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The Spatiotemporal Dynamics of Autobiographical Memory: Neural Correlates of Recall, Emotional Intensity, and Reliving

Sander M. Daselaar[1,2], Heather J. Rice[1], Daniel L. Greenberg[1,3], Roberto Cabeza[1], Kevin S. LaBar[1] and David C. Rubin[1]

[1]Department of Psychology and Neuroscience, Duke University, Durham, NC 27708, USA
[2]Current address: Swammerdam Institute for Life Sciences, University of Amsterdam, Amsterdam, the Netherlands
[3]Current address: Department of Psychology, UCLA, Los Angeles, CA 90095, USA

We sought to map the time course of autobiographical memory retrieval, including brain regions that mediate phenomenological experiences of reliving and emotional intensity. Participants recalled personal memories to auditory word cues during event-related functional magnetic resonance imaging (fMRI). Participants pressed a button when a memory was accessed, maintained and elaborated the memory, and then gave subjective ratings of emotion and reliving. A novel fMRI approach based on timing differences capitalized on the protracted reconstructive process of autobiographical memory to segregate brain areas contributing to initial access and later elaboration and maintenance of episodic memories. The initial period engaged hippocampal, retrosplenial, and medial and right prefrontal activity, whereas the later period recruited visual, precuneus, and left prefrontal activity. Emotional intensity ratings were correlated with activity in several regions, including the amygdala and the hippocampus during the initial period. Reliving ratings were correlated with activity in visual cortex and ventromedial and inferior prefrontal regions during the later period. Frontopolar cortex was the only brain region sensitive to emotional intensity across both periods. Results were confirmed by time-locked averages of the fMRI signal. The findings indicate dynamic recruitment of emotion-, memory-, and sensory-related brain regions during remembering and their dissociable contributions to phenomenological features of the memories.

Keywords: affect, declarative memory, episodic memory, neuroimaging, recollection

Introduction

We view laboratory episodic memory and autobiographical memory as points on a continuum of complexity of memory for unique events. Autobiographical memory is more varied in its temporal and spatial context, emotions, visual imagery, relation to the self, and narrative structure (Cabeza et al. 2004; Rubin 2006). Here, we use autobiographical memory not only for its inherent interest and for its practical applications but also because it is uniquely well suited to functional magnetic resonance imaging (fMRI) research. The retrieval of an unrehearsed autobiographical memory in response to a word cue takes on the order of 10 s, which is much longer than most memory tasks, and results in interesting and complex memories that participants can easily maintain and elaborate for another 10 s. This allows an fMRI study to sample the whole brain many times while the memory is being accessed, and while the memory is being elaborated, and thus to map the time course of brain activations. Moreover, the variability in the time to access a memory is several seconds, which provides an inherent "jitter" between the time of the word cue and the accessing of the memory. Many spatially distributed areas are involved. Therefore, a technique, such as fMRI, which can scan a whole brain with a spatial resolution on the order of millimeters, is ideal. To take full advantage of fMRI to study autobiographical memory, we have participants press a button when they feel they have accessed a memory and use the time measured from this point in our analyses. Because autobiographical memories vary greatly on 2 key properties that have suggested neural bases, we measure, immediately after each memory, the degree to which memories are relived and the extent of their emotional intensity. We can thereby look for areas responsible for such judgments and describe when they are most active over the course of accessing and elaborating autobiographical memories.

We divide the introduction into a brief review of the neural networks involved in autobiographical memory retrieval. Then we provide sections on the spatiotemporal dynamics of autobiographical memory retrieval and of the modulation of these networks by the degree of reliving and emotional intensity of the resulting memories.

The Distributed Network Producing Autobiographical Memory Retrieval

The retrieval of autobiographical memories, that is, the remembering of personally experienced past events, is associated with processing in a distributed neural network (Rubin 2005, 2006; Svoboda et al. 2006), including the medial temporal lobe (MTL) (Eldridge et al. 2000; Daselaar et al. 2001; Gilboa et al. 2004; Squire et al. 2004; Greenberg et al. 2005), visual cortex (Wheeler et al. 2000), posterior parietal midline region (Henson et al. 1999; Shannon and Buckner 2004), and prefrontal cortex (PFC) (Moscovitch and Melo 1997; Buckner et al. 1998; Konishi et al. 2000; McDermott et al. 2000; Stuss and Levine 2002; Wheeler and Buckner 2004). Because autobiographical memories are episodic memories for contextually rich events, areas involved in sensory and emotional processing play additional roles during retrieval (Fink et al. 1996; Andreasen et al. 1999; Konishi et al. 2000; Markowitsch et al. 2000, 2003; Conway et al. 2003; Maguire and Frith 2003; Piefke et al. 2003; Addis et al. 2004; Cabeza et al. 2004; Fitzgerald et al. 2004; Greenberg et al. 2005; Keedwell et al. 2005; Rubin 2005), and their retrieval appears to preferentially recruit left lateralized regions (Conway et al. 1999; Maguire 2001; Piefke et al. 2003; Addis et al. 2004; Svoboda et al. 2006). However, most of the studies showing left lateralization used procedures in which participants also recalled the memories shortly before the scan. In contrast, neuropsychological studies tend to implicate right frontal areas (Kopelman and Kapur 2001). Moreover, during the prolonged retrieval of memories not recently accessed as done here, we might expect to see more effects of the right PFC because participants are attempting to access the memories for longer

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periods and such attempts extend retrieval mode (Tulving 2002; Velanova et al. 2003), which is right lateralized.

The Spatiotemporal Dynamics of Autobiographical Memory Retrieval

Much less is known about the time courses of retrieval-related activity than about its location, although a general anterior-to-posterior trend exists in electrophysiological data. Slow cortical potentials during the retrieval and maintenance of autobiographical memories exhibit a shift from primarily left frontal regions to posterior temporal and occipital regions (Conway et al. 2001, 2003).

It is difficult to distinguish the time courses of fMRI activity in different memory-related brain regions during many episodic memory tasks because the retrieval process occurs so quickly. However, autobiographical memories take much longer to retrieve than memories for items learned in the laboratory. In order to have enough time to separate the processes of access or retrieval from those of elaborating and maintaining memories, and to ensure variability in emotional intensity, in the present study, autobiographical memories were cued using the Galton/Crovitz technique (Galton 1879; Crovitz and Shiffman 1974; for reviews see Rubin 1982; Rubin and Schulkind 1997). Participants were asked to provide a memory of a specific past event for each of a series of generic cue words (e.g., "tree"). In contrast to procedures where individuals create their own personally tailored cue words (Maguire 2001; Greenberg et al. 2005), the retrieval process using the Galton technique takes significantly longer (typically >10 vs. 3 s) because the memories are not rehearsed with the cues prior to magnetic resonance imaging scanning.

By most behavioral, neural, and computational accounts, retrieving an episodic memory from a cue in order to perform a task requires that one memory be selected for retrieval and other competing memories be inhibited (i.e., one set of neural activations dominates). It is at this point that the recovery of a memory occurs, according to Tulving (1983). Next, the selected memory must be maintained and possibly elaborated long enough to perform the required task. Here, we call the earlier processes of finding one memory "memory access" to avoid other terms, which entail stronger theoretical claims. We call the later processes "elaboration" because our participants were asked to maintain and elaborate their memories. Operationally, we take the point when our participants indicate they have accessed a memory, via a button press, as the dividing point between processes that are mostly involved in accessing the memory and those that are mostly involved in maintenance and elaboration. Thus, by comparing activity before and after the button press directly to each other, we can distinguish brain regions primarily associated with memory access versus elaboration. We check the value of this operational definition by examining the activity of fMRI signals within regions of interest (ROIs) to see if they follow the expected time course.

