the recent and remote retrieval conditions as only one interview was obtained in detail outside of the scanner. An additional comparison was conducted between recent retrieval memories and multiple retrieval memories on Day 1 and between remote retrieval memories and multiple retrieval memories on Day 28 to eliminate the possibility of a detail increase due to other factors such as comfort with the interviewer or interview process. The difference between single and multiple retrieval memories was significant for Day 28 but not for Day 1, indicating that the increase in detail count was likely an effect of repetition.

Neuroanatomically, patterns of activation were very similar across all three retrieval conditions, including the hippocampus bilaterally, bilateral perirhinal and parahippocampal gyri, bilateral precuneus, bilateral middle frontal gyrus, left-lateralized inferior frontal gyrus, and bilateral middle and superior temporal gyri. On first pass, effect sizes extracted for each memory retrieval condition were not significantly higher for the multiple retrieval memories within the medial temporal lobe. Several areas outside the medial temporal lobe were slightly increased in the multiple compared to single retrieval conditions. Several regions, including bilateral parahippocampal gyrus, bilateral hippocampus, right amygdala, bilateral precuneus, and left caudate showed significantly stronger activation for the remote retrieval condition, those memories recalled only on

Day 1. This was possibly a result of retrieval effort being greater in the scanner.

To investigate this further, reaction time (RT) data were used in a secondary analysis. While participants were in the scanner they were asked to respond by mouse button press once they had read the memory cue and brought the corresponding memory to mind. For six out of the twelve participants, the mean RTs were matched across all three retrieval conditions by removing 0-3 RT items from the analysis. After equating the portion of the entire duration, 12 seconds, that was spent recalling versus searching, the differences seen in the remote condition were minimized and there were virtually no differences in effect size across retrieval condition.

The behavioral findings suggest that repeated reactivation of memories, but not the mere passage of time, resulted in increased accessibility and increased recall and development of a narrative script over time. Neurobiologically, repetition of autobiographical memories resulted in increased activation within some neocortical regions, possibly as a result of scripting effects, and maintenance of activation within medial temporal lobe structures.

### **Hypermnesia for Autobiographical Events after a One Year Delay**

Chapter two describes a behavioral follow-up study to the original investigation of the role of the hippocampus through time and with repetition (see Appendix A). Results from the original study demonstrated that after a series of five repetitions throughout the course of one month there was an overall increase in detail, both internal and external. I was interested in exploring whether these memories were permanently



altered and that this higher level of detail remained a stable part of the memory “script” or if the memories returned to their initial state, decreasing in detail somewhat since our last recorded measure. Surprisingly, even after one year, the level of detail increased over and above that of the final retrieval session of the original study. In some cases this included details that had not yet been recalled in any of the previous sessions. This finding was consistent for both multiple and single retrieval memories, suggesting that multiple factors are contributing to this increase in recall observed at a long delay.

### **The Influence of Repetition and the Passage of Time on Recent and Remote Autobiographical Memories: A longitudinal fMRI study**

A third and final study, described in Chapter 3, explores the influence of repetition on both recent and remote autobiographical memories using fMRI. In the first experiment (Appendix A) only remote memories were manipulated in order to observe changes that occurred with repetition in the context of the same study. Results suggested that with repetition memories did not show a significant increase in hippocampal activation as was predicted. One explanation for this outcome was that these well-established remote memories had already undergone a high level of reconsolidation from many years of retrieval and possibly reached some asymptotic level of consolidation. Changes over and above this level could be too subtle to detect with use of fMRI. These results begged the question, ‘what would happen to recent, less stable memories under similar manipulations?’ The third experiment incorporates recent memories from within the past one to two months *and* remote memories from five or more years ago. The

second improvement over the original paradigm was the integration of a second scan session at the beginning of the study in addition to the scan session at the end of the month. This enabled a direct comparison of both recent and remote memories after a series of five repeated retrieval sessions. Results suggest that activity within the bilateral posterior cingulate and precuneus increased considerably for both recent and remote conditions with repetition, and no brain regions showed a significant decrease with repetition. Equivalent levels of activity within the hippocampus, surrounding MTL, and neocortex resulted after a series of repetitions. Behavioral results revealed a consistent level of recall of internal details and a decrease in external. Consistent with the predictions of MTT, these findings suggest that autobiographical memories are always dependent upon the hippocampus during retrieval.

## II.

EXPERIMENT 2:  
HYPERMNESIA FOR AUTOBIOGRAPHICAL MEMORIES AFTER A ONE YEAR  
DELAY

## **ABSTRACT**

We recently showed that repeated retrievals of remote autobiographical memories over the course of one month led to an overall increase in reported detail (Nadel, Campbell & Ryan, 2007). The current study examined the retrieval of those same memories one year later in order to determine whether the level of detail remained stable or whether the memories returned to their original state. Participants reported even more details than they had recalled at least one year earlier, including new details that were reported for the first time. This finding was consistent across both multiple and single retrieval conditions suggesting that the critical factor leading to the increase in recall was the passage of time, and any offline reactivations occurring during this interval, not the repetitions serving as part of the initial study. These findings provide evidence for long-term effects on memory content.

## INTRODUCTION

What happens to memories for autobiographical events as time passes and stories are told and retold to family and friends? Despite the importance of this question to the field of memory and to our everyday lives, surprisingly few empirical studies have addressed this fundamental issue. The existing literature has focused almost exclusively on the effect of retrieval on newly acquired information such as word lists, pictures, or stories, but not autobiographical memories. The few studies that exist report mixed results for memories that are repeatedly recollected and retold. For example, Bartlett's observational study of the War of the Ghosts (1932) suggested that the passage of time results in a loss of detail as memories become simplified and distorted, while retaining the core elements, or gist, of the story. Wynn and Logie (1998) also found that although gist persisted across time and over repeated retrievals, new peripheral details were added, potentially for the listener's sake, as first-year students recalled an orientation lecture. In contrast, Gauld and Stephenson (1967) argued that Bartlett's open-ended interview style led to increased errors of recollection, showing that instructions emphasizing strict accuracy resulted in reduced error rates even when using the same test materials as Bartlett.

More recently, in a controlled replication, Bergman and Roediger (1999) reproduced Bartlett's original results, showing that participants forgot details of the folktale over delays of fifteen minutes, one week, and six months. Participants' memories also included the same rationalizations and distortions observed by Bartlett, which increased with lengthening retention intervals and, contrary to Gauld and Stephenson

(1967), did not depend on whether lenient or strict instructions were provided to participants. These results would suggest that memories are indeed simplified, modified, and generally forgotten over time.

A very different view of memory over time and repetition comes from the literature on hypermnesia. Even earlier than Bartlett, Ballard (1913, reviewed in Payne, 1987) reported that children could recall lines of poetry on subsequent memory tests that they could not recall on an initial test. Much later, Erdelyi and Becker (1974) demonstrated that recall for pictures increased over the course of three memory tests with delays, and coined the term hypermnesia to refer to the phenomenon of increased recollection as a function of retrieval practice. Other studies of hypermnesia have resulted in a similar outcome where participants' recall improved for both verbal and visual materials over repeated test sessions (Klein, Loftus, & Kihlstrom, 1989; Payne & Roediger, 1987; Roediger & Thorpe, 1978).

Most hypermnesia studies employ lists of words, sets of pictures, or brief stories as the to-be-remembered materials that are acquired in a single session. Although hypermnesia has been discussed in the context of research relevant to autobiographical memory, including eyewitness testimony (Turtle & Yuille, 1994) and flashbulb memories (Coluccia, Bianco, & Brandimonte, 2006), few studies have investigated the effect of repeated retrievals on episodic memories for life events. In one such study, Bluck and colleagues (Bluck, Levine, & Laulhere, 1999) interviewed participants eight months after the television airing of the O.J. Simpson verdict. Participants were required to recall the details of the event three times over the course of a single hour. Bluck et al. (1999)

reported a significant increase in memory for the details of the event across the three closely spaced retrievals.

Many factors contribute to determining which stimuli are better recalled and which are eventually forgotten over time. Personal relevance, salience, emotionality, and level of associated imagery may all be factors that increase the ability to remember certain material. In the current study we were interested in what happens to rich, personally-relevant, and emotionally-charged autobiographical events as they are recalled and retold over weeks, months, or even years? Do they also lose detail and become gist-like, as Bartlett (1932) and others would suggest? Or does the repeated retrieval and retelling of these stories result in richer, more detailed recollections, as suggested by the studies of hypermnesia?

We first addressed this question in a study that involved repeated recollections of autobiographical memories over the course of a 30 day period (Nadel, Campbell, & Ryan, 2007). Three different retrieval conditions enabled us to observe differences in what participants recalled after the passage of time and repeated retrievals. Memories that were included in the original analysis were rich, containing a high level of detail, personally-relevant life events from individuals' pasts from at least two years ago but widely distributed throughout all life stages, and on average memories were rated as very emotional. In the *Remote Retrieval* condition, 12 memories were recalled twice, 30 days apart on Days 1 and 30. In the *Recent Retrieval* condition, 12 memories were recalled twice, two days apart on Days 28 and 30. In the *Multiple Retrieval* condition, 12 memories were recalled six times at intervals of approximately one week on Days 1, 7,

14, 21, 28, and 30. On Day 30, participants recalled all 36 memories while undergoing fMRI scanning in order to assess any changes in activity; the fMRI results will not be addressed here. On Day 30 all memories were retrieved silently in the scanner, therefore behavioral data are not available for analysis from this retrieval session. As a result, only behavioral changes seen in the Multiple Retrieval condition were observed in the original study. These results indicated a significant increase in memory length and reported internal and external details, or what we refer to as *total* memory details, across the five retrieval sessions. There was also a linear increase across sessions in the repetition of phrases used to describe each memory, a measure we referred to as “phrase consistency”, such that details mentioned during one retrieval session were more likely to be repeated during a subsequent retrieval session. This pattern suggested that as a memory was being recalled, participants recruited additional details to what became a consistent story, or “episodic narrative”. The behavioral results for the Multiple Retrieval condition are depicted in Figure 1.



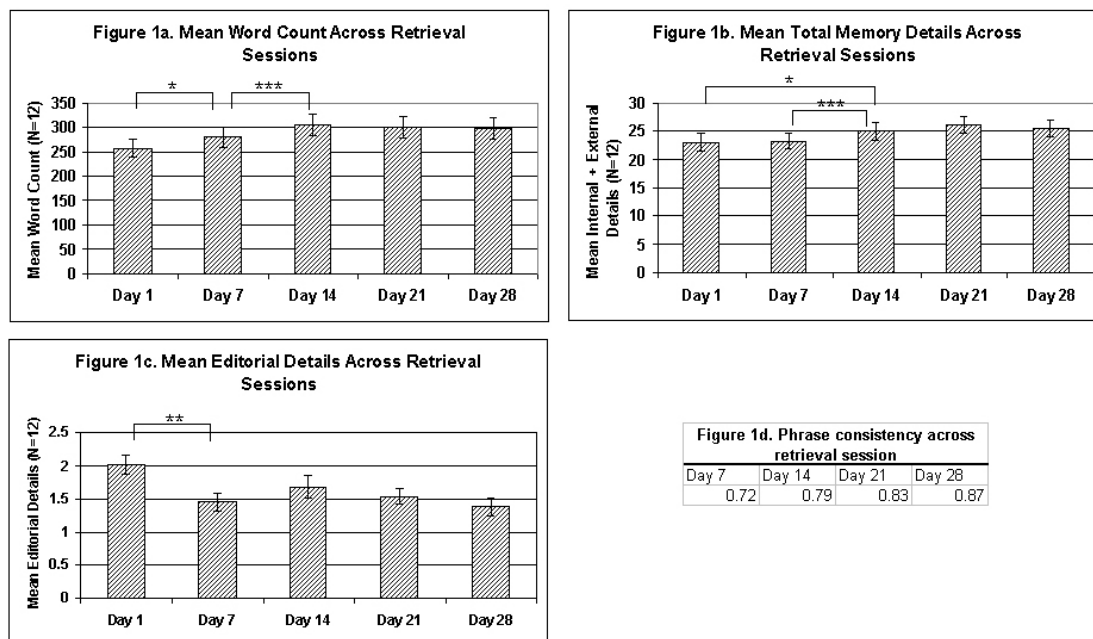


Figure 1. Detail counts and phrase consistency measures for the Multiple Retrieval condition from Nadel et al., (2007), *Neural Plasticity*, 2007, 1-14. Note that these results were taken from all 12 participants, eight of whom participated in the current study. Word count (1a) significantly increased across the first three retrieval sessions. Total memory details (external plus internal, 1b) also increased significantly across the first three retrieval sessions and then remained stable. Editorial details (1c) significantly decreased across the first two retrieval sessions. Note that the scales used for each detail type differ. Phrase consistency (1d) represents the number of details repeated from the previous retrieval session divided by the total details from the previous retrieval session. Phrase consistency also increased across retrieval sessions. (\*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p < .005$ )

In the current study, eight middle-aged participants who had taken part in the original study (Nadel, et al., 2007) agreed to return to the laboratory. These participants were unaware, at the conclusion of the previous study, that we would contact them over a year later. Upon their return, participants recalled all 36 autobiographical memories that were originally recalled in the context of the previous experiment approximately one and a half years prior. We compared these results (time 2) with those from the original study (time 1) for all three conditions. In this way we explored the influence of a long delay,

over one year, after two or six retrieval sessions over the course of one month. According to Multiple Trace Theory, after each retrieval the memories undergo a process of reconsolidation, strengthening the existing memory trace and possibly incorporating new information. We expected to see a further increase or stabilization of the level of detail recalled for the Multiple Retrieval memories as a result of not only repeated exposure to the material but also the associated process of reconsolidation. Since the single retrieval conditions, Remote and Recent, involved only two prior retrieval sessions, the increase in recall could well be less compared to that of the Multiple Retrieval condition.

## METHODS

**Participants.** Data from eight of the original 12 participants are reported here (ages 47-64, mean age 57.4; mean years of education, 16.2; range 12-20; 5 female, 2 male). Participants who agreed to return for the experiment were initially unaware that the current study was related to the earlier study. Three of the original 12 participants were unavailable for the follow-up experiment. One other participant completed the study protocol but did not adequately follow instructions; as a result, this participant's data were excluded from the current analyses. Participants received monetary compensation for their participation.

**Materials.** In the original study, an extended version of the list of common life events described by Levine et al. (2002) was used to generate episodic memories from participants during the initial retrieval session. Participants were instructed to recall only

unique events that had occurred more than two years ago and that took place in a specific place and time. They were instructed to visualize the details of the event, playing it out as if it were a scene in a movie, while verbally describing all of the details that they could remember including what happened, who was there, where they were, what they were feeling, and the time of day. The experimenter then created a specific memory cue for each memory, such as “Mary’s 40<sup>th</sup> birthday party”, that was used to cue recall during subsequent retrieval sessions. The same thirty-six memory cues derived during the original study were used for each participant in the current experiment.

**Procedures.** Participants were interviewed approximately a year and a half after completion of the original study (mean 1.4 years, range 1.2-1.9 years). An interviewer who was not involved in the previous study conducted six interviews in-person, and one participant’s interview was conducted over the phone. The interviewer was instructed not to comment or converse during the recollections, acting only as an engaged listener. Participants were instructed that they were going to discuss the same memories as during the former study, and they were given the exact same retrieval instructions as in the previous study. They were encouraged to retrieve all the details they could remember, even if they had discussed the same details in the past. In addition, they were instructed to include any new information that came to mind that they had not previously discussed. Their recollections were tape recorded and later transcribed for analysis.

Following recollection of each event, participants were asked to rate the memory on several scales, including the importance of the event at the time that it occurred, the

current importance of the memory, the emotionality of the event at the time it occurred, the current emotionality of the memory, how vividly the memory was recalled, and their energy level or arousal at the time of the event. Ratings were made on a 1-5 scale, respectively representing not at all (1), somewhat (2), moderately (3), very (4), or extremely (5). Participants were also asked to rate how positive or negative the event was at the time that it occurred using the following scale: very negative (-3), somewhat negative (-1), neutral (0), somewhat positive (+1), and very positive (+3). Participants had also rated their memories on these same scales following their initial recollection during the original study.

**Script analysis.** Three types of details were identified using methods similar to Levine et al. (2002). Internal details occurred during the time of the event itself. For example, “this was during the summer before I turned sixteen,” describes an internal detail for the memory “taking your first plane flight”, as it identifies the time of the event. External details provided context for the memory or general knowledge that was not unique to the event, occurred outside of the time window of the event, or provided a judgment about the event. For example, “I had gone on train rides in the past, to the Grand Canyon and such”, describes an external detail for the memory “going on a train ride”. Editorial details were statements that reflected uncertainty, such as, “I think this was...” or “Now that I think about it, it had to have been...”. Two raters performed the detail analyses, obtaining an inter-rater reliability on each of the three detail types above 85%. Any discrepancies were evaluated and adjudicated by one of the authors (J.

Campbell). The total number of words spoken while the participant described each event was obtained using the word count option in Microsoft Word.

## RESULTS

**Details and Word Counts.** Contrary to the findings of Bartlett (1932) and others (e.g., Bergman & Roediger, 1999) that forgetting occurs over time and with repeated retrievals, details counts for all three of the original memory conditions increased over a one and a half year delay. The number of details recalled for the initial retrieval session and the follow-up session for each condition were compared (Day 1 versus follow-up for Remote and Multiple, Day 28 versus follow-up for Recent). For the Multiple Retrieval condition, we also compared the details recalled during the fifth and final behavioral retrieval session of the original study on Day 28 with the follow-up session. These results are displayed in Figure 2.

Due to the large variability in the length of memories across participants, details were analyzed at the item level rather than the mean detail count per participant. Four separate 3x2 repeated measures analyses of variance (ANOVA) comparing retrieval condition (Remote, Recent, and Multiple) and time (initial and follow-up) were conducted to determine if word count, internal, external, and editorial details differed between the initial and follow-up retrieval sessions. In every instance participants were able to remember the same 36 memories via cued-recall. Word count generally increased between initial and follow-up, indicated by a main effect of time,  $F(1, 95) = 59.64, p < .001$ , with no interaction effect. Follow-up paired t-tests revealed significant differences

in mean word count between initial and follow-up for Remote  $t(1, 95) = 2.88, p < .005$ , Recent  $t(1, 95) = 5.01, p < .001$ , and for Multiple  $t(1, 95) = 4.77, p < .001$ . External details also increased across time for all three retrieval conditions, indicated by a main effect of time  $F(1, 95) = 92.95, p < .001$ . Paired follow-up t-tests revealed significant differences in mean external details between initial and follow-up for Remote Retrieval memories  $t(1, 95) = 5.68, p < .001$ , for Recent Retrieval memories  $t(1, 95) = 6.21, p < .001$ , and for Multiple Retrieval memories  $t(1, 95) = 4.48, p < .001$ . Editorial details increased across time for all three retrieval conditions, indicated by a main effect of time,  $F(1, 95) = 57.78, p < .001$ . Paired follow-up t-tests revealed significant differences in mean editorial details between initial and follow-up for Remote  $t(1, 95) = 4.04, p < .001$ , Recent  $t(1, 95) = 8.26, p < .001$ , and Multiple  $t(1, 95) = 5.21, p < .001$ . Internal details also generally increased over time,  $F(1, 95) = 14.87, p < .001$ , but this effect was moderated by an interaction between time and retrieval condition  $F(2, 94) = 4.66, p < .01$ . Paired follow-up t-tests for internal details revealed significant differences between initial and follow-up for the Recent condition,  $t(1, 95) = 3.95, p < .0001$ , and the Multiple condition  $t(1, 95) = 3.30, p < .001$ , but not the Remote condition, ns.

