



Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Laboratory-based and autobiographical retrieval tasks differ substantially in their neural substrates

Kathleen B. McDermott*, Karl K. Szpunar, Shawn E. Christ

Washington University in St. Louis, United States

ARTICLE INFO

Article history:

Received 12 September 2008

Received in revised form

21 November 2008

Accepted 21 December 2008

Available online 30 December 2008

Keywords:

Memory

Retrieval

Event memory

Autobiographical memory

Laboratory memory

Retrieval success

Neuroimaging

Meta-analysis

Recognition memory

Free choice recognition

Old/new recognition

fMRI

Activation likelihood estimation

ABSTRACT

In designing experiments to investigate retrieval of event memory, researchers choose between utilizing laboratory-based methods (in which to-be-remembered materials are presented to participants) and autobiographical approaches (in which the to-be-remembered materials are events from the participant's pre-experimental life). In practice, most laboratory studies have utilized old/new recognition memory, and most autobiographical memory studies have used the Galton–Crovitz word cueing technique [Crovitz, H.F., & Schiffman, H. (1974). Frequency of episodic memories as a function of their age. *Bulletin of the Psychonomic Society*, 4, 517–518]. What are the implications of these methodological choices for understanding the component processes and underlying neural substrates of memory retrieval? An Activation Likelihood Estimation (ALE) meta-analysis procedure [Turkeltaub, P., Eden, G., Jones, K., & Zeffiro, T.A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage*, 16, 765–780] was used to construct two whole-brain statistical maps: one showing brain regions that are consistently implicated when the task utilized is old/new recognition memory and one showing regions that tend to emerge when autobiographical event memory is queried. A comparison of the two maps shows very few regions of overlap. This basic methodological choice has a profound impact on the conclusions reached regarding human memory retrieval and its neural substrates.

© 2008 Elsevier Ltd. All rights reserved.

Words to the memory researcher are what fruit flies are to the geneticist: a convenient medium through which the phenomena and processes of interest can be explored and elucidated. . . . Words are of no more intrinsic interest to the student of memory than Drosophila are to a scientist probing the mechanisms of heredity. . . . Tulving, 1983, p. 146.

Broadly speaking, research on human memory has followed two traditions. The first approach is to use laboratory-based methods in the tradition of verbal learning and memory (Hall, 1971). The mindset of this tradition is captured by Tulving's quote above. In this experimental tradition, subjects might be asked to study a list of words and then a few minutes later be tested on that list. The idea is that each word in the study list constitutes a micro-event, and understanding how people recall or recognize such micro-events informs how life events are retrieved.

The second tradition – often referred to as the autobiographical memory or everyday memory approach – is more naturalistic in that researchers study real-life memories from peoples' past. One popular methodological technique is to give participants cue words (e.g., *airplane*) and ask them to use each cue word as a starting point to recall a related memory (Crovitz & Schiffman, 1974; Galton, 1879).

Obviously, the two orientations differ substantially on the surface, but the underlying assumption (certainly in the case of the laboratory-based methods) is that there will be convergence on the conclusions regarding the basic principles of memory. Each tradition has advantages and disadvantages, and considerable debate has arisen regarding the more appropriate approach (Banaji & Crowder, 1989; Koriat & Goldsmith, 1996; Neisser, 1978); we mention just a few of the factors that bear on the decisions of which approach to use.

Studies in the laboratory tradition offer strict experimental control: one can know with certainty what objective events (e.g., words) were present during the encoding phase, and variables can be manipulated during encoding and retrieval phases. One can statistically control for guessing, too, in that false alarm rates can be measured in old/new recognition. These studies, however, entail

* Corresponding author at: Department of Psychology, CB 1125, Washington University, St. Louis, MO 63130-4899, United States. Tel.: +1 314 935 8743.

E-mail address: kathleen.mcdermott@wustl.edu (K.B. McDermott).

compromises in the area of ecological validity. How well does a person's recognition of whether the word "ham" had been read 10 min prior inform understanding of the processes underlying recollection of life events—events that are complex, spatially and contextually rich, emotional, and self-focused? The assumption is that these studies capture core processes of memory and that the social and visuospatial factors that accompany memories from one's life are added in on top of these core memorial processes (Cabeza et al., 2004; Svoboda, McKinnon, & Levine, 2006; Tulving, 1983; Winograd, 1993). The heart of memory, though, is thought to be experimentally tractable through the use of micro-events (e.g., lists of words or pictures).

Studies in the autobiographical memory tradition sacrifice experimenter control in favor of ecological validity. People are asked to remember the events of their lives. Although memory cues can be varied, as can instructions (e.g., the time period from which to remember), there is no experimenter control over the events remembered, and there is no way to know how faithfully a person's recollection accords with the initial experience. The methods differ in time, too, not only in that the events of interest have occurred on different timescales (weeks or years for studies in the autobiographical memory tradition compared with minutes/hours in the laboratory memory tradition): It can take people on the order of 8–12 s to construct a vivid autobiographical memory (Robinson, 1976), compared to recognition memory decisions, which often occur in a second or two. This difference has made direct empirical comparisons of the two approaches challenging (especially with respect to neuroanatomical correlates).

To this point, most empirical studies of human memory have followed from the experimental tradition, and there is little crosstalk between traditions (although see Cabeza et al., 2004 for an exception). This characterization applies not only to the behavioral psychological literature but also to neuroimaging studies. What are the implications of this methodological choice for understanding the neural substrates of memory retrieval?

What might be hypothesized for a comparison of regions involved in laboratory-based and autobiographical memory investigations? Several studies have attempted to contrast the two (e.g., Cabeza et al., 2004; Conway et al., 1999; Fink et al., 1996; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002). Nyberg et al. found that laboratory-based cued recall and recognition tests produced similar brain activity, which differed from that seen with autobiographical memory. Cabeza et al. found many similarities between a laboratory-based and autobiographical memory task, and the differences were in the direction of more activation for the autobiographical memory task within regions interpreted as contributing self-relevant processing (medial prefrontal cortex), visual-spatial memory (occipital and parahippocampal regions) and recollection (hippocampus). Taken together, the results of these two studies highlight the uncertainty surrounding the question. Do laboratory and autobiographical memory have little neural activation in common (as might be concluded from an extrapolation of Nyberg et al.'s finding)? Or is it the case that the two share a core set of processes/regions, but with autobiographical memory calling upon an additional set of processes (e.g., more self-relevant, recollective, and emotional processing, as might be suggested by Cabeza et al.'s findings)?