According to current memory models, memory access includes the reactivation of distributed, stored memory traces, as well as the strategic operations sustaining retrieval search (Tulving 1983; Conway and Pleydell-Pearce 2000; Rugg and Wilding 2000; Moscovitch et al. 2005; Rubin 2005). The candidate regions for these processes are the MTL and right PFC. MTL is hypothesized to be critically involved not only in the formation but also in the reactivation of memory traces (Moscovitch 1995; Eichenbaum 2004; Squire et al. 2004). Right PFC has been linked to retrieval effort (Kapur et al. 1995; Wagner, Desmond, et al. 1998) and to the mental set that guides the retrieval of episodic information—known as retrieval mode (Velanova et al. 2003).

We expected that further elaboration of a memory involves imagery evoked by the retrieved episode, especially regions in the visual system (Greenberg and Rubin 2003; Rubin 2006), as well as controlled attentional and working memory operations related to selecting and keeping retrieved information active in mind. Accordingly, we predicted that the period after a memory was initially formed would be associated with activity in visual cortex regions, as well as the precuneus—a region associated with visual imagery during episodic retrieval (Fletcher et al. 1995). In addition, we predicted activity related to controlling the elaboration process, selecting relevant information, and maintaining this information online. In particular, the left PFC has been associated with cognitive control (Wagner et al. 2001; Buckner 2003), top–down attentional selection of visual information (Hopfinger et al. 2000), and working memory maintenance operations (e.g., Wager and Smith 2003).

The Spatiotemporal Dynamics of Reliving and Emotional Intensity

Two phenomenological properties have played a key role in distinguishing episodic memory retrieval from other forms of memory retrieval. The first property is the extent to which a memory is recollected (relived or reexperienced) as opposed to feeling merely familiar (Tulving 1983; Yonelinas 2001; Dobbins et al. 2002; Yonelinas and Levy 2002). Recollection is a necessary, defining feature of episodic memory, which is often expressed in terms of traveling back in time to relive the event (Tulving 2002). When recalling autobiographical memories for specific events rather than semantic knowledge, it is therefore assumed that some degree of recollection is always involved. To distinguish between degrees of reexperiencing an event, we evaluated ratings of reliving as a continuous phenomenological property of recollection. The ability mentally to time travel to reexperience past events is thought to depend on frontal lobe structures (Wheeler et al. 1997). Furthermore, activity in posterior cortices, especially visual areas (Kosslyn et al. 2001), should be involved in memories associated with a high degree of subjective reliving, as behavioral studies show that the best predictor of the degree of experienced reliving is visual imagery (Rubin et al. 2003; Rubin and Siegler 2004; Rubin 2006).

A second phenomenological property that is important in the retrieval of personal memories is emotional intensity (Talarico et al. 2004). A key question here is how the neural structures supporting emotion modulate memory retrieval. Several neuroimaging studies have shown that the extent of amygdala activation during the initial encoding of emotional pictures or film clips predicts subsequent retention (Cahill et al. 1996; Canli and others 2000; Kensinger and Corkin 2004), which is associated with functional interactions between the amygdala and the hippocampus during encoding (Hamann et al. 1999; Dolcos et al. 2004). However, much less is known about the amygdala's role in memory retrieval. Some episodic or autobiographical memory studies have reported amygdala activation in healthy subjects (Fink et al. 1996; Markowitsch et al. 2000, 2003; Maguire and Frith 2003; Greenberg et al. 2005), but some have not, even when emotions were specifically probed (Damasio et al. 2000; Piefke et al. 2003; Keedwell et al. 2005). Dolcos et al. (2005) found greater activity in and interactions between the

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amygdala and hippocampus for emotional than for neutral memory retrieval, especially for items whose memory was accompanied by a sense of recollection (see also, Sharot et al. 2004). Addis et al. (2004) showed that the hippocampus and amygdala were modulated during retrieval by ratings of emotional intensity. However, in this study, the amygdala effects were subthreshold when considering autobiographical memories that occurred only once (as opposed to repeated events).

The question of when, during the process of retrieving and maintaining an episodic memory, reliving and emotion have their effects is much less well understood. Behavioral studies have indicated that these 2 phenomenological aspects of autobiographical memories tend to be correlated (Talarico et al. 2004), but they may not arise at the same time nor in the same brain regions during recall. Because judgments of reliving are metacognitive judgments (Rubin et al. 2003) that occur behaviorally after the memory has been fully formed based on the quality of information retrieved, we expect the degree to which a memory is reexperienced to be evident in the brain only after the memory is retrieved and being held in mind to be judged.

For emotional intensity, 2 contrasting theoretical predictions exist. Similar to the argument for reliving, subjective ratings of emotional intensity may be made only about a fully formed memory, as emotion is an emergent property of that memory. This argument would follow from appraisal views of emotion (Lazarus 1991), if emotional intensity were not an inherent part of the memory but a judgment made on a memory after it was recovered (James 1890). The contrasting view, which has more support from neurally based studies, is that emotion is an early warning system, a way of preparing the organism for action that is generally appropriate for the situation at hand even before the situation is fully comprehended (Leventhal and Scherer 1987; LeDoux 1996). If one purpose of episodic memory is to provide a detailed record of events that occur under similar cuing situations so an organism can act appropriately, then activity in emotional areas of the brain could occur very early in the retrieval process to signal that a relevant memory is being retrieved before the full complexity of the memory is assembled and in consciousness. Bartlett postulated a similar early role of emotion during the act of remembering: "When a subject is being asked to remember, very often the first thing that emerges is something of the nature of an attitude. The recall is then a construction, made largely on the basis of this attitude, and its general effect is that of a justification of the attitude," where for Bartlett attitude is "very largely a matter of feeling, or affect." (Bartlett 1932/1995).

Thus, although little is known directly about the time course of the phenomenological properties associated with the retrieval of episodic memories, the existing literature allowed us to formulate clear hypotheses about when, and in broad terms where, the effects of the degree of reliving and of emotional intensity should occur. Because metacognitive judgments of reliving depend on the reexperiencing of a memory, they should occur after the button press that indicates that the memory is retrieved, and they should include activity in frontal areas related to recollection and self-reference and visual areas needed to support reliving judgments. The best-supported hypothesis for the effect of emotional intensity is that it will occur in the amygdala and hippocampus as the memory is being formed during the retrieval stage. However, there is also the possibility, though less well supported, of late effects of emotion modulation during memory maintenance and elaboration.

Much is known about the localization of the network involved in autobiographical memory retrieval. Here, we add to this existing knowledge by examining the time course of activation in that network and how it is modulated by the sense of reliving and emotional intensity of the resulting memories. We expected more MTL and right PFC activity when the memory was being accessed and constructed (i.e., before the key press), and more visual cortex, precuneus, and left PFC activity during the subsequent elaboration and maintenance of the memory (i.e., after the key press). We expect that the degree of reliving will modulate frontal areas related to recollection and self-reference as well as visual areas and will do so after the key press, and that emotional intensity will modulate the amygdala before the key press, though there is some support for effects after the key press.

Materials and Methods

Participants

The results of 17 healthy young adults (10 females; age range 18–35) were included in the analyses. All participants were right handed and were negative for histories of psychiatric illness, neurological disorder, and drug abuse. The Institutional Review Board at Duke University Medical Center approved the protocol for ethical considerations. Participants gave written informed consent prior to participation.

Materials

Word cues were chosen from a database of 125 word cues previously shown to elicit autobiographical memories (Rubin 1980). The 80 word cues that most consistently led to the retrieval of an autobiographical memory in 24 additional participants in a behavioral pilot study were selected. These 80 words comprised the final test list used in the scanner. Ten additional words were chosen from the database to create a practice list. Auditory word cues were recorded.

Procedure

The basic procedure was adapted from Greenberg et al. (2005). Because of the importance of visual imagery in autobiographical memory, participants were scanned with eyes closed, and all instructions were given auditorily (including presentation of the memory cues and rating scales), so that any potential effects of visual imagery were not confounded by requirements to visually attend to external task-relevant stimuli. Participants were presented with 80 auditory single-word cues, via headphones, while in the scanner. Within each of 8 runs, 10 cue words were presented in a pseudorandom order, each for a duration ranging from 0.65 to 1.25 s. Twenty-four seconds following stimulus onset, participants heard an instruction to rate the emotional intensity (the words "rate emotion") and an instruction to rate the degree to which they felt they were reliving the events (the words "rate reliving") on 4-point scales (1 = low, 4 = high). These instructions were presented in a pseudorandom order 4.5 s after one another and were followed by a 4.5- or 6-s break between trials, resulting in single-trial durations of 28.5 and 30 s. Participants made all responses via a button box held in their right hand. Participants completed a practice run during acquisition of anatomical scans to ensure task comprehension. Total scan time for each session, including acquisition of anatomical scans, was approximately 70 min.

