Reviews and perspectives

Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation

Julia Spaniol[a,*], Patrick S.R. Davidson[b], Alice S.N. Kim[c], Hua Han[c], Morris Moscovitch[c], Cheryl L. Grady[c,d]

[a] Department of Psychology, Ryerson University, 350 Victoria Street, Toronto, Ontario, Canada M5B 2K3
[b] School of Psychology, University of Ottawa, Canada
[c] Rotman Research Institute, Baycrest and Department of Psychology, University of Toronto, Canada
[d] Department of Psychiatry, University of Toronto, Canada

ABSTRACT

The recent surge in event-related fMRI studies of episodic memory has generated a wealth of information about the neural correlates of encoding and retrieval processes. However, interpretation of individual studies is hampered by methodological differences, and by the fact that sample sizes are typically small. We submitted results from studies of episodic memory in healthy young adults, published between 1998 and 2007, to a voxel-wise quantitative meta-analysis using activation likelihood estimation [Laird, A. R., McMillan, K. M., Lancaster, J. L., Kochunov, P., Turkeltaub, P. E., & Pardo, J. V., et al. (2005). A comparison of label-based review and ALE meta-analysis in the stroop task. *Human Brain Mapping, 25,* 6–21]. We conducted separate meta-analyses for four contrasts of interest: episodic encoding success as measured in the subsequent-memory paradigm (subsequent Hit vs. Miss), episodic retrieval success (Hit vs. Correct Rejection), objective recollection (e.g., Source Hit vs. Item Hit), and subjective recollection (e.g., Remember vs. Know). Concordance maps revealed significant cross-study overlap for each contrast. In each case, the left hemisphere showed greater concordance than the right hemisphere. Both encoding and retrieval success were associated with activation in medial-temporal, prefrontal, and parietal regions. Left ventrolateral prefrontal cortex (PFC) and medial-temporal regions were more strongly involved in encoding, whereas left superior parietal and dorsolateral and anterior PFC regions were more strongly involved in retrieval. Objective recollection was associated with activation in multiple PFC regions, as well as multiple posterior parietal and medial-temporal areas, but not hippocampus. Subjective recollection, in contrast, showed left hippocampal involvement. In summary, these results identify broadly consistent activation patterns associated with episodic encoding and retrieval, and subjective and objective recollection, but also subtle differences among these processes.

© 2009 Elsevier Ltd. All rights reserved.

Contents

1. Introduction

For decades, studies of brain-damaged humans and experimentally lesioned animals have provided the bulk of evidence regarding the brain bases of episodic memory (i.e., conscious memory for personally experienced events within a particular spatio-temporal context; Tulving, 1985). More recently, the advent of non-invasive functional neuroimaging has enabled researchers to examine normal memory processes in the healthy brain. Functional neuroimaging can address questions that the lesion method cannot, for example, the examination of similarities and differences between encoding and retrieval stages and the identification of wide-scale networks of regions that interact to support memory. Since the early 1990s, there has been a dramatic increase in the number of functional neuroimaging studies of episodic memory. The first used positron emission tomography (PET) and block-design functional magnetic resonance imaging (fMRI), and had relatively coarse spatial and temporal resolution (and many did not cover the whole brain). Nevertheless, reviews and meta-analyses of these early findings spurred the generation of novel hypotheses and new directions for research. Current studies generally image the Blood Oxygenation Level Dependent (BOLD) signal from the whole brain using fMRI, and have much greater spatial and temporal resolution than the first generation of studies. In fact, temporal resolution is now sufficient to analyze performance trial-by-trial in an event-related design. However, despite this large number of studies, relatively few reviews and meta-analyses have been conducted, and these have typically been selective. Therefore, this appears to be a particularly important time to perform a comprehensive, quantitative meta-analysis of the burgeoning event-related fMRI (ER-fMRI) literature on episodic memory.

1.1. Two main paradigms for examining memory in ER-fMRI

Currently, researchers typically employ variations of two standard paradigms to examine episodic memory in the scanner. First, in the *successful encoding* method, also referred to as the *subsequent memory* or *difference due to memory* paradigm (Dm; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Paller, Kutas, & Mayes, 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980; Wagner et al., 1998), brain activity is measured when participants are initially exposed to memoranda, and, following a yes–no recognition

memory test, average activations are compared between items that were encoded more successfully (i.e., elicited *hits* on the subsequent recognition test) vs. less successfully (i.e., *misses*). Second, in a *successful retrieval* analysis (e.g., Buckner et al., 1998), participants initially study a list of items and are imaged during the memory test. Activations then are compared between trials in which the person successfully endorsed a studied item (i.e., hits) vs. successfully rejected a new one (i.e., *correct rejections*; *CRs*). In both of the aforementioned methods, a difference in neural activity associated with each kind of response indicates that the two kinds of responses (i.e., hits vs. misses, or hits vs. CRs) are supported by at least partially non-overlapping neural substrates. Researchers can assume that the reason for a person's remembering some items and not others is due to some combination of the characteristics of each item, and each participant's prior experience, traits, and state at the time of encoding and retrieving each item (Gabrieli, 2001).

1.2. Neural structures involved in episodic encoding and retrieval

Following Scoville and Milner's (1957) report on amnesic patient HM, human and animal lesion work focused intensively on the role of the hippocampus and surrounding medial-temporal lobe (MTL) in memory. One of the more surprising findings from early functional neuroimaging reviews, however, was that medial-temporal activations were far from reliable, but activations in other regions were ubiquitous. These other regions included prefrontal and parietal cortices, the cingulate gyrus, the retrosplenial region, and the cerebellum (e.g., Buckner, 1996; Cabeza & Nyberg, 2000; Fletcher & Henson, 2001; Lepage, Habib, & Tulving, 1998; Nyberg, Cabeza, & Tulving, 1996; Schacter & Wagner, 1999).

Current models generally agree that the MTL supports the creation and possibly also retrieval of distributed memory traces that consist of ensembles of MTL and neocortical neurons (e.g., Alvarez & Squire, 1994; Moscovitch, 1992; Moscovitch et al., 2005), but there are still open questions concerning the functional neuroimaging evidence. For example, how reliable is the activity in the medial-temporal region? Early PET and block-design fMRI studies often failed to detect medial-temporal activation, especially during retrieval, and, in a qualitative review, Henson (2005) noted that current studies also often fail to do so. Second, is memory-related activation concentrated in the hippocampus proper, or distributed more broadly across the medial-temporal

lobe, including the parahippocampal gyrus (i.e., perirhinal, entorhinal, and parahippocampal cortices)? This is a question that has received considerable interest in the context of dual-process models of memory (outlined below). Finally, various claims have been advanced regarding the locus of activation along the long axis of the hippocampus during encoding vs. retrieval (e.g., Greicius et al., 2003; Henson, 2005; Lepage et al., 1998; Ludowig et al., 2008; Parsons, Haut, Lemieux, Moran, & Leach, 2006; Schacter & Wagner, 1999). Would a meta-analysis reveal that activation is concentrated more in one segment than another of the hippocampus?

Additional brain systems are proposed to support or modify the basic operations of the MTL. For example, there is evidence for a major contribution of prefrontal cortex (PFC) to successful encoding. Specifically, encoding-related activity in the ventrolateral PFC (VLPFC) has been attributed to selection, maintenance, and control of incoming information, whereas activity in the dorsolateral PFC (DLPFC) is thought to support organization and associative encoding (for reviews, see Blumenfeld & Ranganath, 2007; Paller & Wagner, 2002; Simons & Spiers, 2003). At retrieval, sub-regions of prefrontal cortex have been implicated in various functions, including setting of a retrieval mode, specification of retrieval cues, and post-retrieval monitoring and verification (e.g., Burgess, Dumontheil, & Gilbert, 2007; Dobbins & Han, 2006; Fletcher & Henson, 2001; Moscovitch and Winocur, 2002; Petrides, 2002; Rugg et al., 1998; Shallice, 2002; Simons & Spiers, 2003). There appears to be at least a rough consensus among these models that setting of retrieval mode and specification of cues are more dependent on VLPFC, whereas monitoring and verification are more dependent on DLPFC. Furthermore, according to the hemispheric encoding/retrieval asymmetry (HERA) model (Habib, Nyberg, & Tulving, 2003; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), left PFC activation should be greater for encoding than retrieval, whereas right PFC activation should be greater for retrieval than encoding.

Posterior parietal cortex may also play a role in episodic memory processes. Although the contribution of parietal regions to successful encoding has received relatively little attention (but see Uncapher, Otten, & Rugg, 2006), possible contributions to retrieval have garnered considerable interest. Retrieval success effects in posterior cortex were described as early as the mid-1990s (e.g., Kapur et al., 1995; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996), but explicit theories about parietal involvement in episodic memory are only now being formulated (e.g., Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). According to one view, retrieval-related activity in superior parietal regions tracks the task relevance or salience of cues, whereas activity in inferior parietal cortex is involved in recollection (Vilberg & Rugg, 2008). A related view is that superior parietal cortex facilitates top-down attentional control during retrieval, whereas inferior parietal cortex mediates bottom-up attentional processes (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008).

The potential roles of other regions, including the cingulate gyrus and the cerebellum, are less well-specified, but because the first generation of functional neuroimaging studies tended to identify them as being involved in encoding and/or retrieval, interest in their specific contributions is growing.

1.3. Dual-process models

A major development in the cognitive neuroscience of memory over the last decade has been the ascent of dual-process models positing that retrieval of episodic memories can be accompanied by a vivid sense of re-experiencing ("recollection") or by a sense of familiarity. The view that these subjective experiences reflect the operation of two independent memory processes (e.g., Atkinson & Juola, 1974; Jacoby, 1991; Mandler, 1980; Tulving, 1985; Yonelinas, 1994) has received strong support from behavioural-experimental studies and from neuropsychological dissociations (see Yonelinas, 2002, for review). A growing literature has investigated the neural substrates of recollection and familiarity in healthy individuals using neuroimaging. This research has yielded additional support for the dual-process view (for recent reviews, see Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Mayes, Montaldi, & Migo, 2007; Skinner & Femandes, 2007; Vilberg & Rugg, 2008). With respect to neural correlates, interest has focused mainly on the contributions of medial-temporal sub-regions to the two processes. For example, recently some researchers (Diana et al., 2007; Eichenbaum et al., 2007; see also Bowles et al., 2007; Brown & Aggleton, 2001; Davachi, 2006) have suggested a correspondence between perirhinal cortex and item memory (familiarity), parahippocampal cortex and context memory (familiarity and recollection), and hippocampus and item-context associations (recollection; but see Rutishauser, Schuman, & Mamelak, 2008; Squire, Wixted, & Clark, 2007). In addition, various frontal and parietal sub-regions have been asserted to be differentially involved in recollection and familiarity (for reviews, see Skinner & Femandes, 2007; Vilberg & Rugg, 2008), though there is still considerable controversy about the precise contributions of these regions. One possible reason for the controversy is that two classes of experimental paradigms, objective vs. subjective, have been used to separate recollection and familiarity.

Objective recollection paradigms (also referred to as "relational-recognition tests"; Eichenbaum et al., 2007) include direct tests of memory for associations or contextual features. Tests of source memory are the most commonly used objective recollection tests. Associative recognition and the process-dissociation procedure also fall into the objective recollection category, but we will not discuss them further because relatively few neuroimaging studies have employed this paradigm.

In the class of subjective-recollection paradigms, the most widely used is the Remember–Know procedure (Tulving, 1985). In this procedure, participants are asked to indicate, for each item they classify as "old" on a recognition test, whether their memory is vivid and rich in contextual detail ("Remember"), or whether it is based on a non-specific sense of familiarity ("Know"). Another approach involves confidence judgments, which can be used to plot receiver operating characteristics (ROCs). The shape of the ROC is then analyzed to provide information about the contributions of recollection and familiarity to recognition performance (e.g., Yonelinas, 1994).

