



Published in final edited form as:

Psychol Bull. 2009 July ; 135(4): 638–677. doi:10.1037/a0015849.

Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory?

Karen J. Mitchell and Marcia K. Johnson

Yale University

Abstract

The systematic study of source memory provides a useful approach to investigating the features that give memories their episodic character, the associative, organizational, or binding processes that connect features, and the access and evaluation processes involved in attributing current mental experiences to memories of past events. This review illustrates how neuroimaging is contributing to our understanding of the brain mechanisms involved in source memory. Focusing primarily on functional magnetic resonance imaging (fMRI), we review evidence regarding the roles of various subregions of the medial temporal lobes, prefrontal cortex, posterior representational areas, and parietal cortex in source memory. We also consider relevant studies assessing the qualitative characteristics of episodic memories, the encoding and remembering of emotional information, and false memories, as well as studies of several populations that show disrupted source memory (older adults, individuals with depression, posttraumatic stress disorder, or schizophrenia). Although there is still substantial work to be done, functional neuroimaging is making good on its promise to advance our understanding of source memory. A continued two-way interaction between cognitive theory, as illustrated by the *Source Monitoring Framework* (Johnson, Hashtroudi, & Lindsay, 1993), and evidence from systematic cognitive neuroimaging studies should help further clarify our conceptualization of cognitive processes (e.g., feature binding, retrieval, monitoring), prior knowledge (e.g., semantics, schemas), and specific features (e.g., perceptual and emotional information), and of how they combine to create true and false memories.

In 1993, *Psychological Bulletin* published a paper titled *Source Monitoring* (Johnson, Hashtroudi, & Lindsay, 1993) that outlined a conceptual framework for organizing empirical findings and theorizing about the factors involved in attributing the source of mental experiences (the *Source Monitoring Framework* [SMF]; see also, Johnson & Raye, 1981). Since then, across many labs, the SMF has provided a useful approach to investigating the features that give memories their episodic character, the associative (organizational, binding) processes that connect features, and the access and evaluation processes involved in taking subjective experiences to be representations of past events. In the 1993 paper, Johnson, Hashtroudi, and Lindsay included a brief discussion of the brain areas likely involved in source monitoring that was based primarily on findings from neuropsychological studies of patient populations and cognitive aging studies, but they also made passing reference to the promise of “new developments in neuroimaging” techniques to advance our

Correspondence to: Karen J. Mitchell, Department of Psychology, Yale University, Box 208205, New Haven, CT 06520-8205, karen.mitchell@yale.edu, Phone: 203.432.4654, Fax: 203.436.4617.

Publisher's Disclaimer: The following manuscript is the final accepted manuscript. It has not been subjected to the final copyediting, fact-checking, and proofreading required for formal publication. It is not the definitive, publisher-authenticated version. The American Psychological Association and its Council of Editors disclaim any responsibility or liabilities for errors or omissions of this manuscript version, any version derived from this manuscript by NIH, or other third parties. The published version is available at www.apa.org/journals/bul.

understanding (p. 19). The current paper is an update on those developments: a selective review and discussion of how functional neuroimaging is contributing to our understanding of the cognitive and neural mechanisms involved in source memory. Indications so far are that the approach is making good on its promise. Functional neuroimaging is proving a useful tool for clarifying and testing theoretical characterizations of qualitative features and processes of human memory such as those proposed by the SMF, and conversely, theoretical characterizations such as proposed by the SMF are informing and guiding neuroimaging investigations (see also, e.g., Davachi & Dobbins, 2008; Johnson, Verfaellie, & Dunlosky, 2008 for further discussion of the benefits of such a synergistic approach).

Of course, optimal advance is likely to be made when functional neuroimaging findings are considered in light of the broader cognitive psychology and neuroscience literatures. Thus, although we do not discuss it in detail, important evidence regarding the brain correlates of source memory continues to come from neuropsychological studies of brain-damaged patients (see Eichenbaum, Yonelinas, & Ranganath, 2007; Johnson, Hayes, D'Esposito, & Raye, 2000; Johnson & Raye, 2000; Moscovitch, 1995; Schneider, 2008; Shimamura, 1995; Squire, Knowlton, & Musen, 1993, for reviews), animal studies (see, Eichenbaum, Fortin, Ergorul, & Robitsek, 2008; Eichenbaum et al., 2007; Riccio, Ackil, & Burch-Vernon, 1992; Squire & Zola-Morgan, 1991, for reviews), and human developmental behavioral studies with both children (see, Newcombe, Lloyd, & Ratcliff, 2007, for a review) and older adults (see, Naveh-Benjamin & Old, 2008; Old & Naveh-Benjamin 2008; Zacks & Hasher, 2006, for reviews). and insights also come from neurocomputational modeling (Elfman, Parks, & Yonelinas, 2008; Li, Naveh-Benjamin, Linenberger, 2005; Norman, Detre, & Polyn, 2008; Norman & O'Reilly, 2003) and other quantitative modeling approaches (Banks, 2000; Batchelder & Riefer, 1990; Bayen, Murnane, & Erdfelder, 1996; Glanzer, Hilford, & Kim, 2004; Meiser & Bröder, 2002; Meiser & Sattler, 2007; Rotello, Macmillan, & Reeder, 2004; Slotnick, Klein, Dodson, & Shimamura, 2000; Wixted, 2007).

The present discussion, however, is intended to illustrate how functional neuroimaging is contributing to our understanding of the brain mechanisms involved in source memory. We focus primarily on functional magnetic resonance imaging (fMRI) studies because this technique affords both the possibility to examine item-related brain activity (e.g., associated with correct vs incorrect memory responses) and a degree of spatial resolution that allows fair specificity with respect to the brain areas involved. The interested reader also can find relevant studies that involve positron emission tomography (PET; Anderson, Iidaka, Cabeza, Kapur, McIntosh, & Craik, 2000; Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Henke, Buck, Weber, & Weisser, 1997; Henke, Weber, Kneifel, Wieser, & Buck, 1999; Schacter et al., 1996) and event-related potentials (ERP; Dywan, Segalowitz, & Arsenault, 2002; Johnson, Kounios, & Nolde, 1997; Johnson, Nolde, et al., 1997; Leynes & Phillips, 2008; Swick, Senkfor, Van Petten, 2006; Van Petten, Luka, Rubin, & Ryan, 2002; see also, Friedman & Johnson, 2000; Paller, 2004; Paller, Voss, & Boehm, 2007; Rugg & Curran, 2007, for reviews), the latter of which adds to our understanding of the temporal characteristics of source memory, as well. In addition, studies using transcranial magnetic stimulation (TMS), which permits temporary in vivo disruption of neural functioning in humans in specific brain areas, has begun to provide evidence regarding the causal role in episodic memory of brain areas identified by other methods (Köhler, Paus, Buckner, & Milner, 2004; Rossi et al., 2006).

fMRI findings regarding source memory mechanisms are being reported at an increasingly rapid pace. We have not attempted to provide an exhaustive review, but rather to highlight both the considerable progress that has been made and a number of key theoretical and empirical puzzles still to be solved. Undoubtedly, some of the specific conclusions of the presented studies will be supplanted (or understood differently) in the future. Nevertheless,

this overview should provide behavioral scientists and neuroscientists with useful pointers to an increasingly rich literature on the cognitive neuroscience of source memory. Though we focus on fMRI studies, and use the SMF to guide interpretations in this review, we draw on results from multiple theoretical and experimental approaches to understanding the processes, and neural mechanisms, involved in creating, remembering, and misremembering events.

Because this review is intended to highlight the synergistic relationship between empirical neuroimaging findings and cognitive theory development, we begin with a brief summary of key theoretical tenets of the SMF and then review fMRI evidence that speaks to the roles of various subregions of the medial temporal lobes, prefrontal cortex, posterior representational areas, and parietal cortex in the basic processes involved in source memory. We then consider how fMRI studies are helping to address fundamental issues associated with source memory, including assessing the qualitative characteristics of episodic memories, encoding and remembering of emotional information, and the development of false memories. We also consider what is being learned by studying changes in brain activity associated with the disruptions in source memory often seen in older adults, as well as individuals with depression, posttraumatic stress disorder, or schizophrenia. We end by commenting on progress to date, as well as outlining issues still to be resolved. We believe that optimal scientific progress in our understanding of the cognitive and neural mechanisms of source memory will be best made if empirical evidence is derived from systematic behavioral and neuroimaging studies guided by cognitive theory (e.g., the SMF, Johnson et al., 1993), and theorizing is, in turn, informed and constrained by the empirical findings from such studies.

A THEORETICAL PERSPECTIVE: THE SOURCE MONITORING FRAMEWORK

Critical to the SMF approach (Johnson, 2006; Johnson et al., 1993; Johnson & Raye, 1981, 2000; Lindsay, 2008; Mitchell & Johnson, 2000) is the idea that the features that make up complex event memories, whether derived from perception or thought (e.g., imagination, inference), include perceptual information (e.g., color, size, taste), spatial details (e.g., left or right on the screen, location in a room), temporal details (e.g., time of day, season), semantic information (e.g., gist, category membership, associated items), emotional information (e.g., how we or others felt), records of the cognitive operations engaged (e.g., imaging, carrying out a mathematical calculation), and so on. When bound together, it is such specific details that differentiate one event from another—that make a memory *episodic* (Johnson, 2006). When brought to mind (revived) moments, weeks, months, or even years later, it is these types of details (or some subset of such details) that provide evidence about the *source* of a mental experience. Thus, the concept of *source memory* subsumes, and is more general than, what is commonly thought of as a memory's *context*. It is important to note that the SMF does not assume there is anything inherently special about “items” or “content” as compared to features that might be labeled “context” (see, e.g., Chalfonte & Johnson, 1996 for further discussion). Often, in laboratory studies, the semantic concept referred to by an item is designated as the content and some other feature of the event (e.g., location) is designated as context, but these roles could be reversed for a given task (Glisky & Kong, 2008). For example, in picking out a new TV, the semantics of the program on the screen could be incidental (contextual) to the color contrast of different TV models or to the location of the store where you saw the one you liked best (content).

According to the SMF, mental experiences are attributed to source categories such as perception, memory, dreaming, imagination, belief, etc., and to more specific sources (e.g., “Joe said it”; “it was a blue word on the list”; “it happened yesterday”), according to our assumptions about average differences in the features that characterize sources (e.g., more

affective information for actually experienced events, more cognitive operations for imagined events, Joe's voice has a deeper tone than Mary's voice). Mental experiences vary on continua of clarity or strength. Specific details (e.g., color, sound, feelings) tend to be characterized as varying in *vividness*, a concept that typically encompasses both how intense or clear and how rich or embellished mental experiences are. If information is less differentiated it may give rise to more vague subjective experiences – a feeling of familiarity, recency, or fluency. Both specific details and a general sense of familiarity, recency, and/or fluency can inform a source decision (see also, e.g., Rotello, et al, 2004; Wixted, 2007).

Johnson and colleagues (Johnson et al., 1993) used the term *differentiation* to refer to the idea that as information becomes active it coheres or settles, giving rise to specific characteristics of memories such as perceptual, affective, or contextual details. Information is proposed to be relatively undifferentiated at low levels of cohesion, or if only a single feature is activated, no matter how strongly activated. That is, differentiation is greater when two or more features collectively form the basis of segregating one event from another. But, active information (including a single feature) that does not cohere into fully formed representations can nevertheless affect perception and thought (e.g., masked priming, Higgins & Johnson, 2008; Marcel, 1983). In short, some source attributions are relatively non-specific (“Something about this situation is familiar from somewhere or sometime before”; “I’ve seen this word in the experiment”); usually such attributions are based primarily on relatively undifferentiated information (familiarity, fluency, recency). Others are based on relatively more differentiated information that includes two or more bound specific details (“I remember the word *chair* was *blue*”; “I remember that I was *angry* with *Chuck yesterday*”). Often, less differentiated information is available more quickly than more differentiated information (Gronlund, Edwards, & Ohrt, 1997; Hintzman, Caulton, & Levitin, 1998; Johnson, Kounios, & Reeder, 1994; McElree, Dolan, & Jacoby, 1999).

Source attributions also may involve retrieving additional information, discovering and noting relations, extended reasoning, and so on (Johnson & Raye, 1981; see also, Moscovitch, 1992; Ross, 1997). Such decisions (e.g., “It must have been Julie because Natalie was out of town”) presumably are slower and more controlled. Although the correlation is not perfect, undifferentiated information tends to be processed heuristically and more specific features tend to require relatively more systematic processing. But, according to the SMF, exactly which processes are involved and the specificity of the information they work on are influenced by context. For example, the absence (or presence) of a specific type of feature might be used heuristically in a given situation (e.g., the distinctiveness heuristic, Schacter, Israel, & Racine, 1999). In addition, even ostensibly the same kind of source decision (e.g., Who said it?) can rely on features that are relatively more or less differentiated under different circumstances. In determining which of four speakers made a statement, for example, one might correctly identify the specific speaker or only whether the speaker was male or female (Dodson, Holland, & Shimamura, 1998). Thus, heuristic and systematic are not fixed concepts but rather relative terms for characterizing the complexity of reflective processes involved in a given task—a rough placeholder awaiting more specific characterizations of component cognitive processes (Johnson, 1992).

Both encoding and remembering are constructive and reconstructive; they are selective and influenced by a rememberer's knowledge, beliefs, biases, goals, agendas, and meta-memory assumptions active at the time. Source monitoring processes capitalize on characteristic differences in the kinds and amounts of information generally associated with different types of events using *flexible criteria* that can vary across situations. Individual features typically are combined to make a source decision (Johnson & Raye, 1981; see, e.g., Banks, 2000 for a model instantiating such an idea), and a key feature of the SMF is the idea that the features

are *flexibly weighted* according to the current task agenda (e.g., context, goals). This weighting can determine what information is sought and revived and/or how it is combined and evaluated during the attribution process. For example, given identical encoding, later asking “did you generate this item” would lead to an emphasis (heavier weighting) on cognitive operations information, whereas asking “did you read this item” would be expected to emphasize perceptual information in making a source attribution (Marsh & Hicks, 1998). An agenda also can influence how vivid you require the information to be (Johnson & Raye, 2000). You would likely require less specific detail to attribute a comment to someone if you are reminiscing with friends vs testifying in court, or, you may have more confidence in a fairly vague recollection when attributing an action to something a colleague did at a conference last year vs something that happened yesterday.

These tenets of weighting and flexible criteria have implications for making inferences about the nature of behavioral performance, and brain activity, in laboratory tasks (e.g., which condition has a higher monitoring demand). Take the case of old-new decisions. Whereas relatively undifferentiated fluency or familiarity alone might be used to make a relatively heuristic old-new decision on a standard recognition task, an old-new decision may involve more systematic evaluation of specific information when made in the context of a task that also includes a subsequent confidence, remember/know, or source decision, because such tasks focus people on specific source details (Lindsay & Johnson, 1989; Mather, Henkel, & Johnson, 1997; Zaragoza & Koshmider, 1989). In such situations, specific source information may be monitored (e.g., revived, evaluated) even though it ostensibly is not required by the old-new task, per se.

It should be clear from the discussion thus far that *episodic memory* and *source memory* are not fundamentally different *classes* of memory at a conceptual level (see Johnson, 2005 for further discussion). We *take as episodic memories* those mental experiences for which we have encoded, bound, revived, and evaluated features that induce (and sometimes seduce) us to attribute the *source* of the experience as a unique event that occurred in our personal past (if only the moment before). An explication of episodic memory involves understanding the repertoire of cognitive processes and features involved in source memory, none of which should be presumed to be unique to a particular memory task (Johnson, 2005). In other words, although some *source identification* tasks ask people to explicitly identify the “source” of information (e.g., “Was this item on the left or the right?” “Did you see this information in the video or in the postevent questions?”), many other tasks tap source memory processes, as well. Such procedures include *remember/know*; *context, relational*, or *associative* memory tests; memory *binding* tasks; *inclusion/exclusion* tasks (e.g., *process dissociation procedure*, Jacoby, 1991; Kelley & Jacoby, 2000); *criteria recollection* tasks, which encourage participants to base their memory judgment on whether or not a certain (criteria) feature is remembered (e.g., “say yes only if you recollect a corresponding red word”; Gallo, Weiss, & Schacter, 2004); *list discrimination*; *cryptomnesia (unconscious plagiarism)* tasks; differentiating between presented and non-presented semantically related items (e.g., the *Deese-Roediger-McDermott [DRM]* procedure; Deese, 1959; Roediger & McDermott, 1995); and so on. Of course, recognition and recall tasks require identifying information from a particular source (e.g., the information presented by the experimenter); false positives and intrusions from associations, inferences, items from another list, and so on, reflect failures in source monitoring. Furthermore, free-recall can be coded for the various featural details associated with the memory, or clustering analyses may reveal that a specific feature such as voice of speaker was used systematically to recall items.

The SMF assumes that the pool of underlying processes across all of these episodic memory tasks is basically the same (Johnson, 1992), and what differs is the extent to which any one or more processes are engaged in a given task, and the precise features or other information

(e.g., knowledge, beliefs) involved under a specific set of conditions (see, Dewhurst, Holmes, Brandt, & Dean, 2006 for a similar view applied to Remember/Know decisions). Thus, although neural activity should differ in some respects between specific episodic memory tasks (e.g., associative recognition memory vs free-recall, Staresina & Davachi, 2006), we would also expect much overlap in underlying processes (Steffens, Buchner, Martensen, & Erdfelder, 2000; Yu & Bellezza, 2000), and presumably then, also much overlap in the brain areas involved. One goal of both cognitive behavioral and cognitive neuroimaging studies is to identify the processes and features active under various conditions; neuroimaging studies further provide information about related brain correlates.

The Source Monitoring Framework vs Dual-Process Models

A complete review of dual-process models is beyond the scope of this paper, but, because such models are influential in both cognitive behavioral and neuroimaging studies of source memory (see, e.g., Eichenbaum, et al., 2007; Skinner & Fernandes, 2007; Vilberg & Rugg, 2008; Wais, 2008; Wixted, 2007; for reviews), specifying how they contrast with the SMF deserves special note. Generally-speaking, most dual-process models argue that more specific and less differentiated information arise from, respectively, *recollection* and *familiarity* processes (Jacoby, 1991), or correspond to the subjective experiences of *remembering* and *knowing* (see Gardiner, 2008; Gardiner & Richardson-Klavehn, 2000, for reviews of behavioral Remember/Know studies). These approaches have been very generative, prompting informative studies such as those demonstrating a disproportionate disruption in Remember responses in older adults (Jacoby, Bishara, Hessels, & Toth, 2005; Jennings & Jacoby, 1997) and amnesics (Quamme, Yonelinas, & Norman, 2007; see, Kensinger & Corkin, 2008 for a review; but see, Squire & Shrager, 2008 for a discussion of contrary evidence), and differential brain activity presumed to be associated with recollection and familiarity (see, e.g., Eichenbaum, et al., 2007; Skinner & Fernandes, 2007; Vilberg & Rugg, 2008, for reviews).

The SMF uses the terms recollection and familiarity to refer to types of subjective experience rather than as labels for two distinct processes that give rise to those experiences, and assumes that recollection, like familiarity, is graded. The assumption of graded recollection is supported by behavioral evidence from subjective ratings of memory features (e.g., Memory Characteristic Questionnaires [MCQ], Johnson, Foley, Suengas, & Raye, 1988), as well as behavioral (Dodson et al., 1998; Qin, Raye, Johnson, & Mitchell, 2001; Simons, Dodson, Bell, & Schacter, 2004; Starns, Hicks, Brown, & Martin, 2008; Wais, Mickes, & Wixted, 2008) and neuroimaging (Eldridge, Engel, Zeineh, Bookheimer, & Knowlton, 2005; Maril, Simons, Weaver, & Schacter, 2005; Vilberg & Rugg, 2007) studies showing graded recollection and use of partial source information. Some theorists accommodate such findings by applying a signal-detection approach and proposing that familiarity and recollection both contribute to a memory's "strength"¹ (e.g., Wixted, 2007). Such models share with the SMF a recognition that both more and less specific information can jointly influence a memory judgment, and that the resulting memorial "evidence" often is experienced as continuous.