Participants were given the following instructions. First, after hearing a cue word, they should think of a memory of a specific event from their life related to that word. Memories did not have to be directly related to the cue word; events tangentially related or retrieved through free association with the word were considered valid. When they recalled a specific event, they should push a button on the response box and continue thinking about the memory for the rest of the trial. They should not press the response button until they felt they had fully retrieved a memory but additional information could come after the button press. Second, when they heard the cue rate emotion, they should rate the emotional intensity of the memory using the 4 buttons

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on the response box. They should rate the current intensity, rather than rating how intense the emotion was during the initial event. Third, when they heard the cue rate reliving, they should rate how much they feel they are reliving the initial event again using the 4 buttons on the response box. Fourth, participants were instructed to keep their eyes closed for the duration of each run. At the end of each run, participants heard an instruction to rest and to open their eyes.

Scanning Parameters

Magnetic resonance images were acquired with a 1.5-T General Electric Signa Nvi scanner (Milwaukee, WI) equipped with 41 mT/m gradients. The participant's head was immobilized using a vacuum cushion and tape. The anterior commissure (AC) and posterior commissure (PC) were identified in the midsagittal slice of a localizer series. Thirty-four contiguous slices were prescribed parallel to the AC–PC plane for high-resolution T_1-weighted structural images (repetition time [TR] = 450 ms, echo time [TE] = 20 ms, field of view [FOV] = 24 cm, matrix = 256^2, slice thickness = 3.75 mm). Inverse spiral images sensitive to blood oxygen level–dependent contrast were subsequently acquired using the same slice prescription as the T_1-weighted structural images (TR = 1.5 s, TE = 35 ms, FOV = 24 cm, matrix = 64^2, flip angle = 90°, slice thickness = 3.75 mm, thereby producing 3.75 mm^3 isotropic voxels).

Preprocessing and Data Analysis

Statistical Parametric Mapping software implemented in Matlab (SPM2; Wellcome Department of Cognitive Neurology, London, UK) was used. After discarding initial volumes to allow for scanner stabilization, images were slice-timing corrected and motion-corrected, then spatially normalized to the Montreal Neurological Institute template, and spatially smoothed using a Gaussian kernel of 8 mm full-width half-maximum. Finally, treating the volumes as a time series, the data were temporally smoothed using 3-point filtering and cubic detrending options integrated in Matlab 6.5.

Standard GLM Analysis

To account for the fact that we used a self-paced paradigm in which participants indicated by themselves when they recalled a specific event, we implemented a flexible fMRI design in the context of the general linear model (GLM). The design distinguished 6 components in each trial—4 transient and 2 sustained components. Transient components included the memory cue (immediately at onset of the trial), response-related decision processes (750 ms before the response indicating a memory was recalled), and the 2 ratings (second and third response). Sustained periods included the memory access period (from trial onset to response) and the elaboration period (from response to the first rating). The transient periods were modeled by convolving a canonical hemodynamic response function with a vector representing period onsets, whereas the sustained periods were modeled with a boxcar function representing both period onsets and offsets (see Fig. 1*A*). In order to account for differences in the timing of activations due to the self-paced design, the response indicating a memory was accessed determined the duration of the memory access period as well as the onsets of the response and elaboration periods. To identify activation differences between the memory access and elaboration stages, the parameter estimates (beta weights) for the memory access and elaboration regressors were directly compared using paired *t*-tests at an uncorrected threshold of $P < 0.001$ and a minimum cluster size of 3 adjacent voxels.

Parametric GLM Analysis: Rating Scales Modulation

Within the aforementioned GLM analysis, each of the transient and sustained trial components were additionally modulated parametrically by the 2 ratings, reliving and emotional intensity, using the first-order parametric modulation option integrated in SPM2. To identify brain regions that show modulation of memory access or elaboration activity associated with the 2 ratings, we applied random effects analyses on the parameter estimates of the parametric regressors using the same threshold as for the standard GLM analysis ($P < 0.001$, cluster size = 3).

Time Course Analysis: Cue-locked Analysis

To assess the validity of our flexible fMRI design, we investigated the time courses for fast and slow responses with respect to the self-paced button press indicating that a memory was formed. As a first step, we selected a subgroup of participants showing an adequate range of fast and slow responses. Employing a minimum cutoff of 10 trials with a 3-s range in the response times, we found a group of 8 participants that had sufficient trial numbers to allow a direct comparison between bins of fast (9–12 s) and slow (12.01–15 s) responses. Second, a GLM was created in which trial onsets time locked to the cue were modeled with a finite impulse response basis set of peristimulus time bins of 1.5 s duration (equal to the TR). The resulting parameter estimates were subsequently averaged for each peristimulus time bin, yielding estimates of fMRI signal change across the whole 33 s trial period for both fast and slow bins. Finally, for the actual validation, we used a ROI approach, focusing on perceptual/motor regions. The clusters showing significant ($P < 0.001$, cluster size = 3) cue-related activity in the auditory cortex or response-related activity in the motor cortex based on the GLM analysis were defined as ROIs. Following the fMRI model depicted in Figure 1*A*, we predicted that cue-related activity should not be modulated by response time, whereas the peak of response-related activity should shift depending on whether it was a fast or a slow response.

Time Course Analysis: Response-locked Analysis

To further evaluate the results from the standard GLM analysis, we conducted a second time course analysis using the same procedures as for the cue-locked analysis, but, in this case, time locked to the response and including an additional period 4.5 s before the button press that indicated a memory was accessed. Thus, for this particular analysis, only trials in which the button press occurred within 4.5 s were excluded, so that virtually all the trials from all 17 participants could be included in the response-locked analysis. Based on the model depicted in Figure 1*A*, we predicted that at the onset of the response component, the time courses of regions associated with memory access should be on a downward slope, whereas regions associated with elaboration should be on an upward slope.

Time Course Analysis: Rating Scales Modulation

To validate the parametric modulation analysis, we conducted 4 additional time course analyses time locked to the cue. For each individual subject, we used a median split of the emotional and reliving ratings in order to generate 4 separate fMRI time courses: high and low emotion and high and low reliving.

Results

Behavioral Data

Participants were able to recall an event matching the cue on 90.5% (standard deviation [SD] = 5.3) of the trials. The average ratings of reliving and emotional intensity on a scale of 1–4 were 2.50 (SD = 0.43) and 2.28 (SD = 0.40), respectively. The mean reaction time from the cue to the button press indicating the formation of a memory was 12.25 s (SD = 3.68). Participants were faster for memories that were later rated as high in reliving and high in emotional intensity as measured using a median split of the ratings for each participant, a division we use later in the fMRI analyses. The mean time for high and low reliving were 11.12 s (SD = 0.95) versus 10.32 s (SD = 1.23); for emotional intensity, they were 11.12 s (SD = 0.89) versus 10.14 s (SD = 1.44). The reaction times for the first and second ratings on each trial were 2.24 s (SD = 0.18) and 2.53 s (SD = 0.22), respectively.

