Hippocampal Complex and Retrieval of Recent and Very Remote Autobiographical Memories: Evidence From Functional Magnetic Resonance Imaging in Neurologically Intact People

Lee Ryan,[1]* Lynn Nadel,[1] Katrina Keil,[1] Karen Putnam,[1] David Schnyer,[1] Theodore Trouard,[2] and Morris Moscovitch[3]

[1]*Cognition and Neuroimaging Laboratories, Department of Psychology, University of Arizona, Tucson, Arizona*

[2]*Department of Biomedical Engineering, University of Arizona, Tucson, Arizona*

[3]*Department of Psychology, University of Toronto, Toronto, Ontario, Canada*

ABSTRACT: It has been argued that the role of the hippocampus in memory is time-limited: during a period of memory consolidation, other brain regions such as the neocortex are said to acquire the ability to support memory retention and retrieval on their own. An alternative view is that retention and retrieval of memory for autobiographical episodes depend on the hippocampal complex, regardless of the age of the memory. We examined the participation of the hippocampal complex in a functional magnetic resonance imaging (fMRI) study in which participants were asked to recollect autobiographical events that occurred either within the last 4 years or more than 20 years ago. We found equivalent levels of hippocampal activation in both conditions in all participants (N = 10). In addition, activation in neocortical regions did not differ as a function of the age of the memory, even though most of the recent memories recalled were less than 2 years old and the remote memories more than 35 years old. The results support the notion that the hippocampal complex participates in retention and recovery of even very old autobiographical memories, and place boundary conditions on theories of memory consolidation. *Hippocampus 2001;11:707–714.*

KEY WORDS: hippocampus; consolidation; autobiographical memory; functional MRI; retrieval; medial temporal lobe

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*Correspondence to: Lee Ryan, Ph.D., Department of Psychology, University of Arizona, PO Box 210068, Tucson, AZ 85721-0068.
E-mail: ryant@u.arizona.edu
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INTRODUCTION

Studies of anterograde memory, i.e., the acquisition and storage of new information, suggest that the hippocampal complex[1] plays an essential role in the formation of new memories (Squire et al., 1984; Teyler and DiScenna, 1986). Yet it is the study of retrograde memory, the retention and recovery of previously acquired information, that is needed to investigate an enduring problem in cognitive neuroscience: the role of the hippocampal complex and of the neocortex in memory consolidation, storage, and retrieval. The traditional view, dating to the early part of the century and to the report by Scoville and Milner (1957) on the effects of bilateral medial temporal lobe lesions in humans, is that the role of the hippocampal complex in memory is time-limited; it is needed only until consolidation of the memory trace or engram in neocortex (or elsewhere) is complete, after which memories can be retained and retrieved without hippocampal complex involvement (McLelland et al.,

[1]Terminology here can be quite confusing. The "hippocampus proper" refers to the CA fields and dentate gyrus. The "hippocampal formation" includes the hippocampus proper plus the subiculum. The "hippocampal complex" includes the hippocampal formation plus the entorhinal, perirhinal cortex and parahippocampal gyrus.

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1995; Moscovitch, 1995; Squire and Alvarez, 1995). The alternative view, based on recent evidence using more sensitive scoring techniques to assess remote memory loss following hippocampal complex lesions in humans, is that retention and recovery of memory for autobiographical episodes and possibly public events, but not semantics, depends on the hippocampal complex for as long as the memory exists, even if it is decades old (Moscovitch et al., 1999; Nadel and Moscovitch, 1997; Viscontas et al., 1999). To account both for extensive retrograde amnesia and for the temporal gradient observed in some studies, the multiple trace theory (MTT) was proposed (Nadel and Moscovitch, 1997; Moscovitch and Nadel, 1998; Nadel et al., 2000), which posits that a new hippocampally mediated trace is created when old memories are retrieved, so that old memories are represented by more or stronger traces than are new ones, making them more resistant to partial lesions of the medial temporal lobe.