Arguably the most popular dual-process model used in the neuroimaging domain characterizes recollection as a threshold process (all-or-none, Yonelinas, 1994) and familiarity as a continuous, graded process that can vary by degrees (see, e.g., Yonelinas,

¹From this perspective, memory strength is orthogonal to recollection/familiarity (e.g., you can have a very strong feeling of familiarity) and results that are usually argued by high-threshold dual process models to dissociate recollection and familiarity might sometimes be better explained as reflecting strong vs weak memories, respectively. As discussed in the section on the medial temporal lobes (MTL), such ideas have implications for interpreting fMRI findings purportedly dissociating the roles of various regions of MTL in different aspects of memory (see, e.g., Squire, Wixted, & Clark, 2007; Wais, in press; Wixted, 2007, for further discussion).

1999; Yonelinas, 2002). Proponents of this high-threshold dual-process approach recently clarified a common misinterpretation of the phrase *all-or-none* by emphasizing that it refers to the idea that one can either recollect or not at any given time (that is, recollection can succeed or fail), and not necessarily that one will remember all features of a memory or none at all (Parks & Yonelinas, 2007, p. 189). Hence, even the high-threshold dual-process approach concurs with the SMF that “recollection can be graded” (Parks & Yonelinas, 2007, p. 190). Nevertheless, the dual-process approach generally has largely focused on cases where recollection succeeds or fails, for example, emphasizing differences between recollection and familiarity in the shapes of the resulting receiver operating characteristic (ROC) curves.

Source memory studies examining the shape of ROC curves report contradictory findings on this point (see, Wixted, 2007; Yonelinas & Parks, 2007, for reviews). Some studies show recollection is fit by a threshold model (with linear ROCs) and familiarity by a continuous model (with curvilinear ROCs) (Yonelinas, 1999, 2002), and other studies show that a continuous model fits both recollection and familiarity (Glanzer et al., 2004; Hilford, Glanzer, Kim, & DeCarlo, 2002; Qin et al., 2001; Slotnick et al., 2000). These contradictions likely can be reconciled by considering the complexity and similarity of the events studied. For example, Elfman et al. (2008) reported simulations consistent with a neurobiologically-based computational model (Complementary Learning Systems [CLS], Norman & O’Reilly, 2003) that predicts recollection will fit a threshold model when sources are very distinct and a continuous model when there is similarity (feature overlap) in sources.

Dual process approaches continue to differ from the SMF in another important way, and that is with respect to “false memories”. As discussed above, the SMF builds on a constructive/reconstructive view of memory. This view emphasizes that our interpretations of, and memories for, events are infused with our knowledge, beliefs, desires, as well as products of our imagination (Bartlett, 1932; Bransford & Johnson, 1973; Loftus, 1979; Neisser, 1981). In addition, both our interpretations and our memories are influenced by similarities between events, which can result in the importation of information from other representations (Henkel, Franklin, & Johnson, 2000; Lampinen, Meier, Arnal, & Leding, 2005; Lyle & Johnson, 2006). The SMF thus assumes that true and false memories can be accounted for using the same general principles of memory (Johnson & Raye, 1981, 2000; Lindsay, 2008; Lindsay & Read, 1994; Lyle & Johnson, 2007; Mitchell & Johnson, 2000), and we should thus expect similar brain mechanisms to be at play. From this perspective, the phenomenal experience of remembering, or recollecting, an event does not guarantee that such memories are veridical.

Dual-process theories, on the other hand, historically have accounted for false memories only as resulting from misattribution of familiarity (i.e., familiarity responses not corrected by recollection). False memories reported with high confidence, recollection, or remember responses (see, e.g., Lindsay, 2008; Marsh, Eslick, & Fazio, 2008, for reviews), for example to new items, have been assumed by some dual-process theorists to be situations in which participants simply were not following task instructions properly (e.g., Yonelinas & Parks, 2007, p. 194). Correct old item recognition accompanied by an incorrect source attribution is sometimes argued, from the dual-process perspective, to signal that the memory decision is based on familiarity (e.g., Kirwan, Wixted, & Squire, 2008; Wais, Squire, & Wixted, 2008). From the SMF view, on the other hand, such responses signal that participants sometimes use specific source information that is self-generated (Durso & Johnson, 1980; Gonsalves, Reber, Gitelman, Parrish, Mesulam, & Paller, 2004), or imported from other items (Henkel et al., 2000; Lyle & Johnson, 2006), or prior knowledge (e.g., Deese, 1959; Johnson, Bransford, & Solomon, 1973) in making their decisions. Such differences in the theoretical

assumptions of the SMF vs dual-process approaches regarding false memories have implications for interpreting brain activity associated with such responses (see, e.g., *Medial Temporal Lobes* section below).

In short, some of the apparent theoretical differences that have been noted between some dual-process models and the SMF arose to a large extent from the dichotomous approach of the former that looks to distinguish familiarity from recollection and the focus of the latter on explicating the characteristics of true and false recollection. Both approaches have been productive in guiding neuroimaging investigations of source memory, but each has unique implications for interpreting brain activity associated with various aspects of source memory.

BRAIN REGIONS INVOLVED IN SOURCE MEMORY

Medial Temporal Lobes

This section discusses the memorial roles of regions of the medial temporal lobes (MTL), long known to be associated with episodic memory. The MTL are composed of the hippocampal formation (dentate gyrus, hippocampus proper [including the CA fields], subicular complex, entorhinal cortex), as well as the perirhinal and parahippocampal cortices. A later section on emotion and source memory will discuss the amygdala, also part of the MTL. Although refinements in anatomical (Kirwan, Jones, Miller, & Stark, 2007; Kirwan & Stark, 2007; see Squire et al., 2004 for a review and discussion) and functional (see, Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Mayes et al., 2007 for reviews) specificity of MTL regions are major goals of current neuroimaging work, the spatial resolution of most fMRI studies does not allow differentiating between all of the MTL structures likely important for episodic memory (e.g. the CA fields). Figure 1 shows the areas most commonly identified in episodic memory fMRI studies to date.

Especially important to source memory are processes that bind together (associate, relate, organize) features, or clusters of features, that co-occur physically or cognitively during encoding, revival, and/or evaluation of memories (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye, & D'Esposito, 2000; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000; Naveh-Benjamin, 2000; see also, Johnson & Chalfonte, 1994). Regions within the MTL have been of particular interest to episodic memory researchers because of extensive animal (Brasted, Bussey, Murray, & Wise, 2003; Bussey & Eichenbaum, 1996) and patient (Gold et al., 2006; Hannula, Tranel, & Cohen, 2006; Kroll, Knight, Metcalfe, Wolf, & Tulving, 1996; Myers et al., 2003; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006; Reinitz, Verfaellie, & Milberg, 1996; Squire & Knowlton, 1995) literatures indicating that these regions are involved in memory binding, and associative or relational remembering (see, Aggleton & Brown, 1999; Burgess, Maguire, & O'Keefe, 2002; Cohen & Eichenbaum, 1993; Eichenbaum et al., 2007; Eichenbaum et al., 2008; Kensinger & Corkin, 2008; Squire & Zola-Morgan, 1991, for reviews). Furthermore, there is evidence that amnesics with hippocampal damage show greater deficits in source than item memory (Giovanello, Verfaellie, & Keane, 2003; Yonelinas et al., 2002; see, Mayes, Montaldi, & Migo, 2007 for a review), though this remains controversial (Gold, Hopkins, & Squire, 2006; Stark, Bayley, & Squire, 2002; Stark & Squire, 2003).

Early neuroimaging studies highlighted the role of the hippocampus in relational memory. An early review, largely of PET studies, suggested an anterior-posterior gradient, such that more anterior portions of the hippocampus were proposed to be involved in relational encoding and more posterior regions in retrieval and/or flexible use of relational information during later remembering (Lepage, Habib, & Tulving, 1998). More recent reviews of accumulated fMRI studies, however, failed to find a strong anterior-posterior pattern with

respect to encoding/retrieval (see, Diana, Yonelinas, & Ranganath, 2007; Henson, 2005; Schacter & Wagner, 1999; Squire, Stark, & Clark, 2004; Squire, Wixted, & Clark, 2007; Wais, 2008).

Although possible functional dissociations within the hippocampus itself remains a topic of vigorous empirical investigation (e.g., Giovanello, Schnyder, & Verfaellie, 2009; see also, Kumaran & Maguire, 2009 for a discussion), much of the recent empirical and theoretical work in the neuroimaging of human episodic memory has centered on identifying the relative contributions of the various regions of MTL. Most of these studies have contrasted activity associated with familiarity or novelty on the one hand and recollection or source memory on the other. There have been several recent reviews (e.g., Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Henson, 2005; Mayes et al., 2007; Skinner & Fernandes, 2007; Squire et al., 2007; Wais, 2008); thus, here we highlight converging conclusions, points of controversy, and puzzles for further investigation.

Activity in the hippocampus frequently is greater during encoding and test for items given Remember responses than those given Know responses or for items whose source is correctly identified than those whose source is incorrectly identified (see, e.g., Davachi, 2006; Diana et al., 2007; Henson, 2005; Mayes et al., 2007; Skinner & Fernandes, 2007, for reviews). Such findings support the idea that the hippocampus is involved in binding features into complex episodic memories during encoding, and in remembering item + context information, and this fundamental idea is emphasized in any discussion of hippocampal function (see Figure 2; but see Squire et al., 2004, for a review and arguments against an associative vs non-associative division of labor for MTL regions; see also, Kensinger & Corkin, 2008; Squire et al., 2007 for further discussion of this debate). Mayes et al. (2007) propose that the hippocampus is needed for across-domain associations (e.g., scene-sound; face-voice) because such information does not converge before the hippocampus. (See also the distinction between *relational* vs *configural* [or *unitized*] representations, argued to rely on hippocampus and surrounding MTL cortex, respectively, Eichenbaum, 1994). One possibility that would be consistent with the data cited above, as well as the established role of the hippocampus in both allocentric spatial cognition and temporal memory (and imagery) is that the hippocampus is involved (perhaps in conjunction with entorhinal cortex [Lipton & Eichenbaum, 2008], or midbrain structures [Shohamy & Wagner, 2008]) whenever information is bound, associated, or integrated, across time or space (see, Bird & Burgess, 2008; Burgess et al., 2002; Nadel & Hardt, 2004; for reviews and related discussions). That is, the hippocampus may be especially important for binding and later remembering information that is not initially strictly contiguous (Johnson & Chalfonte, 1994).

Perirhinal cortex typically is not seen in the same fMRI contrasts that produce hippocampal activity and is often more active for incorrect source items than misses. Based on this and other evidence, investigators have proposed that perirhinal cortex supports item memory (Davachi, 2006), including memory for feature-complexes that are “unitized” (Diana, Yonelinas, & Ranganath, 2008; Haskins, Yonelinas, Quamme, & Ranganath, 2008; Preston & Gabrieli, 2008; see, e.g., Diana et al., 2007; Mayes et al., 2007 for reviews and discussion). Mayes et al. (2007) propose that perirhinal cortex supports memory for associations of features within the same domain (e.g., word-word or face-face pairs) because activity for different items within the same domain converges within perirhinal cortex and thus can be bound there.

Generally, the conditions and/or contrasts producing activity in parahippocampal cortex (e.g., Remember > Know; source correct > source incorrect) are more similar to those producing activity in hippocampus than in perirhinal cortex. Whereas Davachi (2006)

suggests that parahippocampal activity primarily reflects processing of spatial context, Diana et al (2007) propose that parahippocampal activity is engaged for contextual information more generally (see also, Bar, Aminoff, & Schacter, 2008), and Mayes et al. (2007) note that the function(s) of parahippocampus remain to be determined.

How to map the functional specificity of MTL regions with respect to familiarity and recollection is also a topic of active theorizing and empirical investigation. Diana et al., (2007) and Mayes et al. (2007) suggest that activity in perirhinal cortex reflects familiarity processes and activity in hippocampus reflects recollection processes (see also, e.g., Eichenbaum et al., 2007). However, perirhinal activity sometimes is associated with *remember* responses when the information to be recollected is item information (e.g., which object was paired with a scene, Awipi & Davachi, 2008). As Diana et al. suggest, hippocampus may always be activated for recollection of inter-item associations. If study context is retrieved (even if incidentally), parahippocampal cortex may also be activated, and, moreover, if one test item prompts revival of an associated item (whether or not it is required by the test), perirhinal cortex also may be involved. This characterization highlights the difficulty of mapping the functional specificity of regions of MTL using global processing concepts such as recollection and familiarity. Rather, theorizing and empirical studies from a number of labs are converging on the idea that it may be more productive to examine which brain areas are associated with memory for which specific features, and combinations of features, and under what circumstances (e.g., what kinds of schemas or mediators have been used to connect features) than to look for brain regions that invariably signal recollection or familiarity (see also Squire et al. 2007, p. 881). For example, there is recent evidence associating perirhinal/entorhinal cortex activity at test with visual but not auditory source memory and parahippocampal cortex with auditory but not visual source memory (Peters, Suchan, Köster, & Daum, 2007; see also, Peters, Koch, Schwarz, & Daum, 2007 for converging evidence from a lesion study). Further replication and extensions under a broader range of conditions, and with other features, will be necessary before any strong conclusions can be drawn.

A more content or feature-based approach perhaps would help resolve another controversy. Squire and colleagues (2007; also Squire, 2004; Wais, 2008; Wixted, 2007) argue that differences between activity in hippocampus and perirhinal cortex that are usually ascribed to recollection and familiarity processes confound memory strength with the basis for that strength (e.g., the experience of recollection or familiarity). To test this idea, Wais, Squire, and Wixted (2008) compared fMRI activity associated with correct and incorrect source judgments for items that were hits on an old-new recognition test that had high confidence ratings and found equal hippocampal activity (relative to old items called new [misses]). They suggested that previous studies failed to find hippocampal activity for incorrect source judgments (assumed to reflect familiarity) because they included low confidence old-new judgments (i.e., weak items).

One problem in trying to resolve the controversy regarding how/whether regions of MTL map onto familiarity and recollection processes is that a common assumption is questionable: that incorrect source judgments reflect familiarity. In particular, some investigators assume that an old item correctly recognized with high confidence at stage one and given an incorrect source attribution at stage two is based on a strong familiarity response (e.g., Kirwan et al., 2008). As previously discussed, however, from the SMF perspective, another viable possibility is that high confidence old responses are sometimes based on recollected (but sometimes erroneous or irrelevant) information. Kirwan et al. (p. 6) note this possibility and dismiss it as untestable, but one could test old-new recognition and source memory in separate runs (or sessions) to minimize the use of source information on item recognition trials, leading to cleaner interpretations of brain activity with respect to

the basis for memory attributions (e.g., Ranganath, Johnson, & D'Esposito, 2000; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000; see also Mayes et al., 2007, Box 2). In any event, it is notable that Wais, Squire, and Wixted (2008) found that high confidence source incorrect items showed activity in perirhinal cortex, and suggested that if one assumes that such items reflect false recollection, this activity argues against the idea that perirhinal cortex reflects familiarity and not recollection.

Mapping functions to various MTL regions is further complicated by the fact that, during retrieval, the change in fMRI signal in the hippocampus and perirhinal cortex tend to go in opposite directions as a function of memory strength: hippocampal activity tends to increase whereas perirhinal activity tends to decrease with memory strength, both in a non-linear fashion (see, e.g., Squire et al., 2007 for a review and discussion). The extent to which this dissociation signals selective sensitivity to, or a preference for, familiar vs novel information, or rather reflects something related to the subjective memorial experiences associated with recollection vs familiarity is a topic of ongoing debate (see, e.g., Diana et al., 2007; Eichenbaum et al., 2007; Squire et al., 2007).

In short, to draw conclusions about the functional specificity of MTL regions with respect to recollection and familiarity, the relation between the information that provides the basis of phenomenal feelings of recollection and of familiarity needs to be better specified. Systematically comparing types of features and feature combinations would help clarify the neural activity associated with different types of recollective experience (e.g., of a face, a word, a color, a place) vs different types of familiarity experience (e.g., of a face, a word, a color, a place).

Prefrontal Cortex

The areas discussed in this section are illustrated in Figure 3 and Figure 4.

Neuropsychological work shows that lesions in frontal cortex disrupt the kind of self-initiated processes (Stuss & Benson, 1986) that should promote feature binding (e.g., by maintaining activation or generating organization or elaborations) and that are likely engaged during the revival and evaluation of source information (see Shimamura, 1995 for a review). Frontal damage often results in deficits on source identification tasks (Ciaramelli & Spaniol, 2008; Duarte, Ranganath, Knight, 2005; Johnson, O'Connor, & Cantor, 1997; Schacter, Harbluk, & McLachlan, 1984; Shimamura & Squire, 1987; Simons, Verfaellie, Galton, Miller, Hodges, & Graham, 2002; see, e.g., Duarte, et al., 2005; Ranganath & Blumenfeld, 2008 for reviews). One of the primary goals of fMRI studies of source memory has been to identify the functional specificity of prefrontal cortex (PFC).

One early hypothesis followed from the SMF and focused primarily on *remembering* (as opposed to encoding). It proposed that right PFC is involved in heuristic evaluation processes and that left, or bilateral, PFC activity is involved in more systematic processes (e.g., self cuing, evaluating specific information; Nolde, Johnson, & Raye, 1998; also see Burgess & Shallice, 1996; Johnson, 1997a,b)². The results of one of the first studies to use event-related fMRI to contrast old-new recognition and source memory judgments (Nolde, Johnson, & D'Esposito, 1998) was consistent with this proposal, finding greater left PFC activity for source memory than old-new recognition. Since then, a large number of fMRI

²Another model that was influential in early neuroimaging studies of episodic memory was the *Hemispheric Encoding/Retrieval Asymmetry [HERA] model* that proposed left PFC is engaged more than right in episodic *encoding* and right PFC engaged more than left in episodic *retrieval* (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; also Habib, Nyberg, & Tulving, 2003; Shallice, Fletcher, Frith, Grasby, Frackowiak, & Dolan, 1994). Lepage, Ghaffar, Nyberg, and Tulving (2000) extended *HERA* by attributing the function of a core network of PFC areas (right and left BA 10, 47/45, and right BA 8/9) to adopting a general retrieval mode (i.e., "set" to remember) that we would expect to operate across various memory tasks.

studies have found that source memory judgments, relative to old-new, are associated with increased activity in left lateral PFC, including superior, middle, and inferior frontal gyri primarily in Brodmann areas (BA) 9, 10, 44, 46, and 47. Left lateral PFC activity associated with source memory has been found for various types of source information (e.g., location, size, cognitive operation performed) and for a broad range of materials (e.g., auditory and visual words, nameable pictures, abstract shapes) (Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Han, 2006; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins & Wagner, 2005; Dudukovic & Wagner, 2007; Henson, Shallice, & Dolan, 1999; Konishi, Uchida, Okuaki, Machida, Shirouzu, & Miyashita, 2002; Mitchell, Johnson, Raye, & Greene, 2004; Mitchell, Raye, McGuire, Frankel, & Johnson, 2008; Nolde, Johnson, & D'Esposito, 1998; Ranganath et al., 2000; Raye et al., 2000; Rugg, Fletcher, Chua, & Dolan, 1999; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Simons, Owen, Fletcher, & Burgess, 2005; Slotnick, Moo, Segal, & Hart, 2003, among others). Right lateral PFC on the other hand, is involved in heuristic judgments based on less differentiated information. For example, Dobbins et al. (2003) compared recency judgments (which can be made based on fluency) and source judgments (encoding task) and found greater right lateral PFC activity for recency judgments and greater left PFC activity for source judgments (see also Dobbins & Han, 2006; Kensinger, Clark, & Corkin, 2003; Mitchell et al., 2004; Raye et al., 2000). Together, these findings support the idea that left and right lateral PFC are engaged for systematic and heuristic monitoring, respectively. Such monitoring is argued to involve evaluation of, respectively, more vs less differentiated information (Nolde, Johnson, & Raye, 1998; see also, e.g., Suzuki et al., 2002).