Behavioural studies of objective and subjective recollection have often provided converging results despite the differences in methodology and in the subjective experiences to which they give rise (Yonelinas, 2002; see also Davidson, Anaki, Saint-Cyr, Chow, & Moscovitch, 2006). Nevertheless, the two types of recollection have been dissociated in frontal (e.g., Ciaramelli & Ghetti, 2007; Duarte, Ranganath, & Knight, 2005; Levine, Freedman, Dawson, Black, & Stuss, 1999) and parietal lesion patients (e.g., Davidson et al., 2008; Simons et al., 2008), as well as in older adults (e.g., Duarte, Henson, & Graham, 2008). Duarte et al. (2008) described diverging fMRI activation patterns for objective and subjective recollection, but the focus of their analyses was on identifying age differences within each type of recollection, rather than on the main effect of recollection type. Indeed, to our knowledge, no previous studies have formally compared the neural correlates of objective and subjective recollection.

1.4. The current study

Several reviews and meta-analyses of ER-fMRI studies of memory have appeared recently, but these have either been limited to a

small subset of data (Naghavi & Nyberg, 2005), specific brain regions (e.g., Ciaramelli et al., 2008; Henson, 2005; Vilberg & Rugg, 2008; Wagner et al., 2005), or the recollection-familiarity distinction (e.g., Eichenbaum et al., 2007; Mayes et al., 2007; Skinner & Femandes, 2007). Accordingly, we conducted a more comprehensive review of ER-fMRI studies of episodic memory.

Rather than performing a qualitative review, we aimed to complete the first *quantitative* meta-analysis of this literature. The benefits of a meta-analysis, in which data from the extant literature are formally integrated into an overall statistical analysis, are many. In particular, this method reduces the bias that can enter more qualitative reviews, and it minimizes the limitations inherent to individual studies that can make it relatively difficult to compare one with another: low statistical power stemming from the small number of participants in each study, variability in the labeling of neuroanatomical regions (e.g., Laird et al., 2005), and idiosyncratic fMRI methods varying from laboratory to laboratory (including differences in image acquisition, smoothing and other pre-processing steps, and statistical analyses, among other factors).

We used the activation likelihood estimation (ALE) method (Turkeltaub, Eden, Jones, & Zeffiro, 2002), in which, for a unidirectional contrast of interest (e.g., Remember–Know), each activation focus reported in the literature is modeled as the peak of a 3D Gaussian probability distribution. The ALE statistic, calculated as the sum of these probabilities across studies, indicates the likelihood that each voxel is active in the task. The ALE method is thus fully automated and quantitative, facilitating statistical inference via thresholding of the concordance maps (Chein, Fissell, Jacobs, & Fiez, 2002; Turkeltaub et al., 2002).

1.4.1. Objective 1: comparing encoding and retrieval success

Our first objective was to synthesize results from the large number of studies that have reported successful-encoding and successful-retrieval contrasts in order to provide standard maps for both contrasts and to allow insight into neuroanatomical similarities and differences between encoding and retrieval networks. As stated above, we expected wide ranging activation across cortical and subcortical regions, but focused our attention on three key areas. First, early studies, and even many current ones, often failed to detect medial-temporal activation (see Henson, 2005). Thus, we were curious as to whether a meta-analysis would yield significant medial-temporal concordance, and, if so, whether it would be concentrated in hippocampus proper or would be more widely dispersed. Comparing encoding to retrieval analyses, we sought to determine whether medial-temporal activity would be concentrated in the anterior, middle, or posterior section of hippocampus, because various analyses have made conflicting claims about the function of the different regions (e.g., Greicius et al., 2003; Henson, 2005; Lepage et al., 1998; Ludowig et al., 2008; Parsons et al., 2006; Schacter & Wagner, 1999).

Second, although we expected widespread concordance in PFC for both encoding and retrieval, we were interested in determining potential differences in the relative involvement of PFC sub-regions during encoding compared to retrieval, as well as differences in the lateralization of PFC activation across studies using verbal and nonverbal materials, as predicted by the HERA model (e.g., Habib et al., 2003; Tulving et al., 1994). Third, although lateral and medial parietal activations during retrieval have been reported widely and several hypotheses as to their functional significance have been proposed (e.g., Ciaramelli et al., 2008; Vilberg & Rugg, 2008; Wagner et al., 2005), we sought to determine whether the same parietal regions were reliably activated in studies of encoding.

1.4.2. Objective 2: comparing objective and subjective recollection

Our second objective was to meta-analyze the ER-fMRI literature on recollection, distinguishing between objective and subjective

measures. As mentioned previously, the neural correlates of these measures have not been formally compared (but see Duarte et al., 2008). As with the more general analyses of encoding and retrieval, brain regions of particular interest included medial-temporal, frontal, and parietal cortex.

Within the medial-temporal region, we sought to establish whether hippocampal activation, thought to be a hallmark of recollective processing (for reviews, see Diana et al., 2007; Eichenbaum et al., 2007; Skinner & Femandes, 2007), would be seen for both objective and subjective recollection. For example, Duarte et al. (2008) reported posterior hippocampal activation, across younger and older participant groups, for subjective but not objective recollection.

Similarly, within PFC, we were interested in identifying subregions sensitive to objective and subjective recollection. We hypothesized that DLPFC and VLPFC regions involved in cognitive control processes would be less strongly activated in subjective than in objective recollection. "Remember" responses, for example, can be based on *any* contextual information that is vividly re-experienced by the participant (Duarte et al., 2008), without necessarily taxing strategic search and post-retrieval monitoring processes (Moscovitch & Winocur, 2002). In contrast, source memory tasks require participants to search for the information specified by the experimenter, and to monitor information retrieved from MTL structures (Dobbins & Han, 2006; Fletcher & Henson, 2001; Simons & Spiers, 2003). Indeed, patients with prefrontal lesions (Ciaramelli & Ghetti, 2007; Duarte et al., 2005) and older adults (Duarte et al., 2008) have been shown to be disproportionally impaired on tests of objective, but not subjective, recollection.

With respect to parietal cortex, it has been proposed that inferior lateral parietal cortex supports mnemonic decisions involving bottom-up attentional capture by the result of a memory search, whereas superior lateral parietal cortex and the intraparietal sulcus track top-down attention during retrieval (Cabeza, 2008; Ciaramelli et al., 2008). Both objective and subjective recollection may engage bottom-up attentional capture by retrieved memory contents, although Duarte et al. (2008) found inferior parietal activation, across younger and older adults, for subjective recollection only. The strategic, top-down component, on the other hand, should be taxed more heavily by objective recollection, which involves search for a specific, experimenter-provided contextual detail (e.g., the spatial location in which an item was presented during encoding). We thus predicted greater involvement of superior parietal cortex in objective recollection, compared to subjective recollection.

2. Methods

2.1. Study selection

We conducted a Pubmed (www.pubmed.org) query using the keyword search "(memory OR recognition OR recall) AND fMRI." We selected studies that were published in 2007 or earlier, used event-related fMRI, reported standard-space stereotactic coordinates of whole-brain activation maxima for at least one of the contrasts of interest (see below), and used a univariate fMRI analysis approach with uniform significance and cluster size thresholds applied throughout the brain. We excluded data from patients and older participants. We identified additional studies by searching through reference lists of studies obtained from the Pubmed query.

2.2. Contrasts of interest

Separate ALE meta-analyses were conducted for each of the four episodic memory contrasts listed below. Because ALE can be applied only to unidirectional pairwise comparisons, deactivations associated with episodic memory were not included. The coordinates of deactivation foci could be submitted to separate meta-analyses, but doing so was beyond the scope of the current objectives.

2.2.1. Encoding success

In the subsequent-memory paradigm (also referred to as "difference in memory" or "DM" paradigm), participants encode stimuli during scanning. Activity during

Table 1
Encoding success studies.

Publication	Encoding task	N	Foci	Stimulus
Brassen, Weber-Fahr, Sommerb, Lehmbecka, and Braus (2006)	Valence ratings	13	9	Words
Buckner, Wheeler, and Sheridan (2001)	Intentional memorizing	14	13	Words
Chee, Westphal, Goh, Graham, and Song (2003)	Animacy judgments	16	2	Words
Clark and Wagner (2003)	Phonological judgments	20	15	Words and non-words
Dennis, Daselaar, and Cabeza (2007)	Semantic category judgments	24	7	Words
de Zubicaray, McMahon, Eastburn, Finnigan, and Humphreys (2005)	Intentional memorizing	14	6	Words
Erk et al. (2003)	Concreteness judgments	10	1	Words
Fletcher, Stephenson, Carpenter, Donovan, and Bullmore (2003)	Pleasantness vs. alphabetical order judgments	10	5	Words
Fliessbach, Trautner, Quesada, Elger, and Weber (2007)	Animacy vs. size vs. alphabetical order judgments	19	7	Words
Fliessbach, Weis, Klaver, Elger, and Weber (2006)	Intentional memorizing	21	4	Words
Garoff, Slotnick, and Schacter (2005)	Size judgments	13	37	Pictures of objects
Gold et al. (2006)	Imagery and intentional memorizing	15	4	Words
Henson, Hornberger, and Rugg (2005)	Animacy vs. alphabetical order judgments	22	19	Words
Kao, Davis, and Gabrieli (2005)	Intentional memorizing	16	9	Pictures of scenes
Macrae, Moran, Heatherton, Banfield, and Kelley (2004)	Trait judgments	22	4	Words
Nichols, Kao, Verfaellie, and Gabrieli (2006)	WM maintenance	16	8	Faces
Otten, Henson, and Rugg (2002)	Animacy judgments	16	7	Words
Otten and Rugg (2001)	Animacy judgments	17	2	Words
Reber et al. (2003)	'Remember' vs. 'forget' instructions	12	4	Words
Schott et al. (2006)	Word stem completion	25	26	Words
Sergerie, Lepage, and Armony (2005)	Gender judgments	18	25	Faces
Sommer, Rose, Weiller, and Büchel (2005)	Manmade/natural judgments	15	17	Pictures of objects
Uncapher et al. (2006)	Animacy judgments	20	4	Words
Uncapher and Rugg (2005)	Animacy judgments	18	14	Words
Wagner et al. (1998)	Concreteness judgments	13	9	Words
Weis, Klaver, et al. (2004), Weis, Specht, et al. (2004)	Building/landscape judgments	16	7	Pictures of scenes

Note: These studies employed post-scan old–new recognition tests and reported "Hit vs. Miss" as the encoding success contrast.

encoding of items that are remembered in a subsequent old–new recognition test (i.e., recognition hits) is contrasted with activity during encoding of items that are subsequently forgotten (i.e., recognition misses). Twenty-six studies reporting this contrast met the criteria for inclusion, yielding a total of 265 foci (see Table 1).

2.2.2. Retrieval success

After studying a list of stimuli, participants are scanned during an old–new recognition test. Activity during correct 'old' responses (hits) is contrasted with activity during correct 'new' responses (correct rejections). Thirty studies reporting this contrast met the criteria for inclusion, yielding a total of 359 foci (see Table 2).

2.2.3. Objective recollection

We included contrasts from several different paradigms assessing recollection with objective performance measures. In source memory studies, participants encode stimuli in two or more different contexts (e.g., spatial positions on the screen) and are scanned during a subsequent-memory test. Source memory tests vary in design, but the most common version has participants make old/new judgments for test items, followed by source judgments for items judged "old." Two-alternative forced-choice versions of this task are also common. For correctly recognized stimuli, activity during correct source judgments (successful recollection and item-based familiarity) is contrasted with activity during incorrect source judgments, which are

Table 2
Retrieval success studies.