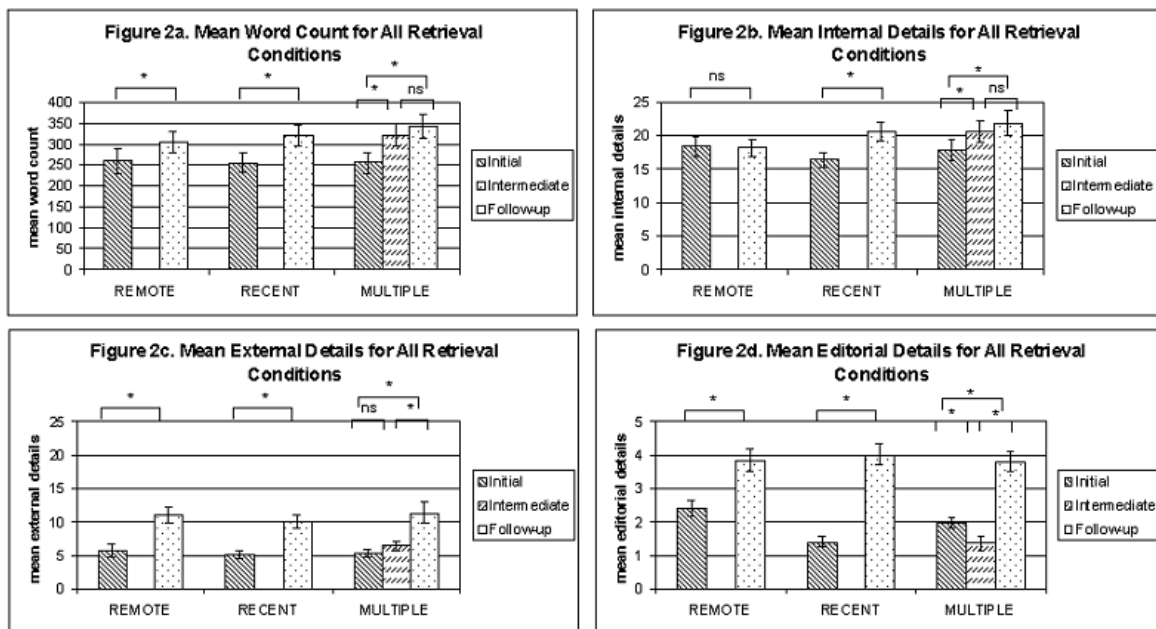


Figure 2. Mean detail counts for Remote, Recent, and Multiple Retrieval conditions from the original study compared to the follow-up retrieval session. Mean word count (2a) increased significantly for all memory conditions between initial and follow-up. Mean internal detail count (2b) increased only for Recent and Multiple, whereas external (2c) and editorial detail counts (2d) increased significantly between initial and follow-up for all retrieval conditions. Note that scales vary by detail type. (Initial = Day 1 for Remote and Multiple Retrieval and Day 28 for Recent Retrieval, Intermediate = Day 28 for Multiple Retrieval, and Follow-up = 1-2 years for all retrieval conditions)

**Ratings.** Rating scores from the current study were compared to those from the original study. Mean rating scores for the three memory conditions are shown in Table 4. Interestingly, although the reported details of memories generally increased over time, the ratings of current emotionality, importance then and now, vividness, and arousal all declined significantly, regardless of the original retrieval condition, with the exception of the event at the time that it occurred. Repeated measure ANOVAs comparing retrieval condition (Remote, Recent, and Multiple) and time (initial and follow-up) were conducted on each rating question. Ratings that declined significantly, indicated by main effects of time, included importance at the time of the event,  $F(1, 93) = 6.88, p < .01$ ,

importance of the event now,  $F(1, 93) = 6.13, p < .05$ , emotionality of the event now,  $F(1, 93) = 12.99, p < .001$ , vividness of recollection,  $F(1, 93) = 14.13, p < .0001$ , and arousal at the time of the event,  $F(1, 93) = 5.12, p < .05$ . Participants' ratings of how emotional the event was at the time that it occurred did not change significantly with time  $F(1, 93) = 1.44, ns$ , nor did their ratings for valence, or how positive or negative the event was at the time,  $F(1,93) = 2.62, ns$ . No interaction effects between time and retrieval condition approached significance for any rating.



Table 1. Mean rating scores for each retrieval condition. Initial ratings were taken after the first retrieval during the original study (1) and follow-up ratings were taken after the single retrieval session of the current study (2). Ratings decreased in nearly every instance between initial and follow-up.

		<i>Importance then</i>	<i>Importance now</i>	<i>Emotionality then</i>	<i>Emotionality now</i>	<i>Vividness of recollection</i>	<i>Positive/ Negative</i>	<i>Arousal level</i>
MULTIPLE	1	4.16	2.27	3.87	2.01	3.69	0.86	3.95
	2	4.05	2.30	3.87	1.90	3.53	0.73	3.79
REMOTE	1	4.32	2.50	4.02	2.13	3.60	0.79	3.87
	2	4.14	2.31	3.97	2.12	3.33	0.85	3.76
RECENT	1	4.36	2.68	4.19	2.39	3.70	0.85	4.00
	2	4.25	2.31	4.00	2.02	3.52	0.61	3.82

**Phrase consistency.** In order to assess whether or not the scripts of the memories at follow-up were consistent with previous recollections, a consistency measure was calculated for memories in the Multiple Retrieval condition by identifying the proportion of total details repeated at follow-up that had been retrieved in the original study on either five, four, three, two, or one occasion. For example, the number of details described in the follow-up that had been mentioned five times in the original study was divided by the total number of details that had previously been retrieved five times. The same calculation was made for four, three, two, and one previous repetition.

Results of this analysis suggested that the consistency effect observed across the original study was moderately maintained in the follow-up retrieval session; the greater the number of previous repetitions, the greater the likelihood that the detail was repeated during the follow-up interview. These results are displayed in Table 2.

Table 2. Mean consistency measure between original and follow-up studies for Multiple Retrieval condition. The proportion of details repeated during the follow-up retrieval session that had previously been retrieved on either five, four, three, two, or one occasion, divided by the total number of items in that particular category.

<b>Number of previous repetitions</b>	Five	Four	Three	Two	One
<b>Probability of repetition</b>	0.65	0.48	0.35	0.31	0.15

In addition to repeating previously retrieved details, participants retrieved new details that were not included in their previous recollections during follow-up. As shown

in Table 3, 40% of the details reported for memories in the Multiple Retrieval condition after one year had not been reported before.

Table 3. Mean proportions of new details to total details from each retrieval session for the Multiple Retrieval condition. Participants recalled new details that had not been previously described at any of the previous retrieval sessions. Across the original study the proportion of new details gradually decreased; the proportion of new details then increased substantially after a one year delay.

**Proportion of New Details to Total Details**

Day 7	Day 14	Day 21	Day 28	Follow-up
0.56	0.39	0.30	0.25	0.40

## DISCUSSION

Despite decades of memory research, surprisingly few studies have asked what happens to memories for events that are salient, emotionally-charged, and important to the story of our lives as they are recounted and conveyed to family, friends, and strangers, over months and years. The present study is an attempt to address that question. In contrast to Bartlett (1932), we find that autobiographical memories become more detailed and contextualized as they are retold after a delay of one and a half years, rather than impoverished. New information is added, and many of the details that were present in previous accounts are expanded. Consider, for example, a single detail taken from a memory on Day 1 (see Appendix B for text). Over the course of a single year, what began as a short sentence of seven words becomes a paragraph, four sentences and eighty words in length. The embellishments are an extension of the memory itself, tying it together with information that will bring the significance of the event into current

perspective, and framing the event in the bigger picture of the speaker's life. The speaker appears to be creating this episodic narrative for the benefit of the listener, and has become, in effect, an expert storyteller.

We believe these results make sense when viewed in the context of the social nature of memories and story telling. Many researchers have emphasized that memories are told for social benefit -- they build relationships amongst people and provide the foundation of our sense of self (Bluck, Alea, & Habermas, 2005), and the specific role they play over our lifespan changes as our goals and social networks change (Hyman & Faries, 1992; Rubin, 1995). Consider how maladaptive our memory system would be if memories become fragmented, devoid of detail, disorganized and confused over time as evidence from Bartlett (1932) and Bergman and Roediger (1999) would suggest. In contrast the virtues of a memory system that allows people to tell their life stories years later through memories that are complete and salient are clear.

In the context of the present study we cannot assess the accuracy of the memories being described. Accuracy of memories over long delays is often the focus of flashbulb memory studies, where accuracy of later recollections can be assessed by directly comparing to the details of the actual event, either obtained from the individual directly after the event or news reports. In one particular study (Schmolck, Buffalo, and Squire, 2000), participants were asked to recall nine specific details of hearing the O.J. Simpson trial verdict. After 15 months, distortions were relatively uncommon, but after 32 months over 42.9% of the details were major distortions. They found that the marked changes in the memory occurred between one and three years after the event. Several other studies

(Bohannon and Symons, 1992; Neisser and Harsch, 1992) also reveal a sharp decrease in accuracy after a 32 month delay. A comparison of flashbulb memories for the terrorist attack of September 11 to the associated event memories by Hirst and colleagues (2009) suggests that after approximately one year content of flashbulb and event memories stabilizes. This comparison also suggests that flashbulb memories may not be as different from event memories as once thought.

It is widely accepted and has been demonstrated in many studies (e.g., Loftus, 1974; Neisser, 1981) that episodic memories are susceptible to revision, with the inclusion of incorrect information or even the development of memories for events that never happened (Ceci, Huffman, Smith, & Loftus, 1994; Loftus & Cahill, 2007). Roediger and his colleagues (Roediger, McDermott, & Goff, 1997) have described these general findings in a review on the paradoxical effects of repeated testing, stating that, “the act of retrieval consolidates the memory and confers easier (and more confident) access later.” This may result in an increase in accurate recollections but could also result in an increase in false information or the creation of false memories. It is likely that the increase in detail we have observed is due to both the accurate addition of internal details (as the hypermnesia literature would suggest) and inaccurate embellishments (as demonstrated by Loftus and others). These inaccurate additions, however, are not necessarily inappropriate, in that the external details used to embellish the memory reflect knowledge derived from prior experiences of a related nature, contributing to the episodic narrative. This process serves to create a rich episodic narrative that is, as Neisser (1981) noted in discussing John Dean’s memory for the Watergate events, not accurate in all

detail but quite truthful to what actually happened. It is clear that our participants did not revise their memories in ways that changed the story in any fundamental way. Each telling of the story was completely recognizable as the story they told in the previous interview, and in this way, as Neisser (1981) pointed out, the question of whether the details are correct or not – whether it was summer or winter, in your backyard or at your cottage – is irrelevant because the critical message of the memory remains intact. Whether the story reflects real details or is filled instead with plausible, but incorrect, contextual details, the memory is "true" at its core and is perceived as truthful by the person conveying it. Neisser referred to this type of memory as “repisodic”.

The memories described by participants in the present study were already well-established, based on events that were rated as important and emotionally rich, and may have already been described and revisited many times in the past. It is also important to note that memory retrievals were not controlled during the period of over one year between the two experiments. Thus, it is possible that these memories were rehearsed during the year preceding our follow-up retrieval test. However, it is unlikely that all 36 memories were repeated in the intervening year, leading us to conclude that these effects probably are not merely a result of non-experimental retrievals. In addition, the increase in detail is consistent and stable across the three retrieval conditions, suggesting that this effect is mostly attributable to the passage of time (over one year) and minimally to the number of retrieval repetitions (three in the Remote and Recent conditions and seven in the Multiple condition).

The results are consistent with the ideas of Multiple Trace Theory (MTT; Nadel

& Moscovitch, 1997; Ryan et al., 2001; Nadel et al., 2007). By this view, memory retrieval initiates both passive (time-based) and active (retrieval-based) processes. Each retrieval, or reactivation, leads to reconsolidation, incorporating the new context and available new information. That is, according to MTT, retrieving a memory can change it. This new memory trace, that interweaves retrieved aspects of the old memory with new information, suggests several things. First, it predicts the incorporation of new and possibly erroneous information into a retrieved memory trace. Second, it raises the possibility that some of the “new” information is not new at all, but rather reflects knowledge derived from related experiences in the past. As a given memory is recalled and reconsolidated, this new information helps create a consistent episodic narrative that becomes the “true” memory in the future.

The present study focuses on previously well-established memories, which raises many questions regarding the specific mechanisms of retrieval and the passage of time. What happens when new memories are consolidated – are they more or less susceptible to this expansion of detail and recruitment of related knowledge? What about the role of emotion? Emotionality possibly confers some benefit to the original consolidation of the memory (LaBar, 2007), but it may also be the case that emotional events happen to be the ones that we are most likely to ruminate about and discuss for days or weeks after the event. It may be that this active process of not only retrieval but also retelling, driven by the emotional content, is critical for laying down the narrative story of our lives for later retelling. Marsh (2007) discusses the distinction between recalling and retelling, highlighting that retellings do not emphasize accuracy as in laboratory recall settings and

as a result may be more malleable and open to distortion.

It is interesting to note that the memories described by participants were rated differently after the passage of another year regarding current emotionality, importance, and vividness, although participants still rated the memories on average as “very important” and “very emotional” as well as “moderately to very” vivid. Of course, the change in these ratings could reflect a simple regression to the mean, but they might also reflect the notion, suggested in the traumatic memory literature (Leskin et al., 1998), that the telling of an event, coupled with the passage of time, decreases the emotional impact of that event, perhaps a small indication that time indeed heals all wounds.

The influence of repeated recall has never been assessed using extended, spaced retrievals of remote, autobiographical memories, although this pattern of retrieval may most closely reflect the way old memories are retrieved and retold in the real world throughout the life span. Our data suggest that the level of event-specific memory information (internal details) remained stable and even increased over time, with virtually no forgetting. Most striking, the memories were embellished by the addition of external details, connecting them to other memories within the larger context of the participants’ lives. These findings are consistent with the original study in which internal and external details were also both seen to increase but under circumstances involving a series of short-term repetitions. While the exact mechanisms of this expansion process are unknown both with short term repetitions and after the passage of very long delays, it appears that Bartlett was at least partly correct in emphasizing the constructive and reconstructive nature of human episodic memory. We are, indeed, storytellers.



**III.****EXPERIMENT 3:  
THE INFLUENCE OF REPETITION AND THE PASSAGE OF TIME ON RECENT  
AND REMOTE AUTOBIOGRAPHICAL MEMORIES: A LONGITUDINAL fMRI  
STUDY**

## **ABSTRACT**

This investigation builds on recent work examining the influence of repetition and the passage of time on remote autobiographical memories (Nadel et al., 2007). Findings led to the question of what would happen to recent memories under similar manipulations. We examined the influence of repetition and the passage of time on remote and recent memories both behaviorally with regard to qualitative and quantitative measures of content and neurobiologically, focusing on changes within the hippocampus and adjacent structures, and how those influences may have differed with respect to the age of the memories. Participants were interviewed a total of five times throughout one month on Days 1, 7, 14, 21, and 28. During the initial interview, participants were asked to retrieve 20 significant life event (autobiographical) memories from different periods of their lives, either within the past several months (10 recent) or more than five years ago (10 remote). During each of the subsequent interviews, the same 20 memories were again recalled. Additionally, fMRI scan sessions were conducted on both Days 2 and 29. This enabled a direct comparison of the same 20 memories before and after a series of repetitions, as well as a comparison of recent and remote memories. The findings contribute to our overall understanding of the neural mechanisms underlying long-term memory consolidation.

## INTRODUCTION

Memories change through time and with repetition, possibly as a function of reconsolidation, a memory process wherein each time a memory is retrieved its underlying neural trace is reinforced. This process of reconsolidation is theorized to involve areas of neocortex as well as medial temporal lobe structures; however, much debate surrounds the nature of the involvement of these brain regions. One perspective regards the role of the hippocampus as time-limited with cortical contributions becoming increasingly strengthened over time, while an alternative view highlights the hippocampus as always necessary in the processes of long-term memory retrieval and consolidation. Additionally, researchers have long been interested in examining the specific behavioral changes that result as time passes and memories are repeated and further understanding which circumstances lead to stronger memories and which to interference.

Ribot (1881) was among the first to note that time was essential to memory stabilization when he observed that brain damage impairs recent memories to a greater extent than remote memories. In contrast, other studies have shown a loss in memory as a result of forgetting over time (Bahrick et al., 2008), and still others have found that learning one set of stimuli can interact or interfere with learning of another set when encoding sessions occur close in time or after reactivation of the original material (Hupbach et al. 2007) or when the encoded information is particularly complex and disjointed (Bartlett, 1932). Memory consolidation, a term first used by Muller & Pilzecker (1900, cited in McGaugh, 2000), seems to predict different behavioral

outcomes depending on time after encoding and the type of information being consolidated.

Neuropsychological data from patients with brain injuries have contributed to a further understanding of memory consolidation and the role of particular brain regions in these processes. Shortly after Hebb originally postulated his dual-trace theory of memory formation (Hebb, 1949), patient HM revealed both retrograde and anterograde amnesia following surgical resection of his medial temporal lobes, specifically the anterior two-thirds of the hippocampal formation, parahippocampal gyrus, and amygdala (Scoville & Milner, 1957). HM exhibited the Ribot gradient with difficulty retrieving recent events, approximately three years prior to surgery, and the inability to form new memories, while maintaining the ability to recall very remote memories from at least 15 or more years ago. This evidence highlighted the hippocampus as a key structure in the process of memory consolidation.

The knowledge of this temporal gradient of consolidation gave way to a prominent view of long-term memory consolidation based in part on the original work of David Marr (1971), who proposed that consolidation involved a transfer of information from hippocampus to areas of neocortex through strengthened synapses and networks. Squire, Cohen and Nadel (1984) took this original idea one step further postulating that consolidation continues and connections within areas of neocortex become strengthened in such a way that the memory may be retrieved solely via areas of neocortex, independent of the hippocampus. This theory of long-term memory consolidation involving a time-limited role of the hippocampus has become widely known as the

standard theory of long-term memory consolidation (Squire & Zola-Morgan 1991; Squire 1992; McClelland et al. 1995) and is mainly supported by instances of retrograde amnesia (Squire & Alvarez 1995).