We used functional magnetic resonance imaging (fMRI) to determine the extent of hippocampal complex activation during recovery of recent and remote autobiographical memories. During scanning, subjects between ages 50–72 were asked to recall the details of 10 recent events (occurring less than 4 years ago) and 10 remote events (occurring at least 20 years ago). We chose these times because we were interested in the long-term consolidation process which has been estimated to last between 3 (Scoville and Milner, 1957; Squire et al., 1984) and about 20 (Rempel-Clower et al., 1996) years according to traditional consolidation theory. Most of the remote events happened when subjects were in their twenties or early thirties, so for some subjects, the events occurred as long as 45 years ago. According to traditional consolidation theory, there should be decreased hippocampal activation and increased neocortical activation during retrieval of the more remote, as compared to the more recent, memories. If, however, our alternative view is correct, comparable hippocampal activation should be observed during the retrieval of remote and more recent memories. Insofar as the memory trace consists of a hippocampal-neocortical ensemble representing the autobiographical event, neocortical activation should also not increase with time.

Because the two views lead to clearly different predictions, the goal of the study was to determine if the hippocampal complex and neocortex would be activated by retrieval of autobiographical memories, and if so, whether activation varied as a function of the age of the memory. The results we report indicate that our technique elicited reliable hippocampal activation during retrieval of recent and remote memories. Although no differences in hippocampal or neocortical activation were found between recent and remote memories, favoring our alternative to the consolidation hypothesis, other interpretations are considered.

MATERIALS AND METHODS

Seven subjects (mean age, 60.3; SD, 4.1; mean years of education, 16; SD, 1.6; range, 13–20) with no prior history of head injury, neurological disroder, or psychiatric disorder participated in the study. Immediately prior to entering the scanner, subjects were given a list of life events such as "learning to drive" and "your wedding day." The list also contained items that were more likely to evoke recent memories, such as "an important career event" and "a recent holiday." Subjects identified items that had occurred in their lives and noted the year of the event and whether it was a positive or negative experience. No other details were obtained at the time. Cues were gathered until the list included 10 remote events and 10 recent events, with relatively equal numbers of positive and negative events within each category.

For the memory recollection task in the scanner, subjects were presented with a visual cue they had chosen from the list, such as "a family picnic," and were instructed to recall that particular event from their past for 20 s. Examples were provided prior to scanning in order to ensure that subjects understood that they were to think about a specific single event from their past rather than generic information associated with events that were repeated many times (such as the routine involved in going on a picnic). Subjects were instructed to focus on details of what happened during a particular episode, and to note where they were, who was there, the time of day and year, how they felt, and perceptual details (e.g., visual, auditory, or olfactory) of the setting.

Two control conditions were also included. The cue "relax" appeared for 16 s before and after each event cue; subjects were instructed to focus their mind on relaxing. Subjects were also periodically shown a set of four sentences with the last word missing, such as "The cat was chased by the _____," and were required to complete each sentence covertly with an appropriate word. Matched sentences, such as "The dog chewed the _____," were used as distractors during a sentence recognition test that was given to subjects immediately after the scanning session was completed. The sentence completion task provided a control that required the retrieval of semantic rather than autobiographical information, and provided a comparison between the retrieval of autobiographical information and the encoding of novel information within the scanning session.

Five functional scans were completed in a single session. Each scan included four event cues (two recent and two remote) and one sentence set, with intervening "rest" periods. After each scan, subjects were again presented with the four memory cues and were asked to describe verbally the details of the memories they recalled, and to rate the memory for vividness of the recollection (0–6), the emotional valence of the memory (−3 to +3), their physical arousal during recollection (0–6), and the importance of the event at the time it occurred (0–6). The scanning and debriefing procedure was repeated five times, so that all 20 event cues and five sets of sentences were presented to a subject.

Functional images were acquired on a 1.5 T whole body scanner (Signa Echospeed, General Electric, Milwaukee, WI), using two-dimensional (2D) single-shot spiral acquisition (Glover and Lee, 1995), TR = 2,000 ms, TE = 40 ms, FOV = 220 × 220 mm^2, matrix = 64 × 64. Sections (17–19) were 5 mm thick, with a 1-mm gap, covering the entire brain. Sections were placed obliquely perpendicular to the long axis of the hippocampus in order to minimize partial voluming effects of the hippocampus. Visual cues (memory cues and the sentences) were presented as a computer projection on a high-resolution set of liquid crystal display (LCD) goggles worn by the subject (Resonance Technologies, Inc.). A bite bar was used to restrain the head to decrease movement artifact. High-resolution anatomical three-dimensional (3D) gradient echo images were obtained in the sagittal plane, 1.5 mm thick, no gap, TR = 22, TE = 5 ms, FOV = 250 × 250 mm^2, matrix = 256 × 256, flip angle = 30°, for localization of functional activity and for registration of fMRI data sets to stereotactic space according to Talairach and Tournoux (1988). Imaging data were analyzed using AFNI software (Cox, 1996). Functional images were reconstructed, 3D re-registered to correct for movement, and normalized to allow the data to be combined across multiple functional runs and across subjects. For each subject and for each comparison condition, the time series data for each voxel were correlated with a reference function derived from an idealized hemodynamic response that identified the contrast of interest. The resulting correlation maps were then thresholded at $P < 0.0001$ (two-tailed). A clustering algorithm was applied so that only clusters of at least three contiguous active voxels (minimum volume = 220 μl) were considered true regions of activation.