Publication	Encoding task	N	Foci	Stimulus
Achim and Lepage (2005a)	Item vs. pair judgments	18	25	Pictures
Daselaar et al. (2001)	Intentional encoding	13	4	Words
Daselaar, Veltman, Rombouts, Raaijmakers, and Jonker (2003)	Pleasantness judgments	17	9	Words
de Zubicaray et al. (2005)	Intentional memorizing	14	12	Words
Donaldson, Petersen, and Buckner (2001)	Abstract/concrete judgments	24	22	Words
Donaldson, Petersen, Ollinger, and Buckner (2001)	Sentence generation using word pairs	9	8	Words
Fliessbach et al. (2006)	Intentional encoding	21	11	Words
Henson et al. (2005)	Deep vs. shallow processing	22	24	Words
Henson et al. (1999)	Lexical decision	12	12	Words
Herron, Henson, and Rugg (2004)	Animacy judgments	12	5	Words
Hornberger, Rugg, and Henson (2006)	Size judgments	17	18	Pictures & words
Iidaka, Matsumoto, Nogawa, Yamamoto, and Sadato (2006)	Deep vs. shallow processing	16	20	Pictures
Kahn et al. (2004)	Imagining vs. reading	17	34	Words
Konishi, Wheeler, Donaldson, and Buckner (2000)	Intentional encoding	14	30	Words
Lepage, Brodeur, and Bourgouin (2003)	Associative encoding/visualization	10	10	Pictures
Leube, Erb, Grodd, Bartels, and Kircher (2003)	Gender judgments	12	2	Faces
Leveroni et al. (2000)	Pleasantness judgments	11	3	Faces (nonfamous)
Lundstrom et al. (2003)	Imagining vs. viewing	21	1	Words
Maratos, Dolan, Morris, Henson, and Rugg (2001)	Intentional encoding	12	15	Words
McDermott, Jones, Petersen, Lageman, and Roediger (2000)	Intentional encoding	24	8	Words
Morcom, Li, and Rugg (2007)	Size or animacy judgments	32	13	Pictures
Ragland et al. (2004)	Intentional encoding	15	5	Words
Ragland et al. (2006)	Deep vs. shallow processing	13	11	Words
Rombouts, Barkhof, Witter, Machielsen, and Scheltens (2001)	Intentional encoding/detecting buildings	9	1	Pictures
Slotnick, Moo, Segal, and Hart (2003)	Intentional encoding	8	6	Pictures
Smith, Henson, Dolan, and Rugg (2004)	Associating object and background	15	10	Pictures
Tsukiura, Mochizuki-Kawai, and Fujii (2005)	Multiple encoding conditions	18	2	Words
van der Veen, Nijhuis, Tisserand, Backes, and Jolles (2006)	Intentional vs. incidental encoding	24	5	Words
Von Zerssen, Mecklinger, Opitz, and von Cramon (2001)	Intentional encoding	12	16	Words
Weis, Klaver, et al. (2004), Weis, Specht, et al. (2004)	Building/landscape judgments	16	17	Pictures

Note: These studies employed old–new recognition tasks and reported "Hit vs. Correct Rejection" as the retrieval success contrast.

Table 3
Objective recollection studies.

Publication	Task, contrast	N	Foci	Stimulus
Cansino et al. (2002)	Source memory, correct vs. incorrect source judgment	17	17	Pictures
Dobbins, Foley, Schacter, and Wagner (2002)	Source memory, correct source judgment vs. correct item recognition judgment	14	21	Words
Dobbins et al. (2003)	Source memory, correct vs. incorrect 2-AFC source judgment	14	24	Words
Dobbins and Wagner (2005)	Source memory, correct vs. incorrect source judgment (recognized items only)	14	31	Pictures
Fan, Snodgrass, and Bilder (2003)	Source memory, correct source judgment vs. correct item recognition judgment	8	6	Pictures
Kahn et al. (2004)	Source memory, correct vs. incorrect source judgment (recognized items only)	17	23	Words
Kensinger and Schacter (2005)	Source memory/reality monitoring, correct vs. incorrect source judgments (conjunction of emotional and neutral words; neutral words-only)	16	20	Words
Lundstrom et al. (2003)	Source memory, correct source judgment vs. correct item recognition judgment	21	1	Words, pictures
Ragland et al. (2006)[a]	Source memory, correct vs. incorrect source judgment (recognized items only)	13	8	Words
Slotnick et al. (2003)	Source memory, correct source judgment vs. correct item recognition judgment	8	6	Pictures
Takahashi, Ohki, and Miyashita, (2002)	Source memory/reality monitoring, correct vs. incorrect source judgment	13	5	Pictures
Weis, Klaver, et al. (2004), Weis, Specht, et al. (2004)	Source memory, correct vs. incorrect source judgment (recognized items only)	12	2	Pictures

[a] Control participants only.

thought to involve predominantly item-based familiarity. We also included studies contrasting activity during correct source decisions with activity during correct old–new decisions (see Table 3). It should be noted that neither of these contrasts provides a "process-pure" measure of recollection. For example, incorrect source judgments may still involve recollective influences (i.e., noncriterial recollection; see Parks, 2007; Yonelinas & Jacoby, 1996), an issue to which we return in Section 4. It is also clear that the two contrasts may capture slightly different mixtures of familiarity and recollection. However, including both contrasts increased the sample size and thus the power of the ALE analysis. It also increased the extent to which results could be generalized across methodologies. To prevent additional heterogeneity, however, we compromised by excluding other source memory contrasts (e.g., correct source decision vs. correct novelty detection), as well as studies using associative recognition, another popular paradigm believed to assess recollection. As the literature grows, a quantitative meta-analytic comparison of these objective-recollection paradigms will be informative; however, this was beyond the scope of the current research. In all, sixteen studies using a variant of the source memory paradigm were included in the objective recollection meta-analysis, providing a total of 164 foci (see Table 3).

2.2.4. Subjective recollection

Seven studies included in the subjective recollection meta-analysis used the Remember–Know procedure. Here, participants are scanned during a recognition test that requires discrimination between old items that are "remembered" (recollection), and old items that are merely "known" (familiarity). The Remember–Know contrast thus yields a measure of subjective recollection. In a variation on the traditional Remember–Know paradigm, Montaldi, Spencer, Roberts, and Mayes (2006) trained participants to discriminate between familiarity and recollection, and to rate their familiarity on a 3-point scale. We included the contrast between "recollected" and "strongly familiar" test trials from this study in the subjective recollection analysis. In another study (Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006), participants were asked to rate their confidence in old–new recognition decisions on a 3-point scale. Using a parametric analysis approach, recollection-sensitive regions were identified as those showing an exponential increase in activation for the highest level of confidence, compared to Levels 1 and 2. In all, nine studies reporting

Table 4
Subjective recollection studies.

Publication	Retrieval task, contrast	N	Foci	Stimulus
Daselaar et al. (2006)	Item recognition with confidence judgments; parametric analysis (see text)[a]	24	8	Words
Eldridge, Knowlton, Furmanski, Bookheimer, and Engel (2000)	Remember–Know procedure; correct remember vs. know judgments	11	15	Words
Fenker, Schott, Richardson-Klavehn, Heinze, and Düzel (2005)	Remember–Know procedure; correct remember vs. know judgments (neutral words only)	20	30	Words
Henson et al. (1999)	Remember–Know procedure; correct remember vs. know judgments	12	4	Words
Johnson and Rugg (2007)	Remember–Know procedure; correct remember vs. know judgments[b]	16	24	Words
Montaldi et al. (2006)	Item recognition with confidence judgments; correct 'recollection' judgments vs. 'very familiar' judgments	13	6	Pictures
Sharot, Delgado, and Phelps (2004)	Remember–Know procedure; correct remember vs. know judgments	13	2	Pictures
Vilberg and Rugg (2007)	Remember–Know procedure; correct remember vs. know judgments[c]	28	13	Pictures
Yonelinas et al. (2005)	Remember–Know procedure; correct remember vs. high-confidence know judgments	16	26	Words

[a] Activations shared by younger and older adult groups.
[b] Exclusively masked with recollection effects specific to each of two encoding conditions.
[c] Exclusively masked with Know vs. Miss contrast.

subjective recollection contrasts met the criteria for inclusion, yielding a total of 131 foci (see Table 4).

2.3. ALE meta-analysis

We ran separate ALE analyses (Turkeltaub et al., 2002) for each contrast of interest. Activation coordinates from studies using the standard space of the Montreal Neurological Institute (MNI) were converted to Talairach space (Talairach & Tournoux, 1988) using the Brett transform (Brett, Christoff, Cusack, & Lancaster, 2001). The activation foci were modeled as the peaks of 3-D Gaussian distributions with a full-width half-maximum (FWHM) of 10 mm. The ALE statistic, representing the probability that a voxel contains at least one of the activation foci, was calculated at each voxel, and the resulting ALE maps were thresholded using 5000 permutations, controlling the false discovery rate (FDR) at $p < .05$. A cluster threshold of 100 mm^3 was applied. Calculation of ALE statistics, permutation testing, thresholding, and cluster analysis were carried out with BrainMap GingerALE Version 1.1 (www.brainmap.org; Laird et al., 2005), using the default values in the program. Thresholded ALE maps were overlaid onto the "colinbrain" Talairach template (Kochunov et al., 2002) and viewed using the Analysis of Functional Neuroimaging program (AFNI; Cox, 1996). Neuroanatomical labels for the ALE maxima were obtained using the Talairach Daemon and visual inspection.

3. Results

3.1. Encoding success

Table 5 and Fig. 1 show the results for the ALE analysis of encoding success studies. Although 12 of the 21 significant clusters were located in the right hemisphere, the greatest concordance in terms of size of region and peak ALE value was observed in the left hemisphere, most notably in dorsolateral and ventrolateral PFC. Other major left-hemisphere clusters were present in parahippocampal gyrus/anterior hippocampus, in fusiform gyrus and neighboring occipitotemporal areas, and in intraparietal sulcus/superior parietal lobe. We discuss the putative roles of these regions in detail below.

Table 5
Results from ALE meta-analysis of encoding success studies.

Cluster	Region(s)	Hem	BA(s)	x	y	z	Volume (mm^3)	Peak ALE value
1	Middle Frontal Gyrus, Inferior Frontal Gyrus	L	9, 45, 46, 47	−42	12	28	17848	0.0331
2	Parahippocampal Gyrus, Hippocampus, Cerebellum	L	37	−32	−36	−10	3552	0.0206
3	Fusiform Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus	L	37, 20	−44	−54	−12	3088	0.0173
4	Intraparietal Sulcus	L	7, 19	−26	−60	36	952	0.0129
5	Superior Parietal Lobule	R	7	28	−58	50	824	0.0155
6	Inferior Frontal Gyrus	R	9, 45	54	14	24	664	0.0120
7	Middle Frontal Gyrus	L	6	−44	0	50	576	0.0150
8	Fusiform Gyrus	R	20	38	−16	−24	536	0.0128
9	Superior Frontal Gyrus, Medial Frontal Gyrus	L	6, 32	0	14	52	456	0.0122
10	Middle Occipital Gyrus	R	19	34	−84	12	432	0.0117
11	Fusiform Gyrus	R	37	40	−56	−12	416	0.0130
12	Middle Frontal Gyrus	R	46	52	34	20	384	0.0130
13	Inferior Parietal Lobule	R	40	50	−48	44	368	0.0125
14	Inferior Temporal Gyrus	R	20	56	−54	−12	312	0.0128
15	Amygdala	R		20	−4	−12	312	0.0119
16	Inferior Frontal Gyrus	L	13	−26	12	−12	304	0.0135
17	Inferior Frontal Gyrus	R	47	26	10	−12	224	0.0131
18	Middle Temporal Gyrus	L	22	−56	−40	6	184	0.0114
19	Inferior Frontal Gyrus	R	9	44	6	22	184	0.0106
20	Intraparietal Sulcus	L	7	−38	−56	54	168	0.0107
21	Intraparietal Sulcus	R	19	30	−76	32	144	0.0116

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. x, y, z coordinates = peak voxel in Talairach space.

