Published in final edited form as:
Neuroimage. 2012 February 1; 59(3): 2908–2922. doi:10.1016/j.neuroimage.2011.09.066.

Routes to the past: Neural substrates of direct and generative autobiographical memory retrieval

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Abstract

Models of autobiographical memory propose two routes to retrieval depending on cue specificity. When available cues are specific and personally-relevant, a memory can be directly accessed. However, when available cues are generic, one must engage a generative retrieval process to produce more specific cues to successfully access a relevant memory. The current study sought to characterize the neural bases of these retrieval processes. During functional magnetic resonance imaging (fMRI), participants were shown personally-relevant cues to elicit direct retrieval, or generic cues (nouns) to elicit generative retrieval. We used spatiotemporal partial least squares to characterize the spatial and temporal characteristics of the networks associated with direct and generative retrieval. Both retrieval tasks engaged regions comprising the autobiographical retrieval network, including hippocampus, and medial prefrontal and parietal cortices. However, some key neural differences emerged. Generative retrieval differentially recruited lateral prefrontal and temporal regions early on during the retrieval process, likely supporting the strategic search operations and initial recovery of generic autobiographical information. However, many regions were activated more strongly during direct versus generative retrieval, even when we time-locked the analysis to the successful recovery of events in both conditions. This result suggests that there may be fundamental differences between memories that are accessed directly and those that are recovered via the iterative search and retrieval process that characterizes generative retrieval.

Keywords

autobiographical memory; retrieval; fMRI; partial least squares

1. Introduction

Autobiographical memories (AM) of past experiences can be often elicited spontaneously; something we encounter in our environment or in our thoughts directly transports us back in time to mentally re-experience that one particular event (Berntsen and Hall, 2004). Other times, however, AM retrieval is much more effortful: we have to actively search for a memory to answer some specific question about our past. Models of AM distinguish

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between these two forms of retrieval. When a specific and personally-relevant cue is encountered (e.g., “breaking my leg”), the ensuing retrieval is described as direct (Conway and Pleydell-Pearce, 2000) or associative (Moscovitch, 1992), as the cue provides a direct entry-point into the specific event. However, when available cues are generic (e.g., “leg”), one must engage in an iterative search and retrieval process, termed generative (Conway and Pleydell-Pearce, 2000) or strategic (Moscovitch, 1992) retrieval, to generate increasingly more specific cues that eventually access a relevant AM.

Direct and generative retrieval are related processes; in both cases, retrieval is successful when an AM that meets the search criteria is recovered. In other words, direct retrieval of a memory is the ultimate endpoint (Conway, 2005), and thus the difference between these processes relates to whether an effortful memory search is required: the *route* to successful retrieval differs. Although informal comparisons of existing studies of direct or generative retrieval give some indication that these processes have different neural signatures, as yet no study has directly contrasted generative and direct retrieval. Svoboda, McKinnon, & Levine (2006) argue that research comparing these two forms of retrieval is important for better understanding the strategic aspects of AM retrieval unique to generative retrieval. Moreover, they assert that the use of multivariate neuroimaging analyses examining the regions associated with AM retrieval would be an important complement to this approach. The current study was designed to achieve these two specific aims.

In direct retrieval studies, personalized cues relating to specific AMs are collected prior to scanning, either at the time of event occurrence (the prospective method; Cabeza et al., 2004; Levine et al., 2004; St. Jacques et al., in press; Svoboda and Levine, 2009) or during a prescan interview with the participant (e.g., Addis et al., 2004b; Maguire and Mummery, 1999; Maguire et al., 2001; Steinvorth et al., 2005) or a close relative (Gilboa et al., 2004), and later used during scanning to elicit direct AM retrieval. Such studies typically report activation of medial and left-lateralized regions, including medial and ventrolateral prefrontal cortex (PFC), medial and lateral parietal cortex, temporal polar cortex and the medial temporal lobes (MTL; for reviews, see Cabeza and St Jacques, 2007; Maguire, 2001; Svoboda et al., 2006). This set of regions is activated quickly upon cue presentation, indicative of direct access to AMs that does not require a protracted search phase. It is proposed that the direct cue interacts with the memory trace (i.e., ecphory; Tulving, 1983) and the hippocampus mediates the reactivation and reintegration of the details comprising the AM stored in posterior cortical regions, enabling distributed memory details to be remembered in a cohesive way (Nadel and Moscovitch, 1998). After a memory is reactivated, the ventromedial and dorsolateral PFC contribute to evaluating the contents of retrieval, to assess whether the AM is a real memory (i.e., reality monitoring; Johnson et al., 1988) and whether it meets the search criteria (Schacter et al., 1998). Ventromedial PFC activity may reflect a quick “feeling-of-rightness” evaluation of retrieved AMs (Moscovitch and Winocur, 2002) as well as the self-referential nature of the retrieved AM (Northoff and Bermpohl, 2004). Consistent with this model of the functional neuroanatomy of AM retrieval, it has been reported that activity in the hippocampus during AM retrieval occurs prior to activity in regions mediating the content of the memory (e.g., posterior visuospatial regions; Daselaar et al., 2008) and post-retrieval monitoring (e.g., medial PFC; Cabeza et al., 2004). In sum, existing neuroimaging studies on direct AM retrieval provide an indication of the neural regions whose activation should be the common end point of both direct and generative retrieval.

When only generic cues are available, a generative search process is required before direct access can occur. If a specific AM is the goal of retrieval, the memory cue is used to launch an iterative search-retrieve-evaluate-elaborate cycle through the different levels of AM: abstract conceptual knowledge about lifetime periods; generic memories of repeated or

extended events; and episodic memories of specific past events (Conway and Pleydell-Pearce, 2000). For instance, if provided with a generic cue such as “dog”, one might first access knowledge of a time when they owned a dog, or general events with their dog (e.g., daily walks). These retrieved memories are evaluated, and if the search criteria are not met, the retrieved information is used as further cues to access a more specific AM (e.g., losing the dog on one occasion; see Table 7 in Conway, 2005, for further examples).

Studies of generative retrieval typically use common nouns as generic cues (i.e., Crovitz cueing paradigm; Crovitz and Schiffman, 1974). The retrieval trial contains a search/construction phase that ends in ecphory that is followed by the elaboration of the event (i.e., fleshing out the event in vivid detail) and post-retrieval processes. Thus, some generative paradigms have had participants indicate (with a button press) when a specific event memory is retrieved to delineate the search phase from subsequent elaboration and post-retrieval processes (Addis et al., 2007; Conway et al., 1999; Daselaar et al., 2008; Hennessey et al., 2011). Early neuroimaging studies of generative retrieval linked AM search processes with left lateral PFC activation (Conway et al., 1999) prior to spreading activation to posterior temporal and occipital cortices reflecting the retrieval of the contents of the memory (Conway et al., 2001; Conway et al., 2003). However, more recent studies have found right-lateralized (Daselaar et al., 2008) or bilateral (Hennessey et al., 2011; St. Jacques et al., 2011; Vandekerckhove et al., 2005) activity in the lateral PFC during generative retrieval.

A recent meta-analysis (Svoboda et al., 2006) called into question the link between generative search processes and ventrolateral PFC: while half of the 24 studies reviewed showed ventrolateral PFC activity, these studies were a mix of both generative and direct retrieval paradigms. Similarly, the studies that did not report ventrolateral PFC engagement also included both studies of generative and direct retrieval. These mixed findings may result from methodological differences. Paradigms differ in their strategic load due to cue type (e.g., personalized cues generated by participants may require less strategic retrieval versus personalized cues provided by relatives) or the age of the AMs (e.g., retrieval of recent AMs may require less strategic search processes). Moreover, the control tasks vary in strategic load and contrasts may therefore result in an apparent absence of lateral PFC activity (Addis et al., 2007). The inconsistent findings regarding both the recruitment and laterality of lateral PFC activity during generative retrieval highlight the need to directly contrast generative retrieval with direct retrieval to identify the unique neural correlates of the search phase of AM retrieval.

Previous research has indicated that general AMs are often retrieved early during the iterative search-retrieval-evaluation-elaboration cycle. For instance, a study sampling the contents of consciousness during generative AM retrieval confirmed that general AMs are accessed prior to specific AMs (Haque and Conway, 2001). Thus, it is likely that neural activity in lateral anterior temporal cortex supporting the retrieval of generic events (Addis et al., 2004a; Graham et al., 2003) will be evident during the early stages of generative retrieval.

The aim of the current study was to contrast direct and generative AM retrieval. To this end, we presented individuals with personalized and generic cues but matched exposure to, and processing of, these cues in a prescan session. As both forms of retrieval ended in specific AM retrieval, it was predicted that there would be evidence of common engagement of regions typically evident in studies of direct retrieval. In addition, we also expected there would be neural differences, with early activity in ventrolateral PFC and anterior temporal cortex evident in the generative AM condition. Because this study was designed to examine two retrieval processes that differ not only in terms of spatial patterns of activity but also in

terms of the unfolding of these processes on a temporal scale, we analyzed these data using spatiotemporal partial least squares (ST-PLS), a multivariate technique that identifies whole brain patterns of activity correlated with tasks across the length of an event (McIntosh et al., 2004). Notably, ST-PLS is not dependent upon assumptions about the shape and time course of the hemodynamic response function (HRF), and can thus be used to examine neural differences between tasks wherever they emerge across the duration of the trial (Addis et al., 2004a). We predicted that direct retrieval should result in the immediate engagement of regions associated with successful AM retrieval (which would be evident in blood oxygen level dependent signal approximately 6–8 seconds after cue onset), while activation of this set of regions would be delayed in generative retrieval, given the need for an initial memory search. However, once a specific AM is recovered in both conditions, these regions should be similarly engaged.

2. Methods

2.1 Participants

Twenty healthy, right-handed young adults with no prior history of neurological or psychiatric impairment were enrolled in this study and provided informed written consent in a manner approved by the Harvard and Massachusetts General Hospital Institutional Review Boards. Two participants dropped out of the study prior to the fMRI session, and three others were excluded due to issues during the fMRI session (i.e., excessive movement, data collection problems, or detection of an anatomical abnormality). Thus, data from 15 healthy participants (9 males; mean age, 22 years; range, 18–33) were analysed.

2.2 Stimuli

Ninety-six highly imageable, frequent and concrete nouns were selected from the Clark and Paivio (2004) extended norms for use in this study. These nouns were divided into lists that did not differ in terms of imagability, frequency or concreteness (F values < .637, p values > .531); see Appendix A. These lists cycled through the conditions comprising the experiment: (1) direct retrieval condition; (2) the generative retrieval condition; (3) the visuospatial control condition; and (4) the semantic processing control condition[1]. Participants were randomly assigned to a counterbalanced version, such that across participants, the same cues were presented in direct, generative, and control conditions.

2.3 Pre-scan Session

Approximately one month prior to scanning, participants completed a 2-hour pre-scan session in the laboratory. The aim of this session was to collect AMs from generic cues that could then be used to create personalized cues to be shown during scanning. Thus, during this session participants silently completed 16 trials in a *"direct retrieval pre-scan"* condition (see Figure 1a). For each of these trials, a generic cue (noun) was shown for 20 seconds, and an instruction to retrieve a specific past event related to the cue, either from the last year or the last 5–20 years. On each trial, participants made a button press when a specific event was retrieved; they then elaborated on the event, generating as much detail as possible, for the remainder of the 20 seconds.