The initial, cellular processes of memory consolidation lasting seconds to hours in which the memory is initially bound into a memory trace have been well documented and the involvement of the hippocampus and surrounding structures in this process is widely accepted (Debiec et al., 2002; Dudai, 2004). The hippocampus' role in the longer lasting and highly complex systems level consolidation process has proven to be less clear cut. Debate surrounding the exact length of the consolidation period poses a serious challenge to the standard theory with some studies suggesting a length of 2 years (Graham and Hodges 1997; Schmidke and Vollmer 1997) and others indicated it may be more than 10 years (Rempel-Clower et al. 1996; Reed & Squire 1998). Different types of memory utilize multiple and distinct neural circuits, multiple memory systems (Tulving, 1999), and patient data suggest semantic and episodic information undergo different processes of consolidation and inevitably rely on different neural substrates during retrieval (Piolino et al., 2003).

Considered together, these facts led to the generation of an alternative perspective of long-term memory consolidation. Nadel and Moscovitch (1997, 1998) proposed their multiple trace theory (MTT) of long-term memory consolidation, stating that each time a memory trace is reactivated it is also reconsolidated, strengthened, and expanded. This expansion may involve an elaboration of the original trace or the formation of a new, additional trace. The reconsolidated trace may also incorporate some contextual

information from the current retrieval environment. According to this view, the hippocampus is always involved in long-term episodic memory retrieval, no matter the age of the memory. The concept that semantic and schematic representations, lacking the recollective experience that accompanies episodic memories, once fully consolidated depend solely on areas of neocortex during retrieval is congruent with both MTT and standard theory.

A particular type of episodic memory, autobiographical memory (AM), refers to life events from one's past that occurred in a specific spatiotemporal context, acquired from as far back as one can remember to the present. According to one view of the function of AM, these past constructions are thought to assist in maintaining continuity of the self through time (Conway & Pleydell-Pearce, 2000). As a result, autobiographical memories serve as an abundant, readily accessible stimulus set for examining remote episodic memory. In addition, the complex constructive nature of these typically vivid and emotional AMs (Conway & Pleydell-Pearce, 2000) is accompanied by robust activation in a well-studied neural network during fMRI scanning (Vandekerckhove et al., 2005; Svoboda, McKinnon, & Levine, 2006; Spreng, Mar, & Kim, 2008). Autobiographical memories have higher ecological validity than controlled, laboratory-generated memories and are more contextually detailed as compared to famous faces or public event memories.

Exploration of the functional neuroanatomy of remote AM retrieval has used various methods while participants undergo functional scanning (for review see Cabeza and St. Jacques 2007). Results have varied with some investigations supporting the time-

limited role of the hippocampus (Haist et al., 2001; Niki & Luo, 2002; Piefke et al., 2003), while others point toward the perpetual role of the hippocampus in retrieval no matter the age of the memory (e.g. Maguire, et al., 2001; Ryan et al., 2001; Gilboa et al., 2004; Rekkas & Constable, 2005; Steinvorth et al., 2006; Viard et al., 2007; Piolino et al., 2008; Svoboda & Levine, 2009). Most imaging investigations contrast recent and remote memories to elucidate the timing of the role of the hippocampus. Since the time frame of systems consolidation is uncertain, the designation of recent and remote varies widely across these studies. Some approaches separate memories into four (Maguire et al., 2000; Maguire & Frith, 2003) or five (Viard et al., 2007; Piolino et al., 2008) time bins throughout the lifespan. Most studies consider recent to be within the past several years (Ryan et al., 2001; Niki & Luo, 2002; Piefke et al., 2003; Gilboa et al., 2004), with only one study examining memories as new as 2.5 days old on average (Rekkas & Constable, 2005). Remote distinctions are from 20+ years ago (Ryan et al., 2001), prior to ten years of age (Piefke et al., 2003), or anything occurring more than several years ago (Niki & Luo, 2002; Rekkas & Constable, 2005; Nadel et al., 2007).

Considering these methodological variables, the present study explored both the neurological and behavioral changes that occur in AM retrieval as a function of the passage of one month interspersed with a series of repetitions. The use of both recent and remote autobiographical memories enables a closer examination into the specific role that time plays in the process of long-term memory consolidation.

Previously, using only remote memories we found that repetition had little to no influence on hippocampal activation which remained stable rather than increasing as

expected (Nadel, et al. 2007). In this paradigm, a subset of memories were repeated on four additional occasions throughout the course of one month and other memories were retrieved only once prior to scan the multiple retrieval memories were compared to those that were only singly retrieved and hippocampal and neocortical contributions remained relatively stable and did not increase with repetition as MTT would predict. However these findings were not in line with standard theory either which would predict a decrease in hippocampal activation and an increase in cortical areas. There are several possible explanations for this flat level of activation. Perhaps these old memories, at least 2 years old but many as old as 20 years, had been recollected, and as a result reconsolidated, many times throughout the years. Or it is also possible that these neuronal changes that are taking place with the multiple retrievals are too subtle to be detectable with the use of fMRI. This high level of consolidation compounded with the passage of much time may have resulted in some asymptotic level of activation in response to retrieval of these remote memories. These results beg the question, ‘what influence does repetition and the passage of time have on more recent, less consolidated memories?’ We hypothesize that hippocampal activation may increase in response to repeated retrieval of memories when those memories are in much earlier stages of consolidation.

Twenty young adults participated in the present study which took place over the course of one month. Each participant came into the lab for five weekly retrieval sessions on Days 1, 7, 14, 21, and 28. During the initial session, participants recalled 20 salient life event memories from two time periods, ten recent memories from within the past few months and ten remote memories from at least five years ago to as far back as the



participants could remember. These same 20 memories were then repeated in each of the subsequent retrieval sessions. Participants also retrieved the 20 memories while undergoing fMRI scanning during two scan sessions on Days 2 and 29. This design enabled a direct comparison of the same memories before and after repetition, while also permitting comparisons between the recent and remote memories.

We anticipated that increases in activation within the hippocampus and parahippocampal gyrus would be evident for very recent, but not remote memories, while extra-MTL cortical regions should show increased activation across the two sessions, replicating our prior results. Consistent with MTT, this finding would demonstrate the expansion of the hippocampal representation with reactivation and reconsolidation of memories. Qualitatively, these memories may be more readily accessible, and as a result an increase in amount of detail recalled may be seen. An increase in recall with repetition as was observed in a previous study (Nadel et al., 2007) would be consistent with the increase in accessibility proposed by MTT, whereas a decline in recall may suggest memories are becoming semanticized with repetition, a prediction made by the standard theory of consolidation.

## **METHODS**

**Participants.** Twenty adults (ages 21-35, mean age 26.5; mean years of education 18.3, range 16-21) with no prior history of serious head injury, illicit drug use, alcohol abuse, neurological disorder, or psychiatric disorder participated in this study. Participants were also screened for potential risks for MRI, including any metal

fragments or implants. Participants were all currently enrolled in a graduate program at the University of Arizona, likely to have experienced significant recent life events while also having salient remote memories for events from over five years ago. Students' flexible schedules and availability on campus facilitated the scheduling of multiple in lab sessions. Participants received monetary compensation for their participation. All participants gave informed written consent prior to beginning the study, and the research protocol was approved by the local ethics committee, Internal Review Board (IRB), at the University of Arizona.

**Materials.** A list of typical life event cues, such as “first plane flight” or “getting a bad grade”, was used to prompt significant life event memories during the initial retrieval session. This list was a modified version of that used by Ryan et al. (2001) which was based on the cues originally used in Levine et al. (2002) and was expanded to include a subset of cues tailored to the many salient recent memories that graduate students may encounter, including “meeting with your advisor” and “moving into your apartment”. Participants were instructed to recall events that happened during two time periods; recent events were those within the past one to two months and remote events occurred at least five years ago and extended as far back as they could remember. Participants were instructed to recall only events that happened in a specific location and time and events that had only happened on one occasion, not regularly occurring repeated events or extended events taking place over multiple days.

Each participant was instructed to visualize the details of the event, playing it out

as if it were a scene in a movie, verbally describing all of the details that they could remember, including what happened, who was there, where the event took place, any physical and perceptual details of the scene, any feelings they experienced during the event, time of day, and time of year. Following the initial retrieval session, participants were explicitly instructed to retrieve any and all details of the event that they could remember, even if they mentioned the details in any previous retrieval session and were asked to also include any new details that came to mind.

Following retrieval of each memory, participants were asked to provide the approximate date of each event to ensure appropriate categorization (recent or remote), and using several descriptive words of their choice, participants were instructed to provide a descriptive title for each memory that would be used as a cue for them during subsequent recall interviews. Participants were also asked to rate each memory on nine scalar qualities. These scales included: the importance of the event at the time it occurred, the importance of the event presently, the emotionality of the event at the time it occurred, the emotionality of the event presently, how vividly the memory was recalled, and their arousal level at the time of the event. Each of these ratings was collected on a one to five scale, 1) not at all, 2) somewhat, 3) moderately, 4) very, or 5) extremely. Participants were also asked to rate how positive or negative the event was at the time it occurred (recent and remote memories) and presently (remote memories only) on the following scale: very negative (-3), somewhat negative (-1), neutral (0), somewhat positive (+1), and very positive (+3).

Participants were also asked to rate their perspective of the event during recall as

either being: 1) through my own eyes, 2) as an onlooker, watching myself, or 3) some combination of the two. Some evidence suggests that as memories become more remote perspective shifts from first to third person (Nigro & Neisser, 1983). Additionally, memories recalled from first person include more details pertaining to psychological states, whereas those recalled from third person report more details related to objective circumstances (Nigro & Neisser, 1983; McIsaac & Eich, 2002). Perspective ratings were collected to observe a possible shift in perspective after a series of repetitions over the course of one month.

**Procedures.** On Day 1, participants were interviewed for detailed recent and remote autobiographical memories from past events using the cues, instructions, and rating qualities described above. After receiving the instruction set, a practice memory was collected to ensure that the instructions were clear and followed correctly. Only memories that were sufficiently detailed were included in the final stimulus set. If the participant described memories that were not specific or not relatively detailed, these memories were not used. The interviewer also kept track of the number of positively- and negatively-rated memories in an attempt to gather approximately equal numbers of each. As some cues were more likely to prompt a positive or negative event, the interviewer provided cues accordingly. One interviewer was assigned to conduct all five retrieval sessions in the same testing room for each participant. Only one interview for one participant was conducted over the phone due to logistical constraints. All sessions were audio tape recorded and later transcribed.

The complete set of 20 salient autobiographical memories, 10 recent and 10 remote, obtained on Day 1 were then again retrieved at each subsequent retrieval session. Participants returned to the laboratory to meet with their original interviewer at a predetermined time once a week for four consecutive weeks. During each visit, they were provided with a newly randomized list of the 20 self-generated cues from Day 1, such as “Accident on 1<sup>st</sup> Street”. Memories were not rated on Days 7, 14, or 21 but were again rated on Day 28.

**Scanning procedure.** Two separate fMRI scan sessions were conducted, one taking place on Day 2 and another on Day 29. Two functional scans were collected at each scan session, an experimental scan and a stability scan. The experimental fMRI scan, lasting approximately seven and a half minutes, consisted of ten memory retrieval blocks and ten control blocks (see Figure 1). During the experimental scan, participants were asked to read verbal stimuli presented using DMDX presentation software (Forster and Forster, 2003) through a pair of high resolution VisuaStim digital goggles (Resonance Technologies, Inc., California) designed for use in the MRI. For the ten memory retrieval blocks, these verbal stimuli included first presentation of the command cue, “RETRIEVE”, followed by two of the memory cues specific to personal memories obtained during the pre-scan interview on Day 1. The order of the memory cues was completely randomized, and presentation of each memory cue was separated by the word “REST” for one second. Participants were instructed to read the memory cue, respond by mouse button press once they brought the corresponding memory to mind, and then

mentally recall all of the details of each memory in their minds, playing it out as if it were a scene in a movie. They were instructed to recall all the details that they could remember as they had done in all previous behavioral retrieval sessions. Each memory cue appeared on the screen for 12 seconds and participants were instructed to ruminate on each memory for the full duration of its presentation.

During each of the ten control blocks, participants first viewed a command cue, either “LIVING” or “NONLIVING”, followed by a sequence of six unrelated words presented for two seconds each for a total of 12 seconds. If participants first saw the cue “LIVING” they were instructed to respond by mouse button press when they saw an item that was living, and when they saw the cue “NONLIVING” to respond when they saw an item that was nonliving. Only one word in the series was a target item, and the timing of a single response in each sequence was matched to that of the anticipated response time of the memory cue to best control for the motor activations elicited by button press as well as visual word presentation. The word “REST” appeared for one second at the end of each control block.

An additional functional scan, lasting approximately two and a half minutes, was also collected as a longitudinal control for scanner stability between the two scan sessions. During this functional scan, participants saw a series of images consisting of houses, human faces, and crosshairs appear on the goggles and were instructed to attend to each stimulus for as long as it appeared on the screen. They were instructed to make judgments on the human faces, right mouse button press if male and left mouse button press if female. To ensure participants attended to the images, they were instructed to

remember the faces and houses that they saw for a possible post-scan recognition test. Participants were also instructed prior to scanning to keep variables consistent from one scan to the next, for example getting a full night's sleep and avoiding caffeine, and all scan sessions were scheduled for the same time of day. Vascular response has been shown to change with caffeine intake (Laurienti et al., 2002) and sleep deprivation (Lim et al., 2007). If changes in the amplitude of activation during the house/face task were to occur, individual baseline data could be used as covariates in across-session analyses, in order to ensure that any changes in signal observed across the two scanning sessions are not attributable to physiologic differences.

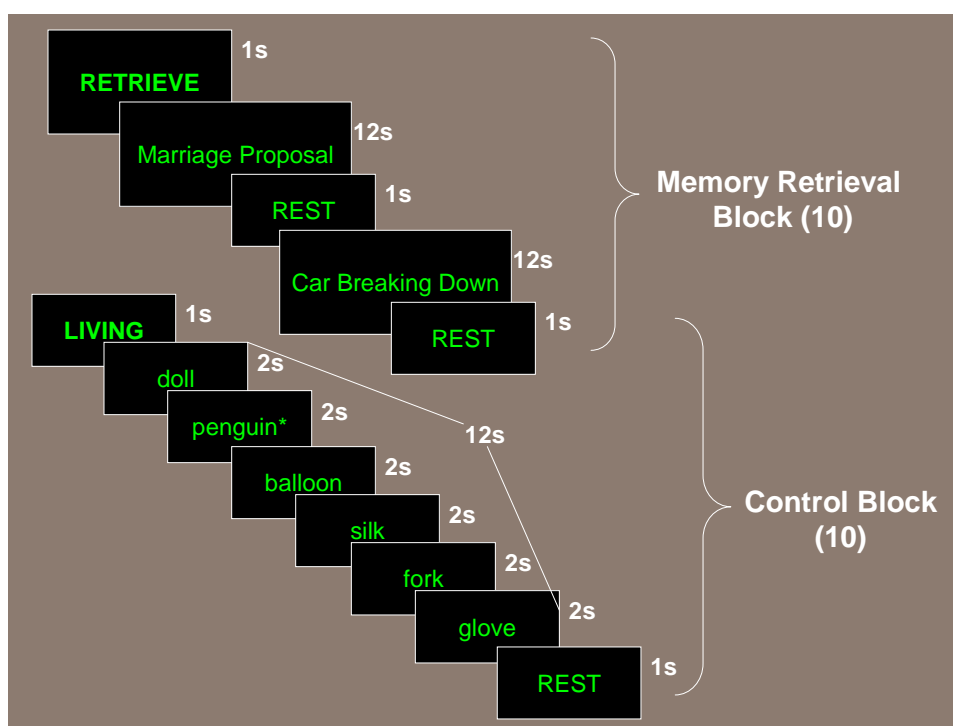


Figure 1. Scanning procedure. Ten memory blocks each containing two memory cues and ten control blocks were administered.

**Imaging parameters.** Images were collected on a General Electric 3.0 Tesla 55cm long-bore whole body Signa Excite VH/i echo-speed magnet currently running 12x software. The magnet is equipped with Optimized ACGD gradients and an 8-channel HR brain phased array coil. A three-plane localizer was collected first for use in aligning T1-weighted anatomical images (matrix = 256 x 256, TR = 500 ms, TE = 14 ms, FOV = 24 cm, sections = 31, thickness = 4 mm, no skip) parallel to the anterior-posterior commissural plane covering the whole brain. Following collection of the T1 images, functional images were acquired in the same alignment as the T1 scans (matrix = 64 x 64, FOV = 24 cm, TR = 2050 ms, TE = 30 ms, flip angle = 90, sections = 31, thickness = 4 mm, no skip), using a single-shot spiral in-and-out pulse sequence (Glover & Lee, 1995; Glover & Law, 2001). A total of 216 volumes were collected for the experimental functional scan, and a total of 78 volumes were collected for the stability functional scan. After reconstruction, the first six volumes of each functional scan were discarded from further analyses to ensure that the net magnetization reached a sufficiently steady state. Lastly, a high resolution 3D spoiled gradient recalled images (SPGR) whole brain anatomical volume was collected (1.2mm sections, matrix 256 x 256, TR = 22 ms, TE = 4 ms, flip angle = 90, FOV = 25 cm) for use in co-registration of images in MNI (Montreal Neurologic Institute) coordinate space.

**Behavioral analysis of memories.** Audio recordings of each of the five retrieval sessions were transcribed for script analysis following methods developed by Levine et al. (2002). Three types of details were identified: internal, external, and editorial. Internal



details refer to information that occurs within the time frame of the event including the time, place, date, and names of individuals, any specifics about the location or what happened during the event. For example, “this was on a Sunday about a month ago” provided the approximate date for the event “going out to dinner”. External details reflect general information not unique to the memory, occurring outside the time frame of the event itself, or provide a judgment about the event based on future or past experience. For example, “my brothers and I camped often and had always wanted to go fishing”, provided context for the event “first time catching a fish” but was not specific to the event itself. Editorial details include statements that reflect uncertainty or judgments, such as, “Now that I think about it, it had to have been...” or “I forget what kind of fish, well I can never really pronounce the name correctly anyway.” These statements provide no extra information regarding the memory being retrieved and include cases where the participant was conversing with the interviewer regarding a detail. Two independent raters performed the script analysis on all memories, with inter-rater reliabilities above 85%. Any discrepancies were discussed and adjudicated by one of the authors (J. Campbell). The total number of words spoken by the participant for each memory was also tabulated using the word counting function in Microsoft Word.