3.2. Retrieval success

ALE results for the retrieval success analysis are shown in Table 6 and Fig. 1. Similar to the encoding success results, the concordance map revealed active regions predominantly in the left hemisphere, but with an emphasis on posterior cortex. The largest cluster was in the left posterior parietal cortex, with local maxima in inferior and posterior lateral parietal cortex, as well as precuneus. A second large cluster was located in left DLPFC. Additional frontal foci included anterior cingulate cortex and left VLPFC. The left posterior parietal clusters were mirrored, albeit to a lesser extent, in the right hemisphere. Other clusters were located in left parahippocampal gyrus, bilateral insula, and bilateral caudate.

3.3. Encoding success vs. retrieval success

Table 7 and Fig. 1 show results for the comparison of encoding success and retrieval success ALE maps. Left inferior frontal gyrus, visual processing regions, and anterior hippocampus were among the primary regions with more concordant activation during successful encoding than during successful retrieval. Several smaller right-hemisphere foci, largely in prefrontal and temporal regions, were also preferentially active for successful encoding. In contrast, regions that were more active during successful retrieval than during successful encoding included left lateral superior parietal cortex and precuneus, as well as bilateral DLPFC and anterior PFC.

3.4. Objective recollection

The results of the objective recollection ALE analysis are shown in Table 8 and Fig. 2. They reveal a largely left-lateralized group of 17 regions. Because the number of foci entering this analysis was small (e.g., compared to the encoding and retrieval success analyses), there was a greater risk for 'outliers' to bias the results. Therefore, for each concordance of interest, we note how many studies report an activation maximum in the same region.

The meta-analyses revealed concordances in left DLPFC (8/12 or 67% of the studies), left VLPFC (75%), and lateral anterior PFC (25%), as well as medial and lateral posterior parietal clusters (precuneus, 25%; intraparietal sulcus/superior parietal lobe, 42%; inferior parietal lobe; 33%). The only significant medial-temporal cluster was located in the left amygdala (25%).

Table 6
Results from ALE meta-analysis of retrieval success studies.

Cluster	Region	Hem	BA	x	y	z	Volume (mm^3)	Peak ALE value
1	Superior Parietal Lobule, Precuneus, Inferior Parietal Lobule	L	7, 40	−34	−60	44	20128	0.0402
2	Inferior Frontal Gyrus, Middle Frontal Gyrus, Precentral Gyrus	L	10, 9, 46, 6, 8	−38	46	0	14808	0.0275
3	Middle Frontal Gyrus, Anterior Cingulate, Superior Frontal Gyrus	L	9, 32, 8	−6	36	30	4352	0.0321
4	Cingulate Gyrus	L	31	−4	−36	34	3224	0.0301
5	Inferior Frontal Gyrus, Insula, Inferior Frontal Gyrus	L	47, 13	−32	20	−6	2336	0.0188
6	Inferior Parietal Sulcus	R	19	34	−66	42	2168	0.0207
7	Superior Parietal Lobule	R	40	48	−44	50	1160	0.0221
8	Caudate	L		−12	8	2	800	0.0192
9	Caudate	R		10	10	−4	776	0.0171
10	Middle Frontal Gyrus	R	10	36	50	8	592	0.0140
11	Inferior Frontal Gyrus	R	47	32	22	−14	456	0.0163
12	Middle Temporal Gyrus	L	21	−62	−40	−4	432	0.0154
13	Superior Frontal Gyrus	L	10	−24	60	10	328	0.0131
14	Parahippocampal Gyrus	L	27	−12	−36	4	320	0.0146
15	Angular Gyrus	R	39	46	−50	28	184	0.0134
16	Superior Frontal Gyrus	R	9	44	36	28	184	0.0134
17	Superior Frontal Gyrus	L	11	−12	44	−14	144	0.0106
18	Insula	R	13	32	18	4	104	0.0126

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. x, y, z coordinates = peak voxel in Talairach space.
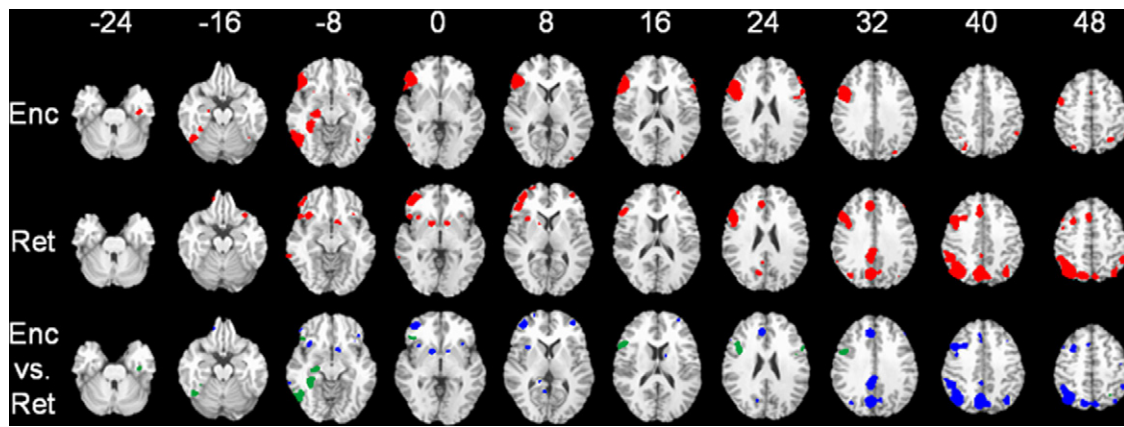
Fig. 1. ALE maps thresholded at $p < .05$, corrected. *Enc* = encoding success; *Ret* = retrieval success. For the *Enc vs. Ret* difference map, areas more active for encoding than for retrieval are shown in green. Areas more active for retrieval than for encoding are shown in blue.

3.5. Subjective recollection

Table 9 and Fig. 2 show ALE results for the subjective recollection analysis. Of the four meta-analyses reported here, the subjective recollection analysis was based on the smallest number of foci, which limited the statistical power of the analysis. Nevertheless, 16 significant clusters emerged, the largest of which was centered on left medial anterior PFC (reported in 6/9 or 67% of individual studies), extending into anterior cingulate cortex. The second largest cluster was situated in left medial-temporal cortex, with local maxima in parahippocampal gyrus (33%) and hippocampus (44%). A final major focus of interest was located in left inferior parietal cortex (78%).

3.6. Objective vs. subjective recollection

Table 10 and Fig. 2 show results for the comparison of objective and subjective recollection ALE maps. A large cluster extending from left DLPFC into left VLPFC, as well as a smaller area in left lateral anterior PFC, were significantly more active for objective recollection than for subjective recollection. Additional major foci with more concordant activity for objective than subjective recollection were located in left intraparietal sulcus and left amygdala. Regions more strongly associated with subjective than objective recollection were found in the left inferior parietal lobe, medial anterior PFC, bilateral parahippocampal gyri, and left hippocampus.

Table 7
Results from an analysis contrasting the ALE maps for encoding success and retrieval success.

Cluster	Region	Hem	BA	x	y	z	Volume (mm³)	Peak ALE value
Encoding > retrieval								
1	Inferior Frontal Gyrus, Middle Frontal Gyrus	L	45, 9	−48	22	14	2856	0.0180
2	Middle Occipital Gyrus, Fusiform Gyrus	L	37	−48	−62	−8	1952	0.0158
3	Cerebellum, Fusiform Gyrus	L	37	−34	−42	−20	1600	0.0109
4	Hippocampus	L	28	−20	−16	−12	816	0.0161
5	Inferior Frontal Gyrus	L	47	−46	32	2	760	0.0119
6	Fusiform Gyrus	R	20	38	−16	−24	312	0.0128
7	Intraparietal Sulcus	R	7	28	−56	52	184	0.0135
8	Amygdala	R		20	−4	−12	168	0.0119
9	Inferior Frontal Gyrus	R	9	54	14	24	152	0.0119
10	Inferior Temporal Gyrus	R	20	56	−54	−12	144	0.0128
11	Fusiform Gyrus	R	37	40	−56	−12	136	0.0123
12	Inferior Frontal Gyrus	R	46	54	32	20	136	0.0126
13	Inferior Frontal Gyrus	R	47	26	10	−12	104	0.0127
Retrieval > encoding								
1	Superior Parietal Lobule, Inferior Parietal Lobule	L	7, 40	−34	−60	44	8656	0.0367
2	Precuneus	L, R	7	−6	−68	36	7272	0.0339
3	Middle Frontal Gyrus, Precentral Gyrus	L	6, 8, 9	−32	10	54	3104	0.0186
4	Inferior Frontal Gyrus	L		−36	48	0	2736	0.0244
5	Cingulate Gyrus	L	31	−4	−36	34	2736	0.0300
6	Medial Frontal Gyrus	L	9, 8	−6	36	30	2584	0.0318
7	Precuneus	R	19	34	−66	42	1304	0.0200
8	Inferior Frontal Gyrus, Claustrum	L	47	−32	20	−6	896	0.0171
9	Caudate	L		−12	8	2	696	0.0184
10	Inferior Parietal Lobule	R	40	46	−44	50	640	0.0187
11	Caudate	R		10	10	−4	576	0.0162
12	Middle Frontal Gyrus	R	10	36	50	8	568	0.0140
13	Parahippocampal Gyrus	L	27	−12	−36	4	384	0.0145
14	Superior Temporal Gyrus	R	39	46	−50	28	256	0.0134
15	Middle Frontal Gyrus	L	10	−22	62	10	216	0.0124
16	Middle Temporal Gyrus	L	21	−62	−40	−4	208	0.0135
17	Insula	R	13	32	18	4	200	0.0124
18	Inferior Frontal Gyrus	R	47	34	22	−12	144	0.0129
19	Middle Frontal Gyrus	R	9	44	36	30	112	0.0123

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. x, y, z coordinates = peak voxel in Talairach space.

Table 8
Results from ALE meta-analysis of objective recollection.