In order to test for differences in magnitude of activation, the time series data for each subject within a given region were averaged across all voxels identified as active during a particular comparison. Differences between conditions were tested with a repeated-measures ANOVA, with time (in 2-s intervals) and condition as within-subject factors. Activation data were analyzed from 2–16 s post-onset of the memory cues. The following comparisons were made: 1) recollection (recent and remote memories combined) vs. rest, 2) recollection (recent and remote memories combined) vs. sentence completion, 3) recent memories vs. remote memories, and 4) sentence completion vs. rest.

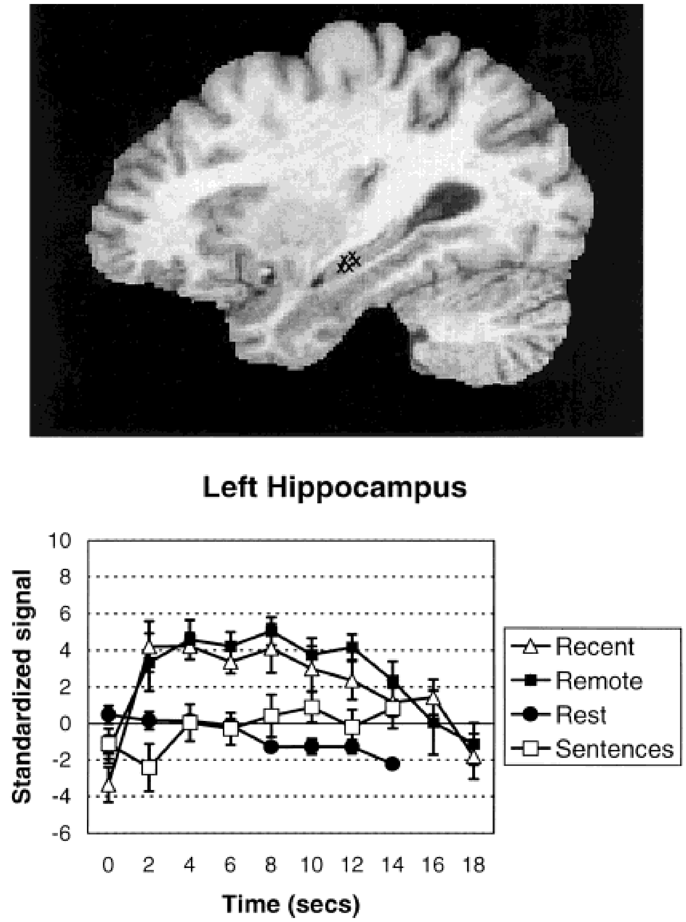

FIGURE 1. Mean (SEM) activation in left hippocampus over a 20-s time period for four conditions: recollection of recent events, recollection of remote events, sentence completion, and a rest period. Data are averaged across six subjects showing activity in the right hippocampal region. Sagittal section shows center of activation (X) for each of the six subjects.

RESULTS

For brevity, only results involving the hippocampal region are described here in detail. First, comparing recollection of all events (recent and remote combined) to either the rest period or the sentence completion task indicated that all 7 subjects showed significant hippocampal activation, 5 bilaterally, 1 in the left hippocampus only, and 1 in the right hippocampus only. Importantly, a direct comparison between recent and remote events yielded no significant differences in hippocampal activation for any subject. Combining data across subjects, the magnitude of hippocampal activation for recent and remote events was greater than either the relax condition or the sentence completion task, and activation did not differ depending on the age of the recalled event. The hippocampus was equally active during the recollection of remote events as it was for recent events, despite the fact that the remote events occurred 20–45 years prior to the scanning session (see Figs. 1, 2). No other regions of the hippocampal complex were activated reliably by retrieval of autobiographical memories. These results are inconsistent with the standard model of memory consolidation, which posits that memories become independent of the hippocampus as they age.