**Image analysis.** Analysis of Functional NeuroImages software (AFNI; Cox, 1996) was used to examine images for motion or other artifact. Images were reconstructed offline and then analyzed in SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>). Pre-processing included realignment to the first volume to correct for movement, spatial

normalization to the standard MNI EPI template (Ashburner & Friston, 1999), and smoothing with an isotropic 7mm FWHM Gaussian kernel. The design was specified such that the onset for each trial matched the memory-specific cue onset and the duration matched the length of each cue presentation. The ensuing BOLD response was modeled by convolving the delta functions from each condition with a canonical hemodynamic response function (HRF) and its temporal and dispersion derivatives (Friston et al., 1998). Contrast vectors were defined for each participant, producing parameter estimates at each voxel for each contrast of interest. Contrast images were then submitted to a second order random-effects group analysis using the general linear model. Regions of significant activation were identified using SPM and were then defined using MarsBar (Brett et al., 2002) to output values of effect size. This was done by combining the resulting group contrast images with either the specified anatomical masks from the MarsBar toolbox or masks drawn using MarsBar based on clusters of activation. The SPM Anatomy Toolbox ([http://www.fz-juelich.de/inb/inb-3//spm\\_anatomy\\_toolbox](http://www.fz-juelich.de/inb/inb-3//spm_anatomy_toolbox); Eickhoff et al., 2005; 2006) was used to transform these coordinates into the Talairach and Tournoux space (1988) and to estimate neuroanatomical regions and the Brodmann's areas. fMRI signal amplitude data were compared across sessions (Day 2, Day 29) and memory types (recent, remote). Estimates of the average magnitude of each individual's activation (average effect sizes) were extracted from the voxels in each ROI for each condition separately. Individual data were then averaged across condition in order to determine the relative contribution.

## RESULTS

**Behavioral Results.** Repeated measures ANOVAs comparing time (recent and remote conditions) and repetition (initial and final retrieval session) were conducted for each detail type: word count, internal, external and editorial details (see Figure 2). Word count did not significantly differ by condition or with repetition as no comparison was significant. For internal details, an interaction between time and repetition resulted,  $F(1,19) = 7.40, p < .01$ , with no significant main effects. Internal details slightly increased within recent condition with repetition, and overall less internal details were recalled for remote than recent memories. Follow-up paired t-tests revealed a significant decrease between recent and remote memories in the final retrieval session,  $t(1,19) = 2.30, p < .05$ . After a series of five repetitions, external details decreased with a main effect of repetition,  $F(1,19) = 4.81, p < .05$ , and no other comparisons were significant. Follow-up paired t-tests revealed a significant decrease in external details for the recent condition,  $t(1,19) = 2.29, p < .05$ . Editorial details showed a main effect of time between recent and remote memories,  $F(1,19) = 8.40, p < .01$ , with no other significant comparisons. Follow-up paired t-tests revealed a significant decrease in editorial details between recent and remote memories during both the initial and final retrieval sessions.

Initially, more details were provided that “staged” each memory (external details) and over time several of those details were omitted and some additional pivotal details (internal details) were recalled but the level of internal details was generally maintained. There were also fewer details mentioned that indicated uncertainty (editorial details) during the final recall session compared to the initial recall session for both recent and

remote conditions.

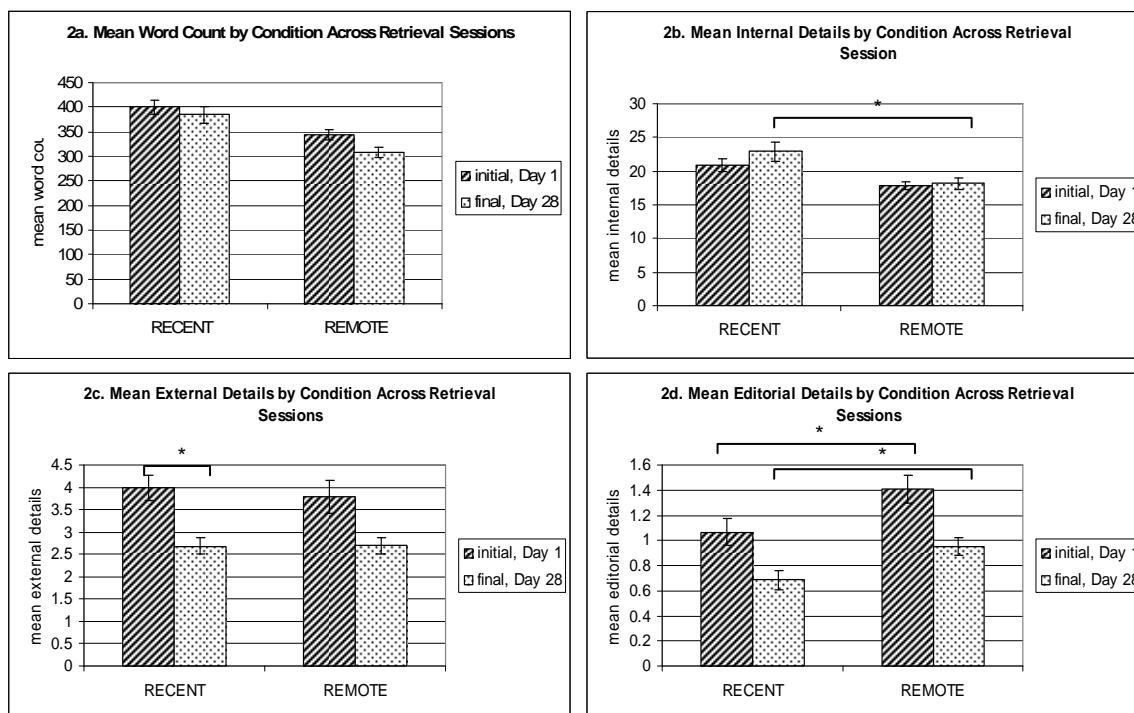


Figure 2. Behavioral detail counts across initial and final retrieval sessions for recent and remote memories: mean word count (1a), mean internal details (1b), mean external details (1c), and mean editorial details (1d). (\*,  $p < .05$ )

**Age of Memories.** Participants were asked to recall memories from two separate time periods, recent memories from within the past one to two months and remote memories for events occurring more than five years ago to as far back as one could remember. From averages based on approximations provided by participants, recent memories occurred approximately 23 days prior to the initial interview, and remote memories occurred approximately 12 ½ years prior to the initial interview (see Table 1). Though the terms recent and remote are used variably, these two groups of memories are clearly temporally distinct.

Table 1. Mean age of all recent and remote memories. Recent memories were calculated in number of days, and remote memories were calculated in number of years. These approximations were provided by participants during the initial interview. Standard errors are noted in parentheses.

<i>Condition</i>	<i>Mean Age</i>
Recent Memories	23.09 days (SEM 1.46; range 1-150)
Remote Memories	12.55 years (SEM 0.39; 5-28)

**Reaction Times.** While in the scanner participants were asked to respond by mouse button press after reading each memory cue and bringing to mind the specific memory. Participants were instructed to then recall all the details of each memory. In this way the reaction time served to indicate at which specific point in time the participant had completed reading and searching and had begun remembering.

A repeated measures one-way ANOVA on participant averages revealed that mean reaction times were significantly longer during the initial scan session compared to the final scan session in response to both recent  $F(1,19) = 27.41, p < .001$  and remote  $F(1,19) = 10.60, p < .005$  memory cues (see Table 2). The difference in reaction time between recent and remote memories at both time points was not significant,  $t's < 1$ . The shorter reaction times observed on Day 29 indicate that over time and with repetition of both recent and remote memories these events were more readily accessible.

Important to note is that RTs were also modeled as covariates in SPM and the results of this analysis did not differ from those without modeling RT. As a result, the RTs were not incorporated into the final imaging statistical model. In Experiment 1, longer RTs may have reflected effort of retrieval which was significantly greater for the remote single retrieval condition. This condition elicited the greatest activation both in

extent and intensity throughout all brain regions. In the current study, the RTs are considerably shorter for Scan 2 than Scan 1. Our imaging data suggest that all brain regions are more robustly activated for Scan 2 than Scan 1. As a result, it is unlikely that the difference in RTs is influencing the results as they are indicated here.

Table 2. Mean reaction times by memory condition. Reaction times were collected while participants were in the scanner and responded by mouse button press to recent and remote memory cues presented visually. Participants were instructed to respond to each cue once they had brought the corresponding memory to mind. Mean reaction times are reported in milliseconds. Standard errors are noted in parentheses.

**Mean Reaction Times (ms)**

<i>Condition</i>	<i>Day 2, Scan 1</i>	<i>Day 29, Scan 2</i>
Recent Memories	1769.47 (44.20)	1259.02 (23.01)
Remote Memories	1643.81 (34.17)	1243.90 (35.24)

**Ratings.** Following recall of each memory during the initial (Day 1) and final (Day 28) behavioral interview sessions, a series of nine qualitative ratings were collected (see Table 3). A repeated measures ANOVA compared the influence of time (recent and remote memories) and repetition (initial and final retrieval sessions) on these ratings. The majority of ratings showed a main effect of time; overall remote memories were rated higher than recent on most rating scales except for vividness of recollection. Only one rating, how positive or negative the event was at the time, showed a main effect of repetition; the majority of ratings did not change with repetition, contrary to our observations in Experiment 1.

Participants' ratings for 'importance then' showed a main effect of time  $F(1,19) = 45.31, p < .001$ , and follow-up paired t-tests revealed that remote memories were rated

higher than recent at both initial  $t(1,19) = 6.26, p < .001$  and final retrieval sessions  $t(1,19) = 5.60, p < .001$ . Ratings for 'emotionality then' showed a main effect of time  $F(1,19) = 57.30, p < .001$ , and follow-up paired t-tests revealed that remote memories were rated higher than recent at both initial  $t(1,19) = 6.23, p < .001$  and final retrieval sessions  $t(1,19) = 8.62, p < .001$ . Participants rated recent memories higher than remote memories for 'vividness of recollection' with a main effect of time  $F(1,19) = 5.32, p < .05$ , and follow-up paired t-tests revealed this increase in recent over remote ratings was significant for the initial retrieval session  $t(1,19) = 2.70, p < .01$ . Participants also rated their 'arousal level' at the time of the event as higher for remote than recent memories with a main effect of time  $F(1,19) = 22.80, p < .001$ , and follow-up paired t-tests reveal this increase is significant at both initial  $t(1,19) = 4.04, p < .001$  and final retrieval sessions  $t(1,19) = 5.16, p < .001$ . Participants rated remote memories as slightly more negative than recent with a main effect of time  $F(1,19) = 6.39, p < .05$  with follow-up paired t-tests revealing a significant difference in the final retrieval session  $t(1,19) = 2.82, p < .01$ . Participants also rated memories more positively after a series of repetitions with a main effect of repetition  $F(1,19) = 11.25, p < .005$  and follow-up paired t-tests showed this effect was significant for remote memories  $t(1,19) = 2.56, p < .05$ . Participants were asked to rate in hindsight 'how positive or negative is the event for you now' only for remote memories and a paired t-test revealed that with repetition memories were rated as less negative on Day 28 than they were on Day 1,  $t(1,19) = 2.55, p < .05$ .

For recent memories, the majority of participants rated their memories as being recalled from first person perspective, some were a combination of first and third and

very few were rated as third. Remote memories were equally rated as being recalled from either first person or some combination of first and third, again with few rated as third person. For this comparison there was a main effect of time  $F(1,19) = 20.34, p < .001$  and follow-up paired t-tests revealed this difference was significant at both initial  $t(1,19) = 3.47, p < .005$  and final retrieval sessions  $t(1,19) = 3.62, p < .005$ . No other comparisons were significant, and no interaction effects between time and repetition were significant.



Table 3. Mean rating scores for the qualitative rating questions asked after recall on Day 1 and Day 28 for Recent and Remote memories. Significance levels are denoted by <sup>1</sup>  $p < .05$ , <sup>2</sup>  $p < .01$ , <sup>3</sup>  $p < .005$ , <sup>4</sup>  $p < .001$ . No other comparisons were significant.

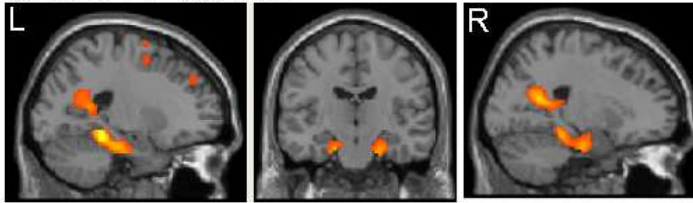
		<i>Importance then</i>	<i>Importance now</i>	<i>Emotionality then</i>	<i>Emotionality now</i>	<i>Vividness of Recollection</i>
Recent	<i>Day 1</i>	2.70 (0.14) <sup>4</sup>	2.10 (0.11)	2.54 (0.14) <sup>4</sup>	1.80 (0.10)	3.73 (0.13) <sup>2</sup>
	<i>Day 28</i>	2.80 (0.17) <sup>4</sup>	1.97 (0.15)	2.48 (0.16) <sup>4</sup>	1.74 (0.13)	3.54 (0.17)
Remote	<i>Day 1</i>	3.58 (0.11) <sup>4</sup>	2.29 (0.15)	3.45 (0.12) <sup>4</sup>	2.04 (0.13)	3.37 (0.10) <sup>2</sup>
	<i>Day 28</i>	3.66 (0.14) <sup>4</sup>	2.18 (0.17)	3.53 (0.14) <sup>4</sup>	1.80 (0.10)	3.26 (0.13)
			<i>Perspective during Recall</i>	<i>Positive/ Negative then</i>	<i>Positive/ Negative now</i>	
Recent	<i>Day 1</i>	2.95 (0.14) <sup>4</sup>	1.56 (0.16) <sup>3</sup>	3.30 (0.12)	-	
	<i>Day 28</i>	2.87 (0.16) <sup>4</sup>	1.65 (0.16) <sup>3</sup>	3.18 (0.11)	-	
Remote	<i>Day 1</i>	3.72 (0.10) <sup>4</sup>	2.02 (0.13) <sup>3</sup>	3.11 (0.11) <sup>1</sup>	3.38 (0.10) <sup>1</sup>	
	<i>Day 28</i>	3.56 (0.12) <sup>4</sup>	1.99 (0.17) <sup>3</sup>	2.86 (0.12) <sup>1</sup>	3.21 (0.11) <sup>1</sup>	

**Imaging Results.** An overall activation map was created from a group contrast of all memory conditions pooled versus all control conditions pooled at a significance level of  $p < .001$  uncorrected and an extent of five contiguous voxels (i.e., Recent 1 + Remote 1 + Recent 2 + Remote 2 > Control 1 + Control 2). Consistent with previous findings, a network of brain regions typically associated with autobiographical memory retrieval was identified, including the medial and ventrolateral prefrontal cortex, medial, lateral and superior temporal, medial and lateral parietal, anterior and posterior cingulate cortices, temporoparietal junction, and amygdala (Vandekerckhove et al., 2005; Svoboda, McKinnon, & Levine, 2006; Spreng, Mar, & Kim, 2008). Of particular interest to the purposes of this study were the medial temporal lobe structures including amygdala, parahippocampal gyrus, and anterior and posterior aspects of the hippocampus proper.

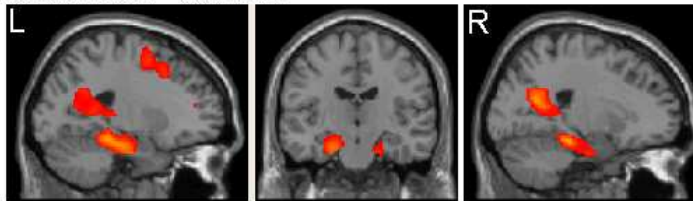
Each of the four memory conditions was then separately compared to control in separate group contrasts at  $p < .001$  uncorrected with an extent threshold of five contiguous voxels; Figure 3 displays a whole brain activation map for each contrast focused on the medial temporal lobe structures. Brain regions that were consistently and robustly activated throughout all four conditions include anterior and posterior hippocampus, parahippocampal gyrus, amygdala, middle temporal gyrus, prefrontal cortex, precuneus, and anterior and posterior cingulate gyrus. The overall activation map was then crossed with each of these regions of interest (ROIs) using MarsBaR. MarsBaR contains a library of ROIs that were anatomically defined by hand on a single brain matched to the MNI / ICBM templates. The ROI definitions are described in Tzourio-Mazoyer et al. (2002). Created specifically for these analyses, the hippocampus was split

at its anatomical center into separate ROIs for anterior and posterior aspects of the hippocampus, and a unitary ROI for the prefrontal cortex was created by convolving a subset of ROIs including orbital frontal, frontal portion of the operculum, and inferior frontal cortex. From the overall activation map, individual datasets of effect size values were extracted for each of the four separate contrasts, each retrieval condition versus control. Design is specified from the individual data and the ROI from which the data is extracted is the result of the overall contrast. Table 4 displays the major ROIs across the four retrieval conditions and the corresponding mean effect sizes, Brodmann's areas, and Talairach coordinates.

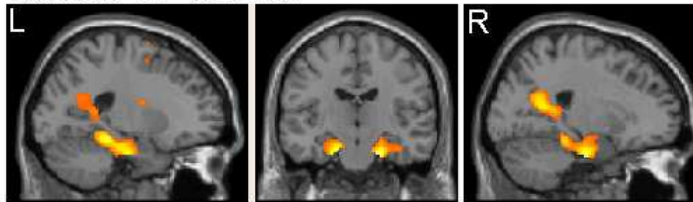
Recent 1 > Control



Recent 2 > Control



Remote 1 > Control



Remote 2 > Control

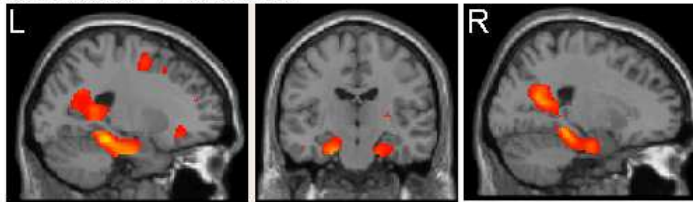


Figure 3. Whole brain activation maps for each retrieval condition versus control condition at  $p < .001$ . These images are shown at coordinates highlighting activation within the medial temporal lobe, which extends bilaterally to areas of parahippocampal gyrus, amygdala, and anterior and posterior aspects of the hippocampus proper. The intensity and extent of activation is increased in nearly every brain region after a series of repeated retrievals. (1 denotes scan 1, 2 denotes scan 2)

Table 4. Mean effect sizes (standard error of the mean) for the four retrieval conditions compared to control at  $p < .001$ . Noted are Talairach coordinates (TAL) and Brodman's Area labels (BA) referencing the center of each activation cluster. (anterior, ant; middle, mid; posterior, post; hippocampus, HC; parahippocampal gyrus, PHG; prefrontal cortex, PFC; 1 main effect of time, 2 main effect of repetition, 3 approaching significant interaction, no other comparisons were significant).