Cluster	Region	Hem	BA	x	y	z	Volume (mm³)	Peak ALE value
1	Middle Frontal Gyrus, Inferior Frontal Gyrus	L	46, 8, 9, 45	−44	28	24	8000	0.0184
2	Medial Frontal Gyrus, Superior Frontal Gyrus	L	8, 9	−6	38	38	3272	0.0161
3	Inferior Parietal Lobe, Intraparietal Sulcus	L	40	−42	−56	48	2128	0.0137
4	Amygdala	L		−18	−6	−18	1344	0.0189
5	Caudate	L		−12	−2	18	1008	0.0134
6	Thalamus	L		−2	−16	0	992	0.0133
7	Middle Frontal Gyrus	L	10	−36	52	0	784	0.0121
8	Postcentral Gyrus	L	5	−28	−42	58	560	0.0112
9	Lingual Gyrus	R	18	12	−84	−6	464	0.0100
10	Inferior Frontal Gyrus	L	47	−28	22	−4	328	0.0089
11	Middle Frontal Gyrus	R	10	38	38	20	296	0.0108
12	Cingulate Gyrus	L	31	−6	−36	38	272	0.0104
13	Caudate	L		−12	18	−4	192	0.0099
14	Middle Frontal Gyrus, Inferior Frontal Gyrus	L	46	−46	46	8	160	0.0076
15	Precuneus	L	7	−2	−64	44	160	0.0085
16	Inferior Parietal Lobe	R	40	62	−36	24	136	0.0079
17	Inferior Temporal Gyrus	R	37	52	−54	−4	128	0.0082

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. x, y, z coordinates = peak voxel in Talairach space.
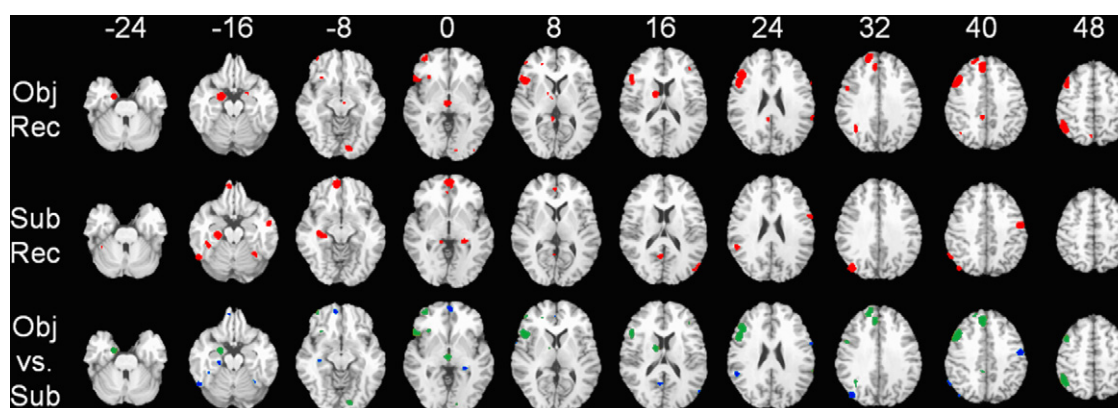

Fig. 2. ALE maps thresholded at *p* < .05, corrected. *Obj Rec* = objective recollection; *Sub Rec* = subjective recollection. For the *Obj vs. Sub* difference map, areas more active for objective than for subjective recollection are shown in green. Areas more active for subjective than objective recollection are shown in blue.

4. Discussion

The ALE meta-analyses revealed robust whole-brain spatial activation patterns related to episodic memory processes, including successful encoding, successful retrieval, and recollection (objective and subjective). In each case, we observed concordant activations across studies that differed in many methodological aspects (experimental paradigms, stimulus types, imaging protocols, etc.). As expected, medial-temporal, prefrontal, and parietal regions contributed the greatest number of significant clusters, particularly in the left hemisphere. We next discuss the specific patterns observed in each meta-analysis.

4.1. Successful encoding and successful retrieval

4.1.1. Medial-temporal regions

Our meta-analysis showed that medial-temporal activation is reliably evident in ER-fMRI studies of memory, during both encod-

Table 9
Results from ALE meta-analysis of subjective recollection.

Cluster	Region	Hem	BA	x	y	z	Volume (mm³)	Peak ALE value
1	Medial Frontal Gyrus, Anterior Cingulate	L, R	10, 32	−6	54	−8	2768	0.0131
2	Parahippocampal Gyrus, Hippocampus	L	35	−22	−22	−16	1608	0.0126
3	Angular Gyrus	L	39	−40	−72	32	1456	0.0141
4	Precentral Gyrus	R	4	52	−8	42	1008	0.0162
5	Precuneus	L	23	−6	−56	18	608	0.0105
6	Fusiform Gyrus	L	20	−36	−40	−18	512	0.0093
7	Inferior Temporal Gyrus	L	20	−52	−56	−14	496	0.0120
8	Superior Temporal Gyrus	L	13	−52	−40	22	408	0.0108
9	Inferior Parietal Lobule	L	40	−54	−54	38	408	0.0091
10	Parahippocampal Gyrus	R	27	24	−32	0	392	0.0098
11	Cerebellum	R		30	−50	−18	352	0.0081
12	Postcentral Gyrus	L	3	−18	−36	58	336	0.0090
13	Middle Temporal Gyrus	R	21	52	−6	−16	320	0.0093
14	Inferior Frontal Gyrus	R	9	58	6	24	320	0.0086
15	Middle Temporal Gyrus	R	39	52	−68	16	304	0.0081
16	Parahippocampal Gyrus	L	27	−10	−36	4	176	0.0075

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. x, y, z coordinates = peak voxel in Talairach space.

Table 10
Results from an analysis contrasting the ALE maps for objective and subjective recollection.

Cluster	Region	Hem	BA	x	y	z	Volume (mm³)	Peak ALE value
Objective > subjective								
1	Middle Frontal Gyrus, Precentral Gyrus, Inferior Frontal Gyrus	L	46, 9, 45	−42	28	24	6440	0.0168
2	Medial Frontal Gyrus, Superior Frontal Gyrus	L	8, 9	−6	38	38	2888	0.0161
3	Intraparietal Sulcus	L	40	−42	−54	50	1088	0.0128
4	Amygdala	L		−18	−6	−20	1000	0.0179
5	Caudate Body	L		−12	−2	18	776	0.0133
6	Middle Frontal Gyrus	L	10	−36	52	0	760	0.0121
7	Thalamus	L		−2	−16	0	720	0.0129
8	Inferior Parietal Lobe	L	40	−34	−52	34	392	0.0101
9	Postcentral Gyrus	L	5	−28	−44	58	320	0.0104
10	Inferior Frontal Gyrus	L	47	−28	22	−4	248	0.0089
11	Middle Frontal Gyrus	R	10	38	38	20	240	0.0106
12	Lingual Gyrus	R	18	12	−84	−6	216	0.0093
13	Caudate Head	L		−12	18	−4	152	0.0093
14	Middle Frontal Gyrus, Inferior Frontal Gyrus	L	46	−46	46	8	152	0.0076
15	Cingulate Gyrus	L	31	−6	−36	38	136	0.0094
Subjective > objective								
1	Inferior Parietal Lobe	L	39	−40	−72	32	936	0.0140
2	Precentral Gyrus	R	4	52	−8	42	784	0.0162
3	Superior Frontal Gyrus	R		2	58	0	384	0.0107
4	Posterior Cingulate	L	23	−6	−56	18	352	0.0105
5	Inferior Temporal Gyrus	L	20	−52	−56	−14	336	0.0120
6	Medial Frontal Gyrus	L	10	−8	52	−10	312	0.0101
7	Superior Temporal Gyrus	L	13	−52	−40	22	280	0.0108
8	Parahippocampal Gyrus	L	35	−22	−24	−16	232	0.0100
9	Inferior Parietal Lobe	L	40	−54	−54	38	232	0.0089
10	Parahippocampal Gyrus	R	27	24	−32	0	168	0.0095
11	Fusiform Gyrus	L	20	−36	−40	−18	144	0.0090
12	Hippocampus	L		−32	−22	−10	120	0.0097

Note: Hem = hemisphere. L = left. R = right. BA = approximate Brodmann area. ALE = activation likelihood estimation. *x, y, z* coordinates = peak voxel in Talairach space.

ing and retrieval (see Henson, 2005). Note, however, that there were differences between the encoding and retrieval paradigms: Regions more strongly associated with encoding than retrieval included left anterior hippocampus (Talairach coordinates: −20, −16, −12) and right amygdala (Talairach coordinates: 20, −4, −12), whereas left parahippocampal gyrus (Talairach coordinates: −12, −36, 4) was preferentially activated during retrieval. Our findings are thus in line with previous proposals that anterior hippocampus supports episodic encoding (Lepage et al., 1998; Parsons et al., 2006; Schacter & Wagner, 1999), whereas more posterior (though not necessarily hippocampal) MTL regions play a stronger role in episodic retrieval (for alternative proposals, see Greicius et al., 2003; Henson, 2005; Ludowig et al., 2008; Schacter & Wagner, 1999; see also Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004). The fact that activation extended beyond hippocampus proper to include the parahippocampal gyrus provides additional evidence that parahippocampal structures (perirhinal, entorhinal, and parahippocampal cortices) make a significant contribution to memory (for recent reviews, see Diana et al., 2007; Eichenbaum et al., 2007; see also Bowles et al., 2007). However, a fine-grained understanding of this contribution requires additional research. One possibility is that parahippocampal activation may reflect heightened attention to contextual details during retrieval as compared to encoding.

Another important consideration is the influence of the specific contrasts used to define encoding and retrieval success. For example, novelty-related hippocampal activation for CRs (e.g., Stark & Okado, 2003) may reduce the chances of detecting hippocampal retrieval success activation with the Hit-CR contrast. As the literature grows, future meta-analyses should be performed for other contrasts (e.g., Hit–Miss at retrieval) to test the generality of the present findings.

4.1.2. Prefrontal regions

Not surprisingly, the encoding success meta-analysis revealed widespread concordance in left DLPFC and VLPFC (see Blumenfeld

& Ranganath, 2007, for a review and discussion of the putative roles of these regions in episodic encoding). In addition, several smaller homologous clusters were present in the right hemisphere. The retrieval success analysis yielded a similar pattern, in addition to clusters in bilateral lateral anterior PFC and left anterior cingulate. According to the hemispheric encoding/retrieval asymmetry model (HERA; Habib et al., 2003; Tulving et al., 1994), a direct comparison of encoding and retrieval maps should show predominantly encoding-related clusters in left PFC, and retrieval-related clusters in right PFC. However, a statistical contrast between the two ALE maps did not support this prediction. Both encoding- and retrieval-dominant regions were situated mainly in left PFC and sensorimotor frontal cortex, and among the few small right-hemisphere clusters, some were encoding-dominant. Given that the majority of the encoding and retrieval studies used verbal materials, it is possible that the overall left-dominant pattern in our results partially reflects the emphasis on verbal processing. However, the proportion of studies using verbal stimuli was similar for both encoding success (20/26; 77%) and retrieval success (19/29; 66%), suggesting that stimulus modality was not a confounding factor in the encoding-retrieval contrasts. We investigated this issue further by conducting separate follow-up analyses for studies using verbal and nonverbal materials, respectively. Within *both* the verbal and the nonverbal analyses, encoding-dominant PFC activations were not strongly lateralized, whereas retrieval-dominant PFC activations were present primarily in the left hemisphere.[1] In sum, both within and across stimulus modalities, our meta-analyses failed to lend support to the HERA model.

To our knowledge, this is the first meta-analytic demonstration that the ER-fMRI literature on episodic memory is inconsistent with HERA, though the results do show some regional differences between encoding and retrieval activations. Specifically, inferior

---

[1] Detailed results for these follow-up analyses are available upon request.

frontal gyrus appears to be more strongly involved in encoding, whereas middle and superior frontal gyri are more strongly involved in retrieval. This finding is consistent with models that emphasize the role of the inferior frontal regions in cue specification and selection at encoding and the superior frontal regions in monitoring (Henson, 2005; Moscovitch & Winocur, 2002). An interesting question for future meta-analysis is whether prefrontal encoding-related activations vary reliably as a function of encoding condition (e.g., with or without orienting task).

4.1.3. Parietal regions

Posterior cortex figured prominently in both encoding and retrieval meta-analyses, offering further evidence for a role of this region in episodic long-term memory generally. However, a direct comparison between the two ALE maps showed parietal cortex to be more strongly associated with successful retrieval than with successful encoding. Retrieval-related activation in intraparietal sulcus and superior parietal lobe eclipsed encoding-related activation. Furthermore, activation in the inferior lateral parietal lobe was almost exclusively associated with retrieval success. To the extent that posterior cortex supports attentional influences on episodic long-term memory (e.g., Cabeza, 2008; Ciaramelli et al., 2008; see also Uncapher et al., 2006; Vilberg & Rugg, 2008), the present findings may be interpreted as suggesting that the attentional requirements of successful retrieval outweigh those of successful encoding. Behavioural data suggest, however, that encoding is generally more vulnerable to the effects of divided attention than is retrieval (e.g., Craik, Naveh-Benjamin, Ishaik, & Anderson, 2000; but see Fernandes & Moscovitch, 2002). Future exploration of the neural bases of the principles governing the relationship between encoding and retrieval operations (e.g., transfer-appropriate processing, cortical reinstatement; see Rugg, Johnson, Park, & Uncapher, 2008) may shed further light on the relative contributions of parietal subregions to episodic memory.