Model Validation: Cue-locked fMRI Time Course Analysis

To assess the validity of our flexible fMRI design, we performed a cue-locked time course analysis in which fast (9–12 s) and slow (12.01–15 s) responses for the button press (indicating a memory was formed) were modeled separately. Based on the model depicted in Figure 1*A*, we predicted that cue-related activity (red line) in the auditory cortex should not be modulated by response time, whereas the peak of response-related

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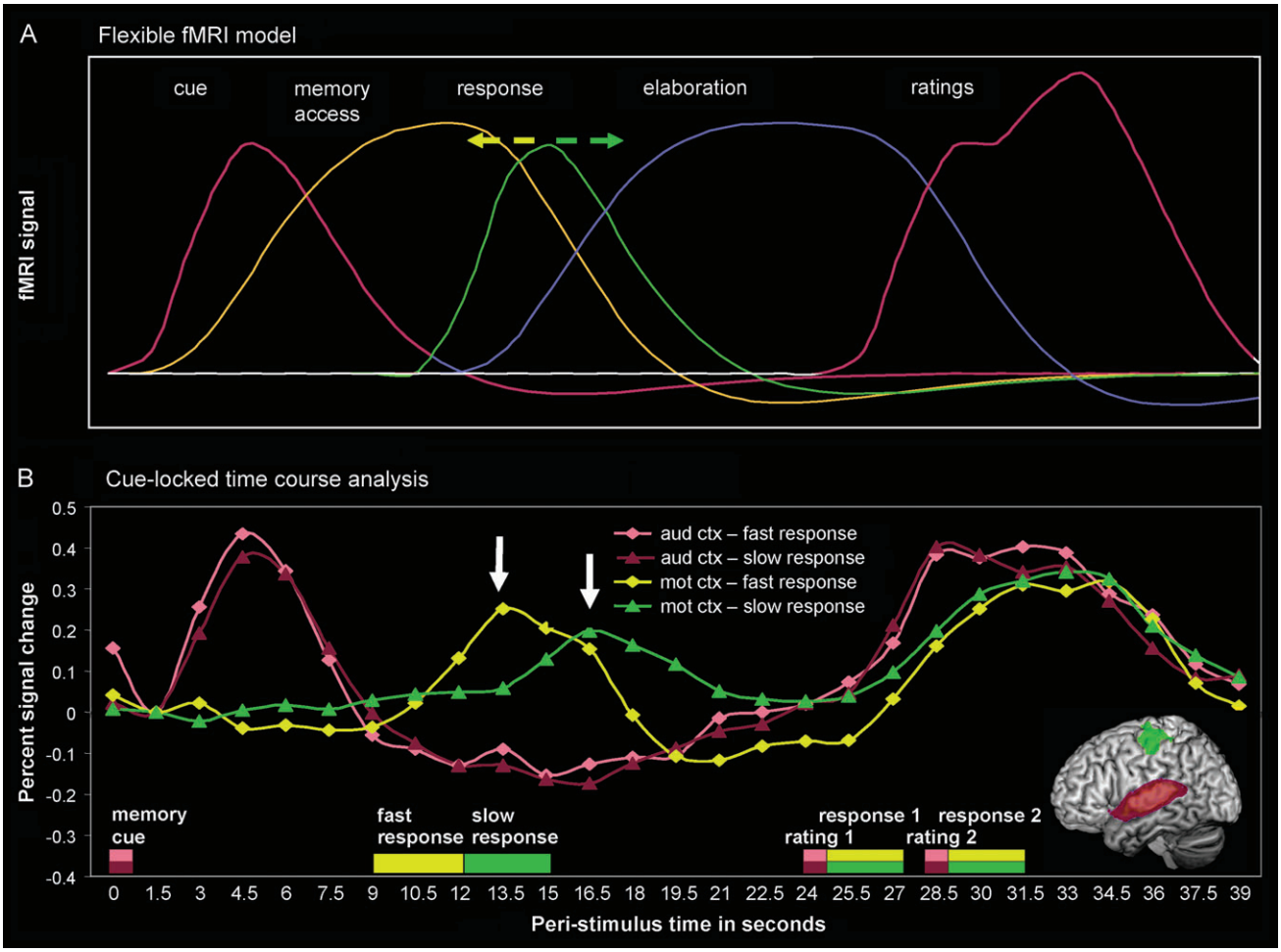

Figure 1. (*A*) The design distinguished 6 components in each trial: the auditory memory cue (left part of red line), the memory access period (yellow line), the response indicating a memory was accessed (green line), the elaboration period (blue line), and the 2 auditory rating cues (right part of red line). As indicated by the arrows, the response time determined the onset of the response component, as well as the offset of the retrieval period, and the onset of the elaboration period. (*B*) Time courses for fast and slow responses were almost identical in the auditory cortex (aud ctx, red lines) but very different in the motor cortex (mot ctx, green lines). The difference in peak latency in the motor cortex (white arrows) matches the 3-s time difference that existed between the fast and slow responses.

activity (green line) in the motor cortex should shift depending on whether it was a fast or a slow response. The results confirmed our predictions. As shown in Figure 1*B*, the time courses for fast and slow responses were almost identical in the auditory cortex (red lines) but very different in the motor cortex (green lines). In particular, there was a large difference in the peak latency corresponding to 2 TRs. This latency difference matches the 3-s reaction time difference that existed between the fast and slow response bins. Yet, at the time that the rating cues are presented (24 s following trial onset), the time courses in auditory and motor cortices join together and show a double bump reflecting the 2 auditory cues and corresponding button presses. The correspondence of the time courses in Figure 1*B* corresponds well to the model depicted in Figure 1*A*, thus validating our approach.

Time Course Analysis: Response-locked fMRI Analysis

Table 1 lists, and Figure 2*A* displays, regions involved in memory access–related and elaboration-related activity. Consistent with our predictions, the memory access period elicited activations in MTL and right PFC regions. The MTL activation was found in the hippocampus, and the right PFC activations included ventrolateral and dorsolateral regions. In addition to these predicted regions, a strong activation was also found in the retrosplenial area of the posterior cingulate cortex. Turning to regions activated during the elaboration period, consistent with our predictions, they included visual cortex, precuneus, left PFC regions, and auditory cortex. The precuneus region was clearly more dorsal than the retrosplenial region associated with memory access. Left PFC activations included ventrolateral and anterior regions.

Confirmation of GLM Results: Response-locked Time Course Analysis

To confirm the results from the GLM analysis, we conducted a time course analysis that was time locked to the response and included a period of 4.5 s before the button press that indicated a memory was accessed. Based on the fMRI model in Figure 1*A*, we predicted a crossover dissociation between memory access–related activity, which should be on a downward slope at the time of the response, and activity associated with subsequent elaboration, which should be on an upward slope. For use as a reference, we extracted the response-locked time course from the motor cortex (green line in the middle graph of Fig. 2*B*). Again, the results confirmed our predictions. As shown in the top part of Figure 2*B*, the mean time courses of the regions

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Table 1
Brain regions associated with memory access and elaboration

Contrast	L/R	BA	Talairach			*t*-values
Region			*x*	*y*	*z*	
Access > elaboration						
Hippocampus	R	—	23	−15	−12	5.35
Retrosplenial ctx	R	29/30	4	−54	20	8.49
Right PFC	R	47	38	29	−14	7.73
	R	46	49	20	27	7.03
	R	9	8	60	28	7.31
	R	6	34	15	61	5.33
Medial PFC	R	10	4	44	−9	4.86
Anterior cingulate ctx	R	8/32	4	13	45	6.42
Cerebellum	L	—	−45	−57	−26	6.05
Elaboration > access						
Visual ctx	L	18/19	−38	−81	−2	5.51
	R	18/19	30	−81	−6	5.12
Precuneus	L	7	−26	−52	58	8.61
Left PFC	L	9	−45	21	41	9.01
	L	10	−42	44	−3	8.70
	L	44	−53	15	13	5.36
Parietal lobe	L	40	−49	−53	38	7.75
	R	40	38	−49	58	4.09
Auditory ctx	L	41/22	−41	−25	8	8.69
	R	41/42	60	−15	4	9.76

Note: BA = Brodmann area; ctx = cortex.

that showed memory access–related activity (i.e., hippocampus, retrosplenial cortex, and right PFC regions) are all on a descending slope at the onset of the motor response, whereas the time courses of the regions associated with elaboration (i.e., visual cortex, precuneus, and left PFC) are all on an ascending slope. The inflection point for these curves is at 1.5 s after the button press; measured in terms of hemodynamic response, this is 3 s before the peak of the motor response for the button press. Hence, the response-locked time course analysis confirmed the results from the standard GLM analysis.