In addition, a careful reading of the separate literatures shows that the focus of interest tends to be on different regions. Qualitative reviews of the autobiographical memory literature (Cabeza & St. Jacques, 2007; Conway, Pleydell-Pearce, Whitecrow, & Sharpe, 2002; Gilboa, 2004; Maguire, 2001; Svoboda et al., 2006) have focused on posterior cingulate, left and medial prefrontal cortices, as well as hippocampus and surrounding regions. Hippocampal activity is less commonly observed in laboratory-based studies of retrieval (but see Diana, Yonelinas, & Ranganath, 2007), for which

the focus of review articles tends to lie on the role of prefrontal cortex and lateral and medial parietal cortices (e.g., McDermott & Buckner, 2002; Nyberg, Cabeza, & Tulving, 1996; Shannon & Buckner, 2004; Wagner, Shannon, Kahn, & Buckner, 2005).

At this point, most neuroimaging studies of memory in the laboratory tradition have utilized old/new (i.e., free choice or yes/no) recognition memory, with relatively few employing other tasks, such as forced choice recognition memory, cued recall, or free recall. Hence, conclusions from this tradition tend to draw heavily on a single task, one that can rely both on vivid recollection of the past and general familiarity (see Yonelinas, 2002 for review). The literature on autobiographical memory is more diverse, as will be reviewed below, but it is generally the case that verbal cues are used as a retrieval cue, and activation in this condition is compared to some baseline task, which varies across studies.

1. The present approach

The goal of the present report is to examine the extent to which regions commonly activated in laboratory-based memory studies overlap with (or differ from) those found in studies of autobiographical event memory. To this end, two quantitative meta-analyses were performed using an Activation Likelihood Estimation (ALE) procedure, which, as will be reviewed, reveals at the whole-brain level the likelihood of activation across the literature.

To examine regions revealed from laboratory-based studies of memory retrieval, we adopted one of the region-definition approaches receiving the greatest focus within this neuroimaging literature—identification of regions seemingly important for "retrieval success," or the feeling of recollection that emerges once one makes contact with a to-be-remembered event. In most such studies, activity on an old/new recognition task for hits and correctly rejected lures has been contrasted (at the whole-brain level). Using the coordinates reported, a reliable estimate can be obtained for the regions that tend to be more active for cases in which a person tries to recollect the past and succeeds (hits) than when the retrieval attempt fails (correctly rejected lures). This specific contrast was chosen because it seems to represent the essence of memory retrieval – the moment of retrieval of one's past (albeit words studied minutes previously) – and because many studies have now reported whole-brain analysis of this contrast (or slight variations).¹ Hence, we can ask which regions – on average – appear when one identifies regions contributing to memory retrieval in this way. We will refer to this approach as being laboratory-based because to-be-remembered information takes place in the laboratory (in contrast to autobiographical memory studies, in which people are asked to retrieve information about their lives prior to participation in the study).

Second, we identified regions that emerge in studies of autobiographical memory. For this analysis, a single prototypical contrast was not possible because there is little convergence across studies with respect to the specific task of interest and even less agreement on the appropriate baseline measure (for discussion see Maguire, 2001). Nonetheless, we can still ask the critical question: What commonalities emerge across studies of autobiographical memory? Indeed, a quantitative meta-analysis is a highly appropriate approach for attempting to identify the core regions contributing to autobiographical memory in that it allows the activations common across the diverse set of approaches to emerge. That is, any individual comparison can easily be criticized for one reason or another, but across all tasks attempting to examine memory for episodes

¹ A cleaner approach would be to contrast hits and misses (so that both item classes had been studied) but in many studies there are too few misses to obtain a reliable signal estimate for this class of items.

in one's past relative to a control task, what brain regions tend to activate?

2. Methods

Articles were initially identified by searching the Medline databases (www.nlm.nih.gov/pubs/factsheets/medline.html) for peer-reviewed articles whose titles, keywords, or abstracts included the terms "retrieval success," or "autobiographical memory" and any of the terms "fMRI," "MRI," "PET," or "neuroimaging." A few additional articles were identified by further related searches. From among these candidate articles, one author (KS) then identified studies reporting conditions of interest (see Appendix A in Supplementary material).

Studies were considered for inclusion if they were published before February 2008, included a voxelwise (i.e., whole-brain) contrast for data of interest, and reported areas of peak activation in a standardized coordinate space (e.g., Talairach and Tournoux, 1988). We restricted our analysis to data from neurologically normal young adults (i.e., no patient populations or older adult participants). Analysis-specific inclusion criteria are presented below.

2.1. Laboratory-based studies

For the laboratory-based analysis, we sought a comparison of retrieval success relative to a condition of retrieval attempt but no success. In most cases ($N = 14$), the comparison was between hits and correctly rejected lures on an old/new recognition test, in which visually presented words, pictures, objects, or faces were encoded and retrieved. Variations can be seen in Appendix B in Supplementary material. We included all studies listed in the meta-analysis, because we were interested in regions generally associated with retrieval success. Exclusion of any particular set of tasks from the analysis (e.g., those using faces as stimuli) did not appreciably influence the overall pattern of results, although with more power such factors may prove to be important. Within the 18 studies, 235 activation foci emerged for inclusion in this analysis (see Appendix B in Supplementary material).

2.2. Autobiographical studies

Studies identified for inclusion in the autobiographical analysis needed to evoke personal event memories and contain a control task that did not invoke laboratory-based methods such as those considered above. Studies using laboratory-based retrieval as a comparison task were excluded as a means of ensuring that regions of overlap between autobiographical and laboratory-based retrieval could be identified (so as not to subtract out such commonalities). Also, comparisons of two autobiographical conditions (e.g., recent vs. remote memories) were excluded. Otherwise, all other comparison tasks were included.² Two instances of duplicate publication of the same dataset were identified, and in those cases only one of the datasets were used (so as not to over-represent those data in the analysis). Several datasets contained more than one relevant contrast, in which case we chose only one of them (with an eye toward capturing variability across studies).

With this approach, 210 foci showing greater activation for autobiographical retrieval than a control task were obtained from 14 studies (see Appendix C in Supplementary material). As with the laboratory-based tasks, these studies were associated with a variety of memory-evoking cues (e.g., words, sentences, pictures). Again, all studies were included in the analysis, and the exclusion of any particular cueing paradigm did not influence the overall pattern of results (but may, with time and an expanding literature, prove to be important).