4.2. Objective and subjective recollection

4.2.1. Medial-temporal regions

One of the more striking results of the recollection analyses is the fact that left hippocampus (Talairach coordinates: -32, -22, -10) was active for subjective recollection as part of a larger MTL cluster, whereas no concordant hippocampal activation was observed for objective recollection. The latter is not surprising, considering that the 164 objective recollection foci on which our analysis was based included only six hippocampal foci (2 in the left hemisphere, 4 in the right hemisphere). This lack of robust hippocampal activation in objective recollection may be due to the influence of noncriterial recollection (e.g., Parks, 2007; Yonelinas & Jacoby, 1996; see also Vilberg & Rugg, 2008), that is, recollection of contextual details other than those required for a correct source judgment. Putatively familiarity-based responses (e.g., source misattributions of correctly recognized items) that form the baseline condition in objective recollection contrasts may thus be "contaminated" with noncriterial recollection. Given this possibility, we refrain from interpreting the null finding as evidence that the hippocampus plays no role in objective recollection. Rather, we suggest that the particular contrasts employed in objective recollection studies may be too constrained to reveal robust hippocampal contributions. Subjective recollection methods, such as Remember–Know and confidence rating procedures, may provide researchers with a greater chance of detecting recollection-related activation in the hippocampus.

Medial-temporal regions outside hippocampus proper were also activated. For objective recollection, significant concordance was present in the left amygdala. This finding is somewhat surprising, given that the amygdala is generally associated with memory for emotional information, whereas the studies included in the present analyses used neutral stimuli.[2] However, the individual studies varied greatly with respect to MTL activation. Three of the twelve objective-recollection studies reported left-amygdala activation (Dobbins, Rice, Wagner, & Schacter, 2003; Kahn, Davachi, & Wagner, 2004; Weis, Klaver, Reul, Elger, & Fernandez, 2004), along with other left-MTL foci. Two additional studies reported right-hemisphere amygdala activation along with right-hemisphere hippocampal activation (Cansino, Maquet, Dolan, & Rugg, 2002; Weis, Specht, et al., 2004). The remaining seven studies reported no activations in MTL. In light of this variability, the concordance results must be interpreted carefully. One possibility is that in the studies that we included in our analysis, some combination of partial voluming, smoothing/filtering, normalization, conversion of MNI to Talairach coordinates, or automated anatomical labeling of the coordinates may have led to a distorted estimate of the exact location of the activation. Thus, although the meta-analysis identified the left amygdala as a likely source of MTL activation in objective recollection, there may also be contributions from anterior hippocampus or parahippocampal gyrus. It is worth noting, however, that independent evidence suggests that amygdala involvement in episodic memory retrieval is not limited to emotional stimuli. A recent single-unit recording study in humans (Rutishauser et al., 2008) revealed retrieval-related spiking activity in both hippocampal and amygdala neurons that was predictive of the success of source memory decisions about nonemotional stimuli. The contribution of the amygdala to objective (but not subjective) recollection is intriguing and awaits additional investigation.

4.2.2. Prefrontal regions

Prefrontal regions were significantly active in both objective and subjective recollection analyses, but a statistical comparison of the two ALE maps revealed significant differences in prefrontal activations. Consistent with our hypothesis, objective recollection was more strongly associated with activation in left DLPFC and VLPFC, and also showed slightly more involvement of left lateral anterior PFC, relative to subjective recollection. The only prefrontal region more active for subjective than objective recollection was medial anterior PFC. Activation in DLPFC, VLPFC, and lateral anterior PFC has been interpreted as supporting cognitive control processes needed to recollect specific contextual details (selection, maintenance, organization; see Badre & Wagner, 2007 and Simons & Spiers, 2003, for reviews). We attribute the absence of lateral PFC activation for subjective recollection to the relatively low demands of Remember–Know and confidence judgments on cognitive control processes, which are more heavily taxed in objective recollection. This account of the data also meshes well with the neuropsychological and developmental dissociations mentioned previously (e.g., Ciaramelli & Ghetti, 2007; Duarte et al., 2005, 2008). However, we cannot rule out an alternative explanation, according to which Remember–Know judgments and confidence ratings tap similar DLPFC/VLPFC-based cognitive control functions for *both* recollection and familiarity-based responses (see also Skinner & Femandes, 2007). Testing the latter account would require separate meta-analysis of familiarity-specific activations. However, relatively few of the studies we included reported such activations. In addition, these studies that did report familiarity-related activations differed greatly with respect to the contrasts used to identify the activations (e.g., Know > Miss, Vilberg & Rugg, 2007; Source Miss > Item Miss, Ragland, Valdez, Loughead, Gur, & Gur,

---

[2] One exception is the study by Kensinger and Schacter (2005), who reported the conjunction, across neutral and emotional items, of correct-vs.-incorrect source memory contrasts. Kensinger and Schacter (2005) reported significant activation in left anterior hippocampus, but not in the amygdala.

2006; correlation with recognition confidence, Yonelinas, Otten, Shaw, & Rugg, 2005). Meta-analysis of familiarity-related activation patterns thus remains a goal for future research.

The involvement of distinct sub-regions of anterior PFC in the two types of recollection also fits in well with previous evidence. It has been noted that activation in medial anterior PFC is associated with fast responding in tasks that direct attention toward one's own cognitive or affective state (Gilbert et al., 2006; Simons, Owen, Fletcher, & Burgess, 2005; see also Burgess et al., 2007; Craik et al., 1999; Moscovitch & Winocur, 2002). Indeed, subjective recollection is by nature introspective (how do I feel about this memory?), and "Remember" responses are typically fast (e.g., Dewhurst & Conway, 1994). In contrast, activation in lateral anterior PFC tends to be observed during tasks with high executive control demands that elicit relatively slow performance (Gilbert et al., 2006; Simons et al., 2005). Objective recollection tasks, such as source monitoring, clearly fall in this category (e.g., Spaniol, Madden, & Voss, 2006).

Neither objective nor subjective recollection contrasts showed right DLPFC involvement. This result suggests that the particular control processes subserved by this region (post-retrieval monitoring and verification; e.g., Cabeza, Locantore, & Anderson, 2003; Henson, Rugg, Shallice, & Dolan, 2000) are either *equally* engaged during recollection and familiarity-based retrieval (see also Skinner & Femandes, 2007), or that they are *more* engaged during familiarity-based responses (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999). As stated above, meta-analysis of ER-fMRI studies of familiarity is a priority for future research.

4.2.3. Parietal regions

A statistical comparison of ALE maps for objective and subjective recollection revealed areas within inferior lateral parietal cortex that were more strongly associated with subjective recollection, as well as one area that was more strongly associated with objective recollection. In superior parietal cortex, a concordant cluster was found for objective recollection only. Thus, whereas inferior parietal regions participate in both objective and subjective recollection, superior parietal cortex appears to be involved in objective recollection only. The association of inferior parietal activity with recollection is in line with current models according to which this region mediates bottom-up attention to (Cabeza, 2008; Ciaramelli et al., 2008) or working memory for (Vilberg & Rugg, 2008) retrieved contents, which are stronger and more salient for recollection than for familiarity. The superior parietal lobe, on the other hand, is thought to be essential for top-down, strategic search processes (Cabeza, 2008; Ciaramelli et al., 2008), thus contributing to the retrieval of specific contextual details. As argued above, these top-down processes may be more characteristic of objective recollection than subjective recollection.

Further clarification of the role of lateral parietal cortex in memory in general, and in the recollection-familiarity dichotomy in particular, may come from studies of focal lesion patients. So far, the few extant studies suggest that lateral parietal patients do not show a severe amnesia or problems with item recognition or objective recollection, but may be impaired on measures of subjective recollection (e.g., Davidson et al., 2008; Haramati, Soroker, Dudai, & Levy, 2008; Simons et al., 2008; see also Ally, Simons, McKeever, Peers, & Budson, 2008).

An interesting question not addressed in the current analyses is whether the regions linked to objective and subjective recollection are also involved during encoding of subsequently recollected material. Given the recent increase in studies of source or associative encoding in the DM paradigm (e.g., Achim and Lepage, 2005b; Chua, Rand-Giovanetti, Schacter, Albert, & Sperling, 2004; Uncapher et al., 2006), this issue will soon be amenable to meta-analysis.

5. Conclusions

Consistent with previous reviews and meta-analyses (e.g., Ciaramelli et al., 2008; Gilbert et al., 2006; Henson, 2005; Naghavi & Nyberg, 2005; Skinner & Femandes, 2007; Vilberg & Rugg, 2008; Wagner et al., 2005), our meta-analysis revealed wide swaths of memory-related activity across temporal, frontal, parietal, and other regions of the brain. Because of the focus of our hypotheses, and the large number of individual results, we concentrated on medial-temporal, prefrontal, and parietal activations in our discussion, but we note that many other regions were active and deserve continued exploration in future research.

Several of our major results lend support to observations previously made on the basis of individual studies or qualitative literature reviews. These results included (a) a generally left-hemisphere-dominant pattern of encoding and retrieval activations that contradicts the HERA model (Habib et al., 2003; Tulving et al., 1994), (b) an anterior–posterior gradient in MTL activations associated with encoding and retrieval (e.g., Lepage et al., 1998), and (c) posterior parietal activation for both encoding and retrieval (e.g., Ciaramelli et al., 2008; Uncapher et al., 2006).

Novel findings included (a) differential involvement of prefrontal sub-regions in objective and subjective recollection, (b) amygdala and superior lateral parietal involvement in objective but not subjective recollection, and (c) reliable hippocampal activation in subjective but not objective recollection. Although the literature (e.g., Duarte et al., 2008) was suggestive of qualitative dissociations between activation patterns for objective and subjective recollection, the current analyses were the first to directly contrast the two types of recollection. Our findings highlight the risk of treating source memory and "Remember" judgments as direct measures of a unitary recollection process (see also Wais, Mickes, & Wixted, 2008). In light of the widespread use of these measures with special populations (e.g., neuropsychological patients, older adults), a challenge for future work lies in the development of behavioural and fMRI paradigms that yield more "process-pure" measures of episodic memory processes.

The concordance maps presented here provide a quantitative synthesis of a large segment of the ER-fMRI literature on episodic memory. As canonical templates, these maps may help guide future research and impose constraints on neurocognitive theories of episodic memory. Some of the more surprising findings, regarding amygdala and hippocampal contributions to different memory processes, open up questions for new research. Finally, several opportunities for future meta-analytic research have been identified. These include alternative measures of retrieval success (e.g., Hit–Miss) and objective recollection (e.g., associative vs. item recognition), the neural correlates of familiarity, and studies of encoding processes that lead to successful recollection.

References

Achim, A. M., & Lepage, M. (2005a). Dorsolateral prefrontal cortex involvement in memory post-retrieval monitoring revealed in both item and associative recognition tests. *NeuroImage*, 24, 1113–1121.

Achim, A. M., & Lepage, M. (2005b). Neural correlates of memory for items and for associations: An event-related functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 17, 652–667.

Ally, B. A., Simons, J. S., McKeever, J. D., Peers, P. V., & Budson, A. E. (2008). Parietal contributions to recollection: Electrophysiological evidence from aging and patients with parietal lesions. *Neuropsychologia*, 46, 1800–1812.

Alvarez, P., & Squire, L. R. (1994). Memory consolidation and the medial temporal lobe: A simple network model. *Proceedings of the National Academy of Sciences*, 91, 7041–7045.

Atkinson, R. C., & Juola, J. F. (1974). Search and decision processes in recognition memory. In D. H. Krantz, R. C. Atkinson, L. R. Duncan, & P. Suppes (Eds.), *Contemporary developments in mathematical psychology: Learning, memory, and thinking* (pp. 243–293). San Francisco: Freeman.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45, 2883–2901.