**RECENT 1 + RECENT 2 + REMOTE 1 + REMOTE 2 > CONTROL 1 + CONTROL 2**

	TAL	BA	RECENT 1	RECENT 2	REMOTE 1	REMOTE 2
L ant HC	-21, -12, -15	34	16.53 (4.73)	19.78 (3.44)	19.67 (4.07)	20.54 (4.34)
R ant HC	26, -12, -17	28, 34	14.86 (3.85)	14.30 (4.31)	17.22 (3.95)	14.48 (3.96)
L post HC <sup>3</sup>	-6, -43, 23	23	16.83 (4.22)	21.56 (5.67)	14.02 (3.28)	19.50 (7.93)
R post HC	7, -42, 20	23	15.82 (3.34)	17.44 (10.43)	13.75 (2.73)	15.73 (4.15)
L PHG	-22, -25, -15	35	24.92 (3.90)	32.14 (4.57)	25.89 (3.70)	29.61 (3.26)
R PHG	25, -25, -14	28	20.43 (3.99)	24.90 (7.20)	20.46 (3.47)	24.00 (3.42)
L amygdala	-22, -4, -16	28	10.10 (5.00)	13.57 (3.95)	10.78 (3.37)	13.60 (3.51)
L mid temporal	-12, 45, 4	10	24.48 (16.05)	34.41 (6.49)	25.12 (5.31)	30.45 (5.11)
R mid temporal	7, 49, 2	10	20.83 (4.42)	27.43 (6.51)	21.15 (3.43)	26.62 (4.53)
L PFC	-50, -21, -8	21	31.71 (6.63)	32.98 (6.86)	34.10 (5.71)	32.54 (5.61)
R PFC	53, -15, -12	21	40.10 (6.49)	48.21 (9.82)	39.09 (5.99)	42.91 (32.21)
L precuneus <sup>1</sup>	-7, -56, 41	31	67.00 (11.32)	90.23 (15.55)	56.30 (10.50)	71.46 (7.90)
R precuneus <sup>1</sup>	9, -52, 35	23, 31	62.04 (10.90)	77.62 (10.48)	51.06 (9.20)	61.92 (8.46)
L post cingulate <sup>1,2</sup>	-22, -34, 2	30	55.69 (9.13)	76.02 (10.50)	47.82 (9.90)	63.19 (11.29)

R post cingulate <sup>1,2</sup>	26, -34, 0	30	41.64 (8.88)	60.65 (9.43)	34.47 (8.86)	48.84 (6.79)
L ant cingulate	-22, -20, -9	27	29.64 (5.72)	31.94 (6.94)	28.52 (5.11)	25.80 (4.99)
R ant cingulate	26, -19, -12	27	23.02 (4.91)	24.05 (6.69)	23.57 (4.43)	21.96 (4.39)

As shown in Figure 3 there was a great deal of overlap in the significant regions of activation throughout the medial temporal lobe structures and extra-cortical areas for each memory condition versus control, however, the intensity and extent of this activation varied between scan 1 and scan 2 within both the recent and remote conditions. The intensity of activation as measured by effect size was seen to increase after the series of repeated retrievals that occurred between scan 1 to scan 2 in nearly every region of interest listed in Table 4. A repeated measures ANOVA comparing time (recent and remote memories) and repetition (initial and final scan sessions) revealed a significant increase in activation in the left posterior cingulate with a main effect of time  $F(1,19) = 6.25, p < .05$  and repetition  $F(1,19) = 7.60, p < .05$ . Follow-up paired t-tests revealed a significant increase in activation between scan 1 and scan 2 for the recent  $t(1,19) = 2.54, p < .05$  and remote memories  $t(1,19) = 2.14, p < .05$  for the left posterior cingulate. There was also a significant increase in activation in the right posterior cingulate with a main effect of time  $F(1,19) = 8.87, p < .05$  and repetition  $F(1,19) = 5.00, p < .05$ . Follow-up paired t-tests showed a significant increase in activation between scan 1 and scan 2 for recent memories  $t(1,19) = 2.15, p < .05$ , and recent memories elicited greater activation than remote at scan 2  $t(1,19) = 2.89, p < .01$  for right posterior cingulate. Right precuneus revealed a significant increase in time between remote and recent memories with a main effect of time  $F(1,19) = 15.51, p < .001$ ; follow-up paired t-tests revealed a significant increase in activation between remote and recent memories at scan 2  $t(1,19) = 3.65, p < .005$ . Left precuneus also revealed a significant increase in activation between remote and recent memory types with a main effect of time  $F(1,19) = 15.04, p < .001$ ; follow-up

paired t-tests revealed a significant increase in activation between remote and recent memories during scan 2  $t(1,19) = 3.73, p < .005$ . The main effect of repetition was approaching significance for left precuneus  $F(1,19) = 3.82, P = .07$ . The interaction between time and repetition was also approaching significance for the left posterior hippocampus  $F(1,19) = 3.60, P = .07$ .

Additionally, direct comparisons were carried out separately for Recent 2 > Recent 1 and Remote 2 > Remote 1 to more closely explore the effect of repetition within condition. The resulting pattern of activation was very consistent for both conditions, and the memory types at each scan session were pooled for the overall direct comparison of Recent 2 + Remote 2 > Recent 1 + Remote 1 (see Table 5). This direct contrast at the significance level of  $p < .005$  uncorrected and an extent of five contiguous voxels revealed significant clusters of activation within the right anterior portion of the superior temporal gyrus, right posterior region of the superior temporal gyrus, right medial frontal, and left cuneus. ROIs based on coordinates of the significant clusters of activation were drawn using the MarsBaR toolbox. Effect sizes were pulled from individual datasets and are reported in Table 5 along with corresponding Brodmann's areas and Talairach coordinates referencing the center of each activation cluster.

Table 5. Mean effect sizes (standard error of the mean) for the direct contrasts of scan 2 memories compared to scan 1 memories (Recent 2 + Remote 2 > Recent 1 + Remote 1) at the  $p < .005$  threshold. Noted are Talairach coordinates (TAL) and Brodman's Area labels (BA) referencing the center of each activation cluster. (anterior, ant; medial, med; posterior, post; superior, sup).

**RECENT 2 + REMOTE 2 > RECENT 1 + REMOTE 1**

Region	TAL	BA	Effect Size
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L cuneus	-9, -104, 2	18	204.65 (60.22)
R ant sup temporal	46, 13, -28	38	135.29 (30.11)
R post sup temporal	64, -50, 17	22	155.03 (46.77)
R med frontal	28, 28, 11	10	92.69 (28.19)

In order to measure stability of scan data across sessions, a series of faces and houses were presented to participants in a separately administered functional scan, highlighting the fusiform face area (FFA; Sergent et al, 1992; Kanwisher et al, 1997) as a functional localizer. This area has been shown to elicit a strong BOLD response to faces, objects, places, and bodies. Direct contrasts were conducted for Face 1 > Face 2 and for the reverse contrast Face 2 > Face 1 for the FFA region of interest. Zero voxels were activated in the Face 2 > Face 1 contrast, but a portion of the left fusiform was activated for the Face 1 > Face 2 contrast with an effect size of 5.79 at a threshold of  $p < .001$  uncorrected. Given that the direction of this result goes against our primary findings, that the majority of brain regions are more activated in scan 2 than scan 1, these data will be taken as further confirmation that our results are not a function of physiological or scanner changes occurring during the two scan sessions.

## DISCUSSION

Autobiographical memory is essentially memory in the real world as it pertains to humans as they age. In order to observe the neural representation of autobiographical memories through time there are two factors that must be considered, repetition and age.

Although the number of repetitions throughout the life of memories is impossible to control, in the context of the current study, both recent and remote memories underwent a series of repetitions. Two scan sessions enabled a direct comparison of these memories before and after a series of repetitions, and two main outcomes resulted. Firstly, behavioral results indicated a decrease in external details, those that provide the supporting details of each memory, between the initial and final retrieval sessions. All other measures, overall word count, external and editorial details decreased between initial and final retrieval sessions. Secondly, neuroimaging results revealed that activation increased between scan sessions 1 and 2 within the bilateral posterior cingulate cortex and bilateral precuneus. Activation did not significantly decrease in any medial temporal or neocortical areas between scan 1 and scan 2.

Contrary to our original findings (Nadel et al., 2007) word count and internal details remained relatively stable, whereas in the previous investigation they increased significantly with repetition. Overall fewer internal details and more editorial details were recalled for remote than recent memories during the final retrieval session. In our previous study, internal and external details were taken together as a combined measure of recall, as the pattern of increase was very similar for both details types. In the current study, the amount of internal details recalled remained stable and external details decreased between initial and final retrieval sessions; as a result, internal and external details were considered separately here. External details are those that stage the memory for the audience, providing peripheral details surrounding the actual event memory or things that occurred outside of the time window of the actual event itself. More of these

details were offered during the initial retrieval session, and over time some of these details were not reported. Consistent with the decrease in external details observed here, Loewenthal (1999) explored repetition and personal memories in a group of ethnically diverse college students and found that fewer orienting details were provided with multiple tellings when the audience was kept constant. Marsh and Tversky (2004) have also shown that we reconstruct a memory each time it is told for different purposes and audiences, and these constructions influence future constructions. Loftus (1979) and others have extensively explored the malleability of memory and have behaviorally demonstrated the plasticity of human memory. Reconsolidation may be the process that enables these modifications, serving to update and advance our memory and inevitably species.

The imaging findings reported here are consistent with the results of our previous investigation (Nadel et al., 2007), which suggested that hippocampal activation remained stable over repeated retrievals. Several methodological modifications were made from the original study. In our previous study, subjects were instructed to recall relatively remote memories for events that occurred at least 2 years ago, however, many of the memories occurred 20 or more years ago (Nadel et al., 2007). The current paradigm incorporated memories that were both recent, events from within the past one to two months, and remote memories, which were on average 12 ½ years old. Another difference in the two studies is the age of the participants. Participants from the original study were middle aged (40-63, mean age 54.6), and participants from the current study were young adults (21-35, mean age 26.5). Possibly the most crucial improvement in the current paradigm is

that the same exact set of memories in both the recent and remote conditions were contrasted directly before and after a series of repetitions. In our previous investigation, different subsets of memories were contrasted across conditions which had either been repeated or not. These factors considered together improved the paradigm considerably and still produced consistent results.

In general, results of the many investigations of the role of the hippocampus through time are variable, and methodological factors may account for these differences. Often the time frame for what are considered recent and remote memories is drastically different, spanning from two days to two years for recent (Rekkas & Constable, 2005; Ryan et al., 2001) and from two years to 50 years for remote (Nadel et al., 2007; Piolino et al., 2008). Additionally, the methods of cueing in the scanner are very different (for review see Cabeza & St. Jacques, 2007). Lastly, the types of memories used vary including autobiographical memories, public events, and semantic details. There are many factors to consider as memory is a complex and ongoing process, but one common result is clear in a multitude of studies: the hippocampus is always involved in memory retrieval regardless of memory age.

We anticipated the changes that occurred with repetition to reflect different patterns of activation in recent and remote memories, however, the results were very similar. Recent memories were rated as slightly less important and emotional than remote memories, while recent memories were rated higher for vividness of recollection. Recent memories also started out as more detailed than remote and the increase observed in internal details was larger for recent than remote. Although these memories were not

exactly qualitatively matched, neuroanatomically the patterns of activation were markedly similar; possibly recency is compensating for the slight decrease in importance and emotionality for recent memories. The direct comparisons between recent and remote memories at both scan intervals did yield some subtle changes throughout the brain overall, but the changes within MTL structures are noteworthy. Remote memory retrieval prior to repetition (Remote 1) robustly activated the hippocampus and parahippocampal gyrus bilaterally when directly contrasted with recent memories prior to repetition (Recent 1). After the series of repeated retrievals direct comparisons did not reveal any significant changes within the MTL. Those remote memories that started off with stronger hippocampal contributions from years of recall and reconsolidation were relatively matched by recent memories after several repetitions, providing further evidence that reconsolidation processes resulting in perpetual hippocampal involvement were indeed induced.

When directly compared, all memories remote and recent pooled showed an increase in activity in right superior temporal gyrus, left cuneus, and right medial frontal as a result of repetition. The activity in the superior temporal cortex may be a result of scripting effects as participants are recalling a memorized verbal version of the details of each memory. However, it is unlikely that participants are recalling these memories from rote, scripted memory which lacks detail because we observed robust activity across many brain regions and this high level of activation remains stable and actually increases for several areas with repetition. It may be that participants are eliciting heightened activity within the right posterior superior temporal gyrus and the left cuneus as these

memories are becoming strengthened both visually and verbally with repetition and are more perceptually rich. The right anterior portion of the superior temporal gyrus was also significantly activated in the direct comparison of all memories after repetition to all memories prior to repetition and this region has been implicated in the neurobiology of insight or the “Aha!” moment during verbal tasks (Jung-Beeman et al., 2004). Possibly as a result of repetition, participants perceived these memories from a more insightful perspective.

The increases in activation that were observed from the direct comparison of recent and remote memories after a series of repetitions compared to the initial scan were not accompanied by a decrease in activation in any other brain regions. No brain regions showed a decrease in activation between the first and second scan sessions, as would be expected from predictions made by the standard theory of consolidation. The changes that were observed within the MTL were very subtle as was anticipated, and although some MTL regions showed a slight increase in activation between scan 1 and scan 2 none reached statistical significance. An improved subsequent approach would be to conduct a higher resolution image analysis of the hippocampus and MTL with use of a similar behavioral paradigm.

In conclusion, hippocampal activation remained stable with repetition during retrieval of both recent and remote autobiographical memories. The most robust increases in BOLD signal were observed in bilateral posterior cingulate and bilateral precuneus for both recent and remote conditions after a series of five reactivations throughout the course of one month. Results were consistent with our previous findings that suggested

that hippocampal activations remained stable in response to repetition of remote memories. Behaviorally, repetition resulted in increased accessibility as suggested by decreased reaction times between the initial and final retrieval sessions and a decrease in external, staging details. Considered together, these data suggest that memories do indeed change through time, as a result of strengthened neural representations. Following encoding, frequent reactivations may work to improve memory as a result of ongoing reconsolidation.

IV.  
GENERAL DISCUSSION



## GENERAL DISCUSSION

Memories have been observed to change through time and with repetition both behaviorally with respect to amount of detail recalled and neurobiologically with respect to the contributions from various brain regions. In some instances the amount of recall increases with repetition, also known as the repetition effect (Roediger & Karpicke, 2006) or hypermnesia (Bluck et al., 1999), and in other cases recall decreases with time as a result of forgetting (Bahrick et al., 2008). In line with the predictions made by the standard theory of consolidation, some imaging studies suggest that the hippocampus is less involved in the retrieval of remote compared to recent memories (Haist et al., 2001; Niki & Luo, 2002; Piefke et al., 2003), and other neuroimaging studies have supported the predictions made by the multiple trace theory that the hippocampus remains involved in the retrieval of episodic memories no matter the age (e.g. Maguire, et al., 2001; Ryan et al., 2001; Gilboa et al., 2004; Rekkas & Constable, 2005; Steinvorth et al., 2006; Viard et al., 2007; Piolino et al., 2008; Svoboda & Levine, 2009).

Results of Experiment 1 indicated that the hippocampus was equivalently activated for remote memories before and after a series of repetitions, contrary to our expectations of an increase in hippocampal activity. It is possible that these older memories reached some asymptotic level of activation or that the changes within the hippocampus were too subtle to be detected with the resolution of fMRI that was used. We were then interested in pursuing the question of what would happen with repetition of newer, less consolidated memories. Possibly these memories because of their age have been retrieved fewer times, reconsolidated less and as a result the effect of repeated

reactivations and any ensuing modifications of the neural representations would be more prominent. The results of Experiment 3 indicated that the repetition of recent memories very closely modeled the effects of repetition of remote memories and our predictions about newer memories eliciting more of an effect were not actualized.

Although hippocampal activation did not increase with repetition of remote memories in either Experiment 1 or 3, the hippocampus was robustly activated and did not decrease with time or repetition. Activation was not modulated with time as few other studies have suggested when contrasting recent and remote memories (e.g. Piefke et al., 2003), instead involvement remained stable regardless of memory age as other studies have shown as well (e.g. Ryan et al., 2001). Activation was also not modulated by repetition but again did not decrease with repetition and equivalent levels of activation were present at both time points, scan 1 and scan 2. No areas showed an increase from the reverse contrast of scan 1 > scan 2, suggesting that no areas significantly decreased with repetition.

One potential criticism of the paradigm is that participants are recalling the memory from the previous retrieval session as opposed to from the original event in the past. As predicted by MTT, we would expect that participants are recalling some conglomerated neural representation that has been reconsolidated from each past recollection including the originally encoded neural representation. If participants were recollecting a verbal, rote script, we would expect to see a simultaneous decrease in hippocampal activation, which we do not. In fact, we observed an increase in visual cortex, left cuneus, as a result of the direct contrast of all memories before and after a

series of repetitions. We also observed a significant increase in activation in bilateral precuneus, known for its role in visuo-spatial imagery (Cavanna and Trimble, 2006), as a result of extracting individual effect sizes from the overall memory versus control contrast. The presence of stable hippocampal contributions in addition to the increase in activation in these visual processing areas suggest that these memories are not becoming condensed or scripted but instead embellished in some way. We also observed an increase in activity within the posterior region of the superior temporal cortex, known for its role in language comprehension (Friederici et al., 2000) which may suggest that the script is also becoming better established and represented in the brain.

Given the similarities in the neural representations of recent and remote memories we must consider the idea that new and older memories are not drastically different on a neural basis. Other studies have suggested similar Behaviorally, some changes in recent and remote memories resulted

Participant age may account for some of the differences observed in the behavioral results between Experiments 1 & 2 and Experiment 3. Participants in Experiments 1 & 2 were middle-aged adults (40-63) and participants in Experiment 3 were young adults (21-35). As a result, the memories retrieved by participants in Experiments 1 & 2 were much older memories, many memories were from events that occurred 20 or more years ago. Remote memories recalled in the context of Experiment 3 were much newer, from five to ten years ago. This is possibly a result of the proximity of the reminiscence bump, which describes the tendency people have for recalling personal events from adolescence and early adulthood (Berntsen & Rubin, 2002), in each group.

The middle-aged adults were more inclined to embellish their memories by including more internal and external details upon each telling, even at a year delay. Young adults were able to maintain their level of recall for internal details and decreased the number of external details mentioned, stripping away any excess details and retrieved only those details that were innately pertinent. It is also important to note that the young adults were graduate students, who are far more accustomed to the strict guidelines of an experimental paradigm. The middle-aged adults, as simply a noteworthy behavioral observation, seemed to truly enjoy recalling the details of their past life events with their young, attentive interviewer and as a result may have been more motivated to recall more details.