All of the compiled foci had been translated previously into a standardized atlas space. The coordinates of the foci had been derived using a variety of analysis methods (e.g., SPM, AFNI), though. To account for differences among the anatomical templates and registration algorithms used for spatial normalization in the various analysis packages, we utilized the Computerized Anatomical Reconstruction and Editing Toolkit (Caret, Van Essen et al., 2001) along with the Population-Average Landmark- and Surface-based (PALS) atlas (Van Essen, 2005) to remap the coordinates into a single common atlas space (for a more detailed description of this approach see Christ, Van Essen, Watson, Brubaker, & McDermott, 2008). This set of mapping procedures corrects for differences in coordinate spaces across analysis methods; such differences are a significant concern because they can lead to variation greater than 1 cm (Van Essen & Dierker, 2007).

2.3. Activation Likelihood Estimation map generation

Following the appropriate coordinate transformation (described above), the methods reported by Turkeltaub, Eden, Jones, and Zeffiro (2002) and the accom-

² Note that we included coordinates from three studies using 'rest' as a comparison task. Although we are aware that this task might engage similar processes as those engaged by autobiographical memory retrieval (Gusnard et al., 2001) and thus mask processes important to autobiographical memory, the exclusion of these studies made little difference to the overall pattern of data. Accordingly, these studies are presented as part of the final analysis.

panying software (available online, <http://csl.georgetown.edu/software/>) were used to generate two whole-brain statistical maps, one representing the likelihood of activation (on a voxelwise basis) for lab-based studies and one for autobiographical memory studies. The ALE approach conceptualizes activation foci not as single points but as probability distributions surrounding each reported peak coordinate. Across studies, these probability distributions are summed, and the result is a whole-brain map in which each voxel represents the activation likelihood within the literature.

Specifically, a three-dimensional Gaussian distribution, with a standard deviation of 6 mm (full-width at half-maximum of 15 mm), was used to model the localization probability distribution for each activation coordinate. Because the question of interest was the probability of a focus lying anywhere within a given voxel (and not just at the center of the 2 mm³ voxel), the resulting values were multiplied by a factor of 8 mm. This process was repeated such that 235 and 210 probability values (for lab-based and autobiographical studies, respectively, one for each of the activation foci) were generated for each voxel. These values were then used to calculate the likelihood that at least one of the activation foci fell within a given voxel. The result was a pair of whole-brain ALE maps: one for laboratory memory and one for autobiographical memory.

We then thresholded the ALE maps to achieve a p -value of .05 using the following procedure. For both maps, 5000 permutations of randomly distributed foci were subjected to the methods outlined above. The resulting values were used to calculate the expected probability value for a given voxel under the null hypothesis at various levels of statistical significance (see Turkeltaub et al., 2002). These data permitted a thresholding of the whole-brain ALE maps so as to achieve a p -value of .05 while controlling for false discovery rate (Genovese, Lazar, & Nichols, 2002; Laird et al., 2005).

The surface data reported here are available for download via the SumsDB database (<http://sumsdb.wustl.edu/sums/directory.do?id=6722273>), and the volumetric data are available from the first author upon request.

2.4. Activation localization

Localization of significant ROIs to geographic regions was based on a probabilistic sulcal identity map generated using the 12 contributing brains of the PALS-B12 atlas (Van Essen, 2005) in combination with a subjective volumetric examination of the activations overlain on a structural image in the same coordinate space; this latter method was especially important for activations along the medial wall, which are currently not described verbally within Caret. Localization to cortical areas was based on maps of cortical areas registered to the PALS atlas from the partitioning schemes of Brodmann (1909) and Öngür, Ferry, and Price (2003).

Center-of-mass coordinates were identified using an automated peak-finding algorithm, which took into account the level of statistical significance and necessitated that peaks be separated by 8 mm.

3. Results

3.1. Laboratory-based studies

The resulting ALE map for laboratory-based tasks can be seen in Fig. 1 (see also Table 1). Here one can see voxels that – across studies – tend to activate under conditions of retrieval success (e.g., more for hits than correctly rejected lures on a recognition memory test). Identified regions fall within bilateral inferior parietal cortex (more pronounced on the left), precuneus, posterior cingulate cortex, left inferior and middle frontal gyri, right middle frontal gyrus, left posterior parahippocampal gyrus, left frontal operculum, and a very small region in right frontal operculum. Center-of-mass coordinates, along with verbal labels and approximate Brodmann Areas (BA, obtained from Caret) are reported in Table 1. Some of these regions have received intense focus in the retrieval literature (e.g., right middle frontal gyrus, precuneus, lateral parietal cortex), whereas others (although consistently reported) have not yet received much attention (e.g., left frontal operculum).

3.2. Autobiographical memory methods

Fig. 2 displays regions that – across studies – are more active for autobiographical memory tasks than baseline comparison tasks. Regions seen here fall within medial prefrontal cortex, left premotor cortex, posterior cingulate/retrosplenial cortex, angular gyrus (predominantly on the left), and bilateral hippocampus/parahippocampal gyri, among other locations. More detail can be seen in Table 2. Many of these regions have been