Two notable alternatives to the systematic/heuristic characterization of left and right PFC activity during tests of episodic memory have been proposed. The *production-monitoring hypothesis* suggested that left PFC is involved in production/generation during memory retrieval and right PFC is involved in memory monitoring (Cabeza, Locantore, & Anderson, 2003). The heuristic-systematic distinction and the production-monitoring hypothesis both predict less differentiated information will be monitored by right PFC and both propose that left PFC is involved in systematic retrieval processes, but these hypotheses differ in that the SMF proposes that left PFC (or left and right) is engaged in the systematic monitoring/evaluation of more specific information while the production-monitoring hypothesis predicts monitoring of all types to be right-based. Rugg and his colleagues have argued, as well, that monitoring generally is associated with right PFC, and note that whether such activity is associated with less or more differentiated information (e.g., whether it is related to familiarity or recollection judgments) depends on which type of information imposes the greater monitoring demand under the current testing situation (e.g., Rugg, Otten, & Henson, 2002; but see Hayama, Johnson, & Rugg, 2008 for a more recent interpretation suggesting that right PFC activity is related to more general decision processes rather than post-retrieval evaluation, per se; see also Dobbins & Han, 2006; Fleck, Daselaar, Dobbins, & Cabeza, 2006 for similar ideas). Rugg and colleagues also acknowledge a role for left lateral PFC during remembering when the task requires specific contextual features (e.g., Rugg et al., 1999), but have stopped short of attributing such activity to monitoring the product of retrieval, noting that the precise function of this activity (e.g., "cue specification" vs "evaluation") is unclear (see, e.g., Rugg & Wilding, 2000 for discussion).

Each of the hypotheses discussed thus far has proven influential in helping to guide and organize early fMRI investigations. As data accumulate, however, it has become apparent that there is a need for greater specificity with respect to both the component processes that encoding and remembering draw upon and regions within left and right PFC that subserve those processes. Evidence to date suggests that anterior prefrontal cortex (aPFC), dorsolateral prefrontal cortex (DLPFC) and ventrolateral prefrontal cortex (VLPFC) may support different aspects of source memory (see Figure 4).

For example, based on a review of neuropsychological and neuroimaging studies of episodic long term memory *encoding*, Blumenfeld and Ranganath (2007; see also Ranganath & Blumenfeld, 2008) proposed that ventrolateral PFC is involved in the kinds of control processes necessary to select and encode the appropriate (i.e., goal-relevant) features of items. Dorsolateral PFC, on the other hand, is more involved in processes that support the kinds of elaboration and organization of multiple features necessary for encoding associations among items. Thus, ventrolateral PFC activity during encoding is more likely to be associated with later successful item memory and dorsolateral PFC with source memory. Consistent with this, Starisina and Davachi (2006) showed that whereas activity during encoding in ventrolateral PFC was associated with both successful associative recognition and recall, activity in left dorsolateral PFC was selectively associated with successful recall. Recall is more dependent on elaboration and organization than is recognition (Guerin, & Miller, 2008; Kintsch, 1968), thus, this pattern of fMRI activity supports the idea that dorsolateral PFC is involved in such processes during encoding.

A dorso-ventrolateral fractionation has been proposed with respect to *remembering*, as well. For example, Petrides proposed that whereas mid-ventrolateral prefrontal cortex involved in the active retrieval and selection of information (e.g., from posterior regions), mid-dorsolateral prefrontal cortex is primarily involved in on-line monitoring and manipulation of information (see, Petrides, 2002 for a review). The activity seen in left PFC during the many long-term source memory studies cited above includes both these regions. It seems likely that this is because several component processes are involved in source monitoring. According to the SMF perspective, *monitoring* minimally encompasses processes involved in both the *revival* (e.g., reactivation, retrieval) and the *evaluation* (e.g., “Is this information characteristic of Source A?”) of information, and we would expect these processes to have different neural correlates. But, assuming revival and evaluation processes are iterative (Johnson & Raye, 2000), it can be difficult to identify the putative brain regions involved specifically in each process using long-term memory tasks (see also, Rugg & Wilding, 2000).

To identify PFC regions involved primarily in *evaluation*, Mitchell et al. (2004) developed a short-term source memory task to maximize the likelihood that information was still active in working memory. This should minimize the need for retrieval of information from long-term memory so that the observed brain activity is relatively more associated with evaluation. Consistent with predictions from the SMF, similar to long-term memory studies, there was greater activation in a large region of left lateral PFC, including middle and inferior frontal gyri (BAs 9, 10, 46, 45), and a smaller region of right, as well, when participants tried to remember which format (picture vs. word) or location (left vs. right) one of four items had appeared in than for old-new recognition. These regions of lateral PFC were equally active in a second experiment when information was tested immediately on a random half of the trials and after a brief filled delay (up to 36 sec) on the other half, suggesting that much of the activity seen in left lateral PFC during source memory tasks is relatively more involved in *evaluating* active source-relevant information than in retrieval from long term memory. In a third experiment, substituting recency for location judgments resulted in an overall shift in task context that produced greater activity in several regions of right PFC associated with the old-new and recency tasks compared to the format task. Again there was left source memory-related activity.

Thus, evidence from both long- and short-term source memory studies supports the idea that the relative contribution of left and right lateral PFC to evaluative processes during source memory will depend on the nature of the information being evaluated (i.e., more- and less-differentiated, respectively) and/or the types of processing (i.e., systematic vs heuristic) required. In addition, given that the areas involved in source evaluation in the short-term

studies tended to be relatively more dorsal than ventral (e.g., Mitchell et al., 2004), the findings also are roughly consistent with the idea (e.g., Petrides, 2002) that left dorsolateral regions may be relatively more involved in online evaluation of active information, as opposed to ventrolateral regions, which tend to be relatively more involved in controlled retrieval and/or selection of relevant information (see also discussion below regarding findings from Mitchell et al., 2008).

An interesting wrinkle in the general pattern of left-lateralized source memory activity comes from a long-term memory study reporting activity in several regions of right posterior ventrolateral and right dorsolateral PFC associated with a size judgment task (Dobbins & Wagner, 2005). The authors emphasized the role of the right posterior ventrolateral region in memory tasks that focus participants on perceptual details of test probes and/or that encourage retrieval of perceptual information, regardless of whether such information is used for familiarity or recollection based memory judgments. For example, in some situations such activity may act to bias the gain on perceptual information in order to differentiate actually-experienced (i.e., old) from novel information, accounting for some of the right lateral PFC activity found in some source memory studies. For example, Mitchell et al. (2008) found activity in a short-term source memory task in right lateral PFC regions similar to those of Dobbins and Wagner (2005) for picture-word source judgments with word test probes and suggested that these regions are engaged not only when participants inspect perceptually present details (e.g., of test probes, as in Dobbins & Wagner) but also when participants reflectively attend to specific perceptual qualities of active mental representations during source memory tasks. Such interpretations dovetail with earlier fMRI evidence showing lateralization of PFC activity during episodic memory tasks, especially in more posterior/inferior regions (e.g., 44/6, 45; see Figure 4), according to materials or information domains: verbal information associated with left PFC activity and nonverbal with right (e.g., Kelley et al., 1998; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Raye et al., 2000; Wagner, Poldrack, Eldridge, Desmond, Glover, & Gabrieli, 1998; see, Buckner & Wheeler, 2001; Wagner, 1999, for reviews).

In considering potential differential sensitivity of specific PFC regions to different types of information, reflectively- or internally-generated information is especially interesting because of the importance of being able to identify oneself as a source (e.g., *reality monitoring*; Johnson & Raye, 1981; Johnson et al., 1993). Our thoughts, and the processes by which we generate them, leave records that can be used to identify the origin of information (Finke, Johnson, & Shyi, 1988). Several long-term memory studies suggest that left anterior ventrolateral PFC and medial anterior PFC are relatively more active during monitoring of internally-generated information, such as the task performed during encoding (e.g., read vs generate) or the conceptual information generated during such tasks, compared to perceptually-derived information such as stimulus size, position on the screen, or list membership (Dobbins & Wagner, 2005; Simons, Davis, Gilbert, Frith, & Burgess, 2006; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005). Consistent with the idea that left anterior ventrolateral PFC is involved in evaluating self-generated information, a short-term source memory study showed that activity in this area was greater during judgments about which encoding task was performed than judgments about format (picture vs. word) (Mitchell et al., 2008). Within medial anterior PFC, long-term memory studies have shown that the more posterior area may be especially sensitive to self- vs other generated information (Simons, Henson, Gilbert, & Fletcher, 2008; Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vinogradov, Luks, Simpson, Schulman, Glenn, & Wong, 2006). One possibility is that medial anterior PFC is involved in representing information about cognitive operations (e.g., self-generation) and left ventrolateral PFC is engaged in evaluating this information. In any event, there do appear to be areas of PFC differentially involved in remembering perceptually-acquired vs reflectively-generated source features.

This should be expected in a system that is capable of not only taking in and synthesizing information from various external sources, but also of generating its own information, and of (at least sometimes) telling these two classes of information apart.

Another aspect of source memory emphasized by the SMF is that it is *agenda-driven*: Source decisions usually involve “paying attention to” (giving more weight to) some information while ignoring (or giving less weight to) other information (for behavioral evidence, see, e.g., Dodson & Schacter, 2001; Lindsay & Johnson, 1989; Marsh & Hicks, 1998; Mather et al., 1997; Rahhal, May, & Hasher, 2002; Zaragoza & Koshmider, 1989; for neuroimaging evidence, see, e.g., Dobbins & Wagner, 2005; Johnson, Nolde, et al., 1997; Johnson, Kounios, & Nolde, 1997; Simons, Gilbert, et al., 2005). From this perspective, remembering usually is not just a matter of a cue reviving information, rather, what information one finds (i.e., what information is activated) during remembering depends on what one seeks³, how one evaluates activated information, including setting criteria for its use (e.g., weighting the importance of features according to the active agenda), and on attributional decision processes (e.g., comparing activated features to expected features) (see also, McDuff, Frankel, & Norman, 2008).

Concepts in the neuroimaging domain consistent with the idea of agenda-driven remembering tend to highlight pre-retrieval control processes—for example, *retrieval orientation* (Rugg & Wilding, 2000), *domain-sensitive biasing* (Dobbins & Wagner, 2005), or *cue-based planning* (Dobbins & Han, 2006). These concepts have tended to be used only in reference to long-term memory retrieval and to emphasize primarily the match between a test cue and what has been encoded (*encoding specificity*; Morris, Bransford, & Franks, 1977; Norman & O’Reilly, 2003; Tulving & Thomson, 1973) (see, e.g., Hornberger, Rugg, & Henson, 2006; Johnson & Rugg, 2007; Otten, 2007; Woodruff, Johnson, Uncapher, & Rugg, 2005). There is growing evidence from studies examining these kinds of pre-retrieval processes in the service of source memory that lateral anterior PFC is involved in identifying and maintaining memory relevant goals, the set to remember, and/or specific source monitoring agenda(s) (e.g., Dobbins & Han, 2006; Lepage, Ghaffar, Nyberg, & Tulving, 2000; see, Ranganath & Blumenfeld, 2008; Simons, in press, for reviews).

Mitchell et al. (2008) found evidence for domain-general cognitive control processes involved in the monitoring/evaluation of active information. In the short-term source memory study discussed above, making source memory decisions about encoding task required evaluating and making attributions about self-generated information while ignoring (presumably) more salient format information. Areas more active on encoding task trials than format included: left mid-ventrolateral PFC, which has been associated with *selection* of relevant information (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; see also Petrides, 2002), left dorsolateral PFC, associated with *foregrounding* (refreshing) a target representation (Dobbins & Han, 2006; Raye, Johnson, Mitchell, Greene, & Johnson, 2007), and anterior cingulate cortex, involved in *detecting conflict* among active representations (Botvinick, Cohen, & Carter, 2004). Thus, Mitchell et al. suggested that, whereas left anterior ventrolateral PFC is involved in evaluating self-generated information, left mid-ventrolateral and dorsolateral PFC activity may be more domain general and, with ACC, involved in selecting relevant features, foregrounding information, and resolving conflict (e.g., from salient but irrelevant active information). Of course, none of these processes need be unique to source memory.

³Related concepts from the cognitive behavioral literature are *cue specification* (Burgess & Shallice, 1996) and *early selection* (Jacoby et al., 2005).

In sum, there is growing consensus that PFC can be functionally fractionated with respect to both the processes and the features involved in source memory (Dobbins & Wagner, 2005; McDermott et al., 1999; see Figure 4). For example, during encoding, ventrolateral PFC tends to be more involved in attention to/encoding of specific item features, which may enhance item memory, whereas dorsolateral PFC tends to be more involved in control processes necessary for organization and relating of multiple features, which should contribute to source memory. With respect to remembering, comparisons of source vs item memory judgments show that whereas left lateral PFC is primarily involved in systematic monitoring of specific information (as during source identification tasks), right lateral PFC is involved in heuristic evaluation of less-differentiated information such as familiarity or recency (as in item recognition). Studies that directly compare activity associated with two source identification tasks suggest that whereas dorsolateral and lateral anterior PFC tend to support domain-general processes engaged during source memory, ventrolateral PFC may be relatively more involved in feature-specific processing. Recent evidence also suggests that there likely are intricate interactions between features and processes, with the functional connectivity between PFC and posterior regions dynamically adjusting to the current context—i.e., specific process-feature combinations (e.g., Protzner & McIntosh, 2008).

Together, findings such as those presented above have encouraged researchers to further refine and specify ideas about the component processes, and the features, involved in source memory under different conditions. Additional systematic investigation is needed before we have a full understanding of PFC specificity with respect to source memory. This understanding will be furthered by investigations looking at how subregions of PFC interact with subregions of MTL or parietal cortex and other regions (see next section) during both encoding and remembering of specific features and combinations of features. Progress also likely will be made as investigators find novel ways to conduct cross-technique studies, such as direct comparisons of TMS and fMRI to examine causal relationships, or that use ERP to examine the timecourse of PFC activity associated with component processes as identified with fMRI.

Parietal Cortex and Other Posterior Brain Regions

Source memory accuracy is related to what specific features of an experience are encoded, how well those features are bound together in memory, and how they are accessed and evaluated during remembering. There is evidence for category specificity in posterior visual areas in episodic memory. For example, different areas of fusiform cortex are differentially involved in encoding various types of materials (e.g., faces [Kuskowski & Pardo, 1999], scenes [Kirchhoff, Wagner, Maril, & Stern, 2000], words [Wagner, et al., 1998]), and these regions are the same as those involved in perception of the corresponding types of information (e.g., *fusiform face area [FFA]*, Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; *parahippocampal place area [PPA]*, Epstein & Kanwisher, 1998; *visual word form area* in left occipito-temporal sulcus [bordering the fusiform gyrus], McCandliss, Cohen, & Dehaene, 2003). In addition, activity in left superior temporal gyrus and retrosplenial/posterior cingulate cortex has been associated with successful encoding of location, and posterior inferior temporal cortex with encoding color source information (Uncapher, Otten, & Rugg, 2006). For visual stimuli, there is some evidence that encoding activity in right fusiform predicts accurate source memory for specific perceptual details and activity in left fusiform predicts accuracy of judgments that can be based on less-specific information (e.g., old-new recognition; Garoff, Slotnick, & Schacter, 2005; see also Simons, Koutstaal, Prince, Wagner, & Schacter, 2003). The precise functional significance of the left fusiform activity for memory is still unclear, but, Simons et al. (2003) have suggested that left fusiform could be involved in processing semantic

information. Findings such as these are consistent with the SMF, in that patterns of posterior brain activity should reflect various specific characteristics of memories.

There also is evidence consistent with the idea that activity in posterior representational areas during encoding is modulated by top-down PFC processes, and that this modulation supports later source memory. For example, a study looking at functional connectivity among regions active during the encoding of face-house pairs found that correlations between face- and place-sensitive voxels in posterior regions and the left dorsolateral prefrontal cortex were related to successful face-house binding (Summerfield et al., 2006).

In contrast to the relatively content-specific activity of some posterior regions, parietal cortex may be more generally involved in encoding and remembering source information. For example, in contrast to the activation associated with successfully encoded individual features (location, color) in the Uncapher et al. (2006) study noted above, activity in intraparietal sulcus (as well as precuneus, another region of parietal cortex) was associated with successful encoding of both source features. In interpreting their results, Uncapher et al. argued that the encoding of multifeatured representations, as opposed to single feature representations, requires initial perceptual binding of the features, which relies on intraparietal sulcus. This interpretation is consistent with behavioral modeling studies suggesting that source judgments of two features tend to be stochastically dependent (Meiser & Broder, 2002; Starns & Hicks, 2005).

With respect to remembering, both long-term (Dobbins et al., 2002; Dobbins & Wagner, 2005; Kahn, Davachi, & Wagner, 2004; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; see also, Wagner, Shannon, Kahn, & Buckner, 2005), and short-term (Mitchell et al., 2008), source memory studies suggest that activity in parietal cortex (especially inferior and lateral posterior areas) differs depending on the specificity of the information being evaluated. For example, Wheeler and Buckner (2004) showed participants words that were paired at encoding with either a related picture or a related sound and reported that during a long-term recognition memory test for the words, activity in an area of left parietal cortex near the intraparietal sulcus was associated with both Remember and Know responses, but two other parietal areas, one more lateral and one more posterior, were more active for Remember than Know responses. Vilberg and Rugg (2007) found that activity in a posterior parietal area similar to Wheeler and Buckner's posterior one showing Remember > Know was associated with the *amount of specific information* recollected (participants remembered a test picture and the picture that was associated with it at study vs. they remembered a test picture but not the picture paired with it at study; see also Okado & Stark, 2003).

Other studies have shown greater activity in parietal cortex (inferior and superior parietal lobules, precuneus) and in posterior cingulate and retrosplenial cortex for hits vs. correct rejections (Wagner et al., 2005). Wagner et al. concluded that several posterior and inferior parietal areas lateral of the intraparietal sulcus, precuneus, and to a lesser extent superior parietal areas, are associated with recollective experience, including amount recollected, but that intraparietal sulcus activity appears more related to familiarity⁴. More recently, Vilberg and Rugg (2008) concluded from a meta-analysis of fMRI studies involving Remember/ Know judgments, that superior parietal cortex, especially in and around intraparietal sulcus, does not seem to be involved in processes directly related to feelings of familiarity or recollection (e.g., the strength of a memory, nature of details), but rather is involved in some (unspecified) processes that respond whenever a stimulus is task relevant (i.e., salient; see

⁴It is interesting that Uncapher et al. (2006) saw both hippocampus and intraparietal sulcus activity associated with successful encoding of both features. Whether this joint activity at encoding results in the kinds of unitized representations discussed by Diana et al. (2007) as leading to a familiarity response at test is an interesting question.

also discussion below of attentional accounts; but see, Vilberg & Rugg, in press). They also argue that inferior parietal cortex appears to be more directly involved in recollection, and they suggest it may correspond to the episodic buffer theorized by Baddeley (2000). In any event, as Wagner et al. noted, lateral parietal, retrosplenial, and posterior cingulate cortices are connected directly or indirectly to the MTL (see also, Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Olson & Berryhill, in press, for further evidence and discussion of parietal cortex's neuroanatomical and functional connections). Thus, it is reasonable that all of these regions have important functions in source memory.