Participants also silently completed 16 trials in a *"generative retrieval pre-scan"* condition (see Figure 1b). For these trials, the 16 nouns that would later be used as generic cues during the scan session were presented. For trials in this condition, participants saw each noun for 20 seconds and an instruction to imagine a future event related to the cue; they pressed a

[1]Participants also completed two other imagination conditions; however, given the focus of this study on AM retrieval, these conditions will not be discussed further.

button when they had an event in mind, and then elaborated or fleshed out the imaginary event for the remainder of the 20 seconds. Importantly, the generation of a future event requires exposure to and processing of the cue, but not in a way that would directly link the generic cue word with one specific past experience. Although it is likely that the simulation of future events activates various AMs or details comprising AMs (Schacter and Addis, 2007), it is highly unlikely that this process would result in the cue word then being a direct pointer to one particular AM.

Trials in both conditions were randomly presented during this pre-scan session. The prescan session ended with a semi-structured interview, where participants were re-presented with each cue and asked to describe the past or future event they had generated for that cue. From this information, the experimenter later created personalized AM cues for use as fMRI stimuli for the direct retrieval condition. Information regarding future events imagined during the pre-scan session was also collected (even though it was not later used during scanning) in order to match exposure and processing of cues in both conditions.

2.4 Scanning session

Participants were familiarized with the task instructions, and introduced to the rating scales they would complete during scanning. Participants then completed six practice trials before entering the MR environment. Participants were aware that following the scan, they would be shown each cue and asked to describe the AM recalled during scanning. Throughout the duration of the scanning session, participants completed 16 trials of each of four conditions: direct AM retrieval, generative AM retrieval, semantic control and imagery control[2]. Each trial was separated by jittered fixation (mean = 4 *s*; range = 2 – 6 *s*). The scanning session was divided into six runs, during which 16 trials were presented in random order. All stimuli were presented using black text on a white background. All responses to the rating scales were made on a five button MRI-compatible response box.

2.4.1 AM tasks—Each personalized cue used in the direct AM retrieval condition identified a specific past event *and* included the cue word shown in the pre-scan session that elicited that AM (see Figure 1c). Participants were instructed to retrieve the memory associated with the personalized cue. For the generative retrieval condition, stimuli consisted of the cue words used to elicit future events in the prescan session (see Figure 1d). Although participants were exposed to these cues previously, we believe they were still generic cues for AM retrieval because in the prescan condition they were used for a different cognitive task (i.e., future simulation), and moreover, the temporal distance was switched. In other words, a cue word used to elicit a *future* event in the next *year* was now used to elicit a *past* event from the past *5–20 years* (see Figure 1). Participants were instructed that all AMs should be specific in time and place, and to remember these events from a field perspective.

For all AM trials, the participant saw a cueing screen for 20 *s*. This screen included the task instruction, the time frame from which the AM should come (past year, past 5–20 years), and the personalized or generic cue (see Figure 1). Once participants had an event in mind, they made a button press and elaborated or fleshed out the memory for the remainder of the trial. Three rating scales then followed, each shown for 5 *s*: (1) level of detail recalled (1 = no/few details; 5 = highly detailed); (2) emotionality of the AM (1 = detachment; 5 = intense emotional experience); (3) the main perspective (field or observer) of the AM (1 = own eyes; 2 = see self).

[2]There were also 32 trials in other imagination conditions that are not part of the current analysis.

2.4.2 Control tasks—In order to isolate regions unique to the AM conditions, two control conditions were also included in this study: a semantic and a visuospatial task (Addis et al., 2007). These two tasks were chosen to control for the fact that AMs, being multifaceted in nature, typically include both semantic and visual elements (Levine et al., 2002). Thus, together these two tasks controlled for general processes associated with retrieving semantic and visual information. Moreover, these tasks were designed to control for the two phases of the autobiographical tasks: 1) the retrieval and integration of information during the construction phase and, 2) during the elaboration phase, the generation of as much detail as possible about the information retrieved during construction.

Specifically, on semantic control trials, participants were presented with a noun; they were instructed to think of two related words, arrange all three words into a sentence, and make a button press. The remainder of the 20 *s* trial involved semantically defining the three words. On visuospatial control trials, participants were presented with a noun and thought of two objects related to the stimulus – one larger and one smaller than the named object – and mentally visualized all three objects in a triangular arrangement. Once the arrangement was in mind, they made a button press and for the remainder of the 20 *s* trial, they focused on the visual features of the three objects. This was followed by three rating scales (shown for 5 *s* each): (1) level of detail of semantic/visual information (1 = no/few details; 5 = highly detailed); (2) relatedness of the words/objects generated to the cue (1= unrelated; 5 = very related); (3) the difficulty of the task (1 = easy; 5 = difficult).

Post-Scan Interview: Immediately after scanning, all participants completed a post-scan interview. They were presented with the direct and generative AM cues they had seen during scanning, and were asked to describe the events they had remembered in response to each cue. Participants also dated each event and indicated when the event had been last rehearsed.

2.4.3 MRI data acquisition—MR data were collected on a 3 Tesla Siemens Allegra MRI scanner. Detailed anatomical data were collected using a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence. Functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (TR = 2000 ms, TE = 23 ms, FOV = 200 mm, flip angle = 90°). Twenty-five coronal oblique slices, each 5mm thick, were acquired at an angle perpendicular to the long axis of the hippocampus in an interleaved fashion.

2.5 Analysis of fMRI data

2.5.1 Pre-processing—Standard pre-processing was conducted using SPM2 (Wellcome Department of Cognitive Neurology, London, UK), including discarding the first four functional images to allow scanner equilibrium effects, rigid-body motion correction and unwarping, slice timing correction, spatial normalization to the Montreal Neurological Institute (MNI) template (resampled at 4×4×4mm voxels) and spatial smoothing (using an 8mm full-width half maximum isotropic Gaussian kernel).

2.5.2 Analysis—Data were analyzed using Spatiotemporal Partial Least Squares (ST-PLS), a multivariate technique that identifies whole brain patterns of activity that are correlated with experimental design (i.e., conditions) across the length of an event (Addis, et al., 2004; Lin, et al., 2003; Lobaugh, West, & McIntosh, 2001; McIntosh, Chau, & Protzner, 2004). PLS is robustly validated (McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh, et al., 2004) and has been used in a number of studies on autobiographical memory and related processes (Addis et al., 2004a; Addis et al., 2009; Burianova and Grady, 2007; Burianova et al., 2010; Spreng and Grady, 2010; Spreng et al., 2010). Although ST-PLS and the more traditional univariate approach are both variations of the general linear model, and detect comparable patterns of activity (e.g., Addis et al., 2009; McIntosh et al., 2004; Salami et al.,

2010), ST-PLS offers a number of advantages. As mentioned earlier, ST-PLS is not dependent upon assumptions about the shape and time course of the HRF, and can identify neural differences between tasks wherever they emerge across the duration of the trial. Moreover, ST-PLS analyses tend to have increased statistical power for several reasons: the increased sensitivity of the multivariate approach (Fletcher et al., 1996; Lukic et al., 2002), especially in situations where the dependent measures are correlated; the conservative nature of univariate random effects analyses (based on Random Field Theory); and the use of a canonical hrf (sensitivity is reduced if the voxel s response differs from the canonical hrf). For instance, some investigations have demonstrated that multivariate covariance-based methods using singular value decomposition – as ST-PLS does – are more sensitive to mean differences in signal than are voxel-wise *t*-tests (e.g., Lukic et al., 2002).

For this analysis, we used the non-rotated version of task ST-PLS (e.g., Addis, Pan, et al., 2009; McIntosh & Lobaugh, 2004; Rajah & McIntosh, 2008), enabling us to specify *a priori* non-orthogonal contrasts. In the current study, two contrasts (design matrices) were specified. The first contrast examined whether direct and generative AM retrieval engaged a common network relative to the control tasks (AM vs. Control). The second contrast examined the differences between direct and generative AM retrieval (Direct vs. Generative AM).

A data matrix was constructed that contained all of the voxels across the length of each event following the onset of each trial (specified as a 10 TR or 20 s temporal window), across all subjects and all conditions. MR signals were normalized within trials with respect to the signal at the onset of the trial. The resulting data matrix was then cross-correlated with the design matrix for the contrast. The dot product of the contrasts with the data matrix was computed, resulting in a matrix of voxel saliences. The weighted value of the salience can be either positive or negative, depending on whether the voxel exhibits a positive or negative relation to the specified contrast of conditions. For example, voxels in which activity (increases or decreases) is associated with a negatively-weighted condition(s) (and other voxels showing the same pattern) will have negatively weighted saliences.

For each *a priori* contrast, the non-rotated analysis produced a series of dot product images (one for each 2 *s* TR) displaying the relative increases and decreases in whole-brain activity related to the positively and negatively weighted conditions. Moreover, brain scores for each condition in each contrast for each subject were also derived; these scores are analogous to factor scores in a factor analysis, as they indicate how much of the spatiotemporal brain pattern is expressed by a subject within a condition. Examination of average brain scores for each condition with confidence intervals indicated how reliably each condition contributed to the spatiotemporal pattern associated with the contrast (i.e., if the error bars crossed zero, a condition was considered to not contribute reliably to the pattern). Moreover, examining average brain scores across the TRs comprising the event (temporal brains cores) enabled identification of the TR(s) when activation for conditions was maximal.

The statistical significance of the results was determined using permutation testing (500 permutations were computed), conducted using the sums of squares of the dot product images (which is equivalent to the ‘singular value’ – the amount of covariance accounted for by the contrast, McIntosh & Lobaugh, 2004). This procedure involved randomly re-ordering the data matrix rows, re-running the non-rotated analysis, and determining the new singular value for each re-ordering. Thus, significance reflects the probability based on the number of times the singular value from the permuted data exceeds the original singular value (McIntosh, et al., 1996). A threshold of $p \leq .05$ was used. Note that as the entire spatiotemporal pattern was assessed in one analytic step rather computing a series of voxelwise statistical tests, correction for multiple comparisons is not required.

The reliability of the voxel saliences was determined using bootstrap estimation of the standard errors. This procedure involved randomly resampling subjects with replacement, and computing the standard error of the saliences after a number of bootstrap samples (McIntosh et al., 1996). In the present study, this sampling and analysis procedure was carried out 300 times. Clusters of 5 or more voxels in which bootstrap ratios were greater than ±2.8 (roughly equal to a *z*-score, and $p < .005$), were considered to represent reliable voxels (Addis, et al., 2004). Note that for the AM>Control contrast, the effect was so robust, most of these saliences survived a more conservative threshold of 3.2 (roughly equivalent to $p < .001$), and for brevity only these saliences are reported here. Moreover, given our focus on regions typically associated with AM retrieval (i.e., the AM retrieval network), we focus our findings on regions identified in the meta-analysis by Svoboda et al. (2006) as core and secondary regions associated with AM retrieval. Local maxima co-ordinates (i.e., voxels showing the highest bootstrap ratios) are reported for each cluster during peak TRs (as determined with reference to the temporal brain score plots). For localization purposes, MNI co-ordinates were converted to Talairach space and localized in reference to a standard stereotaxic atlas (Talairach and Tournoux, 1988).