Experiment 1 suggested that repetition, not time was the critical factor leading to an increase in recall, while experiment 2 suggested it was time and not repetition that was critical for an increase in recall. Experiment 1 involved several short-term repetitions which in other investigations has also resulted in an increase in recall (Roediger & Karpicke, 2006), while Experiment 2 involved a very long-term delay in time. This increase in recall after the passage of one year has to our knowledge is a result that has not been previously represented in the literature. Multiple factors may be contributing to this increase in recall observed at a very long delay of over one year. Although we asked participants not to recall these memories during their involvement in the original study, we did not anticipate their return to the lab one year later and so they were not instructed between Experiment 1 and 2 not to think upon these memories. As a result, it is possible that participants retrieved these memories during the intervening year a number of times

and these repeated reactivations resulted in the increase that we observed in Experiment 2. It would certainly be of interest to have participants from Experiment 3 return to the lab at the one-year delay to see if the same effect would result.

One possible contributing factor to the changes observed in the results of these three experiments involves the method of statistical analysis. In Experiments 1 and 2 the behavioral data were statistically analyzed at the item level due to the large variability in the data and the relatively low number of participants. Experiment 1 had 12 participants, Experiment 2 included eight participants, and Experiment 3 involved 20 participants. Given the higher number of participants in Experiment 3 all behavioral statistical analyses were conducted on participant averages which is a better and more sound statistical approach, however, the lack of statistical power changed the results from previous findings considerably. These data were still largely variable and given a larger number of participants, may have driven some differences in details and ratings to statistical significance.

In conclusion, the exploration of autobiographical memory retrieval is very complex and many factors contribute to the pattern of change that results with time and repetition. Future investigations should consider participant age, memory age, and method of cuing as three factors that could influence results. The retrieval of recent and remote autobiographical memories always activates the hippocampus and surrounding medial temporal lobe structures, and this activation is not modulated by the passage of time, age, or repetition. This finding does not directly support nor contradict the predictions made by the multiple trace theory but does come in opposition to the standard

theory's idea that hippocampal contributions fade with time and repetition. Behaviorally, under some circumstances the level of recall increased with repetition and in others the level of recall was maintained but a decrease in recall of internal details was not observed in any instance. Repetition of autobiographical memories may result in strengthening neural representations and increasing recall.

APPENDIX A

EXPERIMENT 1:  
AUTOBIOGRAPHICAL MEMORY RETRIEVAL AND HIPPOCAMPAL  
ACTIVATION AS A FUNCTION OF REPETITION AND THE PASSAGE OF TIME

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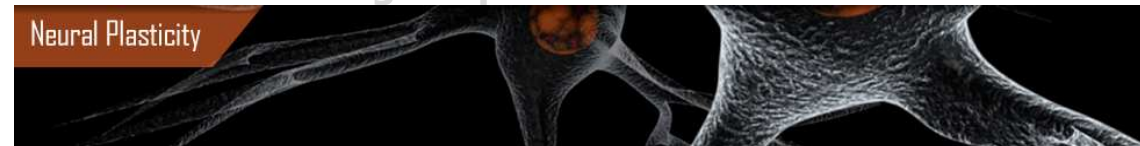
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## Research Article

# Autobiographical Memory Retrieval and Hippocampal Activation as a Function of Repetition and the Passage of Time

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Multiple trace theory (MTT) predicts that hippocampal memory traces expand and strengthen as a function of repeated memory retrievals. We tested this hypothesis utilizing fMRI, comparing the effect of memory retrieval versus the mere passage of time on hippocampal activation. While undergoing fMRI scanning, participants retrieved remote autobiographical memories that had been previously retrieved either one month earlier, two days earlier, or multiple times during the preceding month. Behavioral analyses revealed that the number and consistency of memory details retrieved increased with multiple retrievals but not with the passage of time. While all three retrieval conditions activated a similar set of brain regions normally associated with autobiographical memory retrieval including medial temporal lobe structures, hippocampal activation did not change as a function of either multiple retrievals or the passage of time. However, activation in other brain regions, including the precuneus, lateral prefrontal cortex, parietal cortex, lateral temporal lobe, and perirhinal cortex increased after multiple retrievals, but was not influenced by the passage of time. These results have important implications for existing theories of long-term memory consolidation.

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## 1. INTRODUCTION

Consolidation refers to the idea that, following the experience of an event, the memory for that event undergoes a process of stabilization that renders the memory more resistant to brain injury or interference from similar experiences. Building on the work of Marr [1, 2], Squire et al. [3] suggested that a memory representation or *memory trace* was dependent upon both medial temporal lobe (in particular, the hippocampus proper) and neocortical structures, and that consolidation was the process by which cortical-cortical connections within the trace were strengthened until eventually the memory could be retrieved in the absence of the hippocampus.

The question of whether a consolidated autobiographical memory, dependent primarily on neocortex rather than hippocampus, is qualitatively unchanged from the memory that was first encoded was not addressed explicitly in the Squire et al. [3] proposal. Indeed, the consolidation view inherently assumed that memories over time remained a faithful record of the original event. This assumption was previously ques-

tioned by Bartlett [4], who demonstrated that memory retrieval was a constructive process rather than a mere replay of the past. Using the now famous "War of the Ghosts" story and what he called the method of repeated reproduction, he showed that there was considerable variability in how a story was recalled over time. Repeated reproduction of the story typically led to a shortened, more stereotyped version of it, with details either discarded, transformed, or added anew. Bartlett's study implied that changes in a memory after initial learning affected not only the strength, but the content of that memory as well.

In recent years, two rather different versions of what happens during consolidation have emerged. One version emphasizes that the role of the hippocampus in retrieval is time-limited and that the informational components of memories are represented solely in cortical regions—this has become known as the standard theory of memory consolidation cf. [5, 6]. Thus, the content of memories remains unchanged through the consolidation process. Remote memories retrieved solely from neocortex (as the case in amnesic patients with hippocampal damage) should be as rich and detailed as



remote memories retrieved by comparable controls with an intact hippocampus. Without further hippocampal involvement, the content of consolidated memories should remain stable and consistent over time, a faithful record of the original event. The theory is supported by evidence of temporally graded retrograde amnesia and a correlation between the severity of retrograde amnesia and the severity of anterograde amnesia [7–12].

Nadel and Moscovitch [13] developed an alternative theory of memory consolidation, known as the multiple trace theory (MTT). Similar to the standard theory of consolidation, MTT posits that the establishment of long-term memories involves a lengthy interaction between the hippocampal region of the medial temporal lobes (MTLs) and neocortical regions both adjacent to the MTL (e.g., perirhinal and parahippocampal cortices) and at a distance (e.g., prefrontal cortex). Those memories that are reactivated, it is presumed, are made stronger while others are forgotten. Unlike standard theory, MTT posits that the hippocampus remains an integral part of the memory trace and is thus always involved in retrieval of long-term episodic memories regardless of the age of the memory. Evidence supporting this view comes from neuroimaging studies showing that retrieval of detailed episodic memories activates the hippocampus no matter how old these memories are [14–18] and from studies showing that remote episodic memories retrieved by amnesic patients lack the detail present in remote episodic memories retrieved by an individual with an intact hippocampus [19].

According to MTT, each time an episode is retrieved and rehearsed, a new hippocampally-dependent trace is created. Retrieval, or reactivation, of a memory trace leads to reencoding, which both strengthens and changes that trace making the details of the event more accessible, either through an expansion of the original trace or creation of a new, altered trace. Importantly, the altered trace may incorporate additional components of the context of retrieval, or even new information that is inadvertently (or incorrectly) generated by the act of retrieval. In this regard, MTT provides a mechanism for Bartlett's [4] notion that as memories age and consolidate, they are not just strengthened, but also may be qualitatively altered.

The present study examined the effects of the passage of time and repeated reactivation, or retrieval, on remote autobiographical memories, and how medial temporal lobe and neocortical structures change in response to these two variables using functional magnetic resonance imaging (fMRI). Twelve middle-aged participants recalled autobiographical memories for events that occurred at least two years prior to the time of the study. Each participant retrieved three groups of remote episodic memories. One group of memories was retrieved during a single retrieval session on Day 1 of the study and not again until the day of the scan, which occurred 30 days later (remote retrieval condition). Another group of memories was retrieved repeatedly during multiple retrieval sessions that occurred weekly on Days 1, 7, 14, 21, and 28 of the study and finally in the scanner (multiple retrieval condition). The third group of memories was retrieved during a single retrieval session on Day 28 as well as in the scanner (recent retrieval condition). On Day 30, participants retrieved

all the memories while undergoing fMRI. While the study focused primarily on fMRI patterns of activation within medial temporal lobe and other cortical regions, the design also allowed us to examine the effect of the passage of time and repeated retrieval on qualitative aspects of the retrieved memories.

While neither the standard theory nor MTT makes explicit claims about the qualitative changes that occur to memories as they undergo repeated retrieval, considering the assumptions of MTT outlined earlier, we hypothesized that multiple retrievals would result in the memories becoming more accessible and more detailed over time. We further hypothesized that, contrary to standard theory, activation within the medial temporal lobe, including hippocampus proper, would be either maintained or increased as a function of multiple retrievals in comparison to the mere passage of time.

## 2. METHODS

### 2.1. Participants

Twelve middle-aged participants (ages 40–63; mean age 54.6; mean years of education, 16.2; range 12–20) with no prior history of head injury, neurological disorder, or psychiatric disorder participated in this study. Participants received monetary compensation for their participation.

### 2.2. Materials

A list of typical life events, such as “your wedding day” or “a birthday party,” was used to generate memory prompting cues for the memory retrieval sessions. The list was an extended version of the one developed by Levine et al. [20]. Participants were instructed to recall events that occurred at least two years ago and extending as far back as they could remember. They were asked to provide the approximate date of each memory to ensure that it occurred more than two years ago. They were also instructed to discuss exclusively events that occurred in a specific place and time and that happened only once. Each participant was instructed to visualize the details of the event, mentally playing the event out as if it were a scene in a movie, while verbally describing all the details of the event that they could remember, including what happened, who was there, where they were, the physical details of the scene, and the time of day. Following recollection of each event, participants were asked to rate the memory on several scales, including the importance of the event both at the time it occurred and currently, the emotionality of the event at the time it occurred and currently, how vividly the memory was recalled, and their overall arousal or energy level at the time of the event. Ratings were made on a 1–5 scale, respectively, representing not at all, somewhat, moderately, very, or extremely. Participants were also asked to rate how positive or negative the event was at the time that it occurred using the following scale: very negative (–3), somewhat negative (–1), neutral (0), somewhat positive (+1), and very positive (+3). At the end of the interview session, participants were instructed not to ruminate on any of the memories or relate

the memories to friends or family until completion of the experiment. Participants were told nothing further about the nature of the subsequent interviews.

### 2.3. Procedures

The experimenter used the information derived from the initial retrieval session to create specific cues for each memory for use in subsequent retrieval sessions, for example, "Mary's 40th birthday party." In each of the retrieval sessions that followed, participants were instructed to recall all the details they could remember about the event, even if they had already mentioned them in a previous retrieval session. One interviewer conducted all the initial interview sessions and another interviewer conducted all the subsequent phone interview sessions. The memory cues were presented in a new, randomized order at each retrieval session. All sessions were tape recorded and then transcribed afterwards.

#### 2.3.1. Day 1, one month prior to scan session

In the initial interview session, participants were provided with generic event cues until they generated a list of 24 autobiographical memories as described in Section 3.2. Participants were asked to discuss memories that were particularly memorable and rich in detail. If only a few aspects of a memory were retrieved and no further information came to mind, the participant was asked to move on to another cue. The interviewer kept track of the number of positively and negatively rated memories to ensure that an approximately equal number of each was collected. After the interview, the 24 memories were divided into two lists of 12, with each list including approximately the same number of memories from each lifetime period (childhood, adolescence, young adulthood, and middle age), as well as roughly the same number of positive and negative events. One list was used in the *remote retrieval* condition and the other list was used in the *multiple retrieval* condition. The remote retrieval items were not retrieved again until the day of the scan (Day 30) and the multiple retrieval items were retrieved during four additional weekly phone interviews scheduled throughout the month, and then finally on the day of the scan (Days 7, 14, 21, 28, and 30).

#### 2.3.2. Days 7, 14, 21, and 28

Participants were telephoned at a predetermined time once each week for four weeks. They were provided with the 12 specific memory cues from the multiple retrieval list derived from their memories gathered on Day 1.

#### 2.3.3. Day 28, 2 days prior to scan session

On Day 28, in addition to retrieving items from the multiple retrieval condition as described above, during the final phone session participants were interviewed exactly as they were on Day 1 for 12 additional autobiographical memories. These newly retrieved memories formed the *recent retrieval* condition. The memories met the same criteria as memories

in the other two conditions, having occurred over two years ago, and including a similar number of positively and negatively valenced memories from a similar distribution of life periods.

Thus, memories were obtained and retrieved under three conditions, as depicted in Figure 1: remote retrieval—only retrieved once, 30 days prior to the scan session; multiple retrieval—retrieved five times throughout the course of the month leading up to the scanning session; and recent retrieval—only retrieved once, 2 days prior to the scanning session.

### 2.4. Scanning procedure

During fMRI scanning, stimuli were presented using DMDX presentation software [21] on high-resolution VisuaStim digital goggles (Resonance Technologies, Inc., Ill, USA) worn by the participants while in the scanner. Participants held a mouse in their right hand that was modified for use in the scanner. Participants were presented with all 36 memory cues described earlier in random order. Each memory cue was presented for 12 seconds. Participants were instructed to press the mouse button as soon as they had read the memory cue and were aware of the memory that the cue referred to. They were instructed to recall all of the details of the memory throughout the remainder of the 12-second period, exactly as they had in each previous retrieval session. Each memory cue was followed by a 4-second "REST" period. During this time, participants were instructed to clear their minds and wait for the next cue.<sup>1</sup>

Following scanning, participants were asked a series of follow-up questions regarding their memories. For each memory, they were asked whether or not they had been successful in the scanner in remembering the memory that corresponded to the cue provided, and if so, if they actively retrieved the details of the event for the full 12 seconds that the cue was presented.

### 2.5. Imaging parameters

Images were collected on a General Electric 3.0 Tesla Signa VH/i whole body echospeed scanner equipped with optimized ACGD Gradients. Approximate total scan time was one hour. A sagittal localizer was collected first for use in aligning T1-weighted anatomical images (matrix = 256 × 256, TR = 500, TE = 14 milliseconds, FOV = 24 cm, sections = 31, 4 mm, no skip) parallel to the anteroposterior commissural plane covering the whole brain. Following collection of the T1 images, functional images were acquired in a single functional scan in the same alignment as the T1 scans, using a single-shot spiral in/spiral out sequence [22] (matrix = 64 × 64, FOV = 24 cm, TR = 2040 milliseconds, TE = 30 milliseconds, flip angle = 90°, sections = 31, thickness = 4 mm, no skip). The first 6 volumes were discarded. A total of

<sup>1</sup> An additional sentence completion condition was also included in the scanning session, but these data are not reported here.



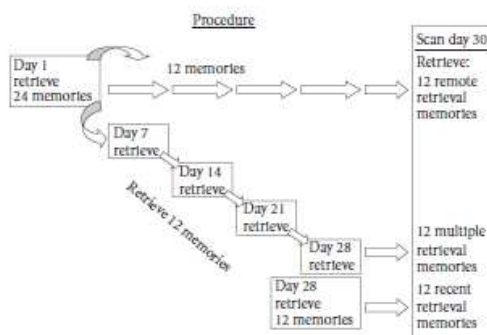


FIGURE 1: Procedure: On Day 1 of the one month study, 24 autobiographical memories were retrieved; 12 of those were not retrieved again until the day of the scan (remote retrieval condition), and 12 were retrieved on four successive sessions throughout the month (multiple retrieval condition). Additional 12 autobiographical memories were retrieved for the first time on Day 28 of the study (recent retrieval condition). All 36 memories were then retrieved in the scanner on Day 30.

400 volumes were collected, taking approximately 14 minutes to complete. Finally, a high-resolution SPGR 3D anatomical volume was acquired (1.5 mm sections covering whole brain, matrix =  $256 \times 256$ , TR = 22 milliseconds, TE = 4 milliseconds, flip angle =  $30^\circ$ , FOV = 25 cm) for coregistration of images in MNI coordinate space.

## 2.6. Behavioral analysis of memories

Audio recordings of each of the five retrieval sessions were transcribed for script analysis. Following methods developed by Levine et al. [20], three types of details were identified: internal, external, and editorial. Internal details referred to information that was central to the memory event itself, including the time, place, date, and names of individuals, any specifics about the location or what happened during the event. These details occurred or were present during the time frame of the event itself. For example, "this was during the summer before I turned sixteen" provided the timing of the event "taking your first plane flight." External details reflected general information not unique to the memory, or referred to events that occurred outside of the time window of the memory event, or provided a judgment about the present based on the past. For example, "I had gone on train rides in the past, to the Grand Canyon and such", provided context for the event "taking your first plane flight" but did not provide specific information about the event itself. Editorial details included statements made by the participant that reflected uncertainty, such as, "I think this was ..." or "Now that I think about it, it had to have been ...", providing no additional information regarding the memory. Two independent raters performed the script analysis on all memories, with inter-rater reliabilities above 85%. Any discrepancies were discussed and adjudicated by J. Campbell.

For the purpose of analyses, internal and external details were added together and are referred to as *total memory detail count*. For each memory the total number of words spoken by

the participant was obtained using the word counting function in Microsoft Word. In addition, three memories from each participant were selected at random for consistent analysis. Essentially, the phrases used to describe each separable detail of each memory were analyzed for consistency across each retrieval session. For retrieval sessions on Days 7, 14, 21, and 28, the number of details that were repeated from the previous retrieval session was measured and expressed as a proportion of the previous session details. For example, if five details were described in the initial retrieval session on Day 1 and four of those details were repeated during retrieval of the same memory on Day 7, the consistency score would be  $4/5$ , or 0.80. Single retrieval memories were retrieved a second time in the scanner on Day 30. As a result, behavioral data from this session are not available for analysis.

## 2.7. Image analysis

Analysis of Functional NeuroImages software (AFNI; [23]) was used to examine images for motion or other artifact. Images were processed and analyzed using Statistical Parametric Mapping 2 (SPM2, Wellcome Department of Cognitive Neurology, University of Glasgow, Glasgow, Scotland). Pre-processing included realignment, normalization to a standard MNI template (<http://www.mrc-cru.cam.ac.uk>), and smoothing using an  $8 \times 8 \times 8$  mm Gaussian filter. The design was specified using a hemodynamic response function (hrf) with partial derivatives for time and dispersion. The onset for each memory trial was specified at 1 second prior to the response time for the memory cue (recall that participants pressed the mouse button when they recognized the cue and began recalling the memory); and duration was specified at the time from the onset (response time - 1 second) to the end of the 12-second stimulus presentation period. This localized the time when the participants were actively recalling the memory and removed time from the analysis when the participant was reading the cue. Other fMRI studies have



similarly modeled RT into the fMRI design by item matching [24], covariate analysis [25], or using RT to temporally model onset of autobiographical memory elaboration [26–28]. Contrast vectors were defined for each participant, producing parameter estimates at each voxel for each contrast of interest. Contrast images were then submitted to a second-order random-effects group analysis using the general linear model. Regions of significant activation were identified using MarsBar [29] by combining the resulting group contrast images with either the specified anatomical masks from the MarsBar toolbox or masks drawn using MarsBar based on clusters of activation.