Rating Scales Modulation fMRI Analysis

The brain regions indicated in Table 2 and Figure 3 were identified using a combined parametric model in which the 2 ratings, reliving and emotional intensity, were entered together as parametric regressors. In Table 2, we present all areas that had a *t*-value that was significant at the same $P < 0.001$ level used in Table 1. One area in the frontal pole was positively correlated with emotional intensity in the elaboration phase and also with emotional intensity at the $P < 0.005$ level in the memory access phase. With this exception, all other areas showed exclusive effects to only one of the 2 ratings and in only one period, with

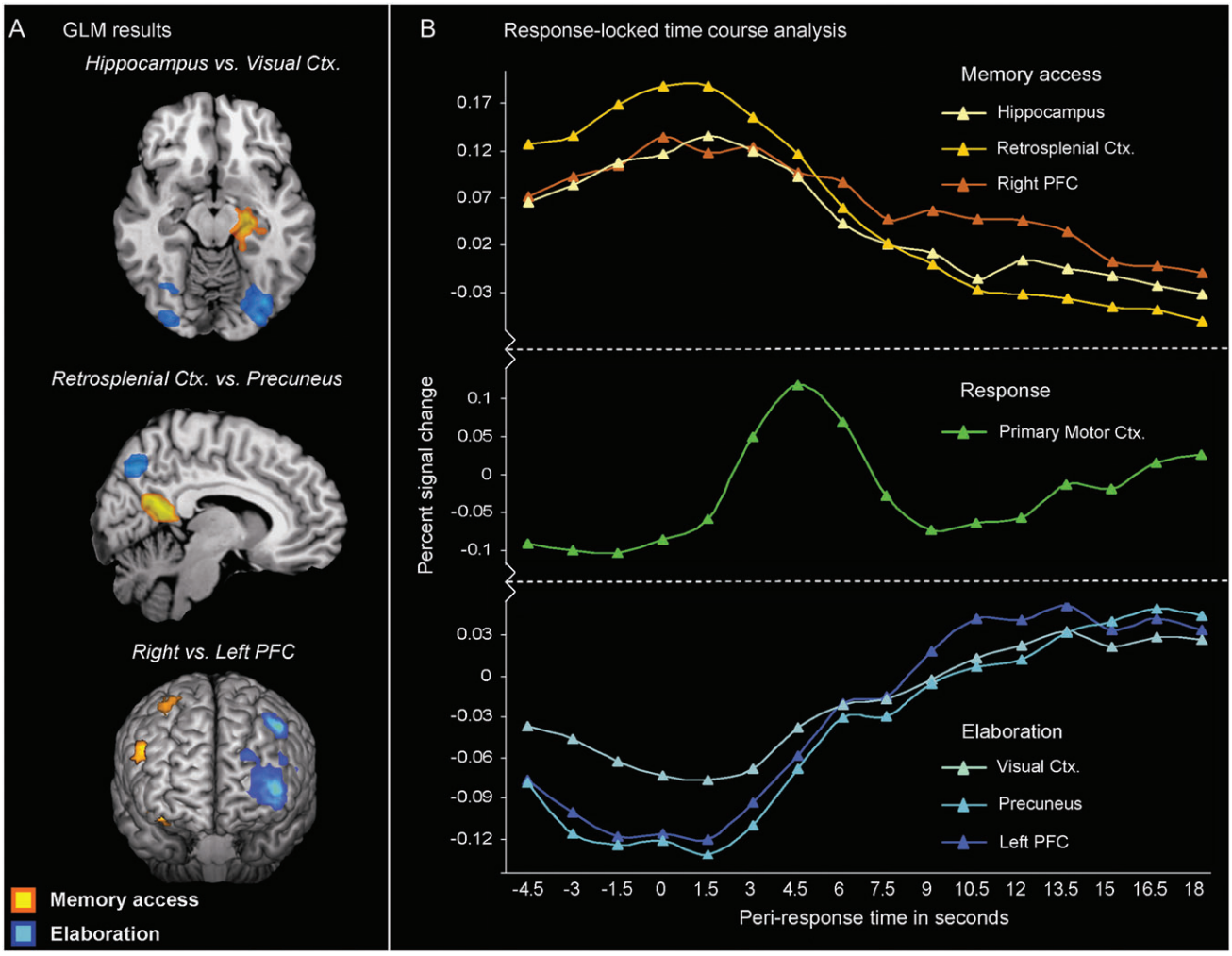

Figure 2. (*A*) Hippocampus, retrosplenial cortex, and right PFC showed greater activity during the retrieval period, whereas visual cortex, precuneus, and left PFC showed greater activity during the elaboration period. (*B*) Regions associated with retrieval showed a descending slope at the time the memory was accessed (top panel), whereas regions associated with elaboration showed an ascending slope (bottom panel). All plots are the average of the cluster. Response-related activity in the motor cortex is displayed as a reference (middle panel).

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the largest nonsignificant t being 1.95. It is also of note that, except for the conjunction area in the frontal pole, all significant positive t-values that came from the memory access period were modulated only by emotional intensity, and all that came from the elaboration period were modulated only by reliving. The negative effects of reliving in right dorsolateral PFC and insula regions during the access memory phase may reflect greater retrieval effort for memories associated with low reliving scores. This interpretation fits with fMRI evidence linking these regions to low-confidence memory decisions (e.g., Fleck et al. 2006). However, given that these negative correlations were not predicted, this interpretation is ad hoc. In summary, the subjective ratings of reliving and emotional intensity of autobiographical memory are temporally dissociable.

Table 2
Brain regions associated with parametric variation in ratings of reliving and emotion

Region	BA	Side	Talairach			Memory access		Elaboration	
			x	*y*	*z*	Reliving	Emotion	Reliving	Emotion
Memory access phase only									
Positive correlations									
Amygdala	—	L	−19	−5	−19	0.92	**4.00**	0.45	0.59
Hippocampus	—	L	−23	−26	−5	−2.21	**7.01**	0.23	−0.67
	—	R	26	−26	−11	−0.70	**4.16**	0.63	0.03
Somatosensory ctx	3	L	−41	−38	65	−1.43	**3.89**	0.00	2.33
	3	R	41	−30	47	0.09	**3.95**	1.47	1.95
Lateral temporal ctx	22	R	56	−52	−10	−1.25	**4.62**	−1.56	0.40
Putamen	—	R	26	−7	11	1.22	**4.49**	1.96	0.77
Negative correlations									
Dorsolateral PFC	6	R	49	−4	49	**−3.99**	1.88	1.07	0.32
Insula	—	R	38	−25	12	**−5.79**	−0.73	0.12	0.25
Superior temporal ctx	42	L	−64	−10	15	**−5.82**	0.91	−0.89	0.69
Elaboration phase only									
Positive correlations									
Visual ctx	19	R	23	−77	7	−0.54	1.18	**3.95**	0.79
Inferior PFC	47	R	52	26	−1	1.20	0.14	**5.15**	−0.72
Putamen	—	L	−15	4	−4	1.20	1.02	**6.79**	−0.08
Anterior cingulate	32	—	0	51	11	0.03	0.38	**6.35**	0.83
	32	R	4	33	−2	−1.19	1.72	**5.29**	1.21
Posterior cingulate	31	R	15	−43	27	1.50	0.20	**6.77**	−0.04
Access and elaboration									
Frontal pole	10	R	23	60	11	0.32	3.25	2.38	**3.72**

Note: All activations with $P < 0.001$ are shown in bold; $t > 1.75$, $P < 0.05$; $t > 2.58$, $P < 0.01$; $t > 2.92$, $P < 0.005$; $t > 3.69$, $P < 0.001$. BA = Brodmann area; ctx = cortex.