3. Results

3.1 Behavioral Results

The number of trials, response time (RT) data, and phenomenological ratings for the various conditions are presented in Table 1. For all conditions, only trials on which a button press (indicating AM retrieval) was recorded were analyzed. For AM trials, analysis was further restricted to trials on which the AM retrieved during scanning was a specific event, and was recounted during the post-scan interview. The resulting number of trials (i.e., bin size) differed by condition, $F_{(2.22,31.02)}=11.26$, $p<.001$, as indicated by a repeated measures analysis of variance (RM-ANOVA). Post-hoc Bonferroni tests indicated that direct retrieval had significantly more successful trials than generative retrieval and the control conditions (p values $< .05$); generative retrieval and both control conditions did not differ (p values $> .66$).

An important manipulation check was to determine whether the presentation of the cues in the generative condition facilitated later retrieval of AMs during the scanning session, despite the fact that during the prescan session these cues were only processed with respect to imagined future events and not retrieved past events. There were two instances of generative retrieval in this experiment that allowed for such a comparison to be made: in the direct AM condition during the prescan session (i.e., the initial retrieval of an AM that was later cued directly during scanning; Figure 1a), and in the generative AM condition during scanning (Figure 1d). The only difference between these instances of generative retrieval was that in the generative condition, the cue had been previously presented and processed during the prescan session (in terms of eliciting an imagined future event). A paired *t*-test of RT data from these two sets of retrieval trials failed to provide any evidence that generative retrieval during scanning was significantly faster than the initial (generative) retrieval of AMs in the direct condition during the prescan session, $t_{(13)}=1.29$, $p = .220$.

We also examined how RTs in the AM and control conditions differed during the scan session. A RM-ANOVA revealed a main effect of condition, $F_{(2.14,30.15)}=40.01$, $p<.001$, and post-hoc Bonferroni tests confirmed that as predicted, RTs for direct retrieval were significantly faster than generative retrieval ($p < .001$). Both AM conditions had significantly faster RTs than the control conditions (p values $\leq .05$). RT did not differ between the control conditions ($p=1.00$).

A chi-square test indicated that the frequencies of field and observer ratings did not significantly differ in frequency between AMs in the direct and generative conditions (χ^2 = .936, p = .432). The phenomenological ratings were compared across AM conditions using Wilcoxon Signed-Rank Tests. Directly retrieved AMs were rated as more detailed (Z=−2.22, p<.05) and more significant (Z=−3.12, p<.01) but not more emotional (Z=−1.36, p=.17) than AMs retrieved through generative retrieval. Given that AMs in the direct task were retrieved more quickly, participants had more time for elaboration, which in turn may have led to inflated detail ratings. To investigate this possibility, we ran correlations of detail ratings and RTs using Spearman s Rho correlations. No significant correlations were found for AMs in either the direct (r_s = −0.181, p=.520) or generative (r_s = −0.145, p=.607) retrieval conditions.

The AMs retrieved in the direct and generative conditions did not differ significantly in terms of event recency (time since the event occurred), $t_{(14)}$=1.21, p=.25. However, as expected, these events differed in rehearsal recency (time since the last rehearsal of the AM), $t_{(14)}$=8.14, p<.001, with direct events last rehearsed at the prescan session 3–4 weeks prior, and general AMs last rehearsed over a year before the scan.

3.2 Non-Rotated ST-PLS – AM versus Control Tasks

The contrast of autobiographical (direct and generative) tasks relative to the control tasks was significant, p<.001, and explained 40.82% of the crossblock covariance. The brain scores plot (Figure 2a) indicates that all four conditions reliably contributed to this overall pattern (as the confidence intervals did not cross zero for any condition). The temporal brain scores plot shows brain scores for both AM conditions and both control conditions, as well as the mean of each pair of conditions (Figure 2b). This plot shows that the differentiation of the autobiographical and control tasks was, in part, related to differing temporal profiles: mean activation associated with the AM tasks peaked between TRs 5–8 (with the highest activity at TR 6), while mean activation associated with the control tasks peaked later during TRs 6–10 (with the highest activity at TR 9).

AM retrieval and control tasks are also differentiated spatially, associated with distinct patterns of neural activity. The regions associated with the control tasks (negative saliences) are provided as supplementary information (Table 2) and are visible in cool colours in Figure 3. The control tasks recruited a set of regions that mapped primarily onto the dorsal attention and fronto-parietal networks, as well as inferior frontal gyrus. In contrast, the regions associated with AM retrieval (indicated by positive saliences; listed in Table 3 and shown in warm colors in Figure 3) included all of the major components of the AM retrieval network (Svoboda et al., 2006): bilateral medial parietal cortices (including posterior cingulate, precuneus and retrosplenial cortex extending into cuneus), MTL (including hippocampus and parahippocampal cortex), lateral temporal cortex, medial PFC (including frontopolar cortex) and left angular gyrus. Examination of HRFs extracted from these regions (Figure 3) supports the overall pattern evident in the temporal brain scores, with activity peaking at approximately TR 6. Interestingly, although the overall result of this contrast demonstrates common activation of these regions during both forms of AM retrieval relative to the control tasks (Figure 2, 3), activity in many regions was stronger for direct relative compared to generative retrieval. This difference is clearly evident in the temporal brain scores (Figure 2), and a t-test on these brain scores at TR 6 indicated this difference was significant, $t_{(14)}$ = 4.65, p <.001. These neural differences were confirmed by our next PLS analysis.

3.3 Non-Rotated ST-PLS – Direct versus Generative AM retrieval

The contrast of direct and generative AM retrieval was significant, p=.006, and explained 25.27% of the crossblock covariance. The brain scores (Figure 4a) indicate that a difference between these two forms of AM retrieval contributed reliably to this result (as the confidence intervals did not cross zero for either AM condition). Interestingly, this plot also shows that the semantic control condition shared some commonalities with the generative retrieval condition. The temporal brain scores (Figure 4b) revealed that brain activity associated with direct retrieval was very strong relative to that associated with generative retrieval, and peaked during TRs 5 and 6. There were also distinct peaks of activity for generative retrieval (confirmed by extracted HRF data) at TRs 2–3 and later at TRs 8–10.

During the peak TRs associated with direct retrieval, regions engaged included: bilateral medial PFC, inferior frontal gyrus, medial parietal cortex (including posterior cingulate, precuneus and retrosplenial cortex, lateral parietal cortex and posterior visuospatial cortices (e.g., cuneus), and the left MTL (including hippocampus, parahippocampal and entorhinal cortices; see Figure 5a and Table 4a). The HRF data extracted from these regions (Figure 5a) illustrates that while there is strong activity during direct retrieval, activation of these regions during generative retrieval is minimal. In contrast, generative retrieval engaged a small set of regions (see Figure 6 and Table 4b) early on during the retrieval process (TRs 2–3), likely reflecting the early search-retrieval processes uniquely associated with generative retrieval. Such regions included left middle and right inferior frontal gyri, bilateral temporal and lateral parietal cortex, and left precuneus. HRF data extracted from these regions confirmed there was an early peak of activation, unique to the generative condition. Later, in TR 8, another subset of regions in left PFC (medial, superior and inferior frontal gyri) exhibited more activity during the generative condition. For example, the HRF data extracted from the inferior frontal gyrus indicates this region showed more sustained activity during the generative AM task.

3.4 Supplementary Non-Rotated ST-PLS Analyses

Although both conditions eventually ended in the successful recovery of an AM, there were still strong neural differences between generative and direct retrieval evident later in the trial when we predicted that both tasks would engage regions comprising the AM retrieval network (Svoboda et al., 2006). Specifically, direct retrieval was associated with increased engagement of bilateral medial prefrontal and parietal cortices and the left MTL. In order to better understand whether this was a true neural difference between direct and generative AMs, or an artifact of differences in bin size, detail of the memories, and/or the time needed for retrieval, a series of additional PLS analyses were conducted.

There were significantly more successful trials for the direct versus generative condition (see Table 1), and because only successful trials were entered into the analysis, this difference may have artificially increased the power to detect activation for the direct AM condition. Additionally, participants assigned significantly higher detail ratings for AMs retrieved directly versus those retrieved generatively (see Table 1), and previous work has demonstrated that constructing more detailed events is associated with more neural activity in AM network regions (e.g., Addis et al., 2004b; Addis and Schacter, 2008; Gilboa et al., 2004; Viard et al., 2007). To rule out these two explanations of neural differences between direct and generative retrieval, we re-ran the PLS analyses using only a subset of direct AM trials that did not differ significantly from generative retrieval in terms of the number of trials and detail ratings. To create these matched subsets of memories, we randomly removed 2–3 direct AM trials from each participant (to match trial numbers) and then compared the detail ratings. This process was repeated until a subset was identified in which the detail ratings of direct and generative AMs did not differ significantly (p values > .05).

We also randomly removed 2–3 control trials, so as to match bin-size across all conditions. Thus, in this matched analysis there were, on average, approximately 13 trials per condition. Both non-rotated ST-PLS contrasts were re-computed. The results were nearly identical to the original analyses, with the contrasts of AM versus Control tasks (p=.006) and Direct versus Generative AM ($p<.001$) both achieving the same level of significance as in the previous analyses, and explaining approximately the same level of cross-block covariance as the original analyses (AM versus Control, 25.81%; Direct versus Generative AM, 40.09%). Inspection of the spatiotemporal pattern of activations revealed that overall, the same brain regions were activated in response to these contrasts as reported above, although the cluster sizes in the matched analysis were slightly increased for regions associated with AM retrieval (versus Control), and Direct AM retrieval (versus Generative). However, some of the clusters associated with Generative AM retrieval (versus Direct) were reduced in extent in the matched analysis. For clarity, we have included notation in Tables 3 and 4 to indicate which activations were evident in both sets of analyses.

Another, possibly more likely, explanation of the difference in the activation of regions comprising the AM retrieval network is that it results from differing time-courses of retrieval. When a direct cue is presented, recovery of the relevant AM ensues more quickly and with a more regular time-course across trials. In contrast, when a generic cue is presented, the time to retrieval is slower given the need for a memory search, and could vary greatly depending on the direct relevance of the cue. In the current experiment, not only were direct AMs accessed more quickly than generative AMs, but the variance of direct AM RTs was nearly half of that for generative AMs (see Table 1); this difference in variance between conditions was significant ($p=.006$). The larger spread of response times for generative AMs may have limited the power to detect neural effects because fewer trials (and associated neural activity) would be occurring at the same time, resulting in apparently lower activity spread across the duration of the trial. To align the neural event of AM recovery in both conditions, we used RT as an anchor by specifying the onset of every trial as 1 *s* before RT. Both non-rotated ST-PLS contrasts were then re-computed.

Both contrasts were still significant (AM versus Control tasks, p=.002; Direct versus Generative AM, p<.001), explaining a significant amount of cross-block covariance (49.96% and 50.04%, respectively). Interestingly, although the amount of covariance explained by the contrast of AM versus Control tasks was similar to the original analysis (40.82%), for the contrast of Direct vs. Generative AM it was nearly double that of the original analysis (25.27%). This increase suggests that accounting for the RT difference had an impact on the contrast of Direct vs. Generative AM. We examined the HRF data from the time-locked analysis extracted from regions that were identified in the original analysis as differentially associated with direct retrieval (see Figure 5b). Although the time-locking resulted in the peaking of the HRF for direct and generative retrieval to be more in line with each other in many regions, this pattern was not evident for all regions (e.g., right posterior hippocampus) and in many regions a considerable difference between levels of activity remained (e.g., left inferior frontal gyrus). These differences in the level of activity were present in similar regions to those identified in the original analysis. For instance, at TR 3 (approximate 4–6 *s* after RT, when activity in the time-locked analysis peaked; see Table 5), direct AM retrieval was associated with more activity in posterior visual processing areas, while generative AM retrieval was associated with lateral temporal regions. Importantly, however, the time-locked analysis revealed new distinctions between direct and generative retrieval that were not evident in the original analysis. One interesting example of this is that differential hippocampal activity was now evident during both retrieval conditions (rather than just the direct retrieval condition): direct AM retrieval was still associated with left hippocampal activity while generative AM retrieval was associated with right hippocampal activity (Figure 7).