Although subjects were free to produce recent events that had occurred within the last 4 years, 75% of the events occurred within the last 2 years (mean age, 1.4 years; SD, 0.8), while the average age of remote events was 35.5 years (SD, 4.8). Verbal reports of the participants' recollections indicated that they truly were retrieving a particular episode while they were in the scanner rather than recounting the scenario of a repeated event, such as vacations at a lake with the family. The participants' ratings of emotionality and vividness attested to their personal involvement in retrieving the event and to the richness of detail of their recollections (Table 1). We found little difference between recent and remote memories in the number of details and the vividness and emotionality of the events, except that subjects tended to report their recollection of recent events as being more vivid. The general lack of difference was likely due to the limited time (20 s) available for recollection in the scanner, since data collected in our laboratory and from other studies indicate that if more time is allotted, the number of details declines with age (Moscovitch et al., 1999). This lack of difference

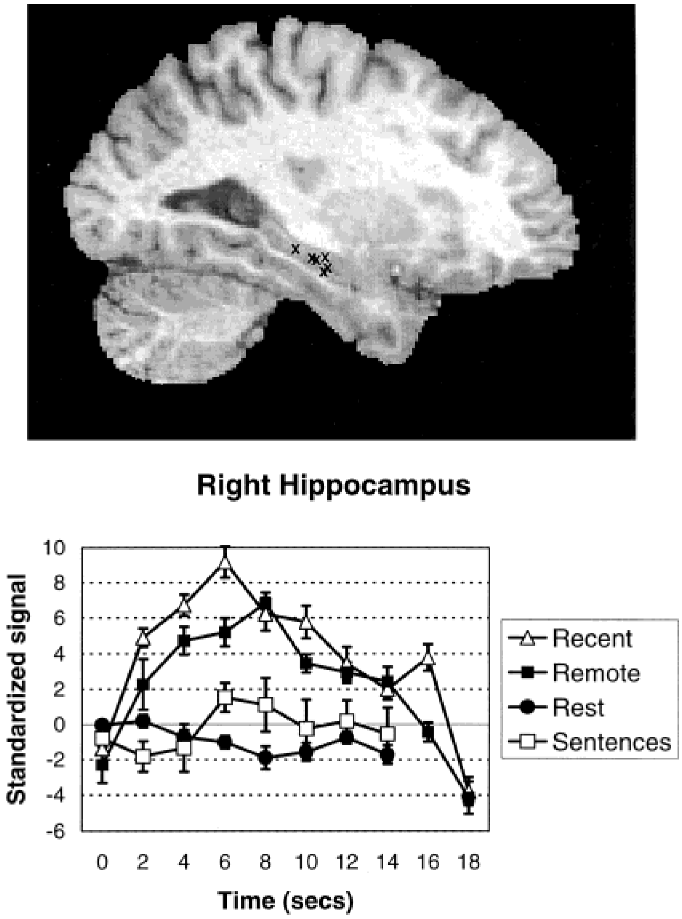

FIGURE 2. Mean (SEM) activation in right hippocampus over a 20-s time period for four conditions: recollection of recent events, recollection of remote events, sentence completion, and a rest period. Data are averaged across six subjects showing activity in the left hippocampal region. Sagittal section shows center of activation (X) for each of the six subjects.

is fortuitous. Otherwise, it would be difficult to attribute hippocampal activation to the age of the memories, rather than the number of details. Given the constraints of the study and its purpose, our data show that if similarly detailed memories are recovered from recent and remote time periods, hippocampal activation is also equivalent.

Other regions showing significant activation during recollection included the bilateral dorsolateral prefrontal cortex, anterior medial frontal cortex, posterior cingulate, bilateral anterior parietal lobe, right cerebellum, bilateral primary visual cortex, and (in 4 of the 7 subjects) thalamus (Table 2). Activation was significantly greater in these regions for recent and remote memories, compared to the rest condition and the sentence completion task. No region showed a significant difference in activation between recent and remote memories, possibly because the old and new events were so similar in attributes such as vividness and emotionality. Finally, the sentence completion task yielded significantly greater activation compared to recollection in the right and left inferior frontal gyri (Brodmann 44), left superior temporal gyrus (Brodmann 22), left middle temporal gyrus (Brodmann 21), and bilateral fusiform gyrus (Brodmann 37), all areas associated with language processes and reading.