Based on comparisons between fMRI activation in control participants and lesion patient data, Simons and colleagues (Simons, Peers, et al., 2008) have suggested that although parietal cortex may often be active in source memory tasks, it might not be necessary for source accuracy. Consistent with this, Simons, Peers, Mazuz, Berryhill, and Olson (2009) found that patients with bilateral parietal lesions were not less accurate than controls on a source memory task (e.g., whether the speaker of a sentence was male or female; which of two judgments about a picture the participant made), but they were less confident in their source judgments. Importantly, they did not differ from controls in old/new recognition or their confidence in their old/new judgments. Interestingly, these same bilateral patients also reported less detail in their autobiographical memories (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). Together, these findings are consistent with the idea that confidence is related to the subjective qualities of memories (see also, e.g., Lyle & Johnson, 2006, 2007), and they add to a growing body of evidence suggesting that parietal cortex plays an important role in representing, or directing reflective attention to, source features that give memories their episodic character.

It seems likely that reflective attention during monitoring of specific source features requires coordinated activity between lateral parietal (and other posterior regions) and prefrontal cortices. This hypothesis is consistent not only with the long-term source monitoring findings just reviewed, but also with evidence that regions of activity in both left dorsolateral PFC and lateral parietal cortex in short-term source memory tasks (Mitchell et al., 2008) overlap with regions active in a working memory task in which people *refresh* (i.e., keep active or foreground) information they just perceived but that is no longer externally present (Raye, Johnson, Mitchell, Reeder, & Greene, 2002; Raye et al., 2007). Together, the findings are consistent with the idea that at least some of the lateral posterior parietal activity during source memory tasks (Dobbins et al., 2002; Dobbins & Wagner, 2005; Kahn et al., 2004; Mitchell et al., 2008; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; Vilberg & Rugg, 2007) reflects processes involved in selectively focusing on and evaluating active information during remembering.

Two conceptually similar hypotheses formalized this idea contemporaneously by suggesting that more superior posterior parietal regions (especially BA 7, but also 19) are involved in top-down modulation of memory retrieval and more inferior posterior parietal regions (BAs 40, 39) are involved in bottom-up attention to active (e.g., perceived or retrieved) information during retrieval (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008; see also, Cabeza et al., 2008; but see, Vilberg & Rugg, in press). Ciaramelli et al. (2008) refer to the relevant areas as superior parietal lobe (SPL) and inferior parietal lobe (IPL) in their hypothesis labeled *Attention to Memory* (AtoM), whereas Cabeza (2008) refers to essentially these same areas as dorsal parietal cortex (DPC) and ventral parietal cortex (VPC), respectively, in his hypothesis labeled the *Dual Attentional Hypothesis* (DAP). Both follow directly from, and are parallel to, Corbetta and Shulman's (2002) hypothesis regarding a perceptual dual-attentional system in the parietal cortex.

Consistent with the SMF idea of iterative heuristic and systematic processes during revival and evaluation (Johnson & Raye, 2000), both the AtoM and the DAP hypothesis suggest an interactive quality to the two “systems” whereby activity in inferior parietal cortex is driven relatively heuristically by incoming stimuli (whether from perception or the product of retrieval) and the superior region participates in, or is modulated by, more controlled processes that are necessary for guided retrieval of information in response to more indirect memory cues (whether externally or internally generated). Whereas both models suggest direct interactions with MTL, the AtoM model more explicitly maps out interactions of parietal cortex with PFC (see Ciaramelli et al., 2008, e.g., Figure 4). Both of these attention-based hypotheses can accommodate a large part of the long-term episodic and source memory findings regarding posterior lateral parietal activations discussed above, as well as much of the patient and neuropsychological data (see Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008, for details). Although both appear to address long-term memory *retrieval* specifically (see also Berryhill et al., 2007), Mitchell et al. (2008) found both inferior and superior lateral parietal activity associated with monitoring specific features (format, location, cognitive operations) in a short-term source memory task that minimizes retrieval from long-term memory, suggesting lateral posterior parietal activity is not uniquely related to retrieval of information from long-term memory but rather will be seen whenever the task requires attention to specific information during remembering.

In any event, this attentional approach makes unique predictions about dissociations among episodic memory tasks that are supported by at least some fMRI data to date. Most notable for current concerns, Ciaramelli et al. (2008) point out that whereas this approach would predict both IPL and SPL activity associated with source memory compared to item memory (IPL activity associated with processing specific active source detail and SPL activity associated with greater need for controlled search in source than item memory tasks), it also would predict SPL activity to show up more during source decisions in source identification tasks than for Remember responses in Remember/Know tasks. This is because source identification tasks ask participants about specific features defined by the task (e.g., location information) whereas Remember responses can be made based on *any* information that comes to mind. This prediction gains some support from Ciaramelli et al.’s review of existing findings, and is consistent with the SMF proposal that although we should expect much overlap in underlying processes among various episodic memory tasks, and thus much overlap in the brain areas involved, neural activity also should differ in some respects between different episodic memory tasks because the precise constellation of component processes and features on which they draw is likely to differ. Likewise, the fact that similar areas of SPL and IPL show up in short-term and long-term source memory tasks highlights the idea that long-term memory and short-term memory consist of overlapping sets of processes, but nevertheless may draw on different component processes and information in any given context (e.g., Johnson & Hirst, 1993; see also, e.g., Dobbins & Han, 2006; Ranganath & Blumenfeld, 2005, 2008).

In sum, as suggested by the evidence reviewed here, attention to different features during source memory tasks is selective (agenda-driven) both at encoding and at test (Johnson, Kounios, & Nolde, 1997; Mitchell et al., 2008). Whether the particular focus adopted produces accurate or inaccurate source memory should depend on whether it biases attention to the most diagnostic features for a particular task. In addition, how successful any particular agenda-driven focus is should also depend on the amount of competition from irrelevant, or less relevant, features—more information is not necessarily better (Mitchell et al., 2008). There is evidence for both feature-specific (e.g., category-selective regions) and feature-general (parietal cortex) posterior activity associated with both encoding and remembering of source information. Understanding how such activity is modulated by specific subregions of PFC and interactions with specific MTL regions is the focus of

current investigations and theorizing (e.g., Cabeza, 2008; Ciaramelli et al, 2008; Dobbins & Wagner, 2005; see also Olson & Berryhill, in press, for a review). Systematic investigation of such relationships should move us a long way toward a better characterization of the subjective experience of source memory.

ADDITIONAL TOPICS OF SPECIAL RELEVANCE TO SOURCE MEMORY

Brain Areas Involved in Assessing the Qualitative Characteristics of Memories

As should be clear from the discussion thus far, the SMF is fundamentally concerned with the specific characteristics of memories that give them an episodic or recollective quality and the differences in qualitative characteristics across memories of different types. Combining Memory Characteristics Questionnaire (MCQ) ratings (Johnson, et al., 1988) with fMRI should be an especially powerful technique for clarifying the neural correlates of the subjective experience of remembering. In particular, identifying brain regions where activity correlates with rated vividness or amount of detail of various types would provide more specific information than simply using, for example, Remember/Know responses. Differentiating between regions that correlate with ratings of different qualities also would be an important step toward understanding the neural bases of subjective memory reports, how they are different from those involved in objective measures, and changes with emotional arousal, age, brain damage, or psychopathology (see later sections).

Surprisingly, there have been few neuroimaging studies using this approach with well-controlled stimuli (e.g., pictures). One possible reason is that such stimuli do not involve the rich array of features and the temporal unfolding of meaningful scenarios involving the self that make up our everyday remembering experiences. Neuroimaging studies examining the neural correlates of autobiographical memory, on the other hand, offer an especially rich platform for investigating the subjective experiences associated with remembering. These studies tend to find regions that overlap with those found in more controlled laboratory episodic memory tasks, including hippocampus and parahippocampus, as well as PFC, retrosplenial/posterior cingulate cortex, precuneus, lateral temporal cortex, and lateral parietal cortex (see, Cabeza & St Jacques, 2007, for a review; see also, Burianova & Grady, 2007; Cabeza et al., 2004, for studies that directly compared a standard laboratory episodic and an autobiographical task). Moreover, a network that additionally includes medial PFC and medial posterior cortical regions is of growing interest because of overlap between activity associated with autobiographical memory tasks and with various other kinds of self-referential tasks (see, Cavanna & Trimble, 2006; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Northoff, Heinzel, de Greck, Bermpohl, Dobrowolny, & Panksepp, 2006; Ochsner et al., 2005; Vogt & Laureys, 2005, for reviews) and “self-projection” tasks (e.g., envisioning future events; Buckner & Carroll, 2007; Hassabis & Maguire, 2007; Schacter, Addis, & Buckner, 2007). Information about the self may contribute to source memory in a number of interesting ways, for example, as a feature of memories (e.g., like other objects), an originator of information (e.g., imagining solutions to problems), or an experiencer of events (e.g., emotional reactions), but this has yet to be systematically explored in fMRI studies.

In one autobiographical memory fMRI study with feature ratings (Ryan et al., 2001) participants recalled autobiographical memories while in the scanner and later rated them for emotional valence, arousal, importance, vividness, and number of details. Recent and remote memories did not differ in ratings and the hippocampus was equally active regardless of the age of the memory. Unfortunately, this study did not report whether hippocampal activity (or activity in any other regions) was associated with vividness or detail of the ratings. Gilboa, Winocur, Grady, Hevenor, and Moscovitch (2004) studied autobiographical memories elicited by photographs obtained from family and friends of the participants.

Participants rated their memories post-scan and hippocampal activity was related to the vividness of the remembering experience, but not the age of the memory (though there was some difference in the distribution of activity within hippocampus, with more recent memories activating the anterior portion). Other findings converge on the conclusion that it is not the remoteness of an autobiographical memory, per se, that is associated with hippocampal activity, but rather its qualitative characteristics, including the level of detail, degree of personal significance, and emotionality (Addis, Moscovitch, Crawley, & McAndrews, 2004). Although a full discussion of the various consolidation theories of memory is beyond the scope of this review, we should note that some researchers (Gilboa et al., 2004; see also Shimamura, 2002) cite evidence of hippocampal activity regardless of remoteness of the memory as evidence against the idea that the hippocampus is only necessary during a time-limited consolidation period (see Kensinger & Corkin, 2008, for further discussion).

With respect to other brain areas, Daselaar et al. (2008) had participants recall autobiographical memories in response to single word cues and examined the timecourse of retrieval; participants also rated emotional intensity and the extent to which they felt they were “reliving” the experience during the time of remembering. Consistent with the notion that the phenomenal experience of remembering includes the retrieval and evaluation of specific qualitative features, initial retrieval of the memory was associated with typical episodic memory areas (e.g., hippocampus, retrosplenial cortex, right and medial PFC), and the subsequent elaboration phase of each trial, during which additional information was remembered, showed activity in posterior visual processing and imagery regions (e.g., BA 18/19, precuneus) as well as in left lateral PFC regions associated with retrieval and/or evaluation of specific source information (BAs 9, 10, 44). Moreover, whereas ratings of emotional intensity were associated with activity in amygdala and hippocampus during the initial retrieval period, they were associated with PFC (frontal pole) during both periods. Degree of “reliving” was related to activity, only during the later elaboration period, in posterior visual areas and right inferior lateral and ventromedial PFC (anterior cingulate cortex, BA 32). The authors suggest that MTL is involved in initial reactivation of memories, which may be mediated by emotion, and further elaboration involves sensory processing and imagery areas (e.g., visual cortex, precuneus) as well as left lateral PFC regions, possibly involved in top-down modulation of the posterior regions during retrieval and/or (re)construction or evaluation of specific details (see also, Botzung, Denkova, Ciuciu, Scheiber, & Manning, 2008). Such an interpretation is supported by studies that have examined more systematically the brain areas involved in memory for emotional information.

Brain Areas Involved in Memory for Emotional Information

The literature on emotion and memory is broad, and our discussion is necessarily limited in several ways. We use the term emotional here to refer to situations in which experimental materials are chosen to be evocative, that is, likely to produce arousal in participants (e.g., negative/positive words [e.g., rape, slime, joy, peace], pictures [e.g., of accidents, war, babies, puppies, faces expressing emotion], emotive film clips). We will not discuss, for example, mood induction studies (see, e.g., Eich, Geraerts, Schooler, & Forgas, 2008 for a review of behavioral mood studies). In addition, although important information has, and continues to be, garnered from both animal and human studies involving, for example, lesions and pharmacological interventions, those studies tend not to include fMRI and thus are not covered here (for reviews see, e.g., Dolcos, LaBar, & Cabeza, 2006; Phelps, 2006). Although valence is an important dimension of emotion, most of the effects in fMRI studies to date suggest arousal as the key factor in the impact of emotion on source memory. Because it is difficult to equate arousal for negative and positive information, most studies

tend to use negative stimuli, or to collapse across valence. Thus, most of the effects discussed below are related to processing negative (or negative and positive), highly arousing stimuli; exceptions are noted.

In short, evidence suggests that emotion (i.e., arousal) can have differential effects on memory for occurrence (e.g., item memory), subjective experience (e.g., vividness, confidence, remember/know ratings), and objective accuracy of details (e.g., source memory)(for reviews and discussion of behavioral findings, see, e.g., Christianson, 1992; Reisberg & Heuer, 2004; for reviews that also discuss specific neural underpinnings of these differences, see, e.g., Kensinger & Schacter, 2008a; Mather, 2007; Phelps & Sharot, 2008). With respect to the brain areas involved, focus has been on the role of the amygdala in modulating the effects of emotion on memory, but other brain areas important for memory such as the hippocampus and prefrontal cortex, also have been implicated.

Behavioral studies show that emotional information not only recruits perceptual attention (e.g., Knight, Seymour, Gaunt, Baker, Nesmith, & Mather, 2007; Most, Chun, Widders, & Zald, 2005) and reflective attention (e.g., Johnson Mitchell, Raye, McGuire, & Sanislow, 2006), it also can enhance perception, even at the lowest levels (e.g., by improving contrast sensitivity, Phelps, Ling, & Carrasco, 2006). Consistent with this, posterior visual regions (e.g., occipital cortex, fusiform gyrus) show greater activity during encoding of emotional than neutral information (Kensinger, Garoff-Eaton, & Schacter, 2007; Mather et al., 2006; Mickley & Kensinger, 2008; Mitchell, Mather, Johnson, Raye, & Greene, 2006; see Phan, Wager, Taylor, & Liberzon, 2002 for a review). This enhanced perceptual processing would help explain the better item recognition of emotional than neutral information in the long term (see Kensinger, 2007; Mather, 2007 for reviews).

In addition, early PET (Cahill et al., 1996; Hamann, Ely, Grafton, & Kilts, 1999) and fMRI (Canli, Zhao, Desmond, Glover, & Gabrieli, 1999) studies showed that there was greater activity in the amygdala during encoding of emotional than neutral items. Such effects obtain for both positive and negative highly arousing stimuli (Hamann et al., 1999; see also, Kensinger & Schacter, 2006; but see Dolcos, LaBar, & Cabeza, 2004; Mickley & Kensinger, 2008 for evidence that some neural mechanisms may be different for positive and negative information). Most important, the amount of activity in the amygdala correlates with amount of emotional, but not neutral, information remembered at the aggregate level (Cahill et al., 1996; Canli et al., 1999; Hamann et al., 1999), and moreover, the amount of amygdala activity during encoding correlates with the online level of emotional reactions to, and later accurate memory for, specific items (e.g., Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). The amygdala is more active also during the retrieval of emotional, compared to neutral, information (e.g., Dolcos, LaBar, & Cabeza, 2005; see, Dolan, Lane, Chua, & Fletcher, 2000 for an earlier PET study).

Evidence also suggests that the amygdala may modulate activation in other regions involved in memory, thereby promoting item recognition. In particular, activity in the amygdala during the successful encoding of emotional information is positively correlated with activity in the hippocampus (e.g., Dolcos et al., 2004; Kensinger & Corkin, 2004). In a study in which patients with damage to either the amygdala or hippocampus (and controls) were scanned during encoding of emotional and neutral words, Richardson, Strange, and Dolan (2004) showed that greater damage to the amygdala was associated with less activity in the hippocampus during encoding and likewise, more hippocampal damage was related to less amygdala activity. Such a pattern highlights the reciprocal influence of the amygdala and hippocampus on encoding emotional information. Ritchey, Dolcos, and Cabeza (2008) showed that the degree of amygdala-hippocampal connectivity is related to how well emotional memories are remembered over time. Consistent with a modulatory role for

amygdala, it also is associated with successful encoding and remembering of neutral information encoded in an emotional, compared to neutral, context (Erk, Martin, & Walter, 2005; Maratos, Dolan, Morris, Henson, & Rugg, 2001; Smith, Henson, Dolan, & Rugg, 2004).

Evidence suggests, as well, that it is the interaction of amygdala and hippocampus that underlies the increased sense of vividness that often accompanies memory for emotional items (i.e., greater rates of Remember responses, higher confidence; see, e.g., Kensinger & Schacter, 2008a; Phelps, 2006, for reviews). For example, in one study (Kensinger & Corkin, 2004) activity in both amygdala and hippocampus during encoding was greater for items later correctly given a remember response (compared to those that were forgotten), and activity in these two regions was correlated for the remembered items. Hippocampus and PFC activity, on the other hand, predicted subsequent remembering of both neutral and negative low-arousal items. Thus, though the amygdala may not be necessary for a later subjective sense of vivid remembering of non-arousing valenced information, it does appear to be engaged when processing involves arousal.

An interesting point from the SMF perspective--one that has not yet been clearly articulated or directly investigated with respect to brain correlates--centers on the difference between source memory for the information that provokes emotion vs memory for the emotion itself as a feature of an event memory. Focus has been primarily on the former, that is, on the modulatory role that emotion (arousal) plays in memory formation and later remembering via involvement of the amygdala and its influence on the hippocampus (presumably via physiological mechanisms such as increasing cortisol levels; see Dolcos et al., 2006; Mather, 2007; Phelps, 2006 for reviews). In this way, arousal often enhances memory for information such as perceptual details, which should lead to the subjective sense of vivid remembering (as discussed above) and more accurate source memory (see below). What has received less attention is the idea that emotion also can serve as a feature of the event which can, much like perceptual detail, serve as evidence for source attributions (e.g., "I know he said it because I remember that I was angry at him for it"). Like remembering perceptual or contextual details, remembering information about how I (or someone else) felt would be expected to lead to more vivid memories attributed with higher confidence, and so on.

A related point is that the precise functional connections involved in remembering emotional information might depend on whether the emotion is subjectively experienced more affectively (i.e., "hot cognition", perhaps reflecting amygdala-hippocampus connectivity), as when we feel again years later the pain of losing a loved one, or more cognitively (i.e., "cold cognition", perhaps reflecting PFC-hippocampus connectivity), as when we factually remember we found a co-worker's comment insulting at the time (see, Kensinger & Corkin, 2004 for a similar point). In other words, the pattern of brain activity observed may depend on whether the emotion is processed, either at encoding or during later remembering, with respect to an affective response or the affective content. In either case the information might serve as a source cue.