Emotional intensity during the retrieval period was parametrically associated with activity in the temporal lobe (amygdala, hippocampus, and lateral temporal cortex), putamen, PFC (superior frontal gyrus and frontopolar cortex), and parietal lobe (inferior parietal lobule and somatosensory cortex). These results support the hypothesis of an early contribution of emotion during the memory retrieval process, including the engagement of 3 regions important in current neurobiological theories of emotion—the amygdala, somatosensory cortex, and frontopolar cortex—as well as canonical memory-related regions (e.g., the hippocampus). The sense of reliving during online maintenance and elaboration of autobiographical memories was parametrically associated with activity in the right inferior and medial PFC, cingulate gyrus (both anterior and posterior subdivisions), extrastriate cortex, cerebellum, thalamus, and brain stem. Activity in the extrastriate cortex (and possibly posterior cingulate cortex) supports our a priori hypothesis of a role of visual imagery during the subjective reliving of autobiographical memories. Because the frontopolar cortex was the only brain region equally sensitive to emotional

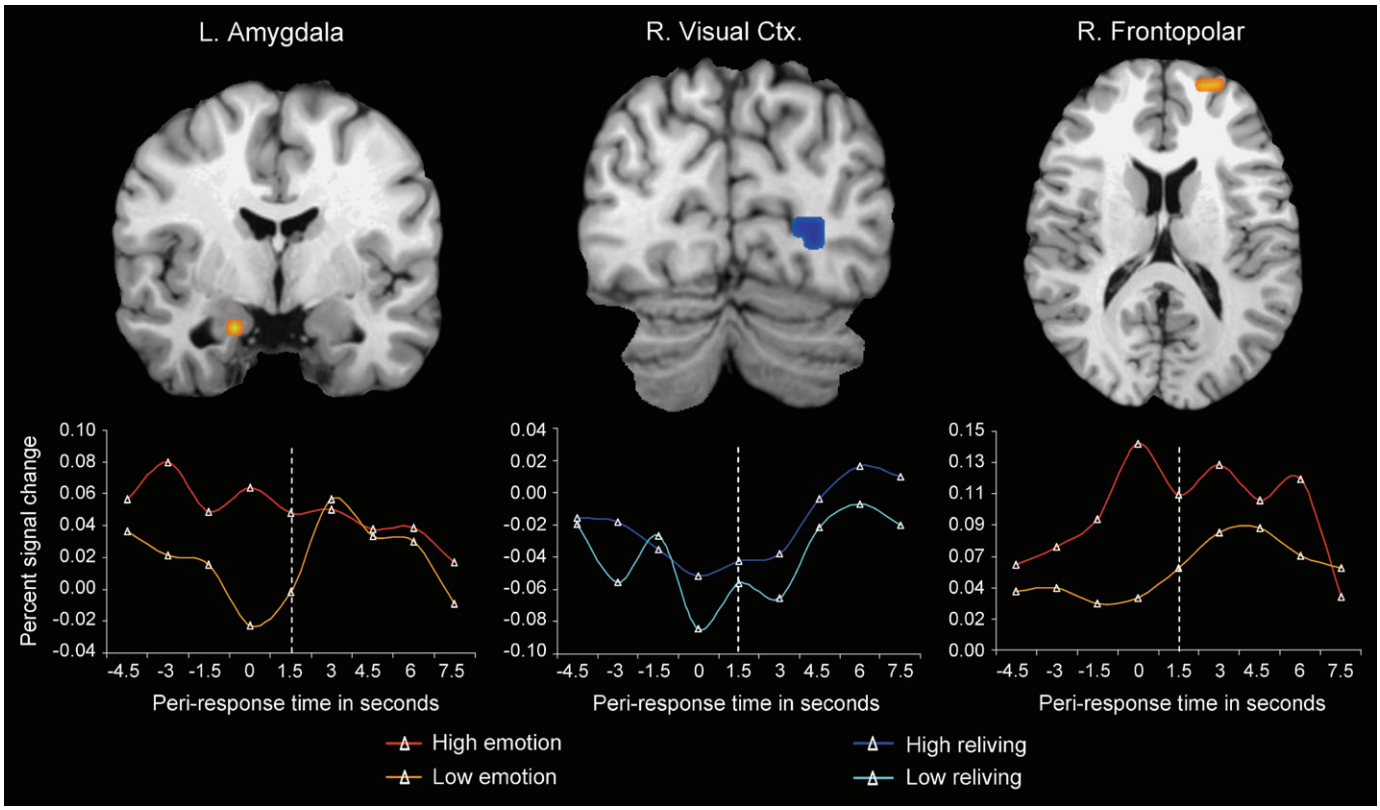

Figure 3. The time course high versus low ratings of emotional intensity and reliving in 3 areas. The plots are for the maximum value. The vertical dotted line shown at 1.5 s marks the inflection point of areas showing increased and decreased activity in Figure 1.

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intensity during both the memory access and elaboration phases, it may serve to maintain emotional representations online as a form of affective working memory during autobiographical recall.

Although the time course analysis based on modulation by the rating scales is a bit noisier than that based on activity, Figure 3 supports the claims of the GLM analyses. To produce this figure, we did a median split for high versus low ratings for each participant and plotted 4 TRs on either side of the 1.5-s post button-press time that was the inflection point for activity in Figure 2. The plots clearly support the analysis shown in Table 2. High emotional intensity ratings produced more activity in the amygdala than did low ratings during the access phase, but not during the elaboration phase. In the right frontal polar area, the emotional intensity effects persisted over both phases. In contrast, high reliving ratings produced more activity in visual cortex from the elaboration phase but not during the access phase.

Discussion

Taking advantage of the protracted time course of autobiographical retrieval, we were able to dissociate brain regions involved in the early and late aspects of remembering personally experienced past events. Initial accessing of memories engaged hippocampal, retrosplenial, and right PFC regions, whereas later elaboration recruited visual cortex, precuneus, and left PFC regions. Online reliving-modulated activity was observed during the elaboration phase in visual cortex, right inferior PFC and the anterior and posterior cingulates. Emotion-modulated activity was observed during the initial retrieval process in the amygdala, hippocampus, somatosensory cortex, and lateral temporal cortex. Thus, our 2 ratings were parametrically associated with activation in different areas of the brain at different time periods, providing both spatial and temporal dissociations. We discuss these results in more detail in the following 3 sections.

Accessing Memories: Hippocampus, Retrosplenial Cortex, and Right PFC

During the first half of each trial, while participants reconstructed a memory of a personal event, the activated brain regions included the hippocampus, the retrosplenial cortex, and the right PFC and medial PFC. The hippocampus showed greater activity during the memory access than during the elaboration period (Fig. 2*A* top), and its time course was on a descending slope at the time participants made a response indicating the end of the memory access period (Fig. 2*B* top). The finding that the hippocampus is involved in memory access operations fits well with evidence from ensemble recording (Hoffman and McNaughton 2002), event-related fMRI studies (Daselaar et al. 2004; Prince et al. 2005), and neuropsychology (Squire et al. 2004; Moscovitch et al. 2005) indicating that MTL is involved in not only the formation but also the reactivation of memory traces. Furthermore, our results provide further support for the critical role of the hippocampus in conscious memory processes (Schacter et al. 1996; Eldridge et al. 2000). Yet, at the same time, our findings show that, although the hippocampus is involved in accessing conscious memories, elaboration of the memories depends on sensory processing regions such as the visual cortex.

Like the hippocampus, the retrosplenial cortex also showed greater activity during memory access than during elaboration (Fig. 2*A* middle) and a time course with a descending slope at the time of the transition from memory access to elaboration (Fig. 2*B* top). The finding that both the hippocampus and the retrosplenial cortex are associated with memory access is in line with clinical evidence showing that damage to the retrosplenial cortex results in memory deficits similar to those following damage to the MTL (Valenstein et al. 1987). This finding is also in line with the strong anatomical connections that exist between these 2 regions (Kobayashi and Amaral 2003). Moreover, in addition to the hippocampus, the retrosplenial cortex also sends dense projections to the anterior thalamic nuclei, which in turn plays a critical role in episodic memory function. Damage to this region results in diencephalic amnesia, and the anterior thalamic nuclei also receive massive hippocampal input (Shibata and Yukie 2003; Van der Werf et al. 2003). In view of these clinical and anatomical findings, it has been suggested that the retrosplenial cortex is an essential node in the communication between the thalamus and the hippocampus (Kobayashi and Amaral 2003; Shibata and Yukie 2003). However, the exact functional coupling between these regions remains a question for future research.