For completeness, we also re-computed this time-locked ST-PLS analysis using only the subset of trials that allowed for matched bin-sizes and detail ratings across the autobiographical conditions. This analysis produced near identical results and, as indicated in Table 5, all activations in the original time-locked analysis were still evident when matching conditions for bin-size and detail.

4. Discussion

It is widely accepted that AMs can be retrieved either directly or generatively depending on the specificity of available cues; however, very little is known about the neural commonalities and differences between these forms of retrieval. The current study was designed to directly compare the two forms of AM retrieval. While both forms of retrieval significantly engaged regions known to comprise the AM retrieval network (Svoboda et al., 2006) relative to the control tasks, important differences also emerged between generative and direct retrieval.

When retrieving an AM from a generic cue, one must engage in an iterative search-retrieve-evaluate-elaborate cycle (Burgess and Shallice, 1996; Conway and Pleydell-Pearce, 2000; Moscovitch, 1992). It has been argued by some that left ventrolateral PFC plays a critical role in the early stages of a controlled and effortful memory search, by mediating the specification and refinement of semantic cues to be used for retrieval (Moscovitch and Winocur, 2002). Using event-related potentials (ERP), Conway found that the left PFC was active during the initial search phase prior to the retrieval of the AM (Conway et al., 2001; Conway et al., 2003). In line with these findings, we found that generic cues that elicit generative retrieval resulted in early activation of the left anterior middle and right inferior frontal gyri. However, there has been some debate as to whether the unique PFC activation associated with generative retrieval is left- lateralized (Cabeza and St Jacques, 2007; Conway et al., 2003), right- lateralized (Daselaar et al., 2008) or bilateral (Hennessey et al., 2011; St. Jacques et al., 2011; Vandekerckhove et al., 2005). For instance, Burgess and Shallice (1996) argue that early specification of retrieval cues – a retrieval stage that is more likely required during generative than direct retrieval – is mediated by the right inferior frontal gyrus. The present results add further support to the idea that bilateral aspects of anterolateral PFC are involved in the early phase of generative retrieval. This finding is consistent with evidence that bilateral aspects of lateral and anterior PFC are involved in the strategic search for AMs, and that these regions interact with medial PFC and MTL during the initial construction of an AM (St. Jacques et al., 2011). Interestingly, St. Jacques et al. found these regional interactions were modulated by the accessibility of the AM during construction, suggesting that the degree of top-down control and strategic search operations needed to recover an AM from a generic cue may influence the activation and interaction of these regions.

The regions uniquely recruited by generative AM retrieval were also associated with the semantic control task. This overlap is not surprising given the early retrieval of conceptual autobiographical information that characterizes generative retrieval. Moreover, like the generative AM task, the semantic task was also generative in nature, such that participants had to engage strategic retrieval processes mediated by lateral prefrontal regions (e.g., Moscovitch and Winocur, 2002) to generate two words related to the presented cue. Another important aspect to the generative process engendered by both tasks concerns the need to select from competing semantic alternatives, a process also known to engage left ventral PFC (Thompson-Schill et al., 1997). Indeed, other studies have reported similar overlap between semantic and autobiographical retrieval tasks. For instance, Nyberg et al. (2002) reported a study examining the similarities and differences between different forms of autobiographical, episodic, and semantic retrieval tasks. Specifically, they found that lateral

prefrontal and temporal regions were common to all tasks requiring retrieval from long term memory (as opposed to working memory tasks). These regions map onto those identified here as being common to the generative AM and semantic tasks. More recently, Burianova & Grady (2007) found overlap in regions recruited by generative AM and semantic retrieval, and consistent with the current findings, these common regions included bilateral ventral anterolateral PFC.

Later during generative retrieval, activity was evident in the left PFC (inferior, superior and medial gyri). Although this activation was not unique to generative retrieval (e.g., left inferior frontal activity was also evident for direct retrieval), it reached higher levels and was sustained longer in the generative condition. Similarly, later activation of the left PFC was also observed in a generative retrieval study by Daselaar et al. (2008); these authors argue this activation reflects control and working memory processes required by the elaboration of recovered AMs. This interpretation fits with the pattern evident here, given that these elaboration processes are recruited during both forms of AM retrieval, but as our results suggest, more so when AMs are retrieved in a generative fashion.

While in most instances, the end goal of this generative retrieval process is the recovery of a specific AM, the search process usually involves the retrieval of conceptual autobiographical knowledge and generic events prior to accessing the specific event that fulfils the search criteria (Graham et al., 2003; Haque and Conway, 2001). Behavioral studies have revealed that general events are typically retrieved prior to the retrieval of specific episodic events (Haque and Conway, 2001). Thus, we predicted that brain regions supporting retrieval of generic AMs, such as lateral temporal cortex (Addis et al., 2004a; Graham et al., 2003) would exhibit early activation. This hypothesis was supported: the generative condition was associated with unique early activity during TRs 2 and 3 in the lateral temporal cortex. Thus, these results converge with behavioral studies indicating that during generative retrieval, recovery of generic conceptual information precedes access of specific event memories.

In contrast to this early activity in lateral temporal cortex, generative retrieval was also associated with later left prefrontal activity, during TR 8. It is likely that this frontal activity is related to the later stage of iterative retrieval process – post-retrieval monitoring. When retrieving an AM from a generic cue, as opposed to direct retrieval, it follows that more monitoring and evaluation of the contents of retrieval are required to determine whether the memory meets the retrieval criteria (e.g., a specific event). That this prefrontal activity was evident after the peak of activity in medial temporal and lateral parietal regions (TR 6) further supports the post-retrieval monitoring interpretation. This finding is broadly consistent with ERP studies that report sustained prefrontal potentials (albeit right-lateralized) following successful retrieval and associated posterior ERP components; similar patterns have been reported for both episodic (e.g., Vallesi and Shallice, 2006; Wilding and Rugg, 1996) and autobiographical (Conway et al., 2001; Conway et al., 2003) memory tasks. Vallesi and Shallice (2006) also found that memories for which confidence was low were associated with increased post-retrieval monitoring demands and more prefrontal activity. It is possible that confidence was lower for memories retrieved via a generative versus a direct route; future behavioural research will be needed to determine if low confidence of AMs is associated with additional prefrontal activity.

In line with an iterative retrieval process, most of the regions comprising the network differentially associated with generative retrieval exhibited a phasic temporal profile of activation. Regions exhibiting this pattern included left lateral prefrontal and temporal cortex, and the right hippocampus. This phasic temporal profile was unique to generative retrieval, consistent with conceptualization of this form of retrieval as protracted and

iterative in nature: pieces of relevant autobiographical information are retrieved and then used to cue more specific AMs (Conway and Pleydell-Pearce, 2000). Summerfield, Hassabis and Maguire (2010) recently observed that regions in the AM network, including the MTL, exhibit a phasic response during scene construction. Summerfield et al. slowed down the process of constructing a scene by having participants construct the scenario one element at a time. They argue that retrieval, integration and working memory operations may be engaged and disengaged throughout the construction of a scene. Although this study was examining imaginary scenes, a similar process likely occurs when re-constructing remembered scenarios - when one has to piece back together the elements of that previous experience (Conway and Pleydell-Pearce, 2000).

In contrast to this phasic activation pattern, direct retrieval resulted in strong activation of AM regions approximately 8 to 12 seconds after the provision of a personalized memory cue. Overall, activity in these regions, including medial prefrontal and parietal cortex and the left hippocampus, was higher during direct than generative retrieval despite the fact that all trials in both conditions ended with the recovery of a specific AM. One explanation of this difference is related to the differing time-courses of retrieval. Unlike direct retrieval, the time to AM retrieval was more variable in the generative condition which may have reduced the power to detect activation of the AM network in this condition. We thus repeated the analysis, time-locking the onset to RT. Although these supplementary analyses still revealed significant differences between direct and generative retrieval, with activity in many regions being lower for generative versus direct AMs, the peaks of the HRFs were more in line with each other indicating that the time-locking analysis was successful in this respect.

However, even after adjusting for the differences related to RT, activation differences remain. One such difference emerged in the hippocampus: the time-locked analysis revealed that direct retrieval was associated with activation of the left hippocampus while generative retrieval was associated with right hippocampal activity. The finding of hippocampal activity in both conditions likely reflects the process of recovering the specific AM (i.e., ecphory; Tulving, 1983), as such activity has been documented previously in both studies using direct and generic cues. The findings in the literature are mixed; although the majority of studies using direct retrieval paradigms have found left-lateralized or bilateral hippocampal activity (for a review, see Svoboda et al., 2006), studies using generative paradigms report activation of the left (Burianova et al., 2010; Vandekerckhove et al., 2005), right (Daselaar et al., 2008) or bilateral (St. Jacques et al., 2011) hippocampus. The current study, however, is the first to directly compare the two forms of retrieval, and although direct and generative retrieval both recruit bilateral hippocampus (as evident by common activity relative to the control task), they *differentially* recruit left and right hippocampus, respectively. We do not have evidence to determine whether direct versus generative AMs differ with respect to levels of narrative and spatial content – which are thought to influence reliance on the left and right hippocampus, respectively (Burgess et al., 2002). A task for future research, however, will be to investigate why these different forms of retrieval exhibit hippocampal laterality differences and how these are related to differences in content.

The overall pattern of findings suggests that, aside from RT differences, there may be other distinctions between AMs that are retrieved directly versus generatively. Direct AMs were associated with stronger activity across the AM network than generative AMs, including increased engagement of posterior visuospatial processing regions, even when the analysis was adjusted for RT differences. In line with the finding of activation in such regions, AMs in the direct retrieval condition were rated as significantly more detailed and personally significant than those retrieved in the generative condition. Together, these results imply that the specificity of the cue and the ensuing retrieval process affects the memory that is ultimately retrieved during that particular reconstruction of the memory. This result is

somewhat surprising, given that the AMs in the direct condition were initially retrieved using generic cues (in the pre-scan session), and thus should not have been affected by a selection bias. One possible explanation is that increased time to elaborate directly retrieved AMs (due to faster RTs) resulted in the production of more detailed memories. The current data speak against this explanation, as detail ratings did not correlate with RT data. Moreover, when we analyzed a subset of data for which the detail ratings did not differ significantly across conditions, the same neural differences were still evident. Another possibility is that the ease of directly accessing an event from a personalized cue results in one assigning a higher detail and significance rating than when retrieval is more effortful. However, previous work examining the phenomenology of AMs directly elicited involuntarily by environmental cues and those generatively retrieved from word cues report little difference in the rated vividness and importance of these AMs (Berntsen and Hall, 2004).

The higher detail ratings of AMs in the direct condition could be attributable to an effect of rehearsal and retrieval practice: AMs in this condition were rehearsed more recently than the AMs in the generative condition, due to retrieval during the pre-scan session. Indeed, this possibility is consistent with the findings of robust “testing effects”, where multiple retrievals of a memory increases the clarity and detail of that representation (e.g., Carrier and Pashler, 1992; for a review, see Roediger and Karpicke, 2006). Interestingly, although Svoboda and Levine (2009) reported that detail ratings of AMs increased with repeated retrievals, they also observed that activity across the AM network decreased when the AM had been rehearsed in the 3 days prior to scanning. This finding would suggest then that if rehearsal was having an appreciable effect on neural activity after one month (the delay between the prescan and scanning session), activity during direct retrieval should be less than that evident during generative retrieval.