### 3. RESULTS

#### 3.1. Behavioral results

The purpose of the behavioral analyses of memories within the multiple retrieval condition was to determine whether or not repeated recollection of the same event resulted in memories that were *less* detailed, stereotyped, or gist-like, as described by Bartlett [4], or *more* detailed and accessible, as predicted by MTT. For the multiple retrieval condition only, item analysis for word count, total detail count, and editorial detail count were conducted within three separate repeated measures analyses of variance (ANOVA) across five retrieval sessions, Days 1, 7, 14, 21, and 28. Because of the large variability in the length of individual memories, we conducted item analyses, with detail counts, and so forth, for each memory included as a separate datum, rather than using averages of memories across each participant. It should be noted, however, that conducting the analyses using participant averages for retrieval sessions did not change the overall pattern of results although some differences across conditions no longer reached statistical significance.

Results for word counts, total details, and editorial details are depicted in Figure 2. Generally, the length of memories as measured by both word count and number of details increased across the first three retrieval sessions (Days 1, 7, 14), and then remained stable across subsequent retrievals (Days 21, 28). A repeated measures ANOVA confirmed that mean word count differed across retrieval sessions,  $F(4,140) = 7.46$ ,  $P < .001$ . Follow-up paired  $t$ -tests indicated that word counts increased between retrieval sessions on Day 1 and Day 7,  $t(1,143) = 2.403$ ,  $P < .05$ , and again between Day 7 and Day 14,  $t(1,143) = 3.215$ ,  $P < .005$ . Word count measures between Day 14 and Day 21 and between Day 21 and Day 28 remained stable ( $t$ 's  $< 1$ , nonsignificant). Similarly, a repeated measures ANOVA confirmed that the total detail counts were significantly different across retrieval session  $F(4,140) = 6.549$ ,  $P < .001$ , with follow-up paired  $t$ -tests indicating significant increases in total detail counts between Day 1 and Day 14,  $t(1,143) = 2.09$ ,  $P < .05$ , and Day 7 and Day 14  $t(1,143) = 2.867$ ,  $P < .005$ . The total detail counts between Day 14 and Day 21 and between Day 21 and Day 28 were not significantly different ( $t$ 's  $< 1$ , nonsignificant).

While word count and total details increased across retrieval sessions, editorial details decreased following the initial retrieval session (see Figure 2), although the overall num-

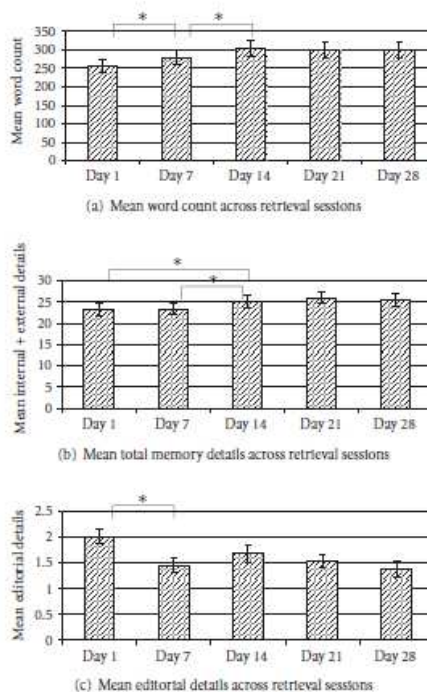


FIGURE 2: Behavioral measures for multiple retrieval memories across retrieval sessions. Mean word count (a) and mean total detail count (b) significantly increased across the first three retrieval sessions and was maintained across the final three retrieval sessions. Mean editorial detail count (c) for the multiple retrieval condition decreased significantly between Day 1 and each subsequent retrieval session.

ber of editorial details was very small (only 2 on average per memory). A repeated measures ANOVA revealed that mean editorial detail measures across retrieval sessions for the multiple retrieval condition on the item level were significantly different  $F(4,140) = 3.692$ ,  $P < .01$ . Follow-up paired  $t$ -tests indicated that editorial details on Day 1 differed from all other days,  $t$ 's(1,143)  $> 2.98$ ,  $P < .01$ , while Days 7–28 did not differ from one another,  $t$ 's  $< 1.62$ , nonsignificant.

As the amount of information in the memories increased over repeated retrievals, so did the consistency of the specific details that were described. The consistency measure for the subset of 36 memories that was evaluated increased across retrieval sessions, suggesting that the story related by the participant was becoming more stereotyped or scripted. It also suggested that, while new details were being added across the early sessions, details provided in earlier sessions were maintained. Table 1 shows that phrase consistency increased

significantly between Day 7 and Day 14,  $t(1,35) = 2.22$ ,  $P < .05$ , and between Day 14 and Day 28,  $t(1,35) = 2.93$ ,  $P < .01$ , with Day 21 falling midway between Days 14 and 28.

### 3.2. Interaction of time and retrieval

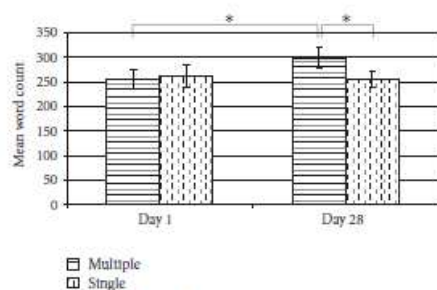
The overall increase in word count and total memory details observed across retrieval sessions could be attributable to multiple successive retrievals but could also be attributable to the participant becoming increasingly comfortable with the interviewer and the interview process. This may have resulted in an increased willingness to report more details about their memories generally, regardless of how many times they were retrieved previously. In order to confirm that retrieval rather than personal comfort levels with the interview process was driving the increase in details, we compared two sets of memories retrieved on Day 1 (remote retrieval, multiple retrieval) with two sets of memories retrieved on Day 28 (recent retrieval, multiple retrieval). We expected that the two sets of memories on Day 1 should not differ from one another in detail or word count, since they were all retrieved for the first time in the same session. On Day 28, if repeated retrieval was responsible for the change over time, then only details for memories in the multiple retrieval condition should increase. If interview comfort was responsible for the change, then all memories retrieved on Day 28, both within the multiple retrieval condition and the newly retrieved memories in the recent retrieval condition, should increase.

A two-factor repeated measures ANOVA was conducted to examine the influence of time (Day 1 versus Day 28) and retrieval (single versus multiple), and indicated a significant interaction between time and retrieval for both word count and total memory details,  $F(1,143) = 6.43$ ,  $P < .01$  and  $F(1,143) = 4.60$ ,  $P < .05$ , respectively. Follow-up  $t$ -tests revealed significant increases between Day 1 and Day 28 for the multiple retrieval condition in both word count,  $t(1,143) = 4.05$ ,  $P < .001$ , and total details,  $t(1,143) = 2.64$ ,  $P < .01$ . On Day 28, word counts and details for memories in the multiple retrieval condition were significantly higher than memories in the recent retrieval condition which were retrieved only once,  $t(1,143) = 2.13$ ,  $P < .05$ ; and  $t(1,143) = 2.46$ ,  $P < .05$ , respectively. In contrast, the differences in word count and details between Day 1 and Day 28 for the two single retrieval conditions (remote retrieval versus recent retrieval) did not approach significance,  $t$ 's  $< 1$ , nonsignificant.

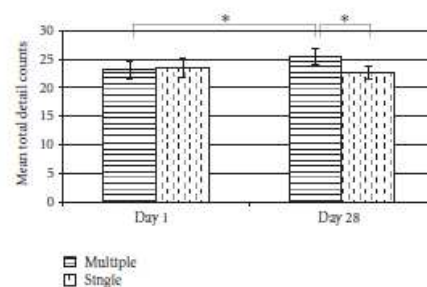
The results strengthen the conclusion that multiple retrieval sessions resulted in memory recollections that were longer, more detailed, and more consistent, and this increase was not due to a change in the reporting characteristics of the participant during the course of the experiment.

### 3.3. Reaction times

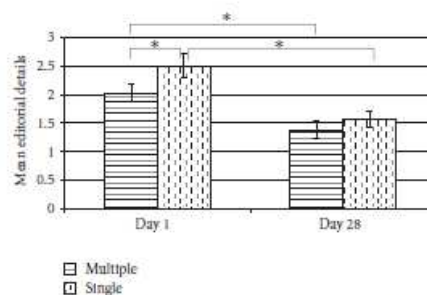
While in the scanner, participants were asked to respond by pressing the mouse button when they had completed reading the memory cue and begun recalling the specific memory. Thus, reaction times may be taken as a general indication of accessibility, or the effort required to retrieve the memory. Reaction times for the three memory conditions are pre-



(a) Mean word count through time for multiple and single retrieval conditions



(b) Mean total memory details through time for multiple and single retrieval conditions



(c) Mean editorial details counts through time for multiple and single retrieval conditions

FIGURE 3: Mean detail measures across retrieval session for multiple and single retrieval conditions. Mean word count (a) and mean total memory detail count (b) significantly increased between Day 1 and Day 28 for the multiple retrieval condition but not for the single retrieval condition. Mean editorial detail count (c) was significantly different between the multiple and single retrieval conditions on Day 1 and between Day 1 and Day 28 for both the multiple and single conditions.



TABLE 1: Mean phrase consistency across multiple retrieval sessions. For each retrieval session of the multiple retrieval condition following Day 1, the number of details repeated from the previous retrieval session was divided by the total details from the previous retrieval session.

Phrase consistency across retrieval session			
Day 7	Day 14	Day 21	Day 28
0.72	0.79	0.83	0.87

TABLE 2: Mean reaction times by retrieval condition. While in the scanner, participants responded by mouse button press after reading the presented memory cue and orienting to the corresponding memory. Mean reaction times are reported in milliseconds (standard error of mean; SEM).

Mean reaction times (ms)		
Condition	Mean	SEM
Remote retrieval	3547.88	226.15
Recent retrieval	3180.15	205.36
Multiple retrieval	2726.87	187.64

sented in Table 2. A repeated measures ANOVA revealed that the mean reaction times differed significantly between the three retrieval conditions  $F(2,128) = 7.70, P < .001$ . Paired  $t$ -tests indicated that mean reaction times were significantly longer for remote retrieval than multiple retrieval memories,  $t(1,129) = 3.71, P < .001$ , and shorter for the multiple retrieval compared to recent retrieval memories,  $t(1,129) = 2.63, P < .01$ . The difference in reaction time between the remote retrieval and recent retrieval conditions was not significant,  $t < 1$ . Note that the same pattern of differences was observed when the analyses were conducted on the average reaction times per participant, one-way ANOVA,  $F(1,10) = 73.76, P < .001$ . For the subject-level analysis, reaction times from one participant were missing due to technical difficulties. The reaction time data suggest that memories in the multiple retrieval session were the easiest to access, followed by recent retrieval memories, and then memories in the remote retrieval condition. This finding has implications for the imaging results that follow.

### 3.4. Imaging results

#### 3.4.1. Similarities across memory retrieval conditions

In separate group contrasts, each memory condition was compared to REST at  $P < .005$  uncorrected, in order to identify the general pattern of brain activation. We expected to see considerable overlap because in all three conditions participants are recalling well-established and vivid memories. Figure 4 depicts the distribution of brain activation observed in each condition compared to REST. The results are consistent with previous studies of autobiographical memory retrieval, indicating activation of bilateral hippocampus, precuneus, lateral prefrontal cortex superior parietal lobules, retrosplenial cortex, and left-lateralized superior temporal gyrus. Regions not commonly observed in studies of mem-

ory retrieval, including bilateral caudate nucleus, thalamus, and orbital frontal cortex, are also activated. Hippocampal activation appears similar across the three conditions, with bilateral activation in the middle region, extending to more posterior regions in the left hemisphere.

Mean effect sizes were assessed using region of interest (ROI) analyses. Because of the significant overlap, a mask was made of common active voxels across the three memory conditions. The mask was then convolved with anatomical masks from MarsBar in order to identify those voxels that fell within major anatomical regions showing activation, including left and right posterior parahippocampal gyrus, left and right hippocampus proper, left and right amygdala, and also bilateral caudate nucleus, superior temporal gyrus, precuneus, and superior temporal gyrus. The mean effect sizes were obtained for each region from individual datasets and were then compared directly across the three memory conditions in SPSS with a repeated measures ANOVA and follow-up paired  $t$ -tests. Table 3 shows the major regions of activation across the three conditions, mean effect sizes, Brodmann's areas, Talairach coordinates, and contrast results for each of the regions. The results show a general pattern of greater activation for remote retrieval memories compared to recent retrieval, multiple retrieval, or both memory types within the hippocampus, parahippocampal gyrus, precuneus, and middle-frontal gyrus. No region showed greater activation for multiple retrieval compared to remote retrieval memories.

#### 3.4.2. Multiple retrieval activations

One problem with interpretation of these results is that the three memory types differed in retrieval effort, as measured by RT. Remote retrieval memories, which were not recalled for over a month prior to scanning, took a significantly longer amount of time to retrieve than either recent or multiple retrieval memories. This difference in RT can influence the amplitude of fMRI signal, particularly since the data were modeled using reaction time to define onset time, which then determined the duration of the item as well. Generally, longer item durations will result in higher amplitude signal.

This issue was approached in several ways. First, a random-effects group analysis directly comparing the multiple and recent retrieval conditions was performed at  $P < .01$ , uncorrected. Both conditions contained memories that had been retrieved only two days prior to the scan, so memories were matched for recency of retrieval. In addition, because the RTs for the multiple retrieval condition were shortest, any increased activations observed in this condition cannot be the result of increased retrieval time. We hypothesized that multiple retrievals would result in increased activation in brain regions associated with recollection, compared to memories in the recent retrieval condition that were recollected only once.

Table 4 shows the results for this analysis, indicating that multiple retrievals resulted in significantly greater activation in cortical, but not medial temporal, regions. Increased activation was observed in frontal, parietal, thalamic, temporal, and precuneus regions. No medial temporal lobe region showed differential activation between

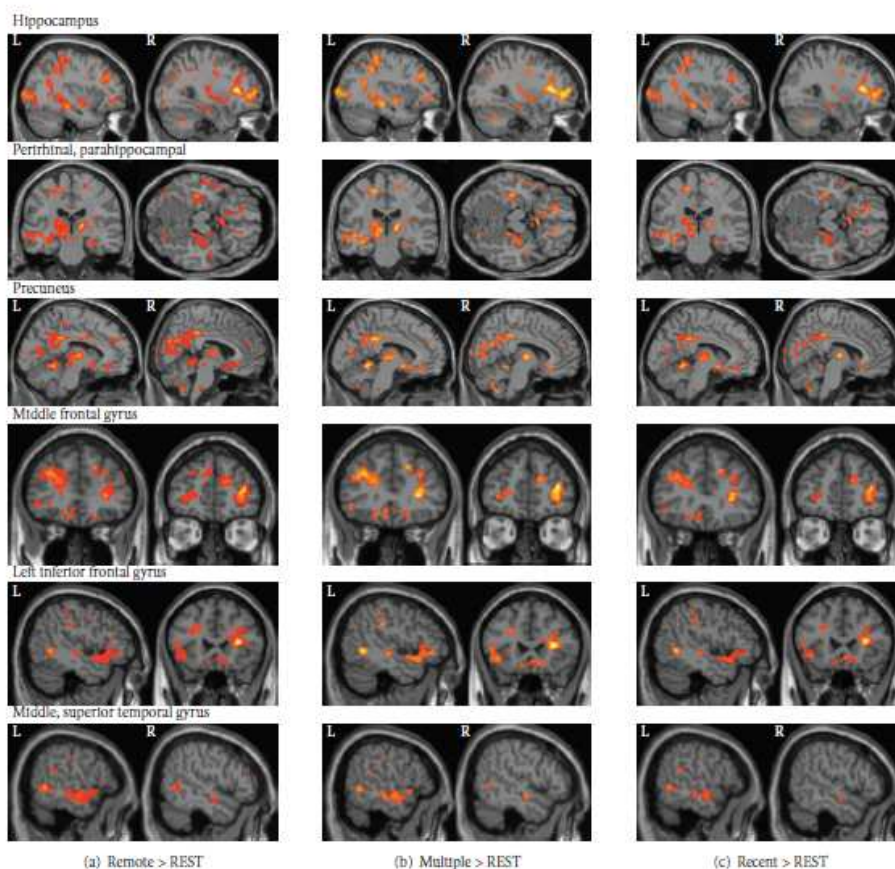


FIGURE 4: Memory conditions > REST ( $P < .005$ ). Each of the retrieval conditions contrasted with REST resulted in common activation patterns throughout the brain, including the hippocampus bilaterally, bilateral perirhinal and parahippocampal gyri, bilateral precuneus, bilateral middle frontal gyrus, left-lateralized inferior frontal gyrus, and bilateral middle and superior temporal gyri.

the two retrieval conditions. In addition, no region showed greater activation for recent retrieval memories compared to multiple retrieval memories, despite the longer RTs for recently retrieved memories.

A second analysis addressing this issue matched memories from each of the three conditions on RTs. The previous analysis suggested that multiple retrievals resulted in increased activation in cortical, but not medial temporal lobe, regions. The same increases should be evident comparing multiple retrieved memories to both recently retrieved and remotely retrieved memories, while controlling for RTs.

One method for dealing with differences in RTs would be to add the RTs as covariates to the model, but this may

be problematic given the relatively small number of items in each memory condition and the assumption of a linear relationship between RT and signal. Instead, memories were matched across the three conditions based on RTs for each individual. Using the criterion of dropping fewer than 3 memories from each condition, we were successful in equating RTs for 6 of the 12 participants, usually dropping either the shortest RTs in the multiple retrieval condition or the longest RTs in the remote retrieval condition. The matched data sets were compared directly in two separate random-effects group analyses comparing multiple retrieval with recent retrieval, and multiple retrieval with remote retrieval. A more liberal threshold ( $P < .05$ ) was applied to the group



TABLE 3: Mean effect sizes (standard error of the mean) for the three retrieval conditions compared to REST at  $P < .01$ . Noted are Talairach coordinates (TAL) and Brodmann's areas (BAs) referencing the center of the activation cluster. The results of various paired sample  $t$ -tests are also reported below the table (parahippocampal gyrus, phg; middle, mid; superior, sup). No other paired comparisons were significant.