Also interesting from the SMF perspective is that the increased sense of vividness or recollective quality associated with memory for emotional information can be dissociated from the accuracy of the source details. As with neutral information, people can give remember ratings to, or have high confidence in, emotional items for which they cannot accurately recollect specific event details (see, e.g., Sharot & Yonelinas, 2008 for a recent behavioral study; see, e.g., Kensinger & Schacter, 2008a for a review of behavioral findings). Hence, source errors can *feel* very *real*, especially if people weight emotional responses or information as more important than other types of details. Sharot, Delgado, and Phelps (2004) showed that with old-new recognition of emotional photos equated, amygdala

activity during retrieval was correlated with remember judgments for emotional photos whereas posterior parahippocampal activity was correlated with remember judgments for neutral photos, suggesting that the neutral items were more likely to be associated with memory for perceptual details than were emotional ones (see also Dolcos et al., 2005; see also, e.g., Kensinger & Schacter, 2005a; Mickely & Kensinger, 2008 for evidence more generally consistent with the idea that source attributions about neutral and emotional information may be based on different characteristics).

Consistent with the idea that source memory is not always better for emotional information, memory for type of encoding task was not found to be better for emotional than neutral information, and in this case, amygdala activity was not correlated with accuracy of source memory (though entorhinal cortex activity was; Kensinger & Schacter, 2006; see also Dougal, Phelps, & Davachi, 2007). Also, in a working memory task in which four pictures and their locations had to be remembered for several seconds, arousal negatively affected source memory for the location of the items (i.e., item-location binding) and there was less activity during encoding in binding related areas, such as the precentral-superior temporal gyrus intersect, for emotional compared to neutral items. On the other hand, arousal increased within-item binding, signaled by better picture memory, and there was greater activity in posterior sensory areas for emotional than neutral items (Mather et al., 2006; Mitchell, Mather, et al., 2006).

But, there also is evidence that source memory for emotional information sometimes may be at least as accurate as, or more accurate than, neutral memories (for reviews of the behavioral evidence, see, e.g., Kensinger, 2007; Mather, 2007). For example, Kensinger and Schacter (2005b) showed that source accuracy for deciding whether an item had been seen as a picture or only imagined during encoding was better for emotional than neutral items. Whereas correct source attribution of emotional items was associated with greater encoding activity in amygdala and orbitofrontal cortex (another emotion processing region), hippocampus activity was associated with memory for both negative and neutral items. In addition, there was a positive correlation between amygdala and hippocampus activity for negative items, suggesting that emotion (amygdala) may have modulated memory binding processes (hippocampus). In addition, Kensinger and Schacter (2007) had participants discriminate between test probes that exactly matched neutral and negative pictures seen at encoding and probes that were similar. Correct source attributions in this case require memory for specific perceptual details. Accuracy was higher for emotional than neutral items. Whereas activity in the fusiform gyrus was related to correct attributions during remembering for all items, amygdala activity was related only to correct attributions for negative items.

Overall, the pattern suggests that while emotion (and amygdala activity) may enhance the encoding and remembering of some source information (e.g., perceptual details) it does not necessarily enhance all contextual details (e.g., cognitive operations engaged). But the key may not be the nature of the feature so much as how one distributes their attention. For example, behavioral studies suggest that thinking about how one is feeling, rather than attending to the perceptual and contextual details of an external event, may lead to good memory about how one felt (Mikels, Larkin, Reuter-Lorenz, & Carstensen, 2005) but poor memory for source specifying perceptual and contextual features (Johnson, Nolde, & De Leonardis, 1996). Consistent with Easterbrook's (1959) cue-utilization hypothesis, Mather (2007) has suggested that whereas arousal enhances binding of intra-object details (i.e., intrinsic features) it does not enhance (and can even impair) object-object and object-context binding, especially when such binding relies on more extended reflective processing. This idea may relate to potential functional differences in MTL regions (see section on MTL

above), although more work is needed to understand fully the brain areas involved in such effects.

In sum, neuroimaging, like earlier behavioral studies, provides contradictory evidence regarding whether arousal enhances or disrupts source memory. Although progress is being made, several critical issues are just beginning to be explored. It seems relatively clear that the amygdala is involved in modulating hippocampally-based memory binding processes during processing of emotional information (see also, e.g., Fenker, Schott, Richardson-Klavehn, Heinze, & Düzel, 2005; also, Kensinger & Schacter, 2008a; Phelps & Sharot, 2008 for further discussion). Brain correlates associated specifically with memory for emotion as a feature of an event, per se, however are less well understood. Based on a review of existing literature, it has been suggested that the temporal pole is an area involved in the binding of perceptual and emotional information (especially with respect to visceral responses; Olson, Plotzker, & Ezzyat, 2007), but more systematic work is needed. Likewise, evidence is just beginning to accumulate regarding differences in the neural underpinnings of memory for emotional content vs emotional contexts (see Smith, Henson, Rugg, & Dolan, 2005 for a review and discussion). In addition, there may be individual differences in responses to emotional information (e.g., related to sex, age, personality, genotype, psychopathology; see, e.g., Haas & Canli, 2008; Hamann & Canli, 2004 for reviews) that influence memory. More systematic consideration of the impact of individual differences on the behavioral and neural correlates of source memory for emotional information and for the impact of emotion on source memory for other features is warranted.

ERRORS, DEFICITS, AND PATHOLOGIES

False Memories As Source Errors

Because neither the processes, nor the representations, involved in source memory are perfect, errors occur. A basic principle of the SMF is that inaccurate source memory (i.e., *source confusions, source misattributions, source errors, source amnesia, source forgetting, phantom recollections, illusory memories, memory distortions, false memories*) and accurate source memory arise via the same component cognitive mechanisms (Johnson, 2006; Johnson & Raye, 1981; Lindsay, 2008; Mitchell & Johnson, 2000), and much has been learned about source memory by using paradigms designed to provoke errors. Source errors can be introduced at the time a memory is initially created (encoded) or as it is accessed and evaluated, or when related memories are accessed. Behavioral studies confirm that anything that disrupts (or inappropriately embellishes) the encoding, consolidation, or remembering of the features of events usually reduces source memory accuracy, for example, dividing attention (Dodson et al., 1998; Gruppuso, Lindsay, & Kelly, 1997; Jacoby, Kelley, Brown, & Jasechko, 1989; Kelley & Sahakyan, 2003). Errors increase when the diagnosticity of source information is reduced, for example, when events from different sources are semantically or perceptually similar⁵ (Hashtroudi, Johnson, & Chrosniak, 1990; Lindsay, Johnson, & Kwon, 1991; Mitchell & Zaragoza, 2001). Errors also increase when lax criteria are used to evaluate mental experiences (Hekkanen & McEvoy, 2002; Lindsay & Johnson, 1989), when less diagnostic features are used (Marsh & Hicks, 1998) or features are weighted inappropriately, or time available to make a source judgment is limited (Benjamin

⁵Source tasks typically involve more “items” than “sources” (e.g., many sentences spoken by two voices). However, source errors occur even in situations with one-to-one mapping (e.g., Schacter, Osowiecki, Kaszniak, Kihlstrom, & Valdiserri, 1994). Any increase in the overlap among features of event memories (whether defined as “item” or “context”) should increase the demands for more specific information to differentiate among them. Interestingly, we often do not take into account the base rate occurrence of a feature in using it as evidence for a source attribution. For example, when you attribute an idea to colleague A (someone you know well) rather than B (someone you do not know well), you are likely to be satisfied that A came to mind without thinking that the probability is higher they will come to mind, independent of their connection to the idea.

& Craik, 2001; Johnson et al., 1994; Zaragoza & Lane, 1998). Motives and social context can influence all of these (Gordon, Franklin, & Beck, 2005).

A particularly interesting type of source error results from confusing thoughts, associations, and imaginations with actual perceptions (Henkel et al., 2000). For example, participants sometimes claim to have seen pictures that they only imagined (Durso & Johnson, 1980), and good imagers are more likely to misattribute imaginations to perceptions (Hyman & Pentland, 1996). Neuroimaging evidence converges with this behavioral evidence in suggesting that rich self-generated perceptual information induces source errors. For example, one study compared source memory for imagined and seen pictures (Gonsalves et al., 2004). Imagined pictures that were later erroneously called seen showed greater activity in precuneus during encoding than imagined items later correctly called imagined. This area is involved during other types of imagery tasks, supporting the idea that perceptual information either generated via active imagination or imported from one item to another (Lampinen et al., 2005; Lyle & Johnson, 2007) lends a sense of vividness to people's false memories for having seen the imagined items. Interestingly, in another study, there was less activity at test in a region of medial anterior PFC when people erroneously remembered seeing items during study that they had in fact only imagined than when they made correct attributions (Turner et al., 2008). As previously discussed, this area is often active in reality monitoring studies, and this finding supports the idea that cognitive operations information (e.g., regarding self-generation) informs accurate reality monitoring decisions (Johnson, Kounios, & Nolde, 1997; Johnson & Raye, 1981).

Okado and Stark (2003) found an area of left parietal cortex in which activity was not different for true and false episodic memories, and the graded pattern of activity suggested that it was related to the amount of memorial information activated: Actually seen items and imagined items called seen showed greater activity than imagined items called new which were greater than unseen items called new (see also, Cabeza, Rao, Wagner, Mayer, & Schacter, 2001 for a similar finding with a different behavioral paradigm). Okado and Stark also found that activity in left lateral PFC (BA 9; BA 10,46) was the same for true and false memories, though unlike parietal cortex, in these PFC areas seen and imagined items called seen and imagined items called new all showed greater activity than new items correctly called new. Together, this pattern is consistent with the data discussed in previous sections associating activity in parietal cortex with amount of information active and in left lateral PFC with monitoring/evaluating that information. Consistent with the SMF, the pattern further suggests that these areas are involved whether the memory is true or false.

It is important to keep in mind that although memories from different sources tend, *on average*, to produce memorial representations that are characteristically different from each other, variability within categories often creates overlap in the distributions of features. For example, representations of some perceived events are less detailed and perceptually vivid than representations of some imagined events, and some imagined events can be highly elaborate and vivid. Thus, although people sometimes believe false memories are true because they have perceptual, emotional, and other details, false memories often differ from true memories, on average, in qualitative characteristics (Anastasi, Rhodes, & Burns, 2000; Henkel et al., 2000; Johnson, Nolde, et al., 1997; Karpel, Hoyer, & Toglia, 2001; Norman & Schacter, 1997). For example, Mather et al. (1997) found that "lures" (e.g., *needle*) were falsely recognized as having been presented in a spoken list because they were semantically related to presented items (*haystack, thread, sharp*; Deese, 1959; Roediger & McDermott, 1995), but these false memories were rated as having, on average, less auditory detail than were accurate memories for items actually presented. Consistent with this, neuroimaging studies suggest that some areas, especially posterior regions (e.g., early visual areas, e.g., BA 17, 18) differentiate true and false visual memories, whereas other posterior areas show

similar activity (e.g., later visual processing areas, e.g., BA 19, 37) (Slotnick & Schacter, 2004; see, Okado & Stark, 2003, for another example of differences in visual areas). Thus, whether a source misattribution error is made may depend on what “level” of perceptual information is being assessed.

Differential activity associated with true and false memories has been observed in other regions as well, including MTL, PFC, and parietal areas (Garoff-Eaton, Kensinger, & Schacter, 2007; Garoff-Eaton, Slotnick, & Schacter, 2006; Kim & Cabeza, 2007a). For example, Kim and Cabeza (2007b) used a semantically-related word procedure and showed that high confidence true memories were associated with activity at test in MTL regions (hippocampus and parahippocampal gyrus) but false memories were associated with activity in PFC and posterior parietal cortex.

Behavioral evidence shows that people can later come to misattribute false information that they themselves generated and that they knew at the time was false (Ackil & Zaragoza, 1998). Hassabis and Maguire (2007) compared memory for recent autobiographical memories with recent *constructed* fictitious experiences (mental experiences that the participants *knew* they were constructing). In this case, the only brain regions more active for real memories were anterior medial PFC and posterior medial cortex (posterior cingulate cortex and precuneus), areas that are associated with self-referential processing (see, Cavanna & Trimble, 2006; Macrae et al., 2004; Northoff et al., 2006; Ochsner et al., 2005; Vogt & Laureys, 2005, for reviews) and “self-projection” tasks such as envisioning future events (Buckner & Carroll, 2007; Schacter et al., 2007). Presumably, the extent to which self-constructed events later come to be misattributed as actual autobiographical events (Hashtroudi et al., 1990; Lindsay, Hagen, Read, Wade, & Garry, 2004; Loftus & Pickrell, 1995) would be related to the amount of imagined information that is revived and evaluated, including information related to the self, and this should be reflected in the amount of brain activity in these medial regions. This remains to be tested. Future fMRI studies such as those noted above that ask participants about specific qualitative features of their memory (see section on assessing qualitative characteristics), rather than just whether an item is remembered (or to rate confidence), and that also manipulate the information people focus on for making source decisions, should be helpful in understanding the neural mechanisms of source errors/false memories.

Aging and Source Memory

Useful information about how source memory processes work, as well as how they can break down, has been obtained from looking at age-related differences in source memory (see, Johnson et al., 1993; Naveh-Benjamin & Old, 2008; Zacks & Hasher, 2006, for reviews; see also Table 1). There is considerable evidence from the cognitive-behavioral literature that, relative to young adults, older adults show memory binding deficits (Chalfonte & Johnson, 1996; Glisky, Rubin, & Davidson, 2001; Mitchell, Johnson, Raye, Mather, & D’Esposito, 2000; Naveh-Benjamin, 2000; Naveh-Benjamin, Brav, & Levy, 2007; O’Hanlon, Wilcox, & Kemper, 2001), source memory deficits that are greater than item memory deficits (see, Kaszniak & Newman, 2000; Spencer & Raz, 1995 for reviews), and reduced recollection along with relatively preserved familiarity-based responding (Anderson et al., 2008; Healy, Light, & Chung, 2005; Parkin & Walter, 1992; Prull, Dawes, Martin, Rosenberg, & Light, 2006; see, Light, Prull, La Voie, & Healy, 2000 for a review; see also, Naveh-Benjamin & Old, 2008, for review of contrary evidence regarding familiarity).

Consistent with this pattern, age-associated neuropathology in medial temporal regions has been demonstrated (Golomb et al., 1996; O’Brien, Desmond, Ames, Schweitzer, & Tress, 1997; Raz, 2000; Raz et al., 2005; Small, Tsai, DeLaPaz, Mayeux, & Stern, 2002). Although

changes in MTL specifically have been noted with the advance of Alzheimer's Disease, MTL volume does shrink with normal aging, with the greatest change in the hippocampus and little, if any, change in surrounding areas such as entorhinal cortex (Raz, Rodrigue, Head, Kennedy, & Acker, 2004). There is evidence of neurochemical changes as well (Driscoll et al., 2003). Although volume and neurochemical changes have been linked to age-related deficits in hippocampally-supported memory tasks (Driscoll et al., 2003), both the relationship between age-related changes in MTL volume and memory function (Van Petten, 2004) and between age-related decrements on MTL-based neuropsychological tests and source memory tasks (Glisky & Kong, 2008; Glisky, Polster, & Routhieaux, 1995; Henkel, Johnson, & De Leonardis, 1998; Mather, Johnson, & De Leonardis, 1999) have been variable.

Aging disproportionately affects the PFC, compared to other brain regions (Raz & Rodrigue, 2006), and these structural and functional changes also have been associated with cognitive dysfunction, though again, the relationships are far from perfect (see, e.g., Dennis & Cabeza, 2008; Raz & Rodrigue, 2006; Small et al., 2008; Valenzuela, Breakspear, & Sachdev, 2007 for reviews). Nevertheless, there are reports of positive correlations between older adults' memory performance and scores on standard neuropsychological tasks sensitive to frontal function (Bunce, 2003; Craik, Morris, Morris, & Loewen, 1990; Glisky et al., 1995; Henkel et al., 1998; Moscovitch & Winocur, 1995), supporting general PFC theories of cognitive decline in aging (Braver et al., 2001; Hasher & Zacks, 1988; Moscovitch & Winocur, 1995; Parkin, 1997; Shimamura, 1995; West, 1996).

Although the number of functional neuroimaging studies of age-related cognitive change is increasing, there still are relatively few fMRI studies that focus specifically on feature binding and/or source memory (see Cabeza, 2006 for a review). The findings to date highlight a particularly interesting piece of the puzzle: Exactly which regions of PFC are functionally coupled with activity in hippocampal or other MTL regions during successful memory encoding (e.g., binding) under different circumstances, and which are affected most by age?

The first fMRI study looking at age-related changes in brain activity associated with memory binding used a short term memory task (Mitchell, Johnson, Raye, & D'Esposito, 2000) to show that, consistent with long-term memory behavioral studies (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000; see Old & Naveh-Benjamin, 2008 for a review), there was an age-related behavioral deficit in memory for object-location combinations that was disproportionate to deficits for either feature alone (see also, e.g., Grady et al., 1995). Moreover, compared to young adults, older adults showed disproportionate attenuation of activity in anterior hippocampus in the combination condition (relative to either feature alone) during the delay period, suggesting an encoding deficit. There was also a suggestive, though not significant, trend in that direction in medial PFC (BA 10), an area involved in maintaining integrated, relative to individual, features in working memory (Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000). Although correlations between these two regions were not conducted, the pattern of regional differences is consistent with the idea that age-related source memory deficits are due, at least in part, to age-related decrements in memory binding during encoding resulting from hippocampal dysfunction, PFC dysfunction, and/or changes in hippocampal-PFC functional connectivity.

A more recent study by Dennis, Hayes, Prince, Madden, Huettel, and Cabeza (2008) looked at brain activity during encoding of face-scene pairs that was associated with subsequent successful long term memory. As in Mitchell et al. (2000), there was an age-related reduction in hippocampal activity, relative to young adults, that was disproportionate to the differences associated with memory for either feature alone. There also was an age-related

reduction in bilateral dorsolateral PFC activity (rather than medial PFC, as in Mitchell et al.) related to pair memory. In addition, the PFC regions demonstrating functional connectivity during encoding with hippocampus were lateral regions (bilateral ventrolateral, right dorsolateral and superior frontal cortex; see also, Gutchess et al., 2005)--areas identified in other studies as engaged in various reflective processes involved in episodic memory tasks. Interestingly, the hippocampal-PFC connectivity was *stronger* in older compared to young adults. That this functional coupling should increase while activity levels in each area decreases is an interesting conundrum, but it suggests that looking at both regional activity and functional relationships will be important in understanding age-related changes. Because the connectivity between the hippocampus and posterior regions (e.g., posterior cingulate, parietal cortex, and inferior temporal regions) was *weaker* in older than young adults, Dennis et al. suggested that age is associated with a posterior-to-anterior shift in the areas that co-activate with hippocampus during encoding (see Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008 for further discussion of this hypothesis of cognitive aging).

The precise reasons for such a shift remain unclear (see section below on compensation hypotheses), but it does raise the question of whether older adults' difficulty in binding features is driven, at least in part, by weak representations of the information in posterior regions (or weak projections from/to posterior regions). Posterior representational areas show less specificity of activation in older adults for distinct classes of information such as faces and scenes (Chee et al., 2006; Park et al., 2004; Payer et al., 2006), and activity during long term memory encoding tasks in a number of these areas is reduced in older, compared to young, adults (Dennis & Cabeza, 2008; Dennis, Hayes, et al., 2008). Although in some cases this may reflect age-related dysfunction of these areas, per se, or age-related differences in perceptual attention to the various types of information (e.g., due to differences in interest), recent evidence suggests an age-related deficit in the modulation of posterior areas during *reflective* attention (Mitchell, Johnson, Higgins, & Johnson, 2009). In addition, the Dennis, Hayes, et al. (2008) face-scene study mentioned above found that age-related differences were greater for source than item subsequent memory effects in the hippocampus and PFC, but not in inferior temporal representational areas (where age deficits were equal for source and item memory). This suggests that older adults may have difficulty in binding features besides a problem of less detailed feature representations, but the relative contribution of each of these problems to older adults' source memory difficulties remains to be determined.