The possibility remains, though, that there are simply fundamental differences in this reconstructive process when personalized rather than generic cues are available. Such reconstruction involves locating the various elements or details that comprise an AM, and reactivating and reintegrating these details into a coherent yet temporary mental representation (Moscovitch, 1992). Is it that when an element of the memory (i.e., the direct cue) is provided, the rest of the memory is reactivated with ease (i.e., pattern completion; McClelland et al., 1995; Schacter et al., 1998) but that when a generic cue is presented, the reactivation of an AM is more piecemeal and possibly incomplete? Indeed, Greenberg and Rubin (Greenberg and Rubin, 2003) have argued that the visual aspects of AMs are most critical to the reactivation of the entire memory trace, and that a direct cue results in a “cascade of activation” of other sensory components of the memory. Although we did not provide visual aspects of the AMs, the direct cues did contain elements of the memory. Moreover, in the direct condition, it is possible that the word cue had become a part of the memory representation: participants had already associated the word cue with the AM during the pre-scan condition, and this reactivation of the memory in conjunction with the cue may have resulted in the cue word being incorporated into the memory trace (episodic memory updating; Hupbach et al., 2007). In contrast, it may be that in generative retrieval, the cues produced during the iterative search process are never as direct as personalized cues and thus the reactivation of the memory trace is not as full. This speculation provides an interesting task for future behavioral research – to understand the differences in the access and the reactivation of a memory trace that result from the specificity of the cue.

In summary, while both direct and generative retrieval engaged regions comprising the AM retrieval network, some important differences between these forms of retrieval emerged. Generative retrieval was distinctly associated with early activity in lateral prefrontal and temporal regions, likely supporting the strategic search operations and initial recovery of

generic autobiographical information. However, many regions comprising the AM network were activated more strongly during direct versus generative retrieval. This result suggests that there may be fundamental differences between memories that are accessed directly and those that are recovered via the iterative search and retrieval process that characterizes generative retrieval.

Acknowledgments

We thank Aleea Devitt, Adrian Gilmore, Melissa Inger, Heidi Koschwanez, Yonatan Matus and Rose McLiver for assistance with data collection, processing and analysis. This research was funded by National Institute of Mental Health grant MH060941 awarded to D.L.S. D.R.A. was supported by a Royal Society of NZ Marsden Grant (UOA0810) and a Grant-in-Aid for Research and Study Leave from The University of Auckland.

Abbreviations

AM	Autobiographical Memory
MTL	medial temporal lobe
PFC	prefrontal cortex
ST-PLS	spatiotemporal partial least squares

References

Addis DR, McIntosh AR, Moscovitch M, Crawley AP, McAndrews MP. Characterizing spatial and temporal features of autobiographical memory retrieval networks: a partial least squares approach. Neuroimage. 2004a; 23:1460–1471. [PubMed: 15589110]

Addis DR, Moscovitch M, Crawley AP, McAndrews MP. Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. Hippocampus. 2004b; 14:752–762. [PubMed: 15318333]

Addis DR, Pan L, Vu MA, Laiser N, Schacter DL. Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. Neuropsychologia. 2009; 47:2222–2238. [PubMed: 19041331]

Addis DR, Schacter DL. Effects of detail and temporal distance of past and future events on the engagement of a common neural network. Hippocampus. 2008; 18:227–237. [PubMed: 18157862]

Addis DR, Wong AT, Schacter DL. Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. Neuropsychologia. 2007; 45:1363–1377. [PubMed: 17126370]

Berntsen D, Hall NM. The episodic nature of involuntary autobiographical memories. Mem Cognit. 2004; 32:789–803.

Burgess N, Maguire EA, O'Keefe J. The human hippocampus and spatial and episodic memory. Neuron. 2002; 35:625–641. [PubMed: 12194864]

Burgess PW, Shallice T. Confabulation and the control of recollection. Memory. 1996; 4:359–411. [PubMed: 8817460]

Burianova H, Grady CL. Common and unique neural activations in autobiographical, episodic, and semantic retrieval. Journal of Cognitive Neuroscience. 2007; 19:1520–1534. [PubMed: 17714013]

Burianova H, McIntosh AR, Grady CL. A common functional brain network for autobiographical, episodic, and semantic memory retrieval. Neuroimage. 2010; 49:865–874. [PubMed: 19744566]

Cabeza R, Prince SE, Daselaar SM, Greenberg DL, Budde M, Dolcos F, LaBar KS, Rubin DC. Brain activity during episodic retrieval of autobiographical and laboratory events: an fMRI study using a novel photo paradigm. J Cogn Neurosci. 2004; 16:1583–1594. [PubMed: 15622612]

Cabeza R, St Jacques P. Functional neuroimaging of autobiographical memory. Trends in Cognitive Sciences. 2007; 11:219–227. [PubMed: 17382578]

Carrier M, Pashler H. The influence on retrieval on retention. Memory and Cognition. 1992; 20:632–642.

Clark JM, Paivio A. Extensions of the Paivio, Yuille, and Madigan (1968) norms. Behavior Research Methods, Instruments and Computers. 2004; 36:371–383.

Conway MA. Memory and the self. Journal of Memory and Language. 2005; 53:594–628.

Conway MA, Pleydell-Pearce CW. The construction of autobiographical memories in the self-memory system. Psychological Review. 2000; 107:261–288. [PubMed: 10789197]

Conway MA, Pleydell-Pearce CW, Whitecross SE. The neuroanatomy of autobiographical memory: A slow cortical potential study of autobiographical memory retrieval. Journal of Memory & Language. 2001; 45:493–524.

Conway MA, Pleydell-Pearce CW, Whitecross SE, Sharpe H. Neurophysiological correlates of memory for experienced and imagined events. Neuropsychologia. 2003; 41:334–340. [PubMed: 12457758]

Conway MA, Turk DJ, Miller SL, Logan J, Nebes RD, Meltzer CC, Becker JT. A positron emission tomography (PET) study of autobiographical memory retrieval. Memory. 1999; 7:679–702. [PubMed: 10659092]

Crovitz HF, Schiffman H. Frequency of episodic memories as a function of their age. Bulletin of the Psychonomic Society. 1974; 4:517–518.

Daselaar SM, Rice HJ, Greenberg DL, Cabeza R, LaBar KS, Rubin DC. The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. Cerebral Cortex. 2008; 18:217–229. [PubMed: 17548799]

Fletcher PC, Dolan RJ, Shallice T, Frith CD, Fracowiak RSJ, Friston KJ. Is multivariate analysis of PET data more revealing than that univariate approach? Evidence from a study of episodic memory retrieval. Neuroimage. 1996; 3:209–215. [PubMed: 9345492]

Gilboa A, Winocur G, Grady CL, Hevenor SJ, Moscovitch M. Remembering our past: functional neuroanatomy of recollection of recent and very remote personal events. Cereb Cortex. 2004; 14:1214–1225. [PubMed: 15166099]

Graham KS, Lee AC, Brett M, Patterson K. The neural basis of autobiographical and semantic memory: new evidence from three PET studies. Cogn Affect Behav Neurosci. 2003; 3:234–254. [PubMed: 14672158]

Greenberg DL, Rubin DC. The neuropsychology of autobiographical memory. Cortex. 2003; 39:687–728. [PubMed: 14584549]

Haque S, Conway MA. Sampling the process of autobiographical memory construction. European Journal of Cognitive Psychology. 2001; 13:529–547.

Hennessey JA, Addis DR, Giovanello KS. Differential neural activity during search of specific and general autobiographical memories elicited by musical cues. Neuropsychologia. 2011; 49:2514–2526. [PubMed: 21600227]

Hupbach A, Gomez R, Hardt O, Nadel L. Reconsolidation of episodic memories: a subtle reminder triggers integration of new information. Learning and Memory. 2007; 14:47–53. [PubMed: 17202429]

Johnson MK, Foley MA, Suengas AG, Raye CL. Phenomenal characteristics of memories for perceived and imagined autobiographical events. Journal of Experimental Psychology: General. 1988; 117:371–376. [PubMed: 2974863]

Levine B, Svoboda E, Hay JF, Winocur G, Moscovitch M. Aging and autobiographical memory: dissociating episodic from semantic retrieval. Psychology & Aging. 2002; 17:677–689. [PubMed: 12507363]

Levine B, Turner GR, Tisserand D, Hevenor SJ, Graham SJ, McIntosh AR. The functional neuroanatomy of episodic and semantic autobiographical remembering: a prospective functional MRI study. Journal of Cognitive Neuroscience. 2004; 16:1633–1646. [PubMed: 15601525]

Lukic AS, Wernick MN, Strother SC. An evaluation of methods for detecting brain activations from functional neuroimages. Artificial Intelligence in Medicine. 2002; 25:69–88. [PubMed: 12009264]

Maguire EA. Neuroimaging studies of autobiographical event memory. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences. 2001; 356:1441–1451.

Maguire EA, Mummery CJ. Differential modulation of a common memory retrieval network revealed by positron emission tomography. Hippocampus. 1999; 9:54–61. [PubMed: 10088900]

Maguire EA, Vargha-Khadem F, Mishkin M. The effects of bilateral hippocampal damage on fMRI regional activations and interactions during memory retrieval. Brain. 2001; 124:1156–1170. [PubMed: 11353732]

McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. Psychological Review. 1995; 102:419–457. [PubMed: 7624455]

McIntosh AR, Chau WK, Protzner AB. Spatiotemporal analysis of event-related fMRI data using partial least squares. Neuroimage. 2004; 23:764–775. [PubMed: 15488426]

Moscovitch M. Memory and working-with-memory: a component process model based on modules and central systems. Journal of Cognitive Neuroscience. 1992; 4:257–267.

Moscovitch, M.; Winocur, G. The frontal cortex and working with memory. In: Stuss, DT.; Knight, RT., editors. Principles of Frontal Lobe Function. 2002. p. 188-209.

Nadel L, Moscovitch M. Hippocampal contributions to cortical plasticity. Neuropharmacology. 1998; 37:431–439. [PubMed: 9704984]

Northoff G, Bermpohl F. Cortical midline structures and the self. Trends Cogn Sci. 2004; 8:102–107. [PubMed: 15301749]

Nyberg L, Forkstam C, Petersson KM, Cabeza R, Ingvar M. Brain imaging of human memory systems: between-systems similarities and within-system differences. Brain Res Cogn Brain Res. 2002; 13:281–292. [PubMed: 11958972]

Roediger HL, Karpicke JD. The power of testing memory: Basic research and implications for educational practice. Perspectives on Psychological Science. 2006; 1:181–210.

Schacter DL, Addis DR. On the constructive episodic simulation of past and future events. Behavioral and Brain Sciences. 2007; 30:299–351. [PubMed: 17963565]

Schacter DL, Norman KA, Koutstaal W. The cognitive neuroscience of constructive memory. Annu Rev Psychol. 1998; 49:289–318. [PubMed: 9496626]

Spreng RN, Grady CL. Patterns of brain activity supporting autobiographical memory, prospection, and theory-of-mind and their relationship to the default mode network. Journal of Cognitive Neuroscience. 2010; 22:1112–1123. [PubMed: 19580387]

Spreng RN, Stevens WD, Chamberlain JP, Gilmore AW, Schacter DL. Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. Neuroimage. 2010; 53:303–317. [PubMed: 20600998]

St Jacques PL, Conway MA, Cabeza R. Gender differences in autobiographical memory for everyday events: Retrieval elicited by SenseCam images versus verbal cues. Memory. in press.