Blumenfeld, R. S., & Ranganath, C. (2007). Prefrontal cortex and long-term memory encoding: An integrative review of findings from neuropsychology and neuroimaging. *The Neuroscientist*, 13, 280–291.

Bowles, B., Crupi, C., Mirsattari, S. M., Pigott, S. E., Parrent, A. G., Pruessner, J. C., et al. (2007). Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proceedings of the National Academy of Sciences of the USA*, 104, 16382–16387.

Brassen, S., Weber-Fahr, W., Sommerb, T., Lehmbecka, J. T., & Braus, D. F. (2006). Hippocampal-prefrontal encoding activation predicts whether words can be successfully recalled or only recognized. *Behavioural Brain Research*, 171, 271–278.

Brett, M., Christoff, K., Cusack, R., & Lancaster, J. (2001). Using the Talairach atlas with the MNI template. *NeuroImage*, 13, S85.

Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*, 281, 1185–1187.

Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of perirhinal cortex and hippocampus? *Nature Reviews Neuroscience*, 2, 51–61.

Buckner, R. L. (1996). Beyond HERA: Contributions of specific prefrontal brain areas to long-term memory retrieval. *Psychonomic Bulletin & Review*, 3, 149–158.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Dale, A. M., Rotte, M., & Rosen, B. R. (1998). Functional-anatomic study of episodic retrieval: II. Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. *NeuroImage*, 7, 163–175.

Buckner, R. L., Wheeler, M. E., & Sheridan, M. A. (2001). Encoding processes during retrieval tasks. *Journal of Cognitive Neuroscience*, 13, 406–415.

Burgess, P. W., Dumontheil, I., & Gilbert, S. J. (2007). The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences*, 11, 290–298.

Cabeza, R. (2008). Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia*, 46, 1813–1827.

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, 9, 613–625.

Cabeza, R., Locantore, J. K., & Anderson, N. D. (2003). Lateralization of prefrontal activity during episodic memory retrieval: Evidence for the production-monitoring hypothesis. *Journal of Cognitive Neuroscience*, 15, 249–259.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition. II. An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12, 1–47.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, 12, 1048–1056.

Chee, M. W. L., Westphal, C., Goh, J., Graham, S., & Song, A. W. (2003). Word frequency and subsequent memory effects studied using event-related fMRI. *NeuroImage*, 20, 1042–1051.

Chein, J. M., Fissell, K., Jacobs, S., & Fiez, J. A. (2002). Functional heterogeneity within Broca's area during verbal working memory. *Physiology and Behavior*, 77, 635–639.

Chua, E. F., Rand-Giovannetti, E., Schacter, D. L., Albert, M. S., & Sperling, R. A. (2004). Dissociating confidence and accuracy: Functional magnetic resonance imaging shows origins of the subjective memory experience. *Journal of Cognitive Neuroscience*, 16, 1131–1142.

Ciaramelli, E., & Ghetti, S. (2007). What are confabulators' memories made of? A study of subjective and objective measures of recollection in confabulation. *Neuropsychologia*, 45, 1489–1500.

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46, 1828–1851.

Clark, D., & Wagner, A. D. (2003). Assembling and encoding word representations: fMRI subsequent memory effects implicate a role for phonological control. *Neuropsychologia*, 41, 304–317.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 29, 162–173.

Craik, F. I. M., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., et al. (1999). In search of the self: A positron emission tomography study. *Psychological Science*, 10, 26–34.

Craik, F. I. M., Naveh-Benjamin, M., Ishaik, G., & Anderson, N. D. (2000). Divided attention at encoding and retrieval: The effects of cognitive control. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 26, 1744–1749.

Daselaar, S. M., Rombouts, S. A., Veltman, D. J., Raaijmakers, J. G., Lazeron, R. H., & Jonker, C. (2001). Parahippocampal activation during successful recognition of words: A self-paced event-related fMRI study. *NeuroImage*, 13, 1113–1120.

Daselaar, S. M., Veltman, D. J., Rombouts, S. A., Raaijmakers, J. G., & Jonker, C. (2003). Neuroanatomical correlates of episodic encoding and retrieval in young and elderly subjects. *Brain*, 126, 43–56.

Daselaar, S. M., Fleck, M. S., Dobbins, I. G., Madden, D. J., & Cabeza, R. (2006). Effects of healthy aging on hippocampal and rhinal memory functions: An event-related fMRI study. *Cerebral Cortex*, 16, 1771–1782.

Davachi, L. (2006). Item, context, and relational episodic encoding in humans. *Current Opinion in Neurobiology*, 16, 693–700.

Davidson, P. S. R., Anaki, D., Saint-Cyr, J. A., Chow, T. W., & Moscovitch, M. (2006). Exploring the recognition memory deficit in Parkinson's disease: Estimates of recollection versus familiarity. *Brain*, 129, 1768–1779.

Davidson, P. S. R., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A. S. N., Murphy, K. J., et al. (2008). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, 46, 1743–1755.

Dennis, N. A., Daselaar, S. M., & Cabeza, R. (2007). Effects of aging on transient and sustained successful memory encoding activity. *Neurobiology of Aging*, 28, 1749–1758.

Dewhurst, S. A., & Conway, M. A. (1994). Pictures, images, and recollective experience. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 20, 1088–1098.

de Zubicaray, G. I., McMahon, K. L., Eastburn, M. M., Finnigan, S., & Humphreys, M. S. (2005). fMRI evidence of word frequency and strength effects in recognition memory. *Cognitive Brain Research*, 24, 587–598.

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.

Dobbins, I. G., Foley, H., Schacter, D. L., & Wagner, A. D. (2002). Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron*, 35, 989–696

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, 41, 318–333.

Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex*, 15, 1768–1778.

Dobbins, I. G., & Han, S. (2006). Cue- versus probe-dependent prefrontal cortex activity during contextual remembering. *Journal of Cognitive Neuroscience*, 18, 1439–1452.

Donaldson, D. I., Petersen, S. E., & Buckner, R. L. (2001). Dissociating memory retrieval processes using fMRI: Evidence that priming does not support recognition memory. *Neuron*, 31, 1047–1059.

Donaldson, D. I., Petersen, S. E., Ollinger, J. M., & Buckner, R. L. (2001). Dissociating state and item components of recognition memory using fMRI. *Neuroimage*, 13, 129–142.

Duarte, A., Henson, R. N., & Graham, K. S. (2008). The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex*, 18, 2169–2180.

Duarte, A., Ranganath, C., & Knight, R. T. (2005). Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience*, 25, 8333–8337.

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, 30, 123–152.

Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, 3, 1149–1152.

Erk, S., Kiefer, M., Grothe, J., Wunderlich, A. P., Spitzer, M., & Walter, H. (2003). Emotional context modulates subsequent memory effect. *NeuroImage*, 18, 439–447.

Fan, J., Snodgrass, G. J., & Bilder, R. M. (2003). Functional magnetic resonance imaging of source versus item memory. *Neuroreport*, 14, 2275–2281.

Fenker, D. B., Schott, B. H., Richardson-Klavehn, A., Heinze, H. J., & Düzel, E. (2005). Recapitulating emotional context: Activity of amygdala, hippocampus and fusiform cortex during recollection and familiarity. *European Journal of Neuroscience*, 21, 1993–1999.

Fernandes, M., & Moscovitch, M. (2002). Factors modulating the effect of divided attention during retrieval of words. *Memory & Cognition*, 30, 731–744.

Fletcher, P. C., & Henson, R. N. A. (2001). Frontal lobes and human memory. *Brain*, 124, 849–881.

Fletcher, P. C., Stephenson, C. M., Carpenter, T. A., Donovan, T., & Bullmore, E. T. (2003). Regional brain activations predicting subsequent memory success: An event-related fMRI study of the influence of encoding tasks. *Cortex*, 39, 1009–1026.

Fliessbach, K., Trautner, P., Quesada, C. M., Elger, C. E., & Weber, B. (2007). Cerebellar contributions to episodic memory encoding as revealed by fMRI. *NeuroImage*, 15, 1330–1337.

Fliessbach, K., Weis, S., Klaver, P., Elger, C. E., & Weber, B. (2006). The effect of word concreteness on recognition memory. *NeuroImage*, 32, 1413–1421.

Gabrieli, J. D. E. (2001). Functional neuroimaging of episodic memory. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging of cognition* (pp. 253–291). Cambridge, MA: MIT Press.

Garoff, R. J., Slotnick, S. D., & Schacter, D. L. (2005). The neural origins of specific and general memory: The role of the fusiform cortex. *Neuropsychologia*, 43, 847–859.

Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Laurie, S. M., Frith, C. D., et al. (2006). Functional specialization within rostral prefrontal cortex (BA 10): A meta-analysis. *Journal of Cognitive Neuroscience*, 18, 932–948.

Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J., & Moscovitch, M. (2004). Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex*, 14, 1214–1225.

Gold, J. J., Smith, C. N., Bayley, P. J., Shrager, Y., Brewer, J. B., Stark, C. E., et al. (2006). Item memory, source memory, and the medial temporal lobe: Concordant findings from fMRI and memory-impaired patients. *Proceedings of the National Academy of Sciences*, 103, 9351–9356.

Greicius, M. D., Krasnow, B., Boyett-Anderson, J. M., Eliez, S., Schatzberg, A. F., Reiss, A. L., et al. (2003). Regional analysis of hippocampal activation during memory encoding and retrieval: fMRI study. *Hippocampus*, 13, 164–174.

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: The HERA model revisited. *Trends in Cognitive Sciences*, 7, 241–245.

Haramati, S., Soroker, N., Dudai, Y., & Levy, D. A. (2008). The posterior parietal cortex in recognition memory: A neuropsychological study. *Neuropsychologia*, 46, 1756–1766.

Henson, R. (2005). A mini-review of fMRI studies of human medial temporal lobe activity associated with recognition memory. *Quarterly Journal of Experimental Psychology*, 58, 340–360.

Henson, R. N., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, 19, 3962–3972.

Henson, R. N., Rugg, M. D., Shallice, T., & Dolan, R. J. (2000). Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience*, 12, 913–923.

Henson, R. N., Hornberger, M., & Rugg, M. D. (2005). Further dissociating the processes involved in recognition memory: An FMRI study. *Journal of Cognitive Neuroscience*, 17, 1058–1073.

Herron, J. E., Henson, R. N., & Rugg, M. D. (2004). Probability effects on the neural correlates of retrieval success: an fMRI study. *Neuroimage*, 21, 302–310.

Hornberger, M., Rugg, M. D., & Henson, R. N. (2006). fMRI correlates of retrieval orientation. *Neuropsychologia*, 44, 1425–1436.

Iidaka, T., Matsumoto, A., Nogawa, J., Yamamoto, Y., & Sadato, N. (2006). Frontoparietal network involved in successful retrieval from episodic memory. Spatial and temporal analyses using fMRI and ERP. *Cerebral Cortex*, 16, 1349–1360.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, 30, 513–541.

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex*, 17, 2507–2515.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional–neuoanatomical correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience*, 24, 4172–4180.

Kao, Y. C., Davis, E. S., & Gabrieli, J. D. E. (2005). Neural correlates of actual and predicted memory formation. *Nature Neuroscience*, 8, 1776–1783.

Kapur, S., Craik, F. I. M., Jones, C., Brown, G. M., Houle, S., & Tulving, E. (1995). Functional role of the prefrontal cortex in retrieval of memories: A PET study. *Neuroreport*, 6, 1880–1884.

Kensinger, E. A., & Schacter, D. L. (2005). Retrieving accurate and distorted memories: Neuroimaging evidence for effects of emotion. *NeuroImage*, 27, 167–177.