Memory access was associated with right PFC. This region showed greater activity during the memory access than during elaboration (Fig. 2*A* bottom) and a descending time course at the time of the button press (Fig. 2*B* top). Early positron emission tomography (PET) studies already highlighted the importance of right PFC in episodic retrieval processes. Based on their PET findings, several researchers proposed that right PFC is involved in retrieval mode, the sustained mental set, which is entered into when episodic memory retrieval is required (Tulving 1983; Kapur et al. 1995; Nyberg et al. 1995). A recent fMRI study that distinguished between transient and sustained responses during retrieval provided support for the retrieval mode hypothesis. Whereas left PFC regions showed a transient response fluctuating on a trial-by-trial basis, right PFC showed sustained activity over trials (Velanova et al. 2003). In contrast, other studies have found transient responses in right PFC during episodic retrieval. For instance, right PFC activity has been found to be modulated by trial-by-trial changes in confidence ratings (Henson et al. 2000; Fleck et al. 2006). The current finding of a transition "within trials" from right to left PFC also does not fit with a sustained role of right PFC in retrieval mode, but rather suggests a more transient role in strategic retrieval operations. However, it should be noted that our analyses did not specifically target sustained activity over trials, leaving open the possibility that sustained and transient retrieval activations involve different subregions of the right PFC.

Finally, memory access was associated with medial PFC, an area that is commonly observed in tasks requiring self-referential processing (e.g., Craik et al. 1999; Gusnard et al. 2001; Kelley et al. 2002). For example, one such study asked participants to decide whether a scene was pleasant versus unpleasant (self-referential) or the scene was indoor versus outdoor (non self-referential), finding more medial prefrontal activity during the pleasant/unpleasant task (Lane et al. 1997). More recent studies have suggested it is not reference to one's self per se driving this region, but more broadly, reference to internally generated information, including one's thoughts or feelings at encoding (e.g., Simons et al. 2005). Another explanation is that this area is involved in a collection of processes including: decision making under uncertainty, control processes providing a "feeling of rightness" and the processing of self-referential information that combine to monitor the veracity of autobiographical memories

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(Gilboa 2004). Both explanations are is consistent with the results of a previous fMRI study in which we found medial prefrontal activity to be greater for autobiographical memory retrieval than for laboratory memory retrieval (Cabeza et al. 2004).

Elaboration of Retrieved Events: Visual Cortex, Precuneus, and Left PFC

During the second half of each trial, while participants maintained personal episodes in working memory, the regions most activated included visual cortex, precuneus, and left PFC. The visual cortex region showed higher activity during the elaboration period than during the retrieval period (Fig. 2*A* top), and its time course was on an ascending slope at the time of the button press indicating the transition from retrieval to elaboration (Fig. 2*B* bottom). The finding that the visual cortex is involved in the elaboration of autobiographical memories is in line with behavioral (Johnson et al. 1988; Rubin et al. 2003), neuropsychological (Greenberg and Rubin 2003), and neuroimaging data (Cabeza et al. 2004) indicating that visual information constitutes a fundamental component of autobiographical memories. Furthermore, the finding that the visual cortex was active during retrieval in the absence of visual stimulation (because our participants had their eyes closed) is in line with fMRI studies showing that sensory regions that are active during encoding of perceptual information are reactivated during retrieval of the same information (Wheeler et al. 2000; Kahn et al. 2004; Prince et al. 2005). In general, our findings confirm the view that the visual cortex plays a key role in autobiographical memory retrieval (Rubin 2005, 2006).

Elaboration also engaged the precuneus. This region showed greater activity during the elaboration period than during the memory access period (Fig. 2*A* middle) and showed an ascending time course after the memory was accessed (Fig. 2*B* bottom). The precuneus is one of the regions most frequently activated during episodic retrieval tasks (Cabeza and Nyberg 2000a). Yet, the role of this region remains unclear (Wagner et al. 2005). According to a popular view based on neuroimaging findings, the precuneus is involved in visual imagery processes during episodic retrieval (Fletcher et al. 1995; Cavanna and Trimble 2006). In support of this idea, activity in this region is greater during retrieval of imageable versus nonimageable words (Fletcher et al. 1995) and during retrieval of imagined versus viewed pictures (Lundstrom et al. 2003). This idea is further substantiated by the strong anatomical connectivity that exists between the precuneus and lateral parietal regions, suggesting a role in visuospatial functions (Kobayashi and Amaral 2003; Cavanna and Trimble 2006). The current finding that the precuneus, together with the visual cortex, was associated with elaboration further supports a role of this region in visual imagery processes during retrieval. Moreover, the finding of activations in perceptual, but not MTL, regions during elaboration fits with memory theories predicting that, once the memory is selected, MTL becomes less important and cortical–cortical coactivation begins to dominate (Damasio 1989; Alvarez and Squire 1994).

Finally, elaboration of personal memories recruited left PFC. This region also showed greater activity during the elaboration period than during the memory access period (Fig. 2*A* bottom) and a time course with an ascending slope after the memory was accessed (Fig. 2*B* bottom). Left PFC is commonly activated during successful item (Konishi et al. 2000; Daselaar et al. 2003) and associative recognition (Prince et al. 2005) memory tasks. Given the current results, this activity could well reflect elaboration of aspects of the study episode. In line with this idea, source memory tasks that require processing visuospatial aspects of recovered episodic information tend to engage left PFC regions (Nolde et al. 1998; Ranganath et al. 2000; Raye et al. 2000; Kahn et al. 2004). The finding that, in the current study, left PFC was associated with elaboration also fits well with fMRI evidence indicating a role of this region in working memory operations (Wager and Smith 2003) and attentional biasing of sensory regions (Hopfinger et al. 2000). Thus, based on findings from the episodic memory, working memory, and attentional literature, left PFC seems an obvious candidate for the top–down control and working memory operations necessary for the elaboration of recalled memories.

The Spatiotemporal Dynamics of Reliving

Participants in this study spent on the average about 12 s retrieving autobiographical memories to the point where they thought their memories were fully formed, followed by about 12 s of continuing to think about and elaborate the memories, as one would do when reminiscing or sharing memories with others, answering questions about them, or abstracting information from them. Our main findings are that online ratings (obtained immediately after this 24 s period) of the degree to which the memory has been relived and the degree of emotional intensity were parametrically associated with activation in different areas of the brain and did so at different times. As expected from assuming that judgments of reliving are metacognitive in nature and made on the basis of fully formed memories, all reliving-modulated activity was observed during the elaboration phase, in the period after the memory was formed. In contrast, nearly all emotion-modulated activity was observed during the initial retrieval process prior to the full formation of the memory.

Judgments of reliving were parametrically associated with activity in areas of the brain involved in visual imagery (extrastriate cortex) (Kosslyn et al. 2001) and a region of right inferior frontal cortex hypothesized to be essential for recollection of episodes from the personal past (Markowitsch 1995). These regions have been observed across several studies of autobiographical memory retrieval using dissimilar comparison tasks, suggesting their involvement is relatively ubiquitous and not simply a function of the chosen subtraction. Previous research suggests the identified posterior regions, which are involved in initial sensory processing during encoding, are often reactivated during retrieval particularly when successful retrieval is biased toward the retrieval of visual details (Wheeler et al. 2000; Kahn et al. 2004; Prince et al. 2005; Gardini et al. 2006). Because our participants were instructed to close their eyes during retrieval, activity within these regions was not related to sensory processing, but rather, were specific to visual imagery associated with autobiographical memory retrieval.