We tested three additional subjects to control for the possibility that participants were recalling the brief exposure they had to the event cues just prior to scanning, rather than recalling the event itself. Instead of asking these subjects to identify events prior to the scanning session, cues were collected from the subjects' spouses, and were presented to the subjects only after entering the scanner. Recollection of the event followed immediately after presentation of the cue. In this way, subjects had no prior exposure to the cues or any way of knowing what events from their past they would be asked to recall. The only other difference in procedure was that subjects were not given the sentence completion task, so analyses were done comparing recent and remote event memories to each other and to the "rest" condition. The results of those analyses indicated that all three subjects, like the earlier group, showed significant bilateral activation in the hippocampus compared to the rest condition, consistent with the placement of activation shown in Figures 1 and 2. Again, direct comparison between recent and remote event recollection yielded no significant differences in hippocampal activation (Fig. 3).

DISCUSSION

The major finding of the study, that the hippocampus is activated equally during retrieval of recent and remote autobiographical memories, favors the alternative view derived from multiple memory trace theory (MTT) over traditional consolidation theory. According to this view, equivalent hippocampal complex activation can arise because the hippocampus is needed to retain and/or retrieve remote as well as recent autobiographical memories. There are, however, alternative interpretations that advise caution in en-

TABLE 1.

Mean (Standard Deviation) Ratings and Number of Details for Recent and Remote Events*

	Remote memories		Recent memories	
	M	SD	M	SD
Emotional valence (−3 to +3)	0.3	0.4	0.2	0.4
Arousal (0–6)	4.3	0.7	4.3	0.4
Importance (0–6)	4.4	0.5	4.7	0.6
Vividness (0–6)	4.5	0.6	5.1	0.6
Number of details	13.0	4.2	14.6	5.3

*Ratings were analyzed using a paired *t*-test in order to determine whether recent and remote memories differed. There were no differences between recent and remote for the valence, arousal, or importance of events ($P > 0.20$). However, there was a trend for new events to be more vividly recollected than remote events ($P = 0.06$).

TABLE 2.

Regions That Were Significantly Active in at Least 4 of 7 Subjects During Remote and Recent Memory Recollection When Compared to Rest Periods and the Sentence Completion Task*

	Talairach (x, y, z)			Brodmann	N
L middle frontal gyrus	−34	8	50	6	6
L middle frontal gyrus	−6	16	60	6	7
R superior frontal gyrus	6	16	54	6	7
L inferior frontal gyrus	−50	20	−1	47	6
R inferior frontal gyrus	50	20	19	45	4
L middle frontal gyrus	−25	40	30	9	4
L inferior frontal gyrus	−50	40	14	46	4
L superior frontal gyrus	−10	58	37	9	6
L superior frontal gyrus	−18	−4	59	6	5
L middle temporal gyrus	−60	−8	−4	21	4
L precentral gyrus	−52	−8	44	4	4
R precentral gyrus	48	−8	44	4	4
L hippocampus	−23	−20	−11	27	6
R hippocampus	25	−20	−12	27	6
L superior temporal sulcus	−51	−28	14	41	5
R pulvinar	14	−32	10		5
Posterior cingulate	5 to −5	−35	24	23	5
L fusiform gyrus	−28	−35	−11	36	4
L inferior parietal	−54	−35	21	40	6
L precuneus	−10	−55	15	23	7
R precuneus	14	−55	15	23	7
R lateral cerebellum	35	−65	−30		7

*Listed are the regions in Talairach coordinates and corresponding Brodmann areas, and the number of subjects with significant activity in the region (N). Coordinates are expressed in millimeters as in the brain atlas of Talairach and Tournoux (1988). x, medial-lateral axis (negative is left); y, anterior-posterior axis (negative, posterior); z, dorsal-ventral axis (negative, ventral); L, left; R, right.

dorsing this view over all others. We consider these interpretations in turn after describing briefly the MTT on which our alternative view is based.