	Remote + Multiple + Recent > REST				
	TAL	BA	Remote	Multiple	Recent
L perirhinal/phg	-22, -31, -10	35	1.88 (0.52) <sup>(1)</sup>	1.71 (0.50)	1.73 (0.51)
R perirhinal/phg	24, -29, -10	35	1.95 (0.43) <sup>(1,2)</sup>	1.79 (0.44)	1.71 (0.44)
L hippocampus	-33, -32, -7	27, 35	1.72 (0.30) <sup>(1)</sup>	1.60 (0.29)	1.59 (0.31)
R hippocampus	30, -21, -10	27	1.66 (0.33) <sup>(2)</sup>	1.55 (0.31)	1.50 (0.31)
L amygdala	-20, -3, -15	34	1.60 (0.48)	1.59 (0.48)	1.51 (0.49)
R amygdala	22, -5, -12	34	2.43 (0.70) <sup>(2)</sup>	2.29 (0.67)	2.18 (0.69)
L precuneus	-6, -53, 31	23	1.72 (0.29) <sup>(1,2)</sup>	1.49 (0.31)	1.43 (0.31)
R precuneus	8, -53, 29	23	1.73 (0.31) <sup>(2)</sup>	1.57 (0.33)	1.45 (0.35)
L caudate head	-7, 10, -8	25	2.06 (0.42)	2.10 (0.44)	2.09 (0.44)
R caudate head	7, 13, -7	25	1.63 (0.47)	1.72 (0.49)	1.62 (0.48)
L caudate body	-15, 17, 12	25	1.42 (0.36) <sup>(1,2)</sup>	1.23 (0.37)	1.21 (0.40)
R caudate body	19, 13, 13	25	1.38 (0.27)	1.25 (0.27)	1.17 (0.32)
L mid/sup temporal	-54, -8, -8	21, 22	1.78 (0.30)	1.70 (0.32)	1.64 (0.35)
R mid/sup temporal	53, -9, -10	21, 22	1.98 (0.48)	1.93 (0.50)	1.85 (0.54)
L inferior frontal	-43, 26, -1	44, 45	1.81 (0.36)	1.74 (0.34)	1.69 (0.39)
L middle frontal	-30, 38, 20	9	1.41 (0.21) <sup>(2)</sup>	1.32 (0.25)	1.21 (0.25)
R middle frontal	36, 37, 13	8	1.38 (0.21) <sup>(2)</sup>	1.30 (0.22)	1.23 (0.24)

<sup>(1)</sup> Remote > Multiple,  $P < .05$ , <sup>(2)</sup> Remote > Recent,  $P < .05$ .

TABLE 4: Mean effect sizes (standard error of the mean) for the multiple and recent retrieval conditions compared to REST at  $P < .01$ . Clusters were taken from the direct comparison of multiple > recent retrieval. Noted are Talairach coordinates (TAL) and Brodmann's areas (BA) referencing the center of the activation cluster (posterior, post; anterior, ant; superior, sup; middle, mid; inferior, inf).

	Multiple > Recent			
	TAL	BA	Multiple	Recent
L orbitofrontal	-1, 33, -17	11, 32	1.32 (0.75)	0.82 (0.72)
R orbitofrontal	9, 31, -11	32	2.11 (0.43)	1.87 (0.43)
L middle frontal	-27, 35, 23	11	1.57 (0.28)	1.37 (0.29)
R inferior frontal	64, 4, 23	6	0.27 (0.43)	0.14 (0.44)
L post cingulate	-13, -33, 14	36	0.15 (0.50)	0.00 (0.50)
R ant cingulate	9, 0, 21	34	0.85 (0.53)	0.66 (0.53)
R thalamus, pulvinar	12, -28, 15	28	0.90 (0.38)	0.72 (0.37)
L sup parietal lobule	-25, -53, 39	31	0.67 (0.53)	0.48 (0.53)
R sup parietal lobule	15, -65, 51	7	0.56 (0.37)	0.28 (0.36)
L precuneus	-15, -47, 52	7	0.87 (0.35)	0.69 (0.35)
R precuneus	9, -67, 48	7	0.62 (0.43)	0.33 (0.43)
R precentral	30, -22, 50	4	0.48 (0.54)	0.30 (0.54)
R mid/inf temporal	46, -8, -21	20	0.78 (0.80)	0.62 (0.79)
R mammillary body	9, 0, -11	25	2.33 (0.91)	2.09 (0.92)

contrasts in order to compensate for the loss of power due to the smaller number of participants.

Table 5 shows the mean RTs for each condition before and after matching. The mean number of memories included in each condition was also well matched. In addition, number of total details, editorial details, and word counts for the selected memories were nearly identical to the detail and word counts for the original memory sets from these partici-

pants, suggesting that our matching procedure did not result in a biased subset of memories being included for analysis.

The random-effects analysis provided results that were consistent with the previous direct comparison of multiple retrieval and recent retrieval memories. Several brain regions showed greater activation for multiple retrieval memories compared to both recent and remote retrieval conditions, including left superior parietal lobule, right precuneus,

TABLE 5: Mean reaction times and number of items before and after matching RTs. A secondary analysis was conducted in which the mean RTs were equated across all three retrieval conditions by removing 0–3 items from the analysis. This analysis was conducted on six out of the twelve participants. Standard errors are noted in parentheses (reaction time (RT), millisecond (ms)).

Condition	Mean reaction times (ms) and number of items			
	Before matching RTs		After matching RTs	
	Mean RT	Number of items	Mean RT	Number of items (mean)
Remote retrieval	3547.88 (226.15)	12	2017.55 (68.35)	10.17
Recent retrieval	3180.15 (205.36)	12	1990.47 (69.96)	10.67
Multiple retrieval	2726.87 (187.64)	12	1993.61 (72.25)	10.83

bilateral retrosplenial cortex, right superior temporal gyrus, and bilateral perirhinal cortex. In the opposite contrasts, no region showed greater activation for either recent or remote retrieval memories compared to the multiple retrieval condition.

We again performed ROI analyses for medial temporal lobe regions as described earlier, this time applied to the matched RT data. The results listed in Table 7 show no significant differences in effect sizes for medial temporal lobe regions across the three memory conditions. The results are consistent with the notion that the earlier differences in activation in medial temporal lobe were driven by differentially longer item durations, particularly for the remote retrieval memories.

#### 4. DISCUSSION

The present study examined the influence of repeated retrievals and the passage of time on the subsequent retrieval of autobiographical memories. Results suggest that multiple retrievals, but not the passage of time, have an impact on the representation of autobiographical memories, reflected in both the quality of the memories during subsequent retrieval and the pattern of regional brain activation as measured by fMRI. We will first discuss the behavioral data and then the fMRI results and their implications for theories of explicit memory consolidation.

Multiple retrievals of well-established memories resulted in three behavioral changes: increased speed of access to the memory, increased consistency in the manner in which memories were described, and a gradual increase in recalled details across repeated retrieval sessions, most prominently across the first three sessions. The increase in speed of access is probably due to the participant's repeated exposure to the identical memory cues as well as repeated rehearsal of the processes involved in search. Daselaar et al. [28] and others have argued that the access component of memory retrieval can be separated from the reconstructive phase of recollection, where participants are actively rebuilding the story of the memory, and these two components may have different neural signatures.

Increased consistency of recall may reflect scripting, or the development and refinement of a narrative over multiple retrievals, that then accompanies a memory. This narrative becomes an integral part of the memory and may be an important vehicle for the additions, deletions, and distortions that can occur in autobiographical memories with time. This

process is different than the changes described by Bartlett [4] where stories are condensed, schematized, and generally lose extraneous detail as they are reproduced multiple times.

The third behavioral change we observed, increased recall of details due to retrieval practice, has been described by other researchers as well. Of particular relevance is the literature on hypermnesia for episodic events, in which more details of an event are brought to mind across several retrieval attempts even after the individual has indicated that they cannot recall any additional details. Although the typical hypermnesia paradigm entails free recall of lists of words or pictures [30, 31], the phenomenon has also been demonstrated using autobiographical memories [32, 33]. Repeated recall of autobiographical memories within a brief period of time (an hour) resulted in recollections that were more consistent [32] and included more details of the original event (e.g., details of the reading of the O. J. Simpson verdict approximately eight months after it was aired on television) [33]. In the present study, we also found increased detailed recollection for events over the first three retrieval sessions even though the retrieval sessions were spaced by weeks, rather than minutes.

Studies of remote autobiographical memory rarely have the ability to clearly address the issue of veracity; that is, whether or not memory details produced by participants actually occurred as they are reported. The present study focuses on changes in recollection over time in response to retrieval, rather than accuracy of the recollections. Studies that address the issue of accuracy most often rely on lists of words, pictures, or newly acquired short stories, at the expense of the rich, emotional detail associated with remote autobiographical memories that have been related many times and in many different contexts, perhaps throughout a lifetime. One notable exception to this is Ulrich Neisser's analysis of the testimony of John Dean [34]. Neisser found that Dean's exhaustive accounts of the intensely emotional and important events surrounding the Watergate scandal occurring during the Nixon administration were generally devoid of correct details, despite the fact that Dean was highly confident in the accuracy of his recollections. Nevertheless, Neisser noted that the general information contained in Dean's memories—who knew what, who did what—was correct, even if the event itself had been revised and reconstructed to a surprising degree, a phenomenon that he dubbed “repisodic memory”. The circumstances in which multiple retrievals increase accuracy (as in hypermnesia) or result in reconstructive and erroneous recollections (as may be the case with



TABLE 6: Mean effect sizes (standard error of the mean) for the direct comparisons of multiple > recent and multiple > remote ( $P < .01$ ) after matching RTs. Noted are Talairach coordinates (TAL) and Brodmann's areas (BAs) referencing the center of the activation cluster (superior, sup).

	TAL	BA	Multiple > Recent	Multiple > Remote
L sup parietal lobule	-22, -48, 48	7	0.17	0.22
R precuneus	13, -52, 59	7	0.27	0.33
R postcentral gyrus	34, -31, 48	2	0.21	0.18
L retrosplenial	-25, -49, 13	19	0.14	0.18
R retrosplenial	26, -67, -3	19	0.18	0.18
R sup temporal gyrus	58, -33, 23	22	0.25	0.18
R precentral	14, -24, 54	4	0.19	0.18
L perirhinal	-20, 2, -24	28	0.23	0.15
R perirhinal	24, 2, -24	28	0.24	

TABLE 7: Mean effect sizes (standard error of the mean) within the MTL for the three retrieval conditions compared to REST at  $P < .01$  matching RTs. No paired comparisons were significant. Noted are Talairach coordinates (TAL) and Brodmann's areas (BAs) referencing the center of the activation cluster. The results of various paired sample *t*-tests are also reported below the table (parahippocampal gyrus, phg).

	Remote + Multiple + Recent > REST (matched RTs)				
	TAL	BA	Remote	Multiple	Recent
L entorhinal/phg	-14, -10, -16	34	1.80 (0.94)	2.37 (0.95)	1.80 (0.88)
R phg	20, -26, -11	28	1.91 (1.20)	1.97 (1.25)	1.82 (1.18)
L hippocampus	-33, -32, -6	35	1.56 (0.46)	1.64 (0.49)	1.60 (0.41)
R hippocampus	22, -26, -9	27	1.70 (0.62)	1.52 (0.60)	1.66 (0.60)
L amygdala	-12, 1, -12	34	1.86 (0.65)	2.22 (0.67)	1.83 (0.61)
R amygdala	6, -1, -13	34	2.37 (0.92)	2.68 (0.99)	2.21 (0.86)

autobiographical memories) have yet to be determined. Recently, Marsh [35] distinguished between the act of repeatedly retelling the story of a life event in social settings with that of repeatedly recalling information in an environment such as a psychology laboratory—the former deemphasizes accuracy and leads to distortions, while the latter emphasizes accuracy and consistency. At this point, however, little empirical evidence exists to support the distinction.

The lability of memories during retrieval has been demonstrated elsewhere with very different types of memory. For example, recent work with animals suggests that the act of retrieval or even partial retrieval destabilizes the memory trace. Nader et al. [36] have shown that following reactivation of a memory trace, injection of a protein-synthesis inhibitor blocks reconsolidation rendering the original memory trace inaccessible. This result has been demonstrated with rats in an amygdala-dependent fear conditioning paradigm [36] and also with appetitive, food-rewarded spatial discrimination tasks mediated by both amygdala and hippocampal regions [37–39].

Consistent with the animal work, Robertson et al. [40] have demonstrated that retrieval or practice of motor skills results in two independent outcomes that are quite consistent with the formulations of MTT. First, the skill memory becomes fragile and susceptible to translation, distortion, or the addition of new components. Second, retrieval allows for reconsolidation of the original event, which results in further strengthening and stabilization of the skill. Thus, a sin-

gle long practice session of a particular skill is less beneficial than several interleaved learning trials which provided multiple opportunities for reconsolidation, reminiscent of the verbal learning paradigms of the 1960's comparing the effects of spaced versus massed retrieval. Robertson and Cohen [41] make the point that memories are not singular but include multiple components which may be strengthened differentially by practice or retrieval, and may be mediated by different brain mechanisms. For example, a rat learning a spatial maze learns the spatial layout of the maze, and also learns the response mapping to obtain the reward. In the present study, it is possible that various behavioral changes observed, such as the speed of access, increased consistency, and increased details, may be relatively independent of one another and are influenced by different variables. This notion is worth pursuing in more detailed studies of autobiographical memory retrieval.

The fMRI results provide further evidence that episodic memory representations change with repeated retrievals, but not with the passage of time. Not surprisingly, all memories showed a similar distribution of activation that has been described in other studies of autobiographical memory retrieval [15, 42]. Memories that were retrieved one month ago (remote retrieval) showed greater activation across virtually all brain regions involved in memory retrieval, including hippocampus, compared with both the recent and multiple memory conditions. Interpretation of this result, however, is complicated by the fact that memories that have not

been retrieved for a period of time (in the present study, one month) are more difficult to access, as measured by response times. After equating RTs across all retrieval conditions, increased activation for memories in the remote condition was no longer observed; in fact, there were no measurable differences between the remote and recent memory conditions, both sets of memories previously retrieved only on a single occasion.

In contrast, compared to the single retrieval conditions, memories that had been retrieved multiple times elicited increased activation in a network of brain regions, most notably in lateral prefrontal, parietal, cingulate, superior temporal, and retrosplenial/precuneate regions, all regions that have been previously observed during memory retrieval for emotional events [15, 43]. In this case, increased activation was associated with decreased reaction times, and hence cannot be attributed to differential effort in accessing the memories. Increased cortical activation is predicted by both the standard theory of consolidation and MTT, which suggest that cortical-cortical connections will be strengthened as a memory is consolidated. However, MTT emphasizes the importance of repeated retrieval for reconsolidation rather than the mere passage of time, while standard theory does not directly address this issue. We assume that these cortical increases are related to the behavioral changes described earlier, but further research is needed to clarify how the specific behavioral changes are related to changes in fMRI signal.

In contrast to cortical regions described above, with the exception of an anterior bilateral region of perirhinal cortex (BA area 28), no differences in activation were observed in hippocampus proper, entorhinal cortex, parahippocampal cortex, or amygdala once memories were equated for accessibility. This does not appear to be the result of decreased power due to smaller numbers of participants, because significant activations for each condition compared to the REST control condition were still observed in medial temporal lobe structures for all three memory types, and clear differences were observed between conditions in other brain regions, including perirhinal cortex. Rather, medial temporal lobe activity was maintained across repeated retrievals, neither increasing nor decreasing. It is important to note, however, that the present study emphasized remote and emotionally salient memories, with nearly two thirds of the events occurring in early childhood, adolescence, or early adulthood. These remote memories may already have reached an asymptotic level of hippocampal activation, and further increases in activity may not be detectable using fMRI. The impact of multiple retrievals and the passage of time on newly formed memories may show a very different pattern of results. For example, there is ample evidence that newly formed memories are reactivated during offline processes occurring largely during sleep [44–46], which may play a larger role during the early stages of the consolidation process.

In summary, the present results demonstrate two consequences of repeated retrieval of remote, well-established autobiographical memories that are consistent with the predictions of MTT. First, repeated retrieval of memories, but not the mere passage of time, resulted in memories that were more accessible and more detailed, and ultimately lead to

a consistent script or narrative that was integrated with the memory. Second, repeated retrievals resulted in increased activation within neocortical regions and maintenance of activation within medial temporal lobe structures. Despite the remote nature of these memories, hippocampal activation was robust and did not decrease across time or repetitions, findings that are contrary to the predictions of the standard theory of consolidation. Whether or not hippocampal activation would actually increase in newer, less well-established autobiographical memories as a function of repeated retrieval and time remains to be seen. Clearly, involvement of hippocampus and cortex in memory retrieval is complex, reflecting both the level of effort required to retrieve old memories and the ongoing alterations of existing representations as memories are retrieved and related. Further research will be needed to disentangle the separate contributions to hippocampal and neocortical regions to the distinct processes involved in memory retrieval.

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## APPENDIX B

EXPANSION OF A SINGLE DETAIL THROUGH TIME AND WITH REPETITION:  
EXAMPLE TAKEN FROM EXPERIMENTS 1 AND 2

The following is an example of a single detail that was mentioned during all six retrieval sessions taken from a description of a memory for the participant's first plane flight. Note the increase in word count and detail between Day 1 and 7, and the general maintenance of the nearly verbatim account of that detail throughout the subsequent retrieval sessions. Most importantly, note the addition of new details at the follow-up retrieval session that occurred over a year later.

Day 1:

"I flew on Frontier Airlines to Flagstaff."

Day 7:

"I bought some stock in Frontier Airlines. The original Frontier Airlines. This was the days before the hub and spoke system became the norm, so they still had point to point flights. So they offered direct service between Tucson and Flagstaff."

Day 14:

"I had got a bunch of stock on Frontier Airlines, the original Frontier not the airline that now operates under that name. And I took a trip that summer to Flagstaff this being before the days of the hub and spoke system came into use in the Airlines, and there was actually a direct flight from Tucson to Flagstaff, they stopped in Phoenix."

Day 21:

"I had purchased some stock in Frontier Airlines. The original Frontier Airlines, not the airline that now operates under that name. This was before the hub and spoke system came into use, there was a direct flight between Tucson and Flagstaff which I believe Phoenix was en route."

Day 28:

"I had purchased stock from Frontier Airlines, the original Frontier Airlines and this being in the days before the hub and spoke system the Airlines still use. There was actually a direct flight from Tucson to Flagstaff with a stop to Phoenix."

1 Year Follow-up:

"At that time many Airlines had programs for younger travelers with discounted fares and other goodies and upgrades. Frontier was one of the major carriers out of Tucson at that time not to be confused with the current version of Frontier Airlines which is a completely different company. At that time this was before the hub and spoke system so you could really fly from point to point. And there was a flight out of Tucson that went through Flagstaff."

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