Together, the findings discussed thus far suggest that there may be multiple ways that PFC, MTL, and posterior regions and/or their functional connectivity during encoding are affected by aging (see Table 1). The pattern of deficits in these regions during encoding predicts age-related decrements in the vividness of older adults' memory for specific source information. Consistent with this, in cognitive-behavioral studies using the Remember/Know procedure, older adults often (but not always) give fewer Remember and more Know responses (Parkin & Walter, 1992; Prull et al., 2006; see, Light et al., 2000; Zacks & Hasher, 2006, for reviews). On the other hand, when older adults are asked to rate specific subjective qualities of their memories such as perceptual, associative, or emotional detail they often rate their memories to be at least as strong or vivid as do young adults, even when a variety of objective memory measures, including source identification, show that they remember less (Hashtroudi et al., 1990; Henkel et al., 1998; Lyle, Bloise, & Johnson, 2006; also Karpel et al., 2001; Norman & Schacter, 1997). For autobiographical memories, as well, they give MCQ ratings as high as (McGinnis & Roberts, 1996) or higher than (Comblain, D'Argembeau, & Van der Linden, 2005; Rubin & Schulkind, 1997) young adults. As Bloise (2008) noted, the different relation between age and subjective memory obtained with different measures (e.g., R/K vs MCQ), and the sometimes lack of correspondence between age differences on subjective and objective measures, suggests that young and older adults

base their subjective reports on different types or combinations of features. Neuroimaging evidence should help assess this possibility.

Using structural equation modeling on structural MR data and Remember/Know responding during recall and recognition tasks, Yonelinas et al. (2007) reported a double-dissociation whereby age-related reduction in hippocampal volume was associated with decreased recollection (but not familiarity) and reduced entorhinal volume was related to decreased familiarity (but not recollection). Using a recognition confidence measure, Daselaar, Fleck, Dobbins, Madden, and Cabeza (2006) showed that older adults demonstrated less recollection-related activity in hippocampus but greater familiarity-related activity in rhinal cortex, relative to young adults. Daselaar and colleagues further found that whereas young adults showed greater functional connectivity between the hippocampus and posterior regions (e.g., parietal and retrosplenial cortex) associated with recollection, older adults showed greater connectivity between rhinal cortex and PFC. This may reflect an increase in frontally-mediated evaluation of familiarity. (See also, e.g., Duarte, Henson, & Graham, 2008; Duverne, Habibi, & Rugg, 2008; Morcom, Li, & Rugg, 2007 for other aging fMRI studies using the Remember/Know procedure). Older adults also show deficits in left lateral PFC during short-term source memory tasks, suggesting they either have problems evaluating specific information or have less information available for evaluation, compared to young adults (Mitchell, Raye, Johnson, & Greene, 2006).

With respect to subjective memory reports, Viard et al. (2007) presented older adult participants with sentence cues to autobiographical memories from 5 time periods of their life that had been obtained from family members (e.g., the *wardrobe falls off of the roof of the car*) and had the older adults recall the events in the scanner and later rate the memories. Although there was no young comparison group in this study, areas of activation common to all time periods included some areas similar to those reported above for young adults, including medial PFC (superior frontal gyrus) and posterior regions (precuneus/posterior cingulate). In addition, they found right hippocampal activity related to the specificity and number of details in postscan reports.

Behavioral studies suggest that source memory for affective information is relatively preserved in older adults, compared to, for example, perceptual information (see, e.g., see Kensinger, in press, for a review), and that older adults may be more likely to use affective information in making source attributions (Hashtroudi et al, 1990; May, Rahhal, Berry, & Leighton, 2005; Rahhal et al., 2002; see also, Johnson & Multhaup, 1992, for discussion). Consistent evidence comes from a study showing age-differences in the brain areas associated with subjective memory ratings for perceptual vs affective information. During an incidental encoding task, Bloise (2008) showed young and older adults labeled photos of various objects and scenes (e.g., *jellyfish; couple on couch*). After several weeks, on a surprise old-new recognition test outside the scanner, they were cued with the names of the pictures and rated their subjective memory for visual details and feelings and reactions associated with items called old. Young adults' encoding activity in right cuneus (a region associated with visual processing and visual imagery, Ganis, Thompson, & Kosslyn, 2004; Hadjikhani & Roland, 1998) was correlated with later visual detail ratings for items correctly identified as old. Activity in medial posterior cingulate cortex (an area associated with self-referential processing; Johnson, Raye, Mitchell, Touryan, Greene, & Nolen-Hoeksema, 2006; Kelley et al., 2002; Ochsner et al., 2004) was positively correlated with subsequent reaction ratings.

For older adults, on the other hand, encoding activity in posterior cingulate cortex was positively associated with subsequent visual detail ratings for correctly identified old items, suggesting that, for older adults, self-referential processing during encoding affected their

later sense of remembering visual details. One possibility is that older adults' engaged in self-referential processing during encoding (e.g., "that looks like the kitchen in my first house") and later the memory for those related, self-generated autobiographical details was misattributed to the studied item (e.g., Henkel et al., 1998; Lyle et al., 2006). That is, older adults may have been influenced by irrelevant information (Hasher, Lustig, & Zacks, 2007), in this case, taking one attribute (e.g., affective or perceptual information associated with their autobiographical memory) as evidence for another (e.g., externally-derived perceptual information associated with the seen pictures). This might inflate perceptual vividness ratings relative to the amount of actual visual detail remembered about the photos. Also interesting was that, for older adults, activity in right inferior frontal gyrus (BA 47) during encoding was negatively associated with subsequent visual detail ratings and positively associated with reaction ratings. A similar area of right inferior frontal gyrus has been found to be active during autobiographical retrieval (Greenberg, et al., 2005), suggesting that as older adults engaged more in autobiographical retrieval during encoding, they processed less of the specific visual details but more of the affective information of the photos.

Bloise's (2008) findings highlight that young and older adults may differ in what they use as evidence for a memory attribution (e.g., what they believe to be diagnostic or how they weight different features in the same nominal situation). In addition, these findings point to two important issues about the relation between emotion/personal reactions during encoding and subsequent memory that require further investigation: (a) specifying the conditions under which personal relevance/emotional reactions during encoding enhance or detract from encoding perceptual and other details, and (b) specifying the conditions under which personal relevance/emotional reactions may later be taken as evidence of perceptual vividness.

Other work is beginning to explore age-related differences and similarities in brain activity associated with source memory for emotional information (see, e.g., Kensinger, in press; Kensinger & Schacter 2008b; Mather, 2004, for reviews). For example, Kensinger and Schacter (2008b) had young and older adults encode positive, negative, and neutral pictures during scanning and later tested recognition memory for pictures that were exactly the same as, similar to, or different than pictures seen in the scanner. Consistent with evidence of relatively preserved amygdala structure and function in aging (see Mather, 2004 for discussion), they found that encoding activity in amygdala and orbitofrontal cortex associated with subsequent accurate memory for both negative and positive emotional items was similar for young and older adults; valence-specific responding was also similar (negative items activated right fusiform cortex and positive items activated left lateral middle and superior temporal regions as well as lateral PFC). Consistent with a positivity bias in older adults (Mather, 2006), the only age difference was for positive items where older adults showed more activity in the medial prefrontal cortex and cingulate gyrus than young adults. Given that these areas also are involved in processing self-referential information, the authors suggested that older adults may be more likely than young adults to process positive emotional information with reference to themselves.

As might be predicted given the evidence discussed thus far, older adults are more vulnerable than healthy young adults to many types of false memories (Budson, Sullivan, Daffner, & Schacter, 2003; Henkel et al., 1998; Karpel et al., 2001; Lyle et al., 2006; Mitchell, Johnson, & Mather, 2003; Multhaup, De Leonardis, & Johnson, 1999; Rybash & Hruby-Bopp, 2000; see, e.g., Schacter, Koutstaal, & Norman, 1997, for a review). For example, perceptual similarity between an imagined and a perceived item increases the proportion of imagined objects erroneously called seen, and disproportionately so for older adults (Lyle et al., 2006; see also Henkel et al. 1998). It seems likely that such errors are related to the age-related disruptions in hippocampus and PFC-mediated binding processes

and the PFC-mediated evaluation processes discussed previously (see also Roediger & Geraci, 2007).

A pair of papers by Dennis, Kim, and Cabeza (2007; 2008) shed light on this issue by investigating false recognition of semantically related lures. Dennis et al. (2007) showed that encoding-related activity in MTL, left ventrolateral prefrontal cortex, and visual cortices associated with subsequent true memory was reduced in older adults, compared to young adults, but that older adults showed increased activity in right ventrolateral PFC. Increased age-related encoding activity in left superior temporal gyrus was seen for both subsequent true and false memories. Similarly, older adults, relative to young adults, showed less activity during correct remembering of presented words in hippocampus but greater activity in retrosplenial cortex; during false remembering of non-presented items, older adults showed relatively greater activity in lateral temporal cortex (Dennis et al., 2008). The authors interpret this overall pattern as consistent with an age-related reduction in encoding and recollection of specific information and increase in more semantically-based (or familiarity-based) responding, which leads to errors in this paradigm. More work looking at age-related false memories under a range of circumstances is needed before the neural correlates associated with age-related increases in source misattributions are completely understood.

Age-related compensatory mechanisms—One topic that has drawn special attention in the neuroimaging of cognitive aging domain is the functional role of additional brain activity in older adults, compared to young adults. Reduced activity in PFC and areas of MTL in older, compared to young, adults is found at both *encoding* (Cabeza et al., 1997; Dennis et al., 2007; Mitchell, Johnson, Raye, & D’Esposito, 2000; Sperling et al., 2003) and *remembering* (Cabeza, Anderson, Locantore, & McIntosh, 2002; Dennis, Kim, & Cabeza, 2008; Mitchell et al., 2006) in source memory tasks (for reviews, see, Cabeza, 2006; Daselaar & Cabeza, 2008; Dennis & Cabeza, 2008; Persson & Nyberg, 2006). These age-related reductions in activity are often, but not always, associated with increased activity in other regions, especially in contralateral PFC regions (see, e.g., Cabeza, 2002; Daselaar & Cabeza, 2008; Grady, 2008; Reuter-Lorenz, 2002, for reviews). This additional activation seen in older adults is sometimes attributed to neural *dedifferentiation* (i.e., a loss of neural efficiency; e.g., Morcom et al., 2007). However, because the additional activity is often greatest for high functioning older adults (according to performance on neuropsychological assessments of frontal functioning, for example, or the primary memory task), it also has been attributed to *compensation* on the part of older adults (Cabeza, 2002; Reuter-Lorenz, 2002). Additional information is gained about the functional significance of such activity when regional activity is directly correlated with performance (Grady, Yu, & Alain, 2008), but it is still unclear whether the added activity represents the recruitment of additional areas to do the same processing or the recruitment of different processes to do the same task (see, e.g., Grady, 2008 for discussion; see Velanova, Lustig, Jacoby, & Buckner, 2007 for an example of how researchers are trying to formalize age-related compensatory models).

What is relatively clear is that age-related behavioral deficits in source memory are due, at least in part, to decreased functioning of the hippocampus and PFC, and/or hippocampus-PFC interactions, which leads to deficits in memory binding and the systematic, controlled processes necessary for reviving and evaluating source information. What is needed are fMRI studies that systematically explore potential differences in age-related decline in various sub-regions of the MTL and PFC, as well as functional connectivity between areas, that may be differentially involved in specific cognitive functions (e.g., *refreshing*, *noting*, *shifting*; Johnson, 1992) relevant to binding and source memory (Johnson et al., 2005; MacPherson, Phillips, & Della Sala, 2002; Rajah & D’Esposito, 2005).

Clinically Significant Deficits in Source Memory

The profound amnesia resulting from damage to MTL, especially the hippocampus, is an extreme source memory deficit in that features do not seem to be bound together to create distinct event memories. The most notable symptom of such damage is loss of event memories rather than simply reduced memory for details, or increased false memories. In contrast, frontal damage, especially combined with damage to certain other areas (e.g., basal forebrain), sometimes results in profound source confusions called confabulations. Psychopathology also can result in increased frequency and/or bizarreness of memory distortions beyond the normal range of everyday errors. Previous reviews have considered the literature on confabulation resulting from brain damage (Burgess & Shallice, 1996; Johnson et al., 2000; Metcalfe, Langdon, & Colheart, 2007), and we focus here on source memory deficits associated with psychopathology.

According to the SMF, clinically significant source memory errors are created by the same factors as are "normal" source misattributions: Inadequate feature binding, disrupted consolidation and revival processes, constructive/reconstructive elaboration, associative importing of features, failure to engage appropriate evaluation processes or to use situationally-appropriate feature weights and criteria (e.g., inappropriate search agendas), poor self-cuing to retrieve related supporting/disconfirming information, and/or failure to access or use general knowledge about the world or the self to offset implausible or bizarre thoughts (Johnson, 1988, 1991; Johnson & Raye, 2000). In addition, deficits in source memory mechanisms may be compounded by motivation (Fotopoulou, Conway, & Solms, 2007), as well as personality and other individual differences (e.g., imagery vividness). It should not be surprising then that fMRI studies are starting to implicate dysfunction in many of the same brain areas discussed throughout this review in the source memory deficits associated with psychopathology. We focus here on three disorders in which poor source memory appears to be a central cognitive factor: schizophrenia, post-traumatic stress disorder, and depression (see Table 1).

Schizophrenia—Schizophrenia is associated with episodic memory deficits (see, Aleman, Hijman, De Haan, & Kahn, 1999; Boyer, Phillips, Rousseau, & Ilivitsky, 2007; Danion, Huron, Vidailhet, & Berna, 2007; Ranganath, Minzeberg, & Ragland, 2008; Weiss & Heckers, 2001, for reviews). In particular, behavioral studies show that schizophrenic patients exhibit deficits in binding multiple features into complex representations (e.g., Burglen et al., 2004; Danion, Rizzo, & Bruant, 1999; Rizzo, Danion, Van der Linden, Grange, & Rohmer, 1996; Waters, Maybery, Badcock, & Michie, 2004). One dominant hypothesis is that schizophrenia-related binding deficits are due to decreased hippocampal volume or function associated with the disorder (see Boyer et al., 2007 for a review). But, there is also evidence for abnormal PFC-hippocampal functional connectivity during working memory tasks in patients (Meyer-Lindenberg et al., 2005), and this would likely contribute to binding deficits. In addition, feature binding during memory encoding of more affective-laden stimuli (pictures) has been associated with activation in an area that includes superior temporal gyrus (STG; e.g., Mather et al., 2006), and a review of MRI findings showed reliable reductions in STG volume in patients with schizophrenia (Shenton, Dickey, Frumin, & McCarley, 2001).

fMRI studies also point to a role for PFC deficits in the associative memory problems seen in schizophrenia. For example, Lepage et al. (2006) scanned patients and control participants as they encoded, and later remembered, either individual items or pairs of items. Behaviorally, although both groups had better item than associative recognition performance, there was an interaction such that the schizophrenic group performed more poorly than controls on the associative but not the item task. At encoding, the control group

showed greater left dorsolateral PFC (BA 9) and anterior cingulate cortex activity in the associative compared to the item memory condition, relative to the patient group (and, in the STG, as well, a point we return to below). At test, control participants showed greater activity, relative to the patient group, for the associative than the item task in left dorsolateral PFC (BA 46) and right inferior PFC (BA 47), as well as medial PFC (including anterior cingulate cortex), and superior parietal lobe (BA 7)--all areas implicated in source memory. Evidence from a transitive inference task during fMRI also implicates a deficit in hippocampal activity during remembering associations on the part of schizophrenic patients (Öngür et al., 2007; see Boyer et al., 2007 for a review across paradigms).

Hallucinations in schizophrenia are believed to result from particular deficits in reality monitoring (differentiating between internally-generated and externally-derived information; see, e.g., Ditman & Kuperberg, 2005 for a review). Consistent with this hypothesis, the smaller schizophrenia patients' left STG, the more severe their hallucinations (Onitsuka et al., 2004) and a small STG seems to be a predisposing factor for the disease rather than a result of it (Rajarethinam, Sahni, Rosenberg, & Keshavan, 2004). The correlation between size of STG and degree of hallucination makes sense if this area aids in the formation of associations among aspects of an event that are critical for later remembering its source (e.g., Mather et al., 2006; Mitchell, Mather, et al., 2006). Consistent with this hypothesis, controls showed greater STG activation than patients with schizophrenia when imagining sentences being spoken in someone else's voice or listening to external speech, suggesting that this area helps create associations between the source of speech and what is said and that it is dysfunctional in schizophrenia (McGuire et al., 1995; Woodruff et al., 1997). Thus, although STG has received relatively little attention in fMRI studies of source memory, the accumulating data point to a functional role for this area, likely in relatively early memorial binding processes. Whether the disruption in binding and source memory seen in schizophrenia is related in particular to emotion-related disruption of processing in STG, a possibility suggested by the Mather et al. (2006) results, remains to be seen.

Interestingly, in a study in which schizophrenia patients who did, and did not, hallucinate were scanned as they made reality monitoring judgments (whether words were previously said or heard), hallucinating patients showed more widespread activity in left BA 40 and 44, areas associated with processing phonological information/inner speech (Woodward et al., 2008; see also, e.g., Hoffman, 2008; Hoffman et al., 2007). Presumably this more extensive activity is associated with more vividly experienced internal speech, making it harder to discriminate internally from externally derived items. In addition, the monitoring of internal speech involves the interaction of areas involved in speech generation (e.g., left inferior frontal cortex) and speech perception (e.g., temporal cortex), and the modulatory relationship between these areas appears to be disrupted in schizophrenic patients with a history of auditory hallucinations (Shergill et al., 2003). One recent study in which schizophrenic participants were scanned as they experienced auditory hallucinations vs generated "normal" inner speech (in separate sessions) suggested that the difference was in the laterality of activation in language areas such as inferior frontal gyrus and superior temporal gyrus (Sommer et al., 2008): left for normal inner speech and right for hallucinations. These laterality differences appeared to be related to the low semantic content and negative emotionality of hallucinations.

It is notable that schizophrenia is associated with dysfunction in medial anterior (i.e., rostral) PFC, an area we previously discussed as being especially sensitive to monitoring self- vs other generated information (Simons et al., 2008; Simons, Davis et al., 2006; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; Turner et al., 2008; Vinogradov et al., 2006; see also Ciaramelli & Spaniol, 2008; see discussion in Simons et al., 2006; but see, Ragland, Valdez, Loughhead, Gur, & Gur, 2006). A recent study showed that schizophrenic

patients were slower and less accurate than control participants at a reality monitoring task requiring them to differentiate whether words were self-generated or read during encoding; moreover, the schizophrenic group showed a deficit in medial anterior PFC activity (medial BA 10) during correct identification of self-generated items (Vinograd, Luks, Schulman, & Simpson, 2008). It remains to be resolved whether schizophrenia patients' difficulty monitoring self-generated information is a primary deficit (e.g., dysfunction of medial anterior PFC) or secondary to a deficit in binding source and content information (e.g., related to dysfunction of STG or hippocampus). In either case, it seems clear that at least some of the cognitive deficits (i.e., memory binding) and clinical symptoms (i.e., hallucinations) associated with schizophrenia are associated with dysfunction in stimulus and speech processing areas, temporal binding areas, and prefrontal areas (e.g., medial PFC) involved in representing and/or monitoring internally-generated information (see, e.g., Allen, Larøi, McGuire, & Aleman, 2008 for further review).