According to MTT, the hippocampal complex always is needed for retention and retrieval of autobiographical memories (Nadel and Moscovitch, 1998; Moscovitch and Nadel, 1998; Nadel et al., 2000). When an autobiographical memory for some event from the past is reactivated, a new memory trace is created, which consists of an ensemble of hippocampal complex and neocortical neurons, and this proliferation of traces renders older memories less susceptible to disruption from brain damage than more recent ones. This mechanism provides a way of understanding the retrograde amnesia gradients sometimes reported after damage to the hippocampal complex, as well as the extensive memory loss for autobiographical events that occurred decades before injury. The extent and severity of retrograde amnesia and the slope of the gradient are related to the amount of damage to the extended hippocampal complex, which includes the hippocampus and adjacent neocortex. This applies only to autobiographical memory and perhaps to detailed memories of public events, personalities, and places. Remote memories for the gist of events, for familiarity with names and faces, and for personal and lexical semantics are

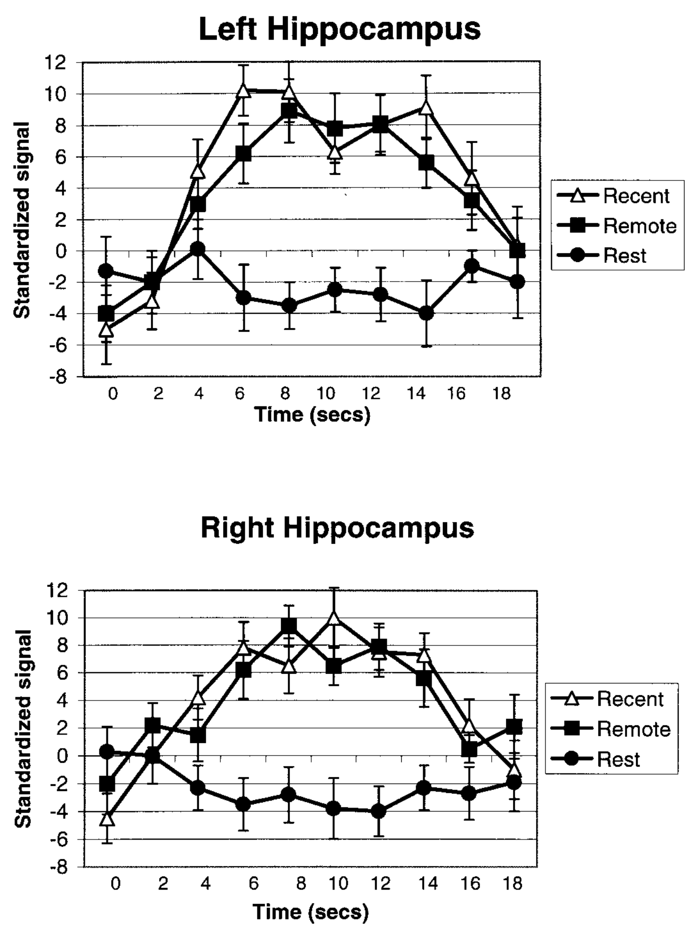

FIGURE 3. Mean (SEM) activations in left and right hippocampus for recollection of recent events, remote events, and rest, from three subjects who were unaware of the event cues that were to be presented in the scanner.

not similarly dependent on the continuing function of the hippocampal complex.

Although the present data support MTT, alternative interpretations are possible. For example, the hippocampal activation described here might be associated with the encoding of a very salient novel event, namely, the experience of the subject recalling old events within a new context (the MRI scanner), rather than with retrieval of the old events themselves. Indeed, MTT posits that each retrieval is accompanied by reencoding of the retrieved information (see Cohen and Eichenbaum, 1993). The greater hippocampal activation during recollection of autobiographical events than during sentence completion, however, suggests that the activation that was observed was related to retrieval rather than to encoding. While subjects were not explicitly instructed to remember the sentences, they were very good at recognizing the sentences afterwards (85% correct or greater). This finding suggests that activation within the hippocampus occurred, at least in part, because of the retrieval of autobiographical events and not solely because of new encoding or reencoding during the scanning experience. We note also that in studies in which other comparison tasks were used, such as retrieval of episodic memories pertaining to oneself (Maguire and Mummery, 1999), episodic memories pertaining to another person (Fink et al., 1996), or general semantic knowledge (Conway et al., 1999), activation was still greater in the hippocampal complex during recollection and recognition of remote autobiographical memories. Similarly, though the time scale was smaller than in our study, no differences in hippocampal activation were noted for material acquired just prior to scanning as compared to a week or 2 weeks earlier (Wiser et al., 2000; Stark and Squire, 2000). Despite this suggestive evidence, we concede that the case against the encoding interpretation would have been stronger had recollection of autobiographical events been compared, in our study, to encoding of complex pictures or other relational information, where hippocampal activation is likely to be more robust (Stern et al., 1996) than in sentence encoding. Until such a study is conducted, an encoding interpretation cannot be dismissed.