Right inferior frontal gyrus has been identified as a crucial region to autobiographical memory retrieval, exhibiting activity in comparisons of autobiographical memory retrieval to category exemplar generation (Greenberg et al. 2005) and to fictitious events (Markowitsch et al. 2000). Furthermore, damage to this region leads to retrograde amnesia (Calabrese et al. 1996; Levine et al. 1998). Evidence from more standard memory paradigms suggest this region is associated with directing attention to or active selection of perceptual, rather than

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conceptual, representations during retrieval (Wagner, Poldrack, et al. 1998; Wagner 1999; Cadoret et al. 2001; Dobbins and Wagner 2005). In the current study, ratings of reliving may be based upon the amount of visual and perceptual detail available, whose retrieval depends on the right inferior frontal gyrus.

The Spatiotemporal Dynamics of Emotional Intensity

Areas modulated by judgments of emotional intensity included brain regions thought to be critical for emotional and somatic signaling (amygdala, frontopolar cortex, and somatosensory cortex) as well as other ones typically engaged during memory retrieval, such as the hippocampus, lateral temporal cortex, and posterior parietal cortex. Interestingly, these canonical memory areas were modulated by emotional intensity before the button press indicating that the participant thought that the memory was formed, suggesting that early detection of high arousal during retrieval may spur and guide efforts at event reconstruction (Bartlett 1932/1995; Reisberg et al. 1988; Markowitsch et al. 2000). Of the emotion-modulated areas, only the frontopolar cortex continued to be sensitive to emotional intensity ratings during the elaboration period, suggesting a role in online maintenance and elaboration of emotional representations (Davidson and Irwin 1999). Thus, despite the behavioral correspondence found between subjective ratings of emotion and reliving during autobiographical recall (Talarico et al. 2004), the present fMRI findings indicate that these phenomenological properties are temporally and spatially dissociable.

The modulation of brain activity of a fully formed memory by its rated degree of reliving is not surprising. For instance, the more activity in visual cortex the more vivid one might expect the memory to be and thus the more strongly it is likely to be judged as highly relived. But how can a rating of emotional intensity done after a memory is fully formed have its effects during the time before, but not after, the memory reaches consciousness? One can consider words in a list as being stored as unitary items and retrieved by what have now become fairly well specified neural areas in the MTL and frontal lobe (Cabeza and Nyberg 2000a, 2000b; Buckner and Wheeler 2001). The relatively rapid reaction times to retrieve such memories compared with the times observed here is consistent with this view. However, it is less plausible to view autobiographical memories involving emotional, visual, auditory, spatial, and other information as being stored as unitary items in contiguous neural locations (Rubin and Greenberg 1998; Greenberg and Rubin 2003; Rubin 2005). Rather, they are more likely to have neural representations that are more distributed, and thus, which are assembled or coactivated at the time of retrieval using the same medial temporal and frontal areas as are used with simpler material, along with other areas.

If this is the case and if emotions function as early warnings through retrieval modulation then emotions may have their greatest effect early in the process, before the memory is assembled. In contrast, visual and other sensory areas may have their greatest effect late in the process, after the memory is assembled. Proust (1928/1934) described something similar in his classic account of autobiographical memory wherein the smell and taste of a "petite madeleine" first produces "an exquisite pleasure … detached, with no suggestion of its origin" and then after a time "the memory returns … immediately the old grey house upon the street … rose up like the scenery of a theatre and with the house the town." In this example, a retrieval cue works quickly to change emotion, but the memory is assembled more slowly, and when it does come, it consists in large part of a visual image. The present study provides some clues as to how these sequences of events during recall unfold in the human brain by capitalizing on the delayed time course of autobiographical memory retrieval using the Galton/Crovitz technique.

Previous neuroimaging studies have generally found a weaker influence of emotion on memory-related brain regions during autobiographical recall (Maguire and Frith 2003; Addis et al. 2004), although some differences in affective valence (positive vs. negative emotions) have been reported in orbitofrontal cortex and various sectors of the temporal lobe (Piefke et al. 2003). However, these prior reports used a prescanning cue generation method where cue words for specific memories were created a few days prior to the study. Under these circumstances, emotional intensity may not play as important a role during the memory reconstruction process because the event was recently retrieved in order to generate the cue words. Using the prescanning cue generation method, we reported similar temporal profiles and functional connectivity between amygdala and hippocampal activation during autobiographical recall, suggesting a reciprocity of emotional and memory functions (Greenberg et al. 2005). In that study, though, online estimates of emotional intensity were not obtained, and the time course of retrieval was much faster (on the order of 3 s) so that the temporal stage of memory processing related to these activation patterns could not be specified. On these points, the present study builds upon and extends prior research, although future work is needed to examine other aspects of emotional processing during recall (e.g., brain regions that parametrically code the degree of physiological arousal) as well as other subjective features of the memories besides emotional intensity and reliving.

Could differences in the words used as cues rather than the memories they cued be the source of our early response to emotion ratings? That is, could the early effects be caused by processing the words themselves and our ratings of the emotional intensity of the autobiographical memories they cue function only through their correlation with the emotional properties of the words? We do not believe this is the case for several reasons. First, the 80 words we used were not especially highly emotional. If we rank them in terms of the emotional intensity of the words themselves, the top 10 emotional words (Bradley and Lang 1999) are anger, ambulance, kiss, joy, fire, thief, trouble, party, love, and mother, and the words occupying the bottom 10 ranks are plant, orchestra, bowl, tree, cottage, street, butter, bird, pencil, and paper. Because parametric scaling was used as the analysis tool (which considers all 4 levels of intensity ratings provided by the participants), the effects could not be driven by just a few emotionally salient items. Second, the pattern of the location of activity shown in Table 1 is more consistent with the retrieval of autobiographical memories than with the semantic processing of words, with the possible exception of the amygdala activity. Third, if we correlate the emotional intensity ratings of the words, drawn from the Affective Norms of English Words database (Bradley and Lang 1999), with the emotional intensity ratings of the memories for each participant, the relationship is weak (mean correlation of .19). These considerations provide supporting evidence that brain areas modulated by emotional intensity ratings reflect the intensity of the specific memory being

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retrieved, not the emotional intensity of the reaction to the meaning of the cue word itself.

Conclusion

The present study provides novel neurobiological insights into some aspects of the retrieval and phenomenology of autobiographical memory. Unlike laboratory-based memories for single items, autobiographical memories are more complex, distributed across a broader network of brain areas, and require more time-consuming reconstructive processes. Employing an autobiographical memory paradigm, the present fMRI study dissociated the activation time courses of brain regions differentially involved in the accessing versus elaboration of personal memories. The memory access period engaged regions associated with access to stored memory traces (the hippocampus and the retrosplenial cortex) and a region associated with maintaining the mental set of episodic retrieval (right PFC). The elaboration period recruited regions associated with visual imagery (extrastriate visual cortex and precuneus) and a region associated with working memory elaboration and top–down attentional control over posterior brain regions (left PFC).

In addition to performing cognitive operations involved in memory access and elaboration, some brain regions were modulated by the subjective properties of the memory itself. Emotional intensity was parametrically associated with activity in the amygdala, temporoparietal regions, and sectors of PFC in the memory access period. Representation of emotional intensity was temporally extended in the frontopolar cortex after the memory was recovered and was actively maintained. The sense of reliving, in which one travels back in time to reexperience the event, was related to subsequent processing (after the memory is accessed) in brain regions that included: ventral and medial PFC, cingulate gyrus, and extrastriate visual cortex. These GLM patterns were confirmed by time course analyses based on time-locked averages of the fMRI signal.

The current study shows that autobiographical memory paradigms are ideally suited to investigate the component processes underlying retrieval of complex events. The findings underscore the diversity of temporal sequencing and spatial localization within the episodic memory network for the processing of subjective features that are central to recalling our personal past. In doing so, we believe that the results are the first fMRI study to reveal the dynamic recruitment of distributed brain regions during distinct periods of episodic remembering.

Notes

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Address correspondence to David C. Rubin, PhD, Department of Psychology and Neuroscience, PO Box 90086, Duke University, Durham, NC 27708-0086, USA. Email: david.rubin@duke.edu.

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