LABORATORY METHODS

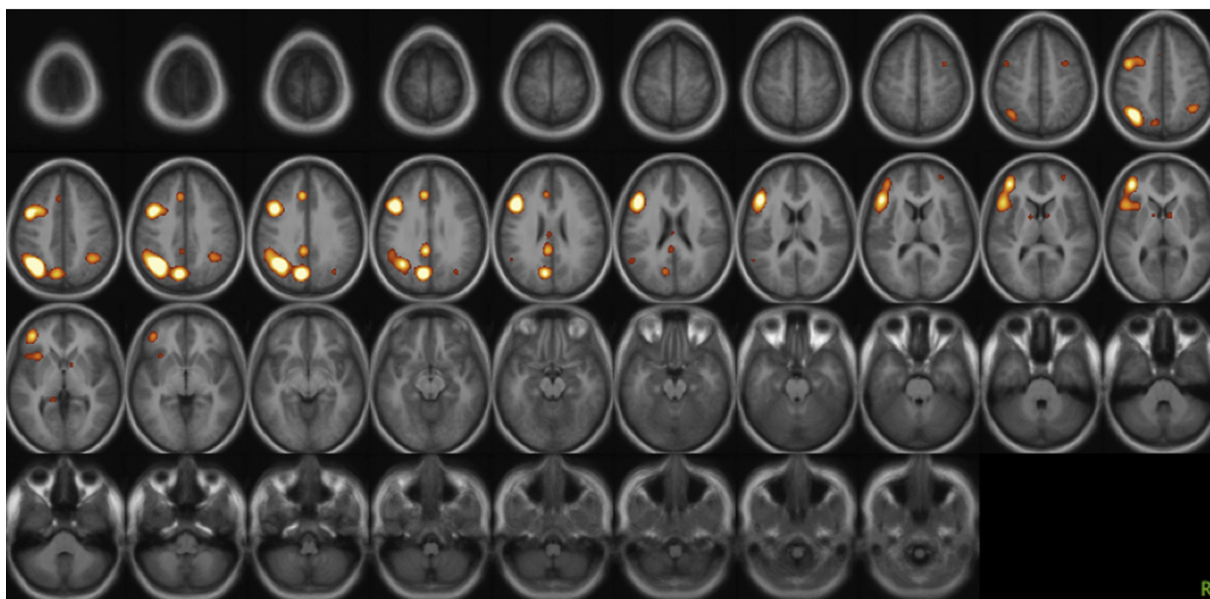


Fig. 1. ALE map for laboratory-based tasks reporting coordinates related to retrieval success. $p < .05$ (FDR-corrected).

identified previously as playing a consistent role in the retrieval of autobiographical memories (e.g., Maguire, 2001; Svoboda et al., 2006). Further, several of these regions (specifically within medial prefrontal cortex, posterior cingulate cortex, and hippocampus) appear to align with those appearing in the “default network” (Gusnard & Raichle, 2001; Raichle et al., 2001), which tends to de-activate during tasks drawing attention away from the internal

environment and onto externally relevant cognitive tasks. This network has been hypothesized to underlie self-referential thoughts such as those engaged during daydreaming, free association, autobiographical memory, and episodic future thought (Addis, Wong, & Schacter, 2007; Szpunar, Watson, & McDermott, 2007), and these cognitive processes appear to be the default processes employed when people are not actively engaged in directing attention toward the external environment (Gusnard & Raichle, 2001).

Table 1

Center-of-mass coordinates and verbal description of regions appearing in the ALE map for laboratory-based memory studies.

Lobe	BA	Peak			Voxels
		x	y	z	
Frontal					
L IFG ^a	44/45/46	-46	18	23	500
L MFG ^a	6/9/44	-42	8	35	478
L MFG ^a	10/46	-40	41	5	439
R MFG	6	32	4	49	53
R MFG	10	29	51	10	37
L operculum		-35	14	2	185
R operculum		30	19	-2	4
Parietal					
L Pcu	7/18/19/39	-9	-73	31	521
L SMG	40	-53	-55	22	70
L IPL	7/39	-36	-62	37	526
R IPL	7	38	-53	40	293
Temporal					
L PHG	27/35	-14	-41	0	27
Occipital					
R SOG	19	33	-70	30	36
L PCC	23/31	-5	-43	28	323
Cingulate	9/24/32	-7	27	31	235
Cingulate	24	-3	-22	23	34
Lentiform nucleus		-13	1	7	25
Caudate		9	2	4	45

Note: L = left; R = right; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; Pcu = precuneus; PCC = posterior cingulate cortex; SMG = supramarginal gyrus; IPL = inferior parietal lobule; PHG = parahippocampal gyrus; SOG = superior occipital gyrus.

^a Represent one contiguous swath of activity.

3.3. Direct comparison

Before considering the direct comparison, we consider a qualitative comparison of Figs. 1 and 2, which appears to reveal large differences. For example, the laboratory-based studies (Fig. 1) show left-lateralized activations within frontal and parietal cortices (in locations not seen with the autobiographical methods, Fig. 2), whereas the autobiographical studies show medial frontal activity in addition to large swaths of activity in and around hippocampus. Both maps exhibit regions within posterior cingulate cortex.

A surfaced-based direct comparison of the two ALE maps is shown in Fig. 3 (projected using Caret software). Here, the points of overlap from the two analyses can be seen (in green), along with the paradigm-selective regions in which no overlap occurs (blue = laboratory; red = autobiographical). A volumetric display of only the overlapping regions can be seen in Fig. 4. The most noticeable feature of Fig. 3 is that the maps are largely non-overlapping. There are points of intersection, however, and these occur within posterior cingulate cortex (BAs 19/31 and 23/31), left inferior frontal cortex (BA 44), and right thalamus. These regions may be particularly important for memory retrieval. Clearly, though, the laboratory memory approach does not activate a subset of regions/processes recruited by autobiographical memory tasks. Instead, the networks underlying the two comparisons seem fairly distinct.

4. Discussion

In summary, three fundamental points emerge from this dataset. First, taken separately, Figs. 1 and 2 are informative in that the iden-

AUTOBIOGRAPHICAL METHODS

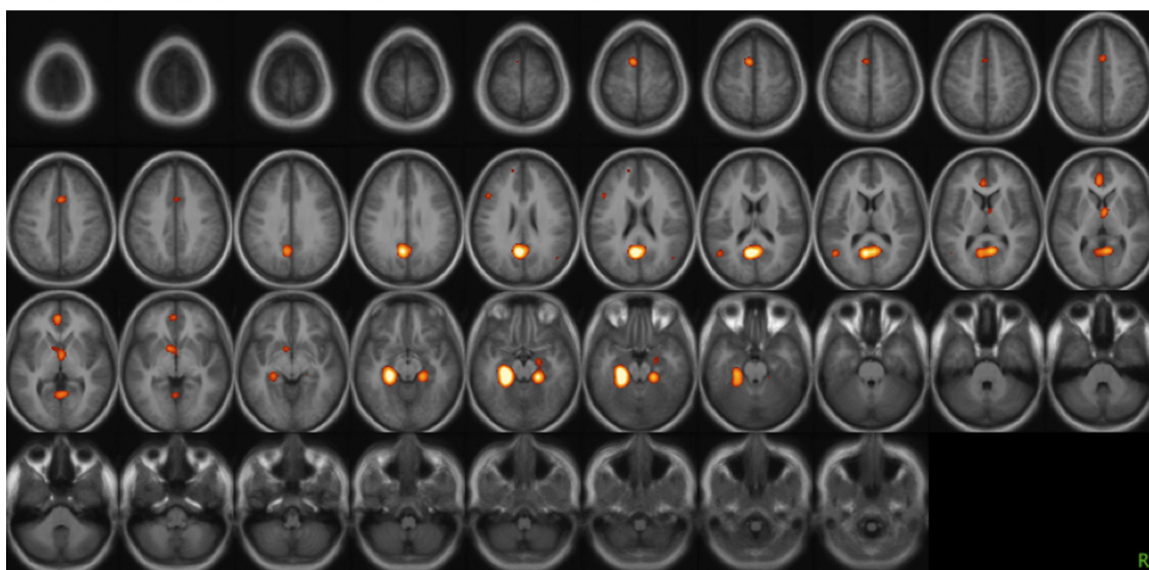


Fig. 2. ALE map for tasks recruiting autobiographical event memory. $p < .05$ (FDR-corrected).