Post-Traumatic Stress Disorder (PTSD)—PTSD is associated with both structural and functional abnormalities in the hippocampus, PFC, and amygdala (see, e.g., Bremner, 2007; Shin, Rauch, & Pitman, 2006, for reviews). It is also associated with both intrusive vivid recollections of the triggering traumatic event and impoverished episodic memory for other events (see, e.g., Bremner, 2007; Brewin, Kleiner, Vasterling, & Field, 2007; Liberzon & Sripada, 2008; McNally, 2006, for reviews). We will deal primarily with the latter.

In addition to less vivid episodic memory (e.g., reduced Remember responses, Tapia, Clarys, El Hage, Belzung, & Isingrini, 2007), PTSD is associated with poor source identification for both emotional (Golier, Harvey, Steiner, & Yehuda, 1997) and neutral (Fichtenholtz et al., 2008) information. In addition, autobiographical memory is often fragmented (i.e., events are de-contextualized), especially, but not only, for the traumatic events (Bremner, Krystal, Southwick, & Charney, 1995; but see, Rubin, Feldman, & Beckham, 2004). Together, this pattern suggests PTSD is related to deficits in encoding processes, especially memory binding, and, perhaps, with difficulty in monitoring specific information during remembering.

We know of no published PTSD fMRI studies to date that have used source identification tasks, or other kinds of subjective or objective measures of source memory (e.g., Remember/Know; MCQ ratings). However, relevant information can be gleaned from studies in which PTSD patients (and control groups) were scanned while encoding and remembering neutral paired-associates. For example, Geuze, Vermetten, Ruf, de Kloet, and Westenberg (2008) scanned male veterans with trauma experience, and who did or did not have PTSD, as they encoded word pairs and then performed a cued-recall task. Behaviorally, the PTSD group did only marginally worse than the control group, consistent with the finding that many of the standard “memory related” brain regions were active in both the PTSD and non-PTSD group (e.g., dorsolateral PFC, anterior cingulate cortex, parietal lobe, parahippocampal gyrus). Nevertheless, during encoding, the PTSD group exhibited less activity than did the control group in several PFC regions including bilateral inferior and left middle and superior frontal gyri (as well as left posterior middle temporal gyrus, and left precuneus) but they exhibited more activity in several temporal regions, including bilateral superior temporal gyrus, right middle and left inferior temporal gyri, as well as right parahippocampal gyrus. Interestingly, correlations showed that activity in the temporal regions was not related to memory performance. Thus, although PTSD patients appeared to recruit temporal areas to a greater extent than controls, perhaps to compensate for less PFC activity⁶, the functional

⁶This apparent anterior-to-posterior shift stands in contrast to the posterior-to-anterior shift associated with aging noted above, perhaps arguing against a strong version of the notion that PTSD is akin to accelerated aging with respect to functional brain changes (Bremner & Narayan, 1998).

role of this activity is unclear. During remembering, the PTSD group showed less activity than did the control group in both PFC (right inferior frontal and precentral gyri) and several temporal regions (left hippocampus/parahippocampal gyrus, middle and superior temporal gyri). Another study compared PTSD patients with mixed trauma history to non-trauma control participants on a face-profession paired-associate task and showed generally similar results (Werner et al., 2009). Although more work is needed, such a pattern suggests a deficit in the functional relationship between the PFC and temporal regions during relational encoding in PTSD. Presumably this dysfunction should lead to less information, or less diagnostic or specific information, being encoded, and/or weaker relationships between items and their context. Although there was only a marginal deficit in behavioral performance in the Geuze et al. study, and no difference in the Werner et al. study, deficits in the functional relationship between brain regions should make it more difficult to later, perhaps after a longer delay (Qin et al., 2003), remember source information.

Whether or not there are source memory deficits for emotional information, in particular, is also of interest. PTSD is associated with increased attention to negative stimuli (e.g., Bleich, Attias, & Furman, 1996). Although the picture regarding neural mechanisms associated with this attentional bias is not entirely clear, differences in several brain areas have been implicated including medial prefrontal cortex, orbitofrontal cortex, parietal regions, anterior cingulate cortex, and amygdala (Liberzon et al., 1999; Rauch et al., 2000; Zubieta et al., 1999). For example, neuroimaging studies that expose PTSD patients and controls to various kinds of emotional stimuli generally show that PTSD patients have a much larger amygdala response to trauma related stimuli and reduced activity in the medial frontal cortex, compared to control participants (see Bremner, 2007 for a review). Within the range of “normal” reactions to emotional information that were discussed above in the section on emotion, increased amygdala activity modulates the hippocampus and is associated with better memory. The hyper amygdala reactions of PTSD patients, on the other hand, appear to be on the downside of the Yerkes-Dodson arousal curve: In some early PET studies, PTSD patients showed less hippocampal activity (even after controlling for reduced volume) than did controls during encoding of emotional paragraphs and also during the recall of emotional word pairs (Bremner et al., 2003). Together, such findings suggest that memory binding for emotional information may be especially affected in PTSD, a possibility under current investigation in our lab.

Also relevant are studies looking at memory for neutral information that had been previously encoded in emotional vs neutral contexts. One event-related fMRI study scanned participants with PTSD (but no depression), depression (but no PTSD), and a trauma matched group without psychopathology as they tried to remember neutral information that had been previously encoded with either emotional or neutral picture backgrounds (Whalley, Rugg, Smith, Dolan, & Brewin, 2008). There were no differences in old-new recognition performance for the items encoded in emotional vs neutral contexts in any group, but both the PTSD and depressed group showed poorer memory overall than controls. Many of the standard memory areas were commonly active during test in all groups (e.g., several regions of left PFC, precuneus). However, relative to the other groups, PTSD participants showed increased activity for old items (regardless of encoding context) in left dorsal amygdala/ventral striatum and right middle occipital cortex and decreased activity in right dorsolateral PFC (BA 46). Relative to the other groups, the PTSD group also showed increased activity for correctly identified items encoded in emotional, compared to neutral contexts, in several areas associated with successful episodic memory including insula, hippocampus, precuneus/posterior cingulate, right occipital cortex. One interpretation of this pattern is that the PTSD group became more aroused during recognition because of incidental activation of some of the emotional context information (as indicated by increased amygdala and occipital cortex), and that this emotional response was taken (appropriately) as evidence that

the item had been seen before. Unfortunately, the authors did not report on the depressed group relative to the other groups: Depression also is associated with episodic memory deficits but we know little about the neural underpinnings, as discussed next.

Depression—People with depression tend to have vague, or over-general, memories compared to non-depressed individuals and they perform more poorly than controls on source memory tasks (e.g., Degl'Innocenti, & Backman, 1999; see, e.g., Hertel, 1992, 2000; Williams et al., 2007 for reviews). Major depression is associated with a memory bias for negative information, and this bias may be related to sustained amygdala activity on the part of depressed individuals related to initial processing of emotional information (Siegle, Steinhauer, Thase, Stenger, & Carter, 2002; Siegle, Thompson, Carter, Steinhauer, & Thase, 2007). On interleaved trials, Siegel et al. (2002) had depressed and non-depressed individuals indicate the valence of some positive and negative words and rate the personal relevance of others. These tasks alternated with trials of a non-emotional task (Sternberg number memory task). Compared to non-depressed individuals, depressed participants showed greater sustained amygdala response for negative but not positive items. The timecourse of the activity suggested that it was sustained for up to 30 seconds after the brief exposure, even though participants were given the interspersed non-emotional task as distraction. Depressed individuals showed less activity than controls, on the other hand, in left dorsolateral PFC (BA 46) related to processing negative information. Interestingly, depressed individuals also showed increased activity for negative items in posterior cingulate and inferior parietal lobe (BA 40), two areas associated with self-referential thinking, as well as episodic and autobiographical remembering. The authors suggested that depressed individuals engage in prolonged self-relevant processing of negative information, as evidenced by a positive correlation between amygdala activity during negative information processing and self-reported rumination in this study.

Studies with non-clinical participants have demonstrated activity in both PFC and amygdala related to emotion regulation (e.g., Goldin, McRae, Ramel, & Gross, 2008) and they provide evidence suggesting top-down modulation of amygdala activity by PFC (e.g., Cunningham, Johnson, Raye, Gatenby, Gore, & Banaji, 2004). Using a blocked design, Siegle et al. (2007) had depressed and non-depressed participants do a non-emotional cognitive task (digit sorting) followed by an emotional task (rating personal relevance of negative, positive, and neutral words) inside the scanner. They replicated the earlier finding (Siegle et al., 2002) of sustained amygdala activity in depressed individuals during the emotional task and also showed that depressed individuals had reduced activity in dorsolateral PFC (primarily left; middle frontal gyrus; BA9, 46) during both tasks. Furthermore, for negative trials, functional connectivity between the rostral cingulate cortex and the amygdala and dorsolateral PFC was somewhat attenuated in the depressed participants relative to controls, consistent with disruption in a control circuit that may be involved in emotion regulation. Certainly, increased processing given to negative information because of a negativity bias would be expected to lead to better item memory among depressed individuals for negative than neutral or positive information. A recent fMRI study (Hamilton & Gotlib, 2008) confirmed such a bias for negative, compared to positive, pictures and moreover, tied it to increased activity in amygdala and greater functional connectivity between the amygdala and hippocampus in depressed individuals.

We know of no fMRI studies that used source identification, relational memory, or other objective or subjective measures of the qualitative characteristics of remembering with clinically depressed individuals. However, given the discussion above about the impact of arousal on item vs source memory (e.g., Mather, 2007), enhanced processing of negative information on the part of depressed individuals might be expected to result in poorer memory for the context of encounter (i.e., source memory) of negative information

associated with depression, relative to controls. A hint of this possibility can be found in the binding study of Mather et al. (2006, Experiment 1, discussed above), in which a random sample of undergraduates showed a negative correlation between scores on a depression measure and accuracy of source memory for arousing picture-location pairings. Whether this pattern obtains in a group of clinically depressed students, and the neural underpinnings, are currently under investigation in our lab (Mitchell, Nolen-Hoeksema, & Johnson, 2009).

In sum, although the findings discussed in this section are informative, more systematic work comparing various patient groups using both emotional and neutral stimuli in source memory paradigms would go a long way toward clarifying dysfunctions of PFC, amygdala, hippocampus, and other regions of the emotion and memory networks that may play a role in the source memory deficits associated with these disorders. In addition, co-morbidity across disorders and heterogeneity within will need to be considered to develop a fuller understanding, as such differences could be related to variation in the precise constellation of brain mechanisms involved. For example, in a behavioral study, Thoma, Zoppelt, Wiebel, and Daum (2006) found that recollection, but not familiarity, appeared to be reduced in a group of schizophrenic patients with greater negative symptoms compared to both controls and schizophrenic patients with less negative symptoms. Based on a constellation of evidence from lesion, metabolic, and neuroimaging studies, they speculated that such a pattern may be related to disruption of connectivity between thalamic and frontal areas as this would be expected to affect both negative symptomology and episodic memory (see Thoma et al., 2006 for their evidence). But, this hypothesis remains to be directly tested. As another example, a recent meta-analysis of behavioral studies looking at source memory in schizophrenia showed that effects were larger for paired-associate tasks than for source identification tasks, but that there were no differences in the size of the effects across various types of source identification tasks (e.g., external-external vs internal-external) (Achim & Weiss, 2008). However this analysis did not consider whether or not the schizophrenics hallucinated, citing too few studies of each type and high variability within type as limiting factors in conducting such a comparison. But, given the evidence discussed above suggesting that difficulty binding voice and content information (related to deficits in STG) is related to degree of hallucination, and that there are deficits in medial anterior PFC during reality monitoring tasks in schizophrenia, differentiating in studies between those who hallucinate and those who do not is necessary to develop a fuller understanding of the cognitive and neural underpinning of the disorder (see, e.g., Brunelin et al., 2006 for behavioral evidence). Challenges for the future also include identifying the pattern of specific component processes, and related brain areas, disrupted in these disorders. Such specificity may help in the development of more targeted treatment options, offer biomarkers for testing the efficacy of such treatments, and advance more generally our understanding of processes contributing to source memory at encoding and during remembering, as well as their disruption in these disorders.

CURRENT STATUS AND FUTURE DIRECTIONS

In their 1993 paper, Johnson, Hashtroudi and Lindsay proposed the SMF for organizing existing empirical findings in the memory domain across a broad range of approaches and paradigms (see also Johnson & Raye, 2000; Lindsay, 2008; Mitchell & Johnson, 2000). In considering what distinguishes the SMF as a general research strategy, primary emphasis was placed on: (a) identifying the specific qualitative characteristics that compose episodic memories of different types; (b) specifying the perceptual and reflective component processes involved in encoding those characteristics, binding them together to form coherent event representations, reviving them in response to both internal and external cues, evaluating them in the context of complex agendas according to flexible criteria, and in making attributional decisions as to their origins; and, (c) understanding how these features

and processes combine under different circumstances to produce the range of phenomenal experiences associated with both true and false memories.

Since 1993, neuroimaging clearly has enriched our understanding of the brain mechanisms supporting source memory. In particular, fMRI studies are beginning to identify brain regions associated with the encoding and remembering of specific types of information (semantic, perceptual, spatial, temporal, emotional, etc.) that give rise to the phenomenal experience of remembering, and to characterize neural activity associated with variations in the subjective qualities (e.g., vividness) of these characteristics. Likewise, studies are beginning to identify the brain areas, and networks of brain regions, associated with specific component cognitive processes (e.g., initiating, refreshing, selecting, reviving, evaluating) and how they combine under different agendas to remember (Dobbins & Han, 2006; Johnson & Hirst, 1993; Ranganath & Blumenfeld, 2005; see also, e.g., Hassabis & Maguire, 2007; Jonides et al., 2008; Uncapher & Rugg, 2008). In addition, the possibility that such component processes are not unique to source memory, but have more general functions, is of growing interest (Dobbins & Han, 2006; Fleck et al., 2006; Hayama et al., 2008; Johnson et al., 2005). Consistent with the SMF, studies are finding substantial overlap, yet still some differences, in neural activity associated with veridical and false memories. Together, all of these findings are helping to elucidate the changes in source memory accompanying development (e.g., normal aging) and pathologies (e.g., schizophrenia, PTSD, depression). Increasing use of cross-method approaches should advance all of these efforts, for example, using ERP with fMRI to isolate the temporal signature of various component processes (e.g., revival vs evaluation of information), or using TMS to explore the causal role of brain areas identified in fMRI studies.

fMRI findings also are prompting investigators to articulate theoretical assumptions (whether explicitly or tacitly held) with greater specificity. For example, as discussed above, making sense of the patterns of activations in subregions of PFC has pushed investigators beyond reference to broad concepts like encoding, retrieval, or monitoring and toward isolating component processes involved in these aspects of remembering. A current hotbed of theoretical debate centers on the role of various subregions of MTL in different aspects of remembering. Consistent with the SMF approach, findings are leading some investigators to focus on the specific features that comprise remembering rather than on more general concepts such as recollection and familiarity (e.g., Davachi, 2006; Diana et al., 2007; Mayes et al., 2007; Squire et al., 2007). Interestingly, the general concept of *memory strength* remains popular (e.g., Squire et al., 2007; Wais, 2008; Wixted, 2007). Some formal models have attempted to reconcile the idea of strength with the SMF idea of undifferentiated vs differentiated features, for example, by suggesting memories are composed of both *global* (i.e., undifferentiated) and *specific* (i.e., differentiated) strength (e.g., Rotello et al., 2004) or by allowing multidimensional memories to be expressed within unidimensional space (e.g., Banks, 2000). Each of these ideas allows remembering to vary on a continuum in a signal-detection fashion. Although such models may accommodate behavioral data such as that produced via ROC curves, precisely how to use them to interpret patterns of brain activity from specific regions remains a puzzle whose solution appears currently to require debatable assumptions (see, e.g., Kirwin et al., 2008 and discussion above in MTL section).

Our position is that continued focus on neural activity associated with specific features and component processes is likely to result in the most gain in our understanding of the phenomenal experience of remembering. Nevertheless, we, like most investigators, would agree that familiarity and recollection are useful summary terms that point to important differences in phenomenal experience. We would argue, however, that given what we already know about how the brain works, the usefulness of these concepts for interpreting and organizing fMRI findings will depend on whether investigators can map them cleanly

onto specific processes (i.e., computations or sets of computations carried out by specific brain areas or orchestrated by networks of areas) that act upon well-defined features or groups of features (e.g., unitized representations). In particular, for the concepts of familiarity and recollection (or others, such as strength) to carry interpretive weight with respect to fMRI findings, a key theoretical and empirical question to be addressed is: What is the relationship between the type of information that yields the experience of familiarity and the type of information that yields the experience of recollection? From the SMF point of view, it is unlikely that familiarity and recollection are based on completely different types of representations but rather they draw upon the same core types of information in different ways under different circumstances (see also, e.g., Banks, 2000 for empirical evidence).

Perhaps the case for recollection is most clear. A sense of recollection arises when fairly well-differentiated features become available which satisfy task goals that require specific information. The “strength” of a sense of recollection (and my confidence in the memory) may then depend on the number and vividness of features that cohere in ways that seem episodic (e.g., bound together, internally consistent, plausible, different from other configurations of features).

Familiarity, though, seems more difficult to characterize. Assuming that no one class of feature (e.g., semantics) is uniquely associated with familiarity but that familiarity may arise from activation of any feature(s) (semantic, perceptual, emotional, etc.), there appear to be at least two “senses” in which we experience familiarity. In one sense, it is as if one or more features are incompletely activated, as if not all processing necessary for a coherent, stable percept or thought has been completed or successful. Familiarity of this type might be experienced when one is given degraded stimuli, a speeded recognition test, or is tested under distraction. In this case, the active information does not have enough definition to constitute specific features or no specific feature “stands out;” the strength of a familiarity response (e.g., confidence) may depend on how many different kinds or classes of information are partially active (or whether only non-lexical information is active, e.g., Johnson & Hirst, 1993). In a second sense, we experience something as *only familiar* if a feature becomes active in isolation and does not include some additional feature(s) that help identify the source of the information. Poor binding during encoding, for example, might lead to a later feeling of familiarity of this type because a feature (e.g., color), no matter how strongly experienced at test, is not able to co-activate features (e.g., semantic concept, location, format) that accompanied it in the original experience. In this case, one does not have enough source-specifying features to differentiate one event from another; the strength of familiarity (e.g., confidence) depends on the properties (e.g., vividness, fluency) of the experienced feature. (Of course, a feeling of familiarity could arise from both of these sources, that is, a single vivid feature accompanied by other incompletely activated features still might not afford a feeling of recollection.)

Thus, in the first sense one feels that *something* is familiar but it is not clear exactly what, whereas in the second sense something *in particular* is familiar (that *face*, that *idea*, that *color*). Although in both cases, the experience is relatively undifferentiated (compared to recollection), either may have functional consequences. The first kind of familiarity provides a rapid signal that can help guide orienting to either the familiar or the novel, depending on what is most important (e.g., finding the well-known person you are picking up at an airport full of strangers vs. finding the new faculty member at a party full of familiar people). The second provides the cue to reflectively attend to other information that may become active (e.g., to shift from perceptually attending to the familiar feature to reflectively attending to activated information that may specify when or where the face, idea, or color were

experienced before) or to self-cuing (i.e., retrieving) or to initiating search of external sources (notes, consulting others).