St Jacques PL, Kragel PA, Rubin DC. Dynamic neural networks supporting memory retrieval. Neuroimage. 2011; 57:608–616. [PubMed: 21550407]

Steinvorth S, Levine B, Corkin S. Medial temporal lobe structures are needed to re-experience remote autobiographical memories: evidence from H.M. and W.R. Neuropsychologia. 2005; 43:479–496. [PubMed: 15716139]

Summerfield JJ, Hassabis D, Maguire EA. Differential engagement of brain regions within a core network during scene construction. Neuropsychologia. 2010; 48:1501–1509. [PubMed: 20132831]

Svoboda E, Levine B. The effects of rehearsal on the functional neuroanatomy of episodic autobiographical and semantic remembering: A functional magnetic resonance imaging study. The Journal of Neuroscience. 2009; 29:3073–3082. [PubMed: 19279244]

Svoboda E, McKinnon MC, Levine B. The functional neuroanatomy of autobiographical memory: A meta-analysis. Neuropsychologia. 2006; 44:2189–2208. [PubMed: 16806314]

Thompson-Schill S, D'Esposito M, Aguirre GK, Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proceedings of the National Academy of Sciences of the United States of America. 1997; 94:14792–14797. [PubMed: 9405692]

Tulving, E. Elements of episodic memory. Oxford University Press; New York, N.Y: 1983.

Vallesi A, Shallice T. Prefrontal involvement in source memory: An electrophysiological investigation of accounts concerning confidence and accuracy. Brain Research. 2006; 1124:111–125. [PubMed: 17070783]

Vandekerckhove MMP, Markowitsch HJ, Mertens M, Woermann FG. Bi-hemispheric engagement in the retrieval of autobiographical episodes. Behav Neurol. 2005; 16:203–210. [PubMed: 16518010]

Viard A, Piolino P, Desgranges B, Chételat G, Lebreton K, Landeau B, Young A, De La Sayette V, Eustache F. Hippocampal activation for autobiographical memories over the entire lifetime in healthy aged subjects: An fMRI study. Cerebral Cortex. 2007; 17:2453–2467. [PubMed: 17204823]

Wilding EL, Rugg MD. An event-related potential study of recognition memory with and without retrieval of source. Brain. 1996:889–905. [PubMed: 8673500]

Highlights

- Personal and generic cues used to elicit direct and generative autobiographical memory retrieval
- Both retrieval tasks engaged regions previous associated with autobiographical memory
- Many of these regions were more active during direct versus generative retrieval
- Generative retrieval differentially engaged lateral prefrontal and temporal cortex

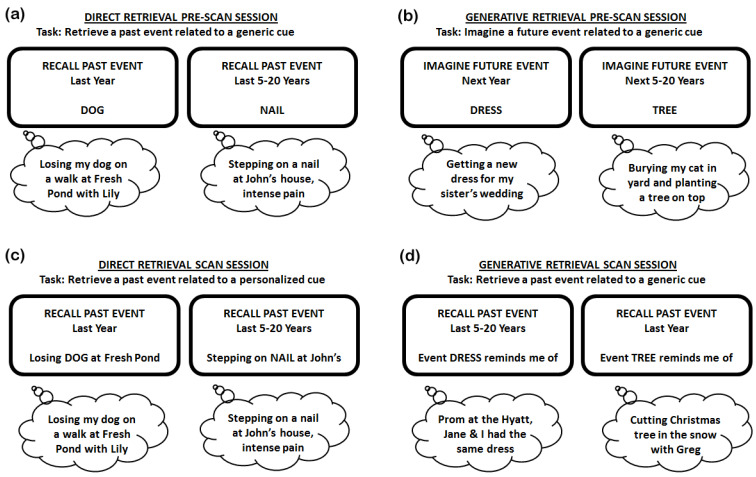

Figure 1. Autobiographical Tasks

For the direct AM condition, participants retrieved AMs in response to nouns (a) and this information was used to create direct cues later shown during scanning to elicit direct AM retrieval (c). For the generative AM condition, participants imagined future events in response to another set of nouns (b) in order to match exposure to and processing of these words that were later used during scanning as general cues to elicit generative retrieval (d).

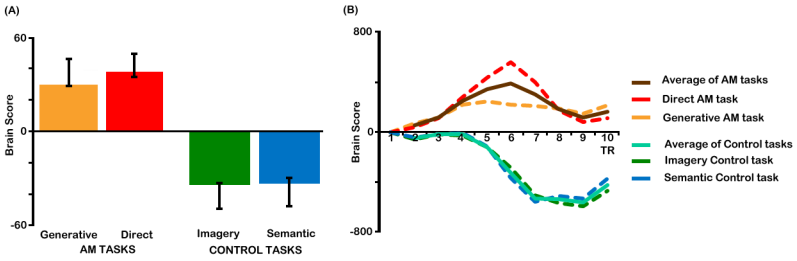

Figure 2. ST-PLS Contrast of AM and Control Tasks

(a) Average brain scores with 95% confidence intervals for the AM (direct, generative) and control (imagery, semantic) tasks. (b) Average brain scores plotted across TRs (i.e., temporal brain scores) for each condition, the average of the AM tasks and the average of the control tasks.

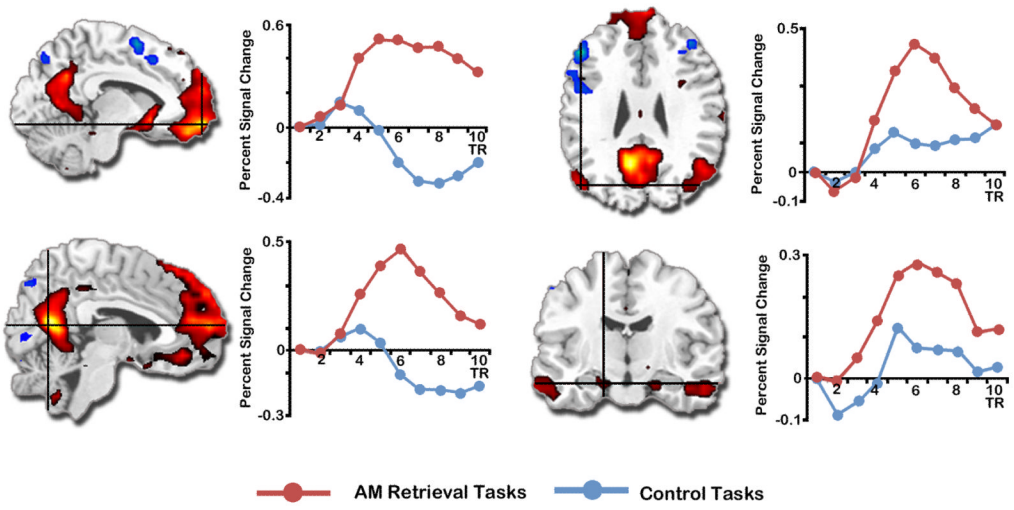

Figure 3. Network Associated with AM Retrieval relative to Control Tasks

Shown in warm colors are the regions comprising the network associated with the AM tasks: right medial prefrontal cortex (upper left panel, xyz = −8 60 −12); left medial parietal cortex (lower left panel, xyz = 4 −60 12); left angular gyrus (upper right panel, xyz = −48 −76 28); and left hippocampus (lower right panel, xyz = −16 −12 −20). The crosshair indicates the location of the peak voxel. Corresponding plots of percent signal change for AM and control tasks extracted from these regions are also presented. Some of the regions comprising the network associated with the control tasks are also visible in the images of activation (in cool colors). Images of activation are superimposed over a standard anatomical template and thresholded using a bootstrap ratio of ±3.2 (equivalent to $p < .001$).

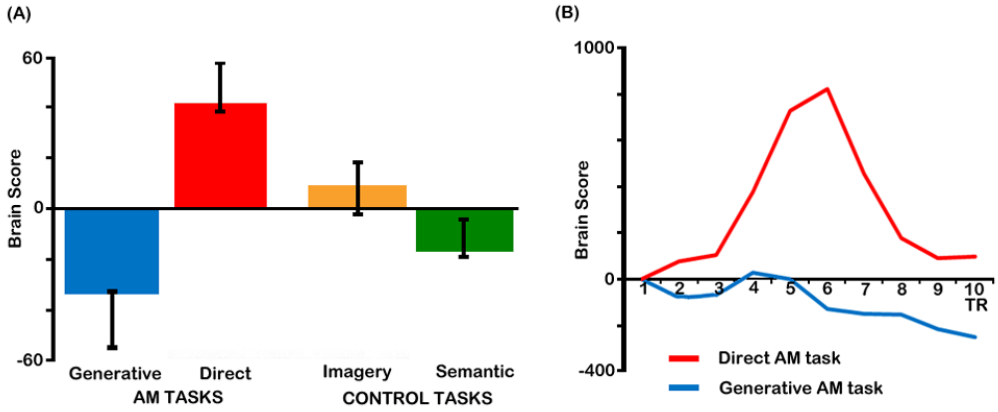

Figure 4. ST-PLS Contrast of Direct and Generative AM Tasks

(a) Average brain scores with 95% confidence intervals for the AM (direct, generative) and control (imagery, semantic) tasks. (b) Average brain scores plotted across TRs (i.e., temporal brain scores) for the direct and generative conditions.

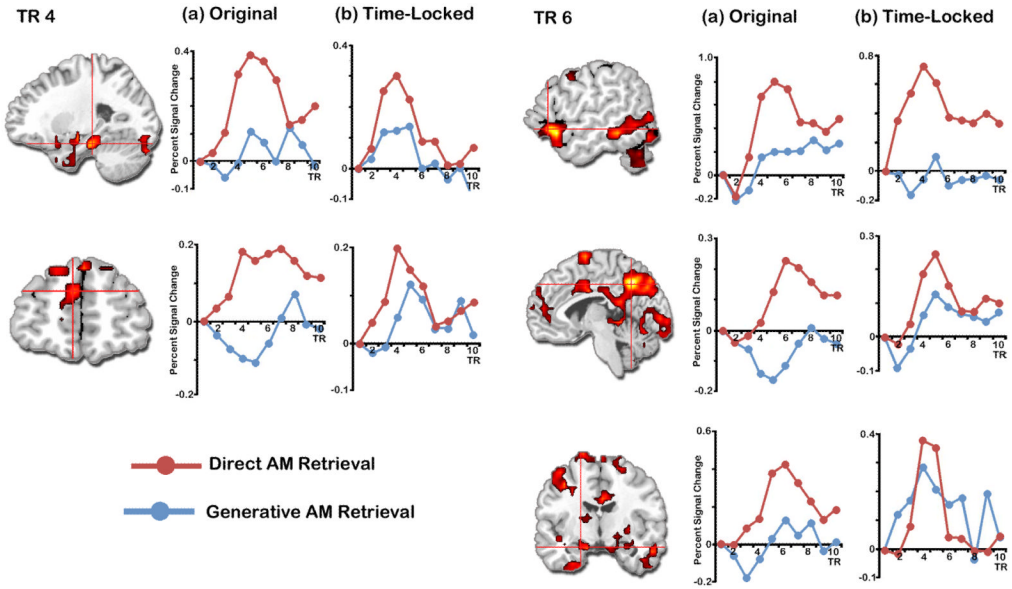

Figure 5. Network Associated with Direct relative to Generative AM Retrieval

Shown in warm colors are the regions comprising the network differentially associated with direct retrieval relative to generative retrieval. At TR 4, this network included left parahippocampal gyrus (upper left panel, xyz = −24 −28 −20) and left medial prefrontal cortex (lower left panel, xyz = −4 52 24). Regions peaking at TR 6 included left inferior frontal gyrus (upper right panel, xyz = −56 24 −8), left medial parietal cortex (middle right panel, xyz = −4 −56 40), left hippocampus/entorhinal cortex (lower right panel, xyz = −12 −8 −20). The crosshair indicates the location of the peak voxel. Corresponding plots of percent signal change for direct and generative AM retrieval extracted from the original analysis (a) and the time-locked analysis (b) are presented. Images of activation are superimposed over a standard anatomical template and thresholded using a bootstrap ratio of ±2.8 (equivalent to $p < .005$).