tification of regions consistently seen for laboratory-based studies of retrieval success and for autobiographical memory is timely and fundamental. These maps are available upon request from the authors and could be used as regions of interest for future investigations. Space precludes a thorough discussion of the specific regions demonstrated and the possible processes contributed by each, although a whole manuscript could be dedicated to such speculation. Indeed, past articles (and even special issues of journals, e.g., Simons 2008) have been dedicated to individual regions emerging from such contrasts.

The primary message from these data is that the regions emerging from the literature on laboratory memory and autobiographical studies of memory retrieval are virtually nonoverlapping. This observation can be seen qualitatively by comparing Figs. 1 and 2 and by a direct contrast (Figs. 3 and 4).

Table 2

Center-of-mass coordinates and verbal description of regions appearing in the ALE map for autobiographical event memory studies.

Lobe	BA	Peak			Voxels
		x	y	z	
Frontal					
mPFC/ACC	24/32/33	-4	40	2	227
L PreM	6/8	-8	5	57	170
L IFG	44	-47	16	23	49
L MFG	9/10	-14	50	22	14
Parietal					
L angular gyrus	39	-47	-62	14	89
R angular gyrus	39	46	-68	22	10
Temporal					
L HF/PHG	20/28/35/36/37	-24	-33	-17	524
R HF/PHG	20/28/35/36/37	20	-36	-16	349
R ant. hippocampus	28	22	-15	-17	77
L PCC	17/19/23/29/30/31	-5	-60	19	525
Cingulate	24/32	1	10	42	147
Thalamus					
Lentiform nucleus		-7	3	-4	113

Note: L = left; R = right; m = medial; PFC = prefrontal cortex; ACC = anterior cingulate cortex; PreM = premotor cortex; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; HF = hippocampal formation; PCC = posterior cingulate cortex; PHG = parahippocampal gyrus; BA = Brodmann's area; ant = anterior.

The third point is that the few regions of overlap *may* point to regions particularly important for memory retrieval (although by no means would we claim they are the only regions critical for memory retrieval). The differences and similarities in laboratory and autobiographical memory tasks are considered below.

4.1. Differences between the two approaches

As noted, the primary finding in the dataset is the overwhelming discrepancy seen in the neural underpinnings associated with memory retrieval as a function of methodological choice. What is the source of such a large discrepancy? Obviously, there are many differences between the tasks under discussion here. For the most part, laboratory studies of the neural substrates of memory retrieval have utilized old/new recognition memory with overt responding (typically a button press), whereas autobiographical studies tend to employ cued recall with covert responding. Lab studies deal with much shorter timeframes (minutes to hours) and tend to use less emotion-laden stimuli not especially relevant to one's sense of self (see Cabeza et al., 2004 for discussion). They stress accuracy and monitoring over extrapolation and gap-filling. They take a second or two to complete (in comparison to autobiographical memory tasks, which can take much longer). They deal (typically) with less complex visuospatial information.

Nonetheless, a reasonable hypothesis would be to see fundamental regions of overlap (with some differences emerging, too). This mindset was captured by Moore (1910), who argued that "we have not one mind for the laboratory and another for the world. The same mental processes that take place in the world are observed in the laboratory, but under different conditions. The change in conditions is in the direction of greater simplification. The mental process of the laboratory is, as it were, a purified product and its true properties can therefore be more easily determined." (p. 116). Tulving (1983) espoused a similar view, claiming "I know of no compelling reasons why the general principles that apply to remembering of mini-events in the laboratory should be greatly different from those governing the remembering of real-life experiences. Rememberers do not leave their brains and minds behind, or switch them off, when they enter the memory laboratory" (p. 146).