Another possible interpretation of our findings is that hippocampal activation is associated with the retrieval process itself, rather than specifically with reactivation of autobiographical memory traces. There is extensive evidence, however, from both the neurological (reviewed in Fujii et al., 2000) and neuroimaging literature (reviewed in Nyberg and Cabeza, 2000) that this statement cannot apply to all memories: retrieval of semantic information, whether personal, public, or lexical, is dependent more on the lateral temporal and prefrontal cortex than on the medial temporal lobes. If one takes the retrieval interpretation to mean that the hippocampus is always implicated in retrieval processes associated with autobiographical memories, as has long been asserted (Shallice, 1988; Warrington and Sanders, 1971; Warrington, 1996), then the view is not markedly different from the one based on MTT, though both are opposed to traditional consolidation theory. What distinguishes the retrieval view from MTT is that according to the former, the hippocampal complex acts only as a retrieval mechanism, whereas according to MTT, its neurons are also crucial constituents of an ensemble, including neurons from the neocortex and other structures that mediate the conscious experience of an event, and that together form the memory trace of that event (Moscovitch, 1995).

In addition to providing information about spatial context, the hippocampal component acts as a pointer to the other neurons of the ensemble that represent information about other aspects of the remembered event (Teyler and DiScenna, 1986). Although our experiment cannot distinguish the retrieval from the memory trace interpretation (in their present formulation, the two may be impossible to distinguish), our results are consistent with both. However, neither of the interpretations nor the results are compatible with consolidation theory, which does not assign a permanent role for the hippocampal complex, either in retrieval or as an integral component of the memory trace.

It is still possible to argue that the results we obtained are merely correlational, as are most neuroimaging data, indicating that hippocampal activation is associated with retrieval of both recent and remote memories, but that the hippocampal complex is needed only for the former. Put another way, one can argue that our data show that the hippocampus may play a role in retrieval of remote memories, but its contribution is not necessary. In cases of hippocampal dysfunction or damage, retrieval can be mediated by the neocortex alone. This position may be construed by some to be consistent with consolidation theory (Eichenbaum, personal communication), but this accommodation can be gained only at the expense of some of the basic assumptions of that theory. The modified view would hold that the hippocampal complex is needed to form, strengthen, and consolidate connections among disparate neocortical neurons. Once consolidation is complete, the hippocampal-neocortical links, though no longer needed, would still be maintained and activated during retrieval.

This hypothesis runs into a number of problems. It contradicts the idea, built into many models of consolidation, that the hippocampal memory system is temporary in a strict sense. Thus, Milner (1989) considered hippocampal-neocortical links to be "soft" in that they are easily and rapidly modified during acquisition and quickly lost during forgetting. Similarly, Alvarez and Squire (1994) incorporated this idea into their formal model and stated that the "learning rate and forgetting rate are greater by an order of magnitude for the connections between cortex and MTL than for the cortical-cortical connections." They subsequently stated, "A key feature of the model is that changes in the connections to and from the MTL area are fast and short-lasting" (Squire and Alvarez, 1995). In referring to the influential paper by McLelland et al. (1995) on consolidation, they correctly stated, "Temporary storage of information is accomplished by rapidly established and short-lived modifications within the hippocampal systems." Similar views were expressed by Paller (2000).

The idea that the hippocampal system is temporally limited is closely linked to the idea that it is also capacity-limited relative to the cortical system. One function of the relatively rapid decay of hippocampal connections that is built into many models is to free space in a limited-capacity system. Thus, it is necessary to shed old hippocampal-cortical connections so as to free hippocampal neurons to form new connections and support consolidation of new memories.