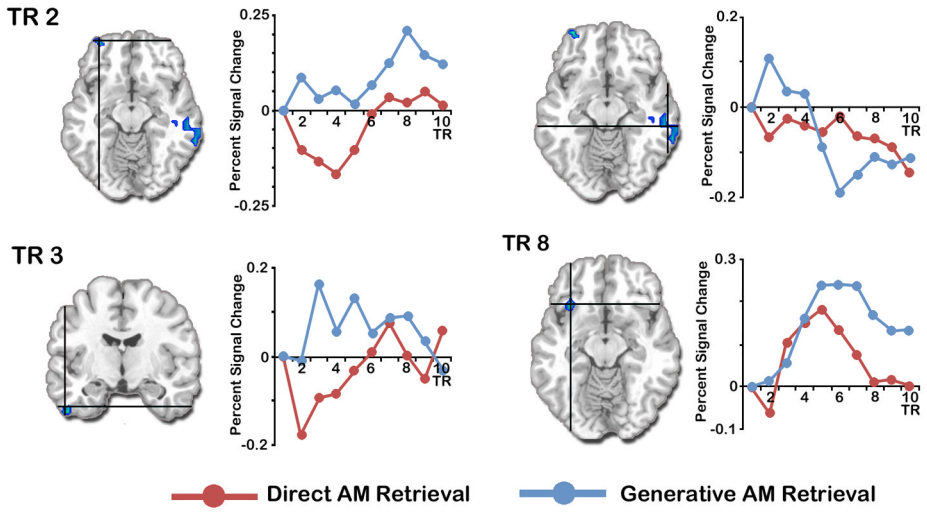

Figure 6. Network Associated with Generative relative to Direct AM Retrieval

Shown in cool colors are the regions comprising the network differentially associated with generative retrieval relative to direct retrieval. Activation of this network emerged early in the trial: in TR 2, this network included left anterior middle frontal gyrus (upper left panel, xyz = −32 60 −12) and right lateral temporal cortex (upper right panel, xyz = 60 −28 −12); and in TR 3, it included left lateral temporal cortex (lower left panel, xyz = −52 −8 −40) and left inferior frontal gyrus (lower right panel, xyz = −32 24 −12). The crosshair indicates the location of the peak voxel. Corresponding plots of percent signal change for direct and generative AM retrieval extracted from the original analysis are presented. Images of activation are superimposed over a standard anatomical template and thresholded using a bootstrap ratio of ±2.8 (equivalent to $p < .005$).

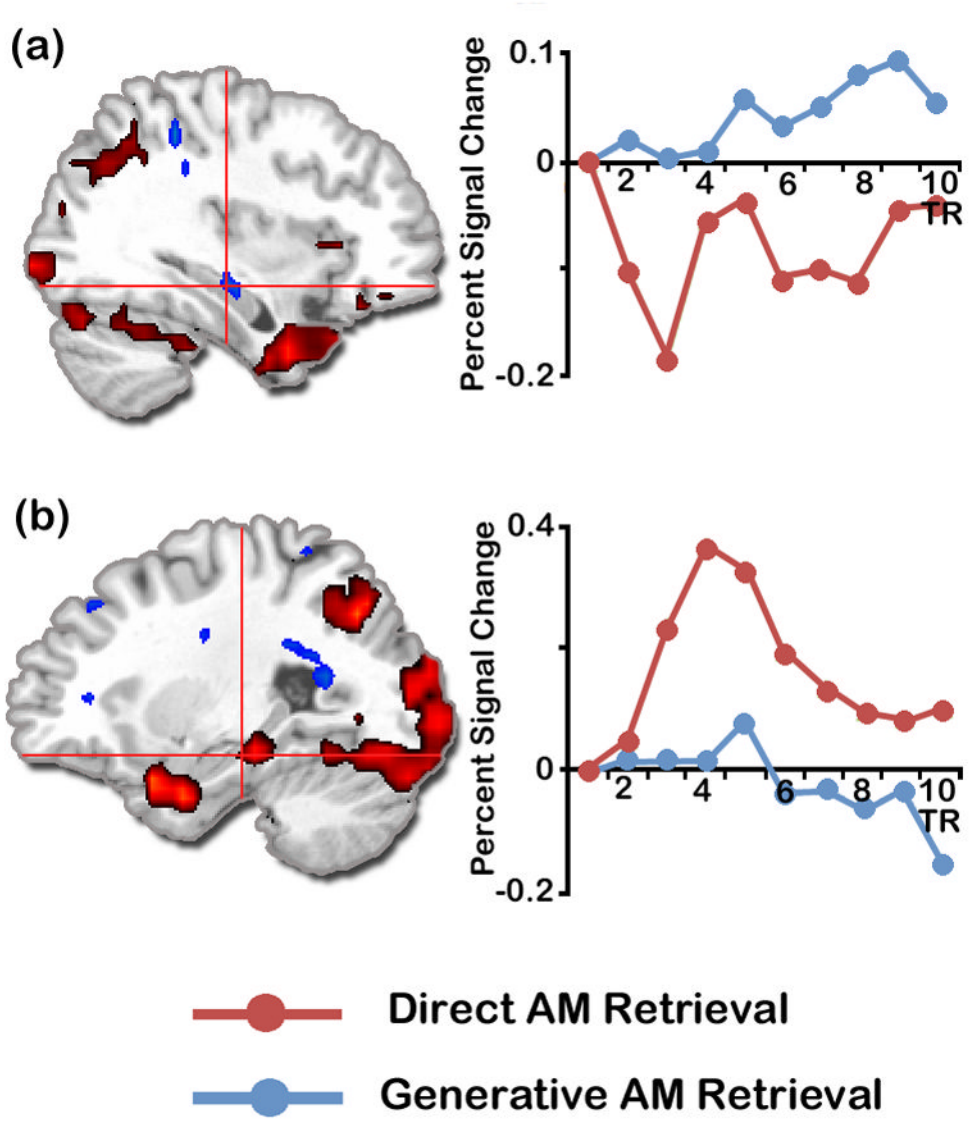

Figure 7. Differential Hippocampal Activity Associated with Direct and Generative AM Retrieval

The PLS analysis time-locked to RT revealed differential hippocampal activity for both AM retrieval conditions: generative retrieval was associated with right hippocampal activity (cool colors; upper panel, xyz = 36 −20 −12) while direct retrieval was associated with left hippocampal activity (warm colors; lower panel, xyz = −24 −20 −16). The crosshair indicates the location of the peak voxel. Corresponding plots of percent signal change for direct and generative AM retrieval extracted from the time-locked analysis are presented. Images of activation are superimposed over a standard anatomical template and thresholded using a bootstrap ratio of ±2.8 (equivalent to $p < .005$).

Table 1

Average behavioral data for AM and Control Conditions

Variable	AM Conditions		Control Conditions	
	Direct	Generative	Semantic	Imagery
Mean reaction time, pre-scan session (ms)	9079.14 (1761.73)	8634.72 (1431.12)		
Mean reaction time, scan session (ms) ***	5126.22[b] (1302.33)	8199.77[a] (1861.68)	9101.44[c] (1840.57)	9300.11[c] (2146.18)
Mean number of successful trials (max. 16)***	15.40[d] (0.83)	12.50[e] (2.47)	14.67[e] (1.72)	14.87[e] (1.25)
Mean number of trials, matched analysis	12.87[e] (0.92)	12.50[e] (2.47)	12.67[e] (1.72)	12.87[e] (1.25)
Mean detail rating (1–5) *	3.00 (0.67)	2.69 (0.57)		
Mean emotion rating (1–5)	2.08 (0.72)	1.87 (0.61)		
Mean personal significance rating (1–5) **	2.32 (0.58)	1.99 (0.41)		
Mean time since event occurrence (years)	4.65 (1.30)	5.25 (1.81)		
Mean time since last rehearsal (weeks) ***	3.82 (0.85)	88.11 (40.47)		
Mean percentage of trials with field perspective	95% (0.06)	94% (0.08)		

Note. Standard deviations are given in parentheses. Main effect of condition:

* $p<.05$;

** $p<.01$;

*** $p<.001$. For repeated-measures ANOVAs, lettering indicates which conditions differ as revealed by post-hoc Bonferroni tests (conditions with different letters differ significantly; conditions with the same letter do not differ). Max = maximum; ms = milliseconds.

Table 2

Regions differentially associated with the control tasks relative to the AM tasks

Brain Region	MNI co-ordinates			BSR	TRs Active
	X	y	z		
TR 6					
R Superior Parietal Lobule (BA 7)	12	−64	48	−4.69	4 5 6* 7 8
TR 7					
L Middle Frontal Gyrus (BA 10)	−48	40	4	−10.06	3 4 5 6 7* 8 9 10
L Medial Frontal Gyrus (BA 6)	−4	4	60	−8.28	4 5 6 7* 8 9 10
Insula	−32	16	4	−6.03	6 7* 8 9 10
TR 8					
L Inferior Temporal/Fusiform Gyrus (BA 37)	−52	−60	−20	−10.78	4 5 6 7 8* 9 10
TR 9					
R Middle Frontal Gyrus (BA 9/46)	48	40	28	−7.44	5 6 7 8 9* 10
L Inferior Frontal Gyrus (BA 45)	−44	16	4	−3.66	9*
TR 10					
L Cerebellum	24	−72	−32	−5.59	5 10*
R Inferior Frontal Gyrus (BA 44)	56	12	24	−4.81	7 8 9 10*
L Superior Parietal Lobule (BA 7)	−20	−80	40	−9.18	4 5 6 7 8 9 10*
R Inferior Parietal Lobule (BA 40)	52	−40	36	−9.74	4 5 6 7 8 9 10*
L Inferior Frontal Gyrus (BA 44)	−56	12	4	−11.98	5 6 7 8 9 10*

Note. Only clusters peaking during TRs 6 – 10 are reported here. For each cluster, the TRs of activation are noted, and the peak of activation (from which the bootstrap ratio and coordinates are taken) is indicated by an asterisk. Bootstrap ratios were greater than ±3.2 (roughly equivalent to $p < .001$), and clusters had a spatial extent of at least 5 voxels ($4\times4\times4$ mm^3). BA = Brodmann area; BSR = Bootstrap ratio; L = left; R = right.

Table 3

Regions differentially associated with the AM tasks relative to control tasks.