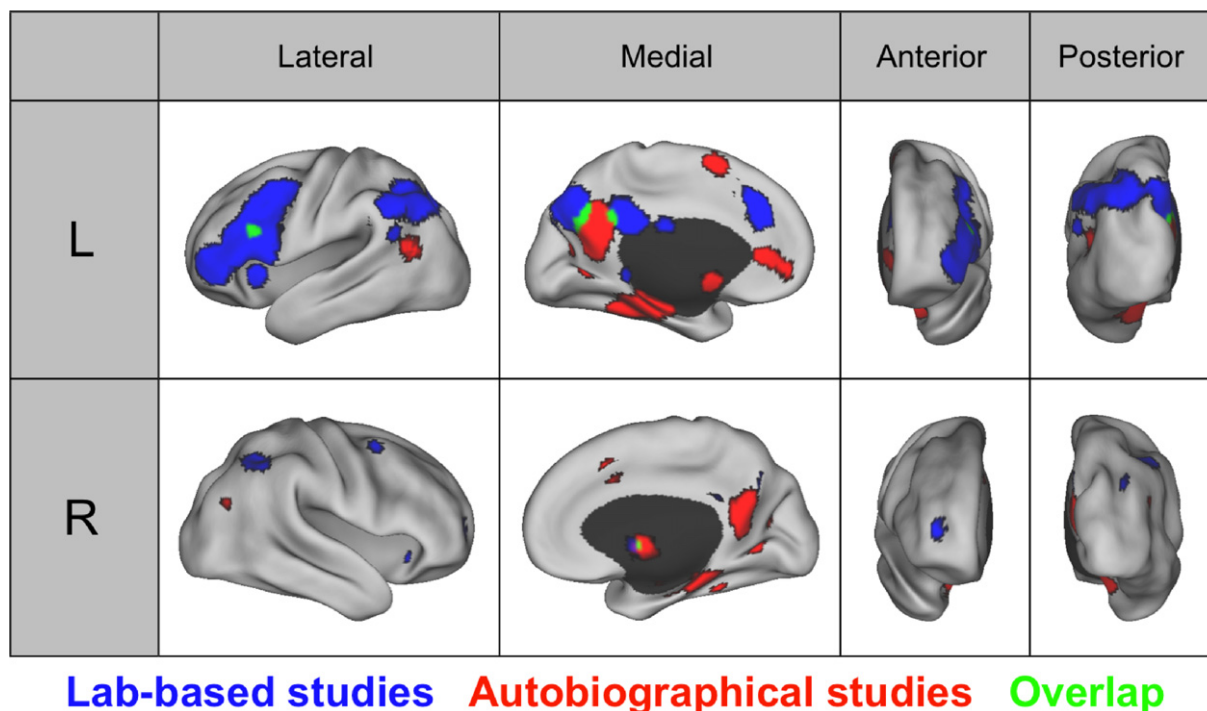


Fig. 3. Similarities and differences between the regions activated by laboratory memory and autobiographical memory tasks viewed on the inflated PALS atlas surface. Voxels shown in blue represent those that (across the literature) activate in laboratory-based studies of retrieval success; those shown in red activate in autobiographical event memory studies; and those in green represent overlap between the two conditions. Top row: left lateral, left posterior, right posterior, and right lateral views. Bottom row: left medial, right anterior, left anterior, and right medial views. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

In line with this viewpoint, one might have expected studies of retrieval success to activate a subset of regions important for autobiographical event memory somewhat like studies of word stem completion activate a subset of regions implicated in word stem cued recall (Buckner et al., 1995; Squire et al., 1992; for discussion see Roediger, Buckner, & McDermott, 1999). Indeed, Cabeza et al. (2004) obtained such a pattern (i.e., a laboratory task activating a subset of regions activated by an autobiographical task), although the specific tasks used were manipulated in an attempt to gain control over many of their differences, with the end result being that the autobiographical task was made more like a laboratory task than usual.

The foregoing comparison between laboratory and autobiographical event memory tasks may also lead one to expect laboratory tasks to have elicited activity in a region (or regions)

responsible for fine-grained monitoring processes, which are not thought to play a large role in autobiographical memory tasks (Cabeza et al., 2004; Gilboa, 2004; Maguire, 2001). Indeed, regions of prefrontal cortex similar or identical to those seen for laboratory memory tasks (Fig. 3) have been interpreted in this manner.

In general terms, what should be made of the striking lack of overlap seen with these two approaches? We suspect that researchers predisposed to prefer one approach to the other may be tempted to conclude that these data are evidence that the non-preferred approach is flawed. For example, one could point to the data while arguing that laboratory memory tasks are artificial and that if the goal of memory researchers is to understand retrieval of life events, one is missing the target by studying old/new recognition memory. This argument could be buttressed by the observation that the regions seen in the autobiographical mem-

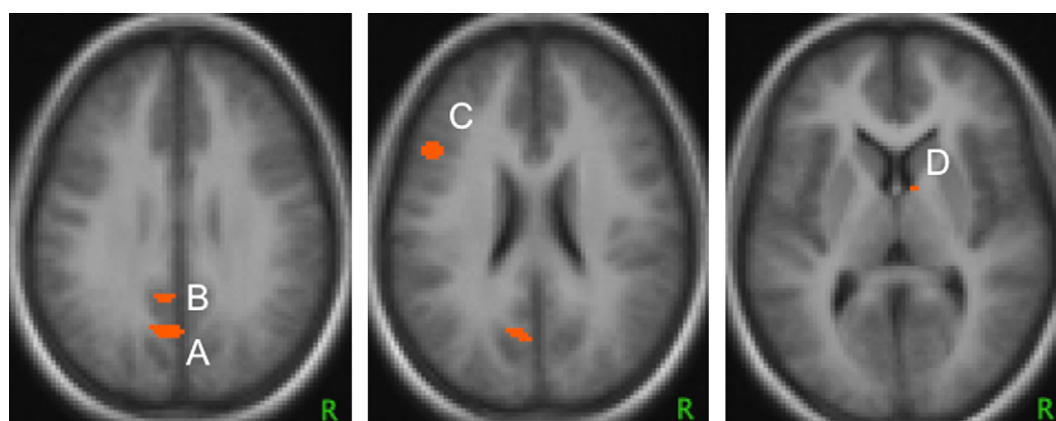


Fig. 4. Volumetric display of overlap between laboratory and autobiographical methods. Centers of mass $-4, -66, 28$ (posterior cingulate, BA 19/31, region A); $-6, -52, 28$ (posterior cingulate, BA 23/31, region B); $-46, 16, 24$ (left inferior frontal gyrus, BA 44, region C); and $8, -2, 6$ (right thalamus, region D).

ory map align naturally with the neuropsychological literature, which has shown that lesions to hippocampal regions (especially on the left, Spiers, Maguire, & Burgess, 2001), thalamus (Zola-Morgan, Cohen, & Squire, 1983), or posterior cingulate/retrosplenial cortex (Valenstein et al., 1987) can lead to memory impairments. Further, the findings that left inferior parietal cortex and anterior prefrontal cortices are consistently implicated in fMRI studies of memory retrieval (with laboratory methods) has been puzzling in that these regions were unanticipated from the neuropsychological literature; it is unclear whether lesions of these regions lead to deficits in memory retrieval. In short, these data could be taken as supporting the choice of autobiographical methods over laboratory methods.

Although there may be some validity to the foregoing claims, it is equally possible for a researcher with another viewpoint to find the data consistent with their own view that autobiographical tasks are flawed. These arguments follow the general story that one has no control over what subjects do during a 10-s trial window (especially one in which no response is required), and whatever the subjects choose to do may not necessarily be related to memory retrieval. Further, even if subjects are covertly performing the task as instructed, there is no way to measure memory accuracy.

We feel it important to note that there are other conclusions, as well, to consider. It could be that the two approaches complement each other well in that when taken together, they recruit a large set of processes fundamental to (albeit not all necessary for) memory, with each approach excelling at isolating different processes. For example, one approach might do a better job at isolating recollective processes, whereas the other approach may draw more upon familiarity, although our attempts to link the maps to the remember/know literature seem to show that some regions in each of the maps appear to align with those underlying remember judgments. A definitive statement regarding this interesting question may await the growth of the remember/know literature to a point where a meta-analysis is possible for that contrast.