Kochunov, P., Lancaster, J., Thompson, P., Toga, A. W., Brewer, P., Hardies, J., et al. (2002). An optimized individual target brain in the Talairach coordinate system. *NeuroImage*, 17, 922–927.

Konishi, S., Wheeler, M. E., Donaldson, D. I., & Buckner, R. L. (2000). Neural correlates of episodic retrieval success. *NeuroImage*, 12, 276–286.

Laird, A. R., McMillan, K. M., Lancaster, J. L., Kochunov, P., Turkeltaub, P. E., Pardo, J. V., et al. (2005). A comparison of label-based review and ALE meta-analysis in the stroop task. *Human Brain Mapping*, 25, 6–21.

Lepage, M., Habib, R., & Tulving, E. (1998). Hippocampal PET activations of memory encoding and retrieval: The HIPER model. *Hippocampus*, 8, 313–322.

Lepage, M., Brodeur, M., & Bourgouin, P. (2003). Prefrontal cortex contribution to associative recognition memory in humans: An event-related functional magnetic resonance imaging study. *Neuroscience Letters*, 346, 73–76.

Leube, D. T., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. (2003). Successful episodic memory retrieval of newly learned faces activates a left fronto-parietal network. *Cognitive Brain Research*, 18, 97–101.

Leveroni, C. L., Seidenberg, M., Mayer, A. R., Mead, L. A., Binder, J. R., & Rao, S. M. (2000). Neural systems underlying the recognition of familiar and newly learned faces. *Journal of Neuroscience*, 20, 878–886.

Levine, B., Freedman, M., Dawson, D., Black, S., & Stuss, D. T. (1999). Ventral frontal contributions to self-regulation: Convergence of episodic memory and inhibition. *Neurocase*, 5, 263–275.

Ludowig, E., Trautner, P., Kurthen, M., Schaller, C., Bien, C. G., Elger, C. E., et al. (2008). Intracranially recorded memory-related potentials reveal higher posterior than anterior hippocampal involvement in verbal encoding and retrieval. *Journal of Cognitive Neuroscience*, 20, 841–851.

Lundstrom, B. N., Petersson, K. M., Andersson, J., Johansson, M., Fransson, P., & Ingvar, M. (2003). Isolating the retrieval of imagined pictures during episodic memory: Activation of the left precuneus and left prefrontal cortex. *NeuroImage*, 20, 1934–1943.

Macrae, C. N., Moran, J. M., Heatherton, T. F., Banfield, J. F., & Kelley, W. M. (2004). Medial prefrontal activity predicts memory for self. *Cerebral Cortex*, 14, 647–654.

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, 87, 252–271.

Maratos, E. J., Dolan, R. J., Morris, J. S., Henson, R. N., & Rugg, M. D. (2001). Neural activity associated with episodic memory for emotional context. *Neuropsychologia*, 39, 910–920.

Mayes, A., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, 11, 126–135.

McDermott, K. B., Jones, T. C., Petersen, S. E., Lageman, S. K., & Roediger, H. L., 3rd. (2000). Retrieval success is accompanied by enhanced activation in anterior prefrontal cortex during recognition memory: An event-related fMRI study. *Journal of Cognitive Neuroscience*, 12, 965–976.

Montaldi, D., Spencer, T. J., Roberts, N., & Mayes, A. R. (2006). The neural system that mediates familiarity memory. *Hippocampus*, 16, 504–520.

Morcom, A. M., Li, J., & Rugg, M. D. (2007). Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cerebral Cortex*, 17, 2491–2506.

Moscovitch, M. (1992). Memory and working-with-memory: A component process model based on modules and central systems. *Journal of Cognitive Neuroscience*, 4, 257–267.

Moscovitch, M., & Winocur, G. (2002). The frontal cortex and working with memory. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 188–209). New York, NY: Oxford University Press.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., et al. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. *Journal of Anatomy*, 207, 35–66.

Naghavi, H. R., & Nyberg, L. (2005). Common fronto-parietal activity in attention, memory, and consciousness: Shared demands on integration? *Consciousness and Cognition*, 14, 390–425.

Nichols, E. A., Kao, Y. C., Verfaellie, M., & Gabrieli, J. D. E. (2006). Working memory and long-term memory for faces: Evidence from fMRI and global amnesia for involvement of the medial temporal lobes. *Hippocampus*, 16, 604–616.

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review*, 3, 135–148.

Otten, L., Henson, R. N. A., & Rugg, M. E. (2002). State-related and item-related neural correlates of successful memory encoding. *Nature Neuroscience*, 5, 1339–1344.

Otten, L., & Rugg, M. E. (2001). Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cerebral Cortex*, 11, 1150–1160.

Paller, K. A., Kutas, M., & Mayes, A. R. (1987). Neural correlates of encoding in an incidental-learning paradigm. *Electroencephalography and Clinical Neurophysiology*, 67, 360–371.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in the Cognitive Sciences*, 6, 93–102.

Parks, C. M. (2007). The role of noncriterial recollection in estimating recollection and familiarity. *Journal of Memory and Language*, 57, 81–100.

Parsons, M. W., Haut, M. W., Lemieux, S. K., Moran, M. T., & Leach, S. G. (2006). Anterior medial temporal lobe activation during encoding of words: fMRI methods to optimize sensitivity. *Brain and Cognition*, 60, 253–261.

Petrides, M. (2002). The mid-ventrolateral prefrontal cortex and active mnemonic retrieval. *Neurobiology of Learning and Memory*, 78, 528–538.

Ragland, J. D., Gur, R. C., Valdez, J., Turetsky, B. I., Elliott, M., Kohler, C., et al. (2004). Event-related fMRI of frontotemporal activity during word encoding and recognition in schizophrenia. *American Journal of Psychiatry*, 161, 1004–1015.

Ragland, J. D., Valdez, J. N., Loughead, J., Gur, R. C., & Gur, R. E. (2006). Functional magnetic resonance imaging of internal source monitoring in schizophrenia: Recognition with and without recollection. *Schizophrenia Research*, 87, 160–171.

Reber, P. J., Siwiec, R. M., Gitelman, D. R., Parrish, T. B., Mesulam, M. M., & Paller, K. A. (2003). Neural correlates of successful encoding identified using functional magnetic resonance imaging. *Journal of Neuroscience*, 22, 9541–9548.

Rombouts, S. A., Barkhof, F., Witter, M. P., Machielsen, W. C., & Scheltens, P. (2001). Anterior medial temporal lobe activation during attempted retrieval of encoded visuospatial scenes: An event-related fMRI study. *NeuroImage*, 14, 67–76.

Rugg, M. D., Fletcher, P. C., Allan, L., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1998). Neural correlates of memory retrieval during recognition memory and cued recall. *Neuroimage*, 8, 262–273.

Rugg, M. D., Fletcher, P. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Differential activation of the prefrontal cortex in successful and unsuccessful memory retrieval. *Brain*, 119, 2073–2083.

Rugg, M. D., Johnson, J. D., Park, H., & Uncapher, M. R. (2008). Encoding-retrieval overlap in human episodic memory: A functional neuroimaging perspective. *Progress in Brain Research*, 169, 339–352.

Rutishauser, U., Schuman, E. M., & Mamelak, A. N. (2008). Activity of human hippocampal and amygdala neurons during retrieval of declarative memories. *Proceedings of the National Academy of Sciences*, 105, 329–334.

Sanquist, T. F., Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1980). Electrocortical signs of levels of procession: Perceptual analysis and recognition memory. *Psychophysiology*, 17, 568–576.

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus*, 9, 7–24.

Schott, B. H., Richardson-Klavehn, A., Henson, R. N. A., Becker, C., Heinze, H.-J., & Düzel, E. (2006). Neuroanatomical dissociation of encoding processes related to priming and explicit memory. *The Journal of Neuroscience*, 26, 792–800.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery and Psychiatry*, 20, 11–21.

Sergerie, K., Lepage, M., & Armony, J. L. (2005). A face to remember: Emotional expression modulates prefrontal activity during memory formation. *NeuroImage*, 24, 580–585.

Shallice, T. (2002). Fractionation of the supervisory system. In D. L. Stuss & R. Knight (Eds.), *Principles of frontal lobe function* (pp. 51–84). New York, NY: Oxford University Press.

Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, 7, 1376–1380.

Simons, J. S., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Anterior prefrontal cortex and the recollection of contextual information. *Neuropsychologia*, 43, 1774–1783.

Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, 46, 1185–1191.

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, *4*, 637–648.

Skinner, E. I., & Fernandes, M. A. (2007). Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia*, *45*, 2163–2179.

Slotnick, S. D., Moo, L. R., Segal, J. B., & Hart, J., Jr. (2003). Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cognitive Brain Research*, *17*, 75–82.

Smith, A. P., Henson, R. N., Dolan, R. J., & Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *NeuroImage*, *22*, 868–878.

Sommer, T., Rose, M., Weiller, C., & Büchel, C. (2005). Contributions of occipital, parietal and parahippocampal cortex to encoding of object-location associations. *Neuropsychologia*, *43*, 732–743.

Spaniol, J., Madden, D. J., & Voss, A. (2006). A diffusion model analysis of adult age differences in episodic and semantic long-term memory retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*, 107–117.

Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews Neuroscience*, *8*, 872–883.

Stark, C. E. L., & Okado, Y. (2003). Making memories without trying: Medial temporal lobe activity associated with incidental memory formation during recognition. *Journal of Neuroscience*, *23*, 6748–6753.

Takahashi, E., Ohki, K., & Miyashita, Y. (2002). The role of the parahippocampal gyrus in source memory for external and internal events. *Neuroreport*, *13*, 1951–1956.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.

Tsukiura, T., Mochizuki-Kawai, K., & Fujii, T. (2005). The effect of encoding strategies on medial temporal lobe activations during the recognition of words: An event-related fMRI study. *NeuroImage*, *25*, 452–461.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, *26*, 1–12.

Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences*, *91*, 2016–2020.

Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-Analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage*, *16*, 765–780.

Uncapher, M. R., Otten, L. J., & Rugg, M. D. (2006). Episodic encoding is more than the sum of its parts: An fMRI investigation of multifeatural contextual encoding. *Neuron*, *52*, 547–556.

Uncapher, M. R., & Rugg, M. D. (2005). Encoding and the durability of episodic memory: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *25*, 7260–7267.

van der Veen, F. M., Nijhuis, F. A., Tisserand, D. J., Backes, W. H., & Jolles, J. (2006). Effects of aging on recognition of intentionally and incidentally stored words: An fMRI study. *Neuropsychologia*, *44*, 2477–2486.

Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*, *45*, 2216–2225.

Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, *46*, 1787–1799.

Von Zerssen, G. C., Mecklinger, A., Opitz, B., & von Cramon, D. J. (2001). Conscious recollection and illusory recognition: An event-related fMRI study. *European Journal of Neuroscience*, *13*, 2148–2156.

Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., et al. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*, 1188–1191.

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.

Wais, P. E., Mickes, L., & Wixted, J. T. (2008). Remember–Know judgments probe degrees of recollection. *Journal of Cognitive Neuroscience*, *20*, 400–405.

Weis, S., Klaver, P., Reul, J., Elger, C. E., & Fernandez, G. (2004). Temporal and cerebellar brain regions that support both declarative memory formation and retrieval. *Cerebral Cortex*, *14*, 256–267.

Weis, S., Specht, K., Klaver, P., Tendolkar, I., Willmes, K., Ruhlmann, J., et al. (2004). Process dissociation between contextual retrieval and item recognition. *Neuroreport*, *15*, 2729–2733.

Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *20*, 1341–1354.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.

Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, *25*, 3002–3008.

Yonelinas, A. P., & Jacoby, L. L. (1996). Noncriterial recollection: Familiarity as automatic, irrelevant recollection. *Consciousness and Cognition*, *5*, 131–141.