The modified consolidation hypothesis, and all that it entails, may account for the neuroimaging data we report in this study, but still remains vulnerable to data from lesion studies. According to this hypothesis, insofar as autobiographical memory is concerned, representations mediated by hippocampal-neocortical connections are similar to those mediated by neocortical-neocortical connections. Consequently, this hypothesis predicts that when remote memories are retrieved in cases of amnesia or memory impairment, the memories should be as detailed as memories retrieved with the aid of the hippocampus. Studies of remote episodic and spatial memory in people with hippocampal complex lesions have shown that some autobiographical memories are retained, but only if they were acquired decades earlier in childhood or adolescence (Reed and Squire, 1998), well beyond the time-frame initially postulated for consolidation to occur. Also retained are some spatial memories from that time which contain information about salient landmarks, routes, and direction, which are adequate for navigation (Teng and Squire, 1999). However, our own studies of amnesic patients indicate that even those very remote autobiographical memories are not as detailed as in normal subjects (Moscovitch et al., 1999; Viscontas et al., 1999). Using a refined measure of episodic memory that scored for the number of details that were recollected, we found persistent deficits extending back to very early childhood in severely amnesic patients and even in people with unilateral temporal lobectomies whose memory loss was mild by comparison. In addition, spatial memories lack information about environmental features that allow one to conjure up rich, spatial representations of a neighborhood (Rosenbaum et al., 2000). Thus, people with hippocampal complex damage may sometimes retain the gist of a memory but not its details (Reyna and Brainerd, 1995; Schacter et al., 1998; for similar arguments, see also Cipolotti et al., 2001).

As this discussion indicates, the case for MTT, supported by our neuroimaging data, is strengthened by evidence from studies of patients with medial temporal lobe lesions. The data from lesion studies are remarkably consistent: people with lesions that include the hippocampus and other portions of the hippocampal complex have a retrograde amnesia for autobiographical events that extends from at least a decade to a lifetime. The only inconsistency is found in the handful of studies on people with lesions restricted to the hippocampus proper, whose retrograde amnesia can vary from months to years (Fujii et al., 2000; Cipolotti et al., 2001). These lesion and neuroimaging data delineate the boundary conditions needed to account for the neuropsychological basis of remote memory. The lesion and neuroimaging data argue against the traditional view of the consolidation theory that states that neural connections between the hippocampal complex and neocortex are maintained only until consolidation is complete. To remain viable, consolidation theory would need to be modified drastically, as we noted, to explain the pattern of hippocampal and neocortical activation found in this study, and also the decades-long retrograde amnesia which sometimes has no temporal gradient that is observed in people with large medial temporal lobe lesions. For its part, MTT would have to account for the contributions of the various regions of the hippocampal complex to remote autobiographical memory. Both theories still need to explain differences between autobiographical and semantic memory in the pattern of memory acquisition and loss.

A similar picture in favor of MTT emerges from recent studies of memory consolidation in other species (Murray and Bussey, 2001). Riedel et al. (1999) found that when the hippocampus was temporarily inactivated 2 weeks after rats had learned the location of a hidden platform in a water maze, they could no longer find the quadrant in which the platform was located, but they showed that they remembered the gist of the experience by searching repeatedly in one of the wrong quadrants. Even when performance on a previously learned maze was preserved following hippocampal lesions made some time after training, as it was in another study (Kubie et al., 1999), the rats could not learn a new maze. The authors concluded that in the absence of the hippocampus, a less effective memory survived, one that could not support flexible behavior in space. These studies are important because they indicate that even when performance on remote tests of memory in rats is relatively preserved following hippocampal damage, closer analyses indicate that the type of memory that is retained may be different in crucial respects from one that is recovered when the hippocampus is intact.

In another study (Bontempi et al., 1999), imaging analyses of rats' brains were used to show that 25-day-old memories activated the cortex, whereas 5-day-old memories activated the hippocampus. The authors of this study used their results as support for the standard model of consolidation, but a closer look at their data suggests another interpretation. After 15 days it is indeed the case that hippocampal activation has greatly diminished, but it is also the case that performance is considerably reduced as well. This result suggests to us that at this retention interval the episodic detail has been lost, and this loss is reflected both in reduced performance and in diminished hippocampal activation.

Taken together with the present fMRI results and evidence from amnesic patients, these findings cast doubt on the view of the hippocampus as merely a temporary memory system,[2] with storage and retrieval of older, consolidated memories being dependent only on the neocortex. Instead, it appears that the hippocampus either is essential for the long-term availability of particular aspects of memory, namely, episodic detail (Tulving, 1983), or, at the very least, participates in the recovery of these memories. In the absence of the hippocampus, some aspects of memory can be retrieved, such as gist or semantic information gleaned from a specific event. But such retrieval will not reach the level of normal recollection that allows one virtually to reexperience an event.

[2]Two recent studies found results consistent with our findings, i.e., similar hippocampal activation with retrieval of remote or recent spatial (Nunn et al., 2000) and autobiographical (Conway et al., 1999) memories.

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