We now return to the more basic point that these two methodological approaches may be complementary such that each excels at isolating a certain set of memorial processes. In this scenario, increasing the crosstalk between domains would be fruitful for researchers on both sides of the fence. Limiting our understanding of the component processes or the neural substrates of memory to a single methodological approach may prevent a more complete understanding of memory retrieval.

It is possible that the overlap obtained in the present data is underestimated due to Type II error. After all, many of the same principles are seen in the laboratory and autobiographical memory literatures (e.g., the importance of distinctiveness; the role of proactive and retroactive interference; the effectiveness of cues at reminding one of a previously inaccessible memory; the role of self-relevance in enhancing later memory, Roediger & Marsh, 2003).

Importantly, it could be that other laboratory-based tasks (e.g., free recall) would more closely approximate the processes used in recall of autobiographical event memories. The literature is not yet mature enough to permit a meta-analysis examining this question with respect to free recall; most of the neuroimaging literature has relied upon variants of recognition memory, just as the autobiographical memory literature has focused on the Galton word-cueing technique. Methodological issues prevent a single definitive study being able to address the similarities and differences in the neural substrates of recognition memory and free recall or between the Galton cueing technique and other methods of studying autobiographical event memory. Hence, at this point it would be premature to conclude that the regions of overlap seen in the present inves-

tigation are the only ones that could be seen in a comparison of laboratory and autobiographical methods.

Indeed, a fruitful avenue for future research would be to attempt to bridge the gap between methodological approaches by taking small steps with independent variables. For example, one could begin with a simple recognition memory task for word lists and gradually make the task more life-like by first introducing multimodal complexity to the stimuli, then adding self-relevance to the multimodal stimuli, then moving to recall, then lengthening the retention interval, and so on. Such steps could probably bridge the gap between the two approaches now in common use. Importantly, if such a pattern occurred, it would suggest that it is the current implementation of laboratory and autobiographical approaches (and not the approaches themselves) that differs so markedly.

4.2. Similarities between the two approaches

Although the primary picture emerging from the data presented here is that the two methodologies lead to strikingly different activation maps, there were some areas of overlap, and those are considered here. These regions are of interest largely because one would expect any regions necessary for retrieval to appear in both maps (assuming sufficient power to develop reliable maps). We begin by examining the two regions in posterior cingulate (Fig. 4A and B). These two regions emerge from the intersection of three distinct regions (a laboratory-based posterior cingulate region, a laboratory-based precuneus region, and an autobiographical posterior cingulate region), as can be seen in Fig. 3. It remains unclear to what extent (if at all) the overlap seen represents true functional overlap. Although processes central to (and possibly even necessary for) memory retrieval may be contributed by these regions, future research is necessary to address whether these overlap regions are indeed functionally distinct, or whether their appearance represents a source of noise unaccounted for in the dataset. For example, the ALE approach takes into account only the location of peak activations reported in articles and not the shape of reported regions of interest; it therefore assumes a spherical ROI centered on each peak activation focus, an assumption that may not be valid. Hence it could be that the spatial extent of the three regions mentioned above is over-estimated (or under-estimated) by the present methods.

On the other hand, it seems reasonable to expect that any regions that are regularly identified *both* in studies that have used laboratory-based methods to examine retrieval success and in studies using autobiographical procedures to examine retrieval of life events might represent core regions important for memory retrieval. Further, as mentioned previously, damage to regions in or near those seen in posterior cingulate/retrosplenial cortex can lead to memory impairment (Valenstein et al., 1987). Our conclusion at this point is that these regions can be considered candidates for contributing fundamental processes to retrieval of event memory but that definitive statements in this regard await future research.

The third region of overlap appeared within left inferior frontal cortex (BA44). This region seems less susceptible to the concerns outlined above regarding spatial extent, as the activity seen in autobiographical studies lies in the heart of a much larger swath of activity observed by laboratory-based studies. Both literatures make reference to left frontal cortex, and the present analysis clarifies that observation. In autobiographical memory studies, a region within BA44 tends to activate, whereas in laboratory studies of retrieval success, much of left frontal cortex is activated reliably. It seems likely that the unconstrained nature of the autobiographical memory task comparisons resulted in variability in the locale of frontal activations, such that only one region emerges consistently across studies.

The fourth region is actually a very small intersection of activation within right thalamus. Neither literature tends to focus much on its discussion; here we note that laboratory-based studies tend to activate thalamus more anteriorly than those using autobiographical methods and that (as with posterior cingulate) the neuropsychological literature demonstrates that thalamic lesions can cause memory impairment (see Svoboda et al., 2006 for review).

4.3. Summary

Research involves construction of a persuasive narrative. Even when whole-brain analysis is used in neuroimaging, data analysis and discussion often focus on a subset of the observed regions. Methodological choices influence these biases, which are therefore self-perpetuating. Hence, methodological assumptions are key in determining what we know about memory retrieval. The present quantitative meta-analysis suggests that tasks typically employed to study autobiographical memory do not simply involve most of the same processes as those employed for laboratory-based memory studies but with more emotional and self-referential processing occurring for the former and more monitoring occurring for the latter. The neural substrates (and underlying processes) associated with the two tasks differ much more fundamentally than such a heuristic would suggest. The present analysis highlights both the gap between these approaches and the importance of bridging the gap in an effort to understand the factors that lead to these differences. A re-examination of how these approaches differ and adoption of broader approaches to studying these questions could prove beneficial in enhancing understanding of memory retrieval and its neural substrates.

Acknowledgements

The authors appreciate the assistance of David Van Essen, John Harwell, and Donna Dierker in developing the Caret software and providing assistance with the data analysis and presentation. Constructive comments on this work were provided by Roberto Cabeza, Jason Chan, Steve Nelson, Heather Rice, Roddy Roediger, David Rubin, and Steve Petersen. Discussions with Endel Tulving inspired much of the work presented here, and we are grateful to be able to include this article in a special issue in his honor.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2008.12.025.