Brain Region	MNI co-ordinates			BSR	TRs Active
	X	y	Z		
TR 5					
R Inferior Frontal Gyrus (BA 47)	32	32	−24	7.09	4,5*,6,8,9
L Middle Temporal Gyrus (BA 21)	−56	12	−32	9.03	5*,6,7,8,9,10
L Lingual Gyrus (BA 19)	−20	−84	−16	4.48	5*
TR 6					
L Middle Frontal Gyrus (BA 6)	−40	12	52	4.49	6*
R Superior Frontal Gyrus (BA 6)‡	8	12	64	3.99	6*
L Uncus/Parahippocampal Gyrus (BA 28/35)	−20	8	−24	4.28	6*,7,9
L Parahippocampal Gyrus (BA 35) §	−24	−28	−16	5.93	5,6*,7,8,9
L Hippocampus/Parahippocampal Gyrus (BA 34)	−16	−12	−20	4.81	6*,7,8
L Angular Gyrus (BA 39)	−48	−76	28	6.34	5,6*,7,8
L Middle Occipital Gyrus (BA 18)	−32	−96	4	4.24	6*
TR 7					
L Superior Frontal Gyrus (BA 9)	−20	40	36	5.23	4,7*
R Middle Temporal Gyrus (BA 39)	52	−68	24	7.02	4,5,6,7*,8,9,10
L Parahippocampal Gyrus (BA 37)	−36	−52	−8	3.77	7*
R Medial Parietal Cortex (BA 23/30/31)	4	−60	12	12.21	4,5,6,7*,8,9,10
TR 8					
L Medial Frontal Gyrus (BA 10)	−8	60	−12	13.65	4,5,6,7,8*,9,10
R Hippocampus/Parahippocampal Gyrus (BA 28)	20	−12	−20	5.66	6,7,8*,9
L Parahippocampal Gyrus (BA 36)‡	−32	−16	−24	3.69	8*
L Cerebellum	−36	−88	−40	7.72	5,6,7,8*,9

Note. Only clusters peaking during TRs 4 – 8 and falling within the AM network (core and secondary regions; Svoboda et al., 2006) are reported here. For each cluster, the TRs of activation are noted, and the peak of activation (from which the bootstrap ratio and coordinates are taken) is indicated by an asterisk. Bootstrap ratios were greater than ±3.2 (roughly equivalent to $p < .001$), and clusters had a spatial extent of at least 5 voxels (4×4×4 mm^3). BA = Brodmann area; BSR = Bootstrap ratio; L = left; R = right;

‡Peak voxel not active when controlling for detail and bin-size;

§Cluster extends into hippocampus when controlling for detail and bin-size.

Table 4

Regions differentially associated with direct or generative AM retrieval

Brain Region	MNI co-ordinates			BSR	TRs active
	x	y	z		
Direct Retrieval					
TR 5					
L Middle Frontal Gyrus (BA 9)	−32	48	28	5.78	5* 7 9 10
L Medial Frontal Gyrus (BA 9)	−4	52	24	4.63	3 4 5* 6 8
R Medial Frontal Gyrus (BA 10)	4	64	16	5.96	2 3 4 5* 6 7 8 9 10
L Middle Temporal Gyrus (BA 21/37)	−56	−44	−8	6.58	5* 6 7 8 9 10
R Middle Temporal Gyrus (BA 21)	56	−4	−24	10.5	4 5* 6
L Hippocampus/Amygdala	−20	−8	−20	9.64	4 5*6
L Parahippocampal Gyrus/HC (BA36)	−24	−28	−20	5.56	4,5*,6,7,9,10
L Inferior/Superior Parietal Lobule (BA 7/40)	−36	−64	52	8.97	4,5*,6,7,8,9,10
R Cuneus (BA 18/19)	20	−84	20	4.2	5*,6,7
TR 6					
B Medial Prefrontal Cortex (BA 10)	0	64	16	4.86	3 6*
L Inferior Frontal Gyrus (BA 45/44)	−56	24	−8	7.36	3 4 6* 9 10
R Inferior Frontal Gyrus (BA 47/45)	55	28	−8	5.33	3 4 5 6* 7 9 10
L Superior Frontal Gyrus (BA 6)	−8	4	72	6.36	4,5,6*
L Middle Frontal Gyrus (BA 11)	−32	44	−8	3.53	4,6*
R Parahippocampal Gyrus (BA28)	16	8	−28	6.78	3 4 5 6* 7 9 10
L Hippocampus/Entorhinal Cortex (BA 34)	−12	−8	−20	5.30	6* 7
R Inferior/Middle Temporal Gyrus (BA 37)	48	−60	−20	6.49	5 6* 7 8 9 10
R Middle Temporal Gyrus (BA 39)	36	−60	24	4.14	6*
L Medial Parietal Cortex(BA 7/23/31)†	−4	−56	40	7.34	4 5 6* 7 8 9 10
L Inferior Parietal/Supramarginal Gyrus (BA 40)	−64	−36	28	5.29	5,6*,7
R Inferior/Superior Parietal Lobule (BA 7/40)	36	−52	40	7.38	4,5,6*,7,8,9,10
L Occipital Cortex (BA 17/18/19)	−4	−68	0	5.10	3,4,5,6*,7,8,9,10
R Middle Occipital Gyrus (BA 19)	52	−80	−8	4.71	5,6*,7
Generative Retrieval					

Brain Region	MNI co-ordinates			BSR	TRs active
	x	y	z		
TR 2					
L Middle Frontal Gyrus (BA 10)	−32	60	−12	−5.05	2* 9
R Inferior Frontal Gyrus (BA 44) ‡	56	12	16	−3.83	2* 8
L Middle Temporal Gyrus (BA 21)	−56	−32	−4	−3.48	2*
R Middle Temporal Gyrus (BA 21)	60	−28	−12	−4.03	2*
L Precuneus (BA 31) ‡	−12	−72	20	−3.62	2*4
L Inferior Parietal Lobule (BA 40) ‡	−48	−40	40	−3.24	2*
R Inferior Parietal Lobule (BA 40) ‡	52	−36	40	−3.26	2*
R Middle Occipital Gyrus (BA 19)	28	−92	20	−4.33	2*
R Cerebellum	48	−68	−40	−4.67	2* 4 5 6 7 8 10
TR 3					
L Middle Frontal Gyrus (BA 9) ‡	−36	28	40	−4.46	2 3* 4
L Inferior Temporal Gyrus (BA 21)	−52	−8	−40	−4.82	3*
TR 8					
L Medial Frontal Gyrus (BA 8/9)	−12	36	32	−4.60	8*
L Inferior Frontal Gyrus (BA 47)	−32	24	−12	−5.74	7 8* 10
L Inferior Frontal Gyrus (BA 45)	−44	32	4	−4.20	8*
L Superior Frontal Gyrus (BA 10)	−20	48	8	−3.64	8* 9

Note. Only clusters falling within the AM network (core and secondary regions; Svoboda et al., 2006) are reported here. Reported clusters peak during TRs 4–7 for direct retrieval and TRs 2–3 and 8–10 for generative retrieval. For each cluster, the TRs of activation are noted, and the peak of activation (from which the bootstrap ratio and coordinates are taken) is indicated by an asterisk. Bootstrap ratios were greater than ±2.8 (roughly equivalent to $p < .005$), and clusters had a spatial extent of at least 5 voxels (4×4×4 mm^3). BA = Brodmann area; BSR = Bootstrap ratio; L = left; R = right.

† Extends bilaterally;

‡ Peak voxel not active when controlling for detail and bin-size.

Table 5

Regions differentially associated with direct or generative AM retrieval from the time-locked PLS analysis

Brain Region	MNI co-ordinates			BSR	TRs active
	x	Y	z		
Direct Retrieval					
R Superior/Medial Frontal Gyrus (BA 6)	−4	4	60	3.97	3* 4 5
L Middle Frontal Gyrus (BA 6)	−36	−4	56	4.27	3* 4 5
R Middle Frontal Gyrus (BA 46)	60	28	24	8.40	3* 4 5
L Inferior Frontal Gyrus (BA 44)	−56	8	32	9.11	2 3* 4 5 6 7 8
L Hippocampus	−24	−20	−16	3.31	3* 4 5 6 7
R Uncus (BA 28)	24	4	−32	7.05	3* 4
L Inferior Parietal Lobule (BA 40)	−36	−56	48	7.08	2 3* 4 5 6
L Supramarginal Gyrus (BA 39/40)	−60	−56	24	3.43	3* 4
R Superior Parietal Lobule (BA 7)	28	−68	40	5.04	2 3* 4 5 6
R Occipital Cortex (BA 17/18/19)	20	−84	−16	7.92	2 3* 4 5
Generative Retrieval					
R Medial Frontal Gyrus (BA 6)	12	−8	60	−3.85	3*
R Orbitofrontal Gyrus (BA 11)	8	48	−28	−3.52	2 3*
R Cingulate Gyrus (BA 24)	4	−8	40	−4.64	2 3*
L Superior Temporal Gyrus (BA 22/39)	−32	−56	16	−5.07	3*
R Superior Temporal Gyrus (BA 22)	48	−8	0	−4.31	3*
R Hippocampus	36	−20	−12	−4.36	2 3* 6 7 8 9
R Posterior Cingulate Gyrus (BA 31)	12	−24	44	−3.82	3* 9
L Inferior Parietal Lobule (BA 40)	68	−28	24	−3.90	3* 7 9
R Inferior Parietal Lobule (BA 40)	36	−40	48	−4.59	3*
R Superior Parietal Lobule (BA 7)	24	−56	64	−6.00	3*
L Cerebellum	−4	−56	−16	−5.19	3*

Note. Only clusters peaking during TR 3 and falling within the AM network (core and secondary regions; Svoboda et al., 2006) are reported here. Note all clusters were evident when controlling for detail and bin size. For each cluster, the TRs of activation are noted, and the peak of activation (from which the bootstrap ratio and coordinates are taken) is indicated by an asterisk. Bootstrap ratios were greater than ±2.8 (roughly equivalent to $p < .005$), and clusters had a spatial extent of at least 5 voxels (4×4×4 mm^3). BA = Brodmann area; BSR = Bootstrap ratio; L = left; R = right.

Appendix A

Lists of Cue Words

List A	List B	List C
PENCIL	DOLL	CAR
OVEN	HORSE	BOWL
INSTRUMENT	SUGAR	POTATO
ANKLE	KETTLE	CANDY
TRUCK	REVOLVER	STAR
ROCK	FOX	TREE
STAIN	LIP	FLOWER
TOBACCO	PEACH	LEMON
BOOK	CAT	UMBRELLA
STRAWBERRY	SHOES	PEPPER
INSECT	LETTER	BOTTLE
PHOTOGRAPH	MEAT	COFFEE
TOAST	SNAKE	IRON
FLAG	PIANO	JELLY
WINDOW	BRAIN	FUR
BULLET	LOBSTER	DOOR

List D	List E	List F
WINE	DRESS	STRING
TOY	TABLESPOON	CHAIR
BABY	ARM	BIRD
SHIP	BODY	MOSS
FIREPLACE	REFRIGERATOR	TOWER
RATTLE	MICROSCOPE	FORK
GRASS	PIPE	CLAW
TICKET	POLE	BEAVER
COIN	DOLLAR	VEHICLE
NEWSPAPER	PAPER	BUTTER
CLOCK	HAMMER	ELEPHANT
COTTON	APPLE	TOOL
TABLE	PLANT	PALACE
CORN	SALAD	DIAMOND
SLIPPER	NAIL	LIME
ENGINE	FROG	BUTTERFLY