References

- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, *45*, 1363–1377.
- Banaji, M. R., & Crowder, R. G. (1989). The bankruptcy of everyday memory. *American Psychologist*, *44*, 1185–1193.
- Brodman, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Leipzig: J.A. Barth.
- Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience*, *15*, 12–29.
- Cabeza, R., Prince, S. E., Daselaar, S. M., Greenberg, D. L., Buddle, M., Dolcos, F., et al. (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience*, *16*, 1583–1594.
- Cabeza, R., & St. Jacques, P. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences*, *11*, 219–227.
- Christ, S. E., Van Essen, D. C., Watson, J. M., Brubaker, L. E., & McDermott, K. B. (2008). The contributions of prefrontal cortex and executive control to deception: Evidence from activation likelihood estimate meta-analyses. *Cerebral Cortex*, doi:10.1093/cercor/bhn189
- Conway, M. A., Pleydell-Pearce, C. W., Whitecrow, S. E., & Sharpe, H. (2002). Brain imaging autobiographical memory. *Psychology of Learning & Motivation: Advances in Research & Theory*, *41*, 229–263.
- Conway, M. A., Turk, D. J., Miller, S. L., Logan, J. M., Nebes, R. D., Meltzer, C. C., et al. (1999). A positron emission tomography (PET) study of autobiographical memory retrieval. *Memory*, *7*, 679–702.
- Crovitz, H. F., & Schiffman, H. (1974). Frequency of episodic memories as a function of their age. *Bulletin of the Psychonomic Society*, *4*, 517–518.
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, *11*, 379–386.
- Fink, G. R., Markowitsch, H. J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. D. (1996). Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *Journal of Neuroscience*, *16*, 4275–4282.
- Galton, F. (1879). Psychometric experiments. *Brain*, *2*, 149–162.
- Genovese, C., Lazar, N., & Nichols, S. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, *15*, 870–878.
- Gilboa, A. (2004). Autobiographical and episodic memory—one and the same? Evidence from prefrontal activation in neuroimaging studies. *Neuropsychologia*, *42*, 1336–1349.
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, *2*, 685–694.
- Hall, J. F. (1971). *Verbal learning and retention*. Philadelphia: Lippincott.
- Koriat, A., & Goldsmith, M. (1996). Memory metaphors and the real-life/laboratory controversy: Correspondence versus storehouse conceptions of memory. *The Behavioral and Brain Sciences*, *19*, 167–228.
- Laird, A., Fox, P., Price, C., Glahn, D., Uecker, A., Lancaster, J., et al. (2005). ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Human Brain Mapping*, *25*, 155–164.
- Maguire, E. A. (2001). Neuroimaging studies of autobiographical event memory. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *356*, 1441–1451.
- McDermott, K. B., & Buckner, R. L. (2002). Functional neuroimaging studies of human memory retrieval. In L. R. Squire & D. L. Schacter (Eds.), *Neuropsychology of memory* (pp. 166–171). New York: Guilford Press.
- Moore, T. V. (1910). *The process of abstraction: An experimental study*. California University Publications in Psychology.
- Neisser, U. (1978). Memory: What are the important questions? In M. M. Gruneberg, E. E. Morris, & R. N. Sykes (Eds.), *Practical aspects of memory* (pp. 3–24). San Diego, CA: Academic Press.
- Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review*, *3*, 135–148.
- Nyberg, L., Forkstam, C., Petersson, K. M., Cabeza, R., & Ingvar, M. (2002). Brain imaging of human memory systems: Between-systems similarities and within-systems differences. *Cognitive Brain Research*, *13*, 281–292.
- Öngür, D., Ferry, A., & Price, J. (2003). Architectonic subdivision of the human orbital and medial prefrontal cortex. *Journal of Comparative Neurology*, *460*, 425–449.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 676–682.
- Robinson, J. A. (1976). Sampling autobiographical memory. *Cognitive Psychology*, *8*, 578–595.
- Roediger, H. L., Buckner, R. L., & McDermott, K. B. (1999). Components of processing. In J. K. Foster & M. Jelicic (Eds.), *Memory: Systems, processes, of function?* (pp. 31–65). Oxford: Oxford University Press.
- Roediger, H. L., & Marsh, E. J. (2003). Episodic and autobiographical memory. In A. F. Healy & R. W. Proctor (Eds.), *The handbook of psychology* (pp. 475–497). New York: Wiley.
- Shannon, B. J., & Buckner, R. L. (2004). Functional-anatomic correlates of memory retrieval that suggest nontraditional processing roles for multiple distinct regions within posterior parietal cortex. *Journal of Neuroscience*, *24*, 10084–10092.
- Spiers, H. J., Maguire, E. A., & Burgess, N. (2001). Hippocampal amnesia. *Neurocase*, *7*, 357–382.
- Squire, L. R., Ojemann, J. G., Miezin, F. M., Petersen, S. E., Videen, T. O., & Raichle, M. E. (1992). Activation of the hippocampus in normal humans: A functional anatomical study of memory. *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 1837–1841.
- Svoboda, E., McKinnon, M. C., & Levine, B. (2006). The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia*, *44*, 2189–2208.
- Szpunar, K. K., Watson, J. M., & McDermott, K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 642–647.
- Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.
- Turkeltaub, P., Eden, G., Jones, K., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage*, *16*, 765–780.
- Valenstein, E., Bowers, D., Verfaellie, M., Heilman, K. M., Day, A., & Watson, R. T. (1987). Retrosplenic amnesia. *Brain*, *110*, 1631–1646.
- Van Essen, D. C. (2005). A population-average, landmark- and surface-based (PALS) atlas of human cerebral cortex. *NeuroImage*, *28*, 635–662.
- Van Essen, D. C., & Dierker, D. (2007). On navigating the human cerebral cortex: Response to 'in praise of tedious anatomy'. *NeuroImage*, *37*, 1050–1054.
- Van Essen, D. C., Drury, H. A., Dickson, J., Harwell, J., Hanlon, D., & Anderson, C. H. (2001). An integrated software suite for surface-based analyses of cerebral cortex. *Journal of the American Medical Informatics Association*, *8*, 443–459.

- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9, 445–453.
- Winograd, E. (1993). Memory in the laboratory and everyday memory: The case for both. In J. M. Puckett & H. W. Reese (Eds.), *Mechanisms of everyday cognition* (pp. 55–70). Hillsdale, NJ: Erlbaum.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory & Language*, 46, 441–517.
- Zola-Morgan, S., Cohen, N. J., & Squire, L. R. (1983). Recall of remote episodic memory in amnesia. *Neuropsychologia*, 21.