Of course, even with this level of specificity, interpreting brain activity with respect to familiarity and recollection could be problematic. As noted above, in laboratory experiments, semantic features are often viewed as central (e.g., the “item”) and other features such as format, location, or speaker, are considered as source or contextual features. Given that content and context are arbitrary, conclusions about brain regions associated with familiarity and recollection need to avoid the risk of confounding type of feature with type of subjective experience (see, e.g., Diana et al., 2007; Squire et al., 2007 for similar points). Equating the “strength” of familiarity and recollection by looking at only the extremes on a rating scale (e.g., confidence), for example, may not clarify the neural correlates of these subjective experiences (see also Skinner & Fernandes, 2007). By definition, the experience of familiarity (no matter how strong) is missing something that the experience of recollection has (no matter how weak)---specificity, vividness, multiple features. In addition, recollection no matter how vivid, and familiarity no matter how strong, are not necessarily veridical.

In conclusion, there is preliminary evidence that sub-regions within MTL, PFC, and posterior cortex are involved in representing or processing specific source features, whereas other sub-regions are involved in general processes that act across features. In addition, there is growing consensus that component processes are shared across different cognitive tasks (e.g., attention, long and short term memory, decision making). To further advance a neuroscience of source memory (see Table 2), we need: (a) a better mapping of the specific brain regions associated with memory for different features and particular combinations of features that are well-defined (and specification of conditions under which feature combinations act as a “unit”); (b) systematic studies of how variations in activity in those regions is related to subjective reports of strength of familiarity and vividness of recollection; (c) investigation of the conditions (e.g., task set, feature set, context) that modulate the relations identified in (a) and (b). This approach should not only help us further specify representational and binding regions (and networks), but also clarify whether familiarity arises from activity in the same representational regions that are involved in recollection and whether there is some specific region that cumulates activity (including sub-recollection activity) from representational regions into a familiarity signal. It should also help further distinguish the brain regions (networks) where activity is related to the representation, or processing, of different types of information from regions where activity is related to relatively general cognitive functions (e.g., refreshing, selecting, evaluating).

A continued two-way interaction between cognitive theory, as illustrated by the SMF, and evidence from systematic cognitive fMRI studies, including those exploring memory deficits associated with aging, focal brain damage, and various clinical populations, should help further clarify our conceptualization of cognitive processes (e.g., feature binding, retrieval, monitoring), prior knowledge (e.g., categories, scripts, schemas), and specific features (e.g., semantic, perceptual, spatial, emotional information), and of how they combine to create true and false memories.

Acknowledgments

Preparation of this review was supported by NIA grants AG09253 and AG15793. We are grateful to Carol Raye and Mara Mather for many thoughtful discussions of the issues covered here and comments on an earlier draft. We thank Kathleen Muller for help organizing references.

References

- Achim AM, Weiss AP. No evidence for a differential deficit of reality monitoring in schizophrenia: A meta-analysis of the associative memory literature. *Cognitive Neuropsychiatry* 2008;13:369–384. [PubMed: 18781492]
- Ackil JK, Zaragoza MS. Memorial consequences of forced confabulation: Age differences in susceptibility to false memories. *Developmental Psychology* 1998;34:1358–1372. [PubMed: 9823517]
- Addis DR, Moscovitch M, Crawley AP, McAndrews MP. Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus* 2004;14:752–762. [PubMed: 15318333]
- Aggleton JP, Brown MW. Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences* 1999;22:425–489. [PubMed: 11301518]
- Aleman A, Hijman R, De Haan EHF, Kahn RS. Memory impairment in schizophrenia: a meta-analysis. *American Journal of Psychiatry* 1999;156:1358–1366. [PubMed: 10484945]
- Allen P, Larøi F, McGuire PK, Aleman A. The hallucinating brain: A review of structural and functional neuroimaging studies of hallucinations. *Neuroscience and Biobehavioral Reviews* 2008;32:175–191. [PubMed: 17884165]
- Anastasi JS, Rhodes MG, Burns MC. Distinguishing between memory illusions and actual memories using phenomenological measurements and explicit warnings. *The American Journal of Psychology* 2000;113:1–26. [PubMed: 10742841]
- Anderson ND, Ebert PL, Jennings JM, Grady CL, Cabeza R, Graham SJ. Recollection- and familiarity-based memory in healthy aging and amnesic mild cognitive impairment. *Neuropsychology* 2008;22:177–187. [PubMed: 18331160]
- Anderson ND, Iidaka T, Cabeza R, Kapur S, McIntosh AR, Craik FIM. The effects of divided attention on encoding- and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience* 2000;12:775–792. [PubMed: 11054920]
- Awipi T, Davachi L. Content-specific source encoding in human medial temporal lobe. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:769–779.
- Baddeley A. The episodic buffer: a new component of working memory? *Trends in Cognitive Sciences* 2000;4:417–423. [PubMed: 11058819]
- Badre D, Poldrack RA, Paré-Blagoev EJ, Insler RZ, Wagner AD. Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron* 2005;47:907–918. [PubMed: 16157284]
- Banks WP. Recognition and source memory as multivariate decision processes. *Psychological Science* 2000;11:267–273. [PubMed: 11273383]
- Bar M, Aminoff E, Schacter DL. Scenes unseen: The parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *The Journal of Neuroscience* 2008;28:8539–8544. [PubMed: 18716212]
- Bartlett, FC. *Remembering: A study in experimental and social psychology*. Cambridge, England: Cambridge University Press; 1932.
- Batchelder WH, Riefer DM. Multinomial processing models of source monitoring. *Psychological Review* 1990;97:548–564.
- Bayen UJ, Murnane K, Erdfelder E. Source discrimination, item detection and multinomial models of source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1996;22:197–215.
- Benjamin AS, Craik FIM. Parallel effects of aging and time pressure on memory for source: Evidence from the spacing effect. *Memory & Cognition* 2001;29:691–697.
- Berryhill ME, Phuong L, Picasso L, Cabeza R, Olson IR. Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience* 2007;27:14415–14423. [PubMed: 18160649]
- Bird CM, Burgess N. The hippocampus and memory: insights from spatial processing. *Nature Reviews Neuroscience* 2008;9:182–194.

- Bleich A, Attias J, Furman V. Effect of repeated visual traumatic stimuli on the event related P3 brain stress disorder potential in post-traumatic stress disorder. *International Journal Neuroscience* 1996;85:45–55.
- Bloise, S. Yale University; 2008. Aging and the subjective experience of remembering. Unpublished doctoral dissertation
- Blumenfeld RS, Ranganath C. Prefrontal cortex and long-term memory encoding: An integrative review of findings from neuropsychology and neuroimaging. *The Neuroscientist* 2007;13:280–291. [PubMed: 17519370]
- Botvinick MM, Cohen JD, Carter CS. Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences* 2004;8:539–546. [PubMed: 15556023]
- Botzung A, Denkova E, Ciuciu P, Scheiber C, Manning L. The neural bases of the constructive nature of autobiographical memories studied with a self-paced fMRI design. *Memory* 2008;16:351–363. [PubMed: 18432480]
- Boyer PA, Phillips JL, Rousseau FL, Ilivitsky S. Hippocampal abnormalities and memory deficits: New evidence of a strong pathophysiological link in schizophrenia. *Brain Research Reviews* 2007;54:92–112. [PubMed: 17306884]
- Bransford, JD.; Johnson, MK. Considerations of some problems of comprehension. In: Chase, W., editor. *Visual information processing*. New York: Academic Press; 1973. p. 383-438.
- Brasted PJ, Bussey TJ, Murray EA, Wise SP. Role of the hippocampal system in associative learning beyond the spatial domain. *Brain* 2003;126:1202–1223. [PubMed: 12690059]
- Braver TS, Barch DM, Kelley WM, Buckner RL, Cohen NJ, Miezin, et al. Direct comparison of prefrontal cortex regions engaged by working and long-term memory tasks. *NeuroImage* 2001;14:48–59. [PubMed: 11525336]
- Bremner JD. Neuroimaging in posttraumatic stress disorder and other stress-related disorders. *Neuroimaging Clinics of North America* 2007;17:523–538. [PubMed: 17983968]
- Bremner JD, Krystal JH, Southwick SM, Charney DS. Functional neuroanatomical correlates of the effects of stress on memory. *Journal of Traumatic Stress* 1995;8:527–553. [PubMed: 8564272]
- Bremner JD, Narayan M. The effects of stress on memory and the hippocampus throughout the life cycle: Implications for childhood development and aging. *Development and Psychopathology* 1998;10:871–885. [PubMed: 9886231]
- Bremner JD, Vythilingam M, Vermetten E, Southwick SM, McGlashan T, Nazeer A, et al. MRI and PET study of deficits in hippocampal structure and function in women with childhood sexual abuse and posttraumatic stress disorder. *American Journal of Psychiatry* 2003;160:924–932. [PubMed: 12727697]
- Brewin CR, Kleiner JS, Vasterling JJ, Field AP. Memory for emotionally neutral information in posttraumatic stress disorder: A meta-analytic investigation. *Journal of Abnormal Psychology* 2007;116:448–463. [PubMed: 17696700]
- Brunelin J, Combris M, Poulet E, Kallel L, D'Amato T, Dalery J, Saoud M. Source monitoring deficits in hallucinating compared to non-hallucinating patients with schizophrenia. *European Psychiatry* 2006;21:259–261. [PubMed: 16545546]
- Buckner RL, Carroll DC. Self-projection and the brain. *Trends in Cognitive Sciences* 2007;11:49–57. [PubMed: 17188554]
- Buckner RL, Wheeler ME. The cognitive neuroscience of remembering. *Nature Reviews Neuroscience* 2001;2:624–634.
- Budson AE, Sullivan AL, Daffner KR, Schacter DL. Semantic versus phonological false recognition in aging and Alzheimer's disease. *Brain & Cognition* 2003;51:251–261. [PubMed: 12727179]
- Bunce D. Cognitive support at encoding attenuates age differences in recollective experience among adults of lower frontal lobe function. *Neuropsychology* 2003;17:353–361. [PubMed: 12959501]
- Bunsey M, Eichenbaum H. Conservation of hippocampal memory function in rats and humans. *Nature* 1996;379:255–257. [PubMed: 8538790]
- Burgess N, Maguire EA, O'Keefe J. The human hippocampus and spatial and episodic memory. *Neuron* 2002;35:625–641. [PubMed: 12194864]
- Burgess PW, Shallice T. Confabulation and the control of recollection. *Memory* 1996;4:359–411. [PubMed: 8817460]

- Burglen F, Marczewski P, Mitchell KJ, van der Linden M, Johnson MK, Danion J-M, Salamé P. Impaired performance in a working memory binding task in patients with schizophrenia. *Psychiatry Research* 2004;125:247–255. [PubMed: 15051185]
- Burianova H, Grady CL. Common and unique neural activations in autobiographical, episodic, and semantic retrieval. *Journal of Cognitive Neuroscience* 2007;19:1520–1534. [PubMed: 17714013]
- Cabeza R. Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging* 2002;17:85–100. [PubMed: 11931290]
- Cabeza R. Prefrontal and medial temporal lobe contributions to relational memory in young and older adults. In: Zimmer, D.; Mecklinger, A.; Lindenberger, U., editors. *Binding in human memory: A neurocognitive approach*. New York: Oxford University Press; 2006. p. 595–626.
- Cabeza R. Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia* 2008;46:1813–1827. [PubMed: 18439631]
- Cabeza R, Anderson ND, Houle S, Mangels JA, Nyberg L. Age-related differences in neural activity during item and temporal-order memory retrieval: A positron emission tomography study. *Journal of Cognitive Neuroscience* 2000;12:197–206. [PubMed: 10769316]
- Cabeza R, Anderson ND, Locantore JK, McIntosh AR. Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage* 2002;17:1394–1402. [PubMed: 12414279]
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M. The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience* 2008;9:613–625.
- Cabeza R, Locantore JK, Anderson ND. Lateralization of prefrontal activity during episodic memory retrieval: Evidence for the production-monitoring hypothesis. *Journal of Cognitive Neuroscience* 2003;15:249–259. [PubMed: 12676062]
- Cabeza R, Mangels J, Nyberg L, Habib R, Houle S, McIntosh AR, Tulving E. Brain regions differentially involved in remembering what and when: a PET study. *Neuron* 1997;19:863–870. [PubMed: 9354332]
- Cabeza R, Prince SE, Daselaar SM, Greenberg DL, Budde M, Dolcos F, LaBar KS, Rubin DC. Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience* 2004;16:1583–1594. [PubMed: 15622612]
- Cabeza R, Rao SM, Wagner AD, Mayer AR, Schacter DL. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proceedings of the National Academy of Sciences* 2001;98:4805–4810.
- Cabeza R, St Jacques P. Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences* 2007;11:219–227. [PubMed: 17382578]
- Cahill L, Haier RJ, Fallon J, Alkire MT, Tang C, Keator D, et al. Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings for the National Academy of Sciences of the United States of America* 1996;93:8016–8021.
- Canli T, Zhao Z, Brewer J, Gabrieli JDE, Cahill L. Event-related activation in the human amygdala associates with later memory for individual emotional experience. *The Journal of Neuroscience* 2000;20:1–5. [PubMed: 10627575]
- Canli T, Zhao Z, Desmond JE, Glover G, Gabrieli JDE. fMRI identifies a network of structures correlated with retention of positive and negative emotional memory. *Psychobiology* 1999;27:441–452.
- Cansino S, Maquet P, Dolan RJ, Rugg MD. Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex* 2002;12:1049–1056.
- Cavanna AE, Trimble MR. The precuneus: A review of its functional anatomy and behavioural correlates. *Brain* 2006;129:564–583. [PubMed: 16399806]
- Chalfonte BL, Johnson MK. Feature memory and binding in young and older adults. *Memory & Cognition* 1996;24:403–416.
- Chee MWL, Goh JOS, Venkatraman V, Tan JC, Gutchess A, Sutton B, Hebrank A, Leshikar E, Park D. Age-related changes in object processing and contextual binding revealed using fMRI adaptation. *Journal of Cognitive Neuroscience* 2006;18:495–507. [PubMed: 16768356]
- Christianson, S-Å., editor. *The handbook of emotion and memory: Research and theory*. Hillsdale, NJ: Lawrence Erlbaum Associates; 1992.

- Ciaramelli E, Grady CL, Moscovitch M. Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 2008;46:1828–1851. [PubMed: 18471837]
- Ciaramelli, E.; Spaniol, J. Ventromedial prefrontal damage and confabulation impair source but not associative memory. 2008. Manuscript under review.
- Cohen, NJ.; Eichenbaum, H. *Memory, amnesia, and the hippocampal system*. Cambridge, MA: MIT Press; 1993.
- Comblain C, D'Argembeau A, Van der Linden M. Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research* 2005;31:173–189. [PubMed: 15981795]
- Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience* 2002;3:201–215.
- Craik FIM, Morris LW, Morris RG, Loewen ER. Relations between source amnesia and frontal lobe functioning in older adults. *Psychology & Aging* 1990;5:148–151. [PubMed: 2317296]
- Cunningham WA, Johnson MK, Raye CL, Gatenby JC, Gore JC, Banaji MR. Separable neural components in the processing of black and white faces. *Psychological Science* 2004;15:806–813. [PubMed: 15563325]
- Danion J-M, Huron C, Vidailhet P, Berna F. Functional mechanisms of episodic memory impairment in schizophrenia. *The Canadian Journal of Psychiatry* 2007;52:693–701.
- Danion J-M, Rizzo L, Bruant A. Functional mechanisms underlying impaired recognition memory and conscious awareness in patients with schizophrenia. *Archives of General Psychiatry* 1999;56:639–644. [PubMed: 10401510]
- Daselaar, S.; Cabeza, R. Episodic memory decline and healthy aging. In: Byrne, J.; Eichenbaum, H., editors. *Memory systems. Learning and memory: A comprehensive reference*. Vol. Vol. 3. Oxford: Elsevier; 2008. p. 577-599.(Series Ed.) (Vol. Ed.)
- Daselaar SM, Fleck MS, Dobbins IG, Madden DJ, Cabeza R. Effects of healthy aging on hippocampal and rhinal memory functions: An event-related fMRI study. *Cerebral Cortex* 2006;16:1771–1782. [PubMed: 16421332]
- Daselaar SM, Rice HJ, Greenberg DL, Cabeza R, LaBar KS, Rubin DC. The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex* 2008;18:217–229. [PubMed: 17548799]
- Davachi L. Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology* 2006;16:693–700. [PubMed: 17097284]
- Davachi L, Dobbins IG. Declarative memory. *Current Directions in Psychological Science* 2008;17:112–118. [PubMed: 20011622]
- Davis SW, Dennis NA, Daselaar SM, Fleck MS, Cabeza R. Que PASA? The Posterior-Anterior Shift in Aging. *Cerebral Cortex* 2008;18:1201–1209. [PubMed: 17925295]
- Deese J. On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology* 1959;58:17–22. [PubMed: 13664879]
- Degl'Innocenti A, Backman L. Source memory in major depression. *Journal of Affective Disorders* 1999;54:205–209. [PubMed: 10403166]
- Dennis, NA.; Cabeza, R. Neuroimaging of healthy cognitive aging. In: Craik, FIM.; Salthouse, TA., editors. *Handbook of aging and cognition: Third edition*. Mahwah, NJ: Erlbaum; 2008. p. 1-54.
- Dennis NA, Hayes SM, Prince SE, Madden DJ, Huettel SA, Cabeza R. Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:791–808.
- Dennis NA, Kim H, Cabeza R. Effects of aging on true and false memory formation: An fMRI study. *Neuropsychologia* 2007;45:3157–3166. [PubMed: 17716696]
- Dennis NA, Kim H, Cabeza R. Age-related differences in brain activity during true and false memory retrieval. *Journal of Cognitive Neuroscience* 2008;20:1390–1402. [PubMed: 18303982]
- Dewhurst SA, Holmes SJ, Brandt KR, Dean GM. Measuring the speed of the conscious components of recognition memory: Remembering is faster than knowing. *Consciousness and Cognition* 2006;15:147–162. [PubMed: 16019226]

- Diana RA, Yonelinas AP, Ranganath C. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends in Cognitive Sciences* 2007;11:379–386. [PubMed: 17707683]
- Diana RA, Yonelinas AP, Ranganath C. The effects of unitization on familiarity-based source memory: Testing a behavioral prediction derived from neuroimaging data. *Journal of Experimental Psychology: Learning, Memory and Cognition* 2008;34:730–740.
- Ditman T, Kuperberg GR. A source-monitoring account of auditory verbal hallucinations in patients with schizophrenia. *Harvard Review of Psychiatry* 2005;13:280–299. [PubMed: 16251167]
- Dobbins IG, Foley H, Schacter DL, Wagner AD. Executive control during episodic retrieval: Multiple prefrontal processes subservise source memory. *Neuron* 2002;35:989–996. [PubMed: 12372291]
- Dobbins IG, Han S. Cue-versus probe-dependent prefrontal cortex activity during contextual remembering. *Journal of Cognitive Neuroscience* 2006;18:1439–1452. [PubMed: 16989546]
- Dobbins IG, Rice HJ, Wagner AD, Schacter DL. Memory orientation and success: separable neurocognitive components underlying episodic recognition. *Neuropsychologia* 2003;41:318–333. [PubMed: 12457757]
- Dobbins IG, Wagner AD. Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex* 2005;15:1768–1778. [PubMed: 15728740]
- Dodson CS, Holland PW, Shimamura AP. On the recollection of specific-and partial-source information. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1998;24:1121–1136.
- Dodson CS, Schacter DL. "If I had said it I would have remembered it": Reducing false memories with a distinctiveness heuristic. *Psychonomic Bulletin & Review* 2001;8:155–161. [PubMed: 11340861]
- Dolan RJ, Lane R, Chua P, Fletcher P. Dissociable temporal lobe activations during emotional episodic memory retrieval. *NeuroImage* 2000;11:203–209. [PubMed: 10694462]
- Dolcos F, LaBar KS, Cabeza R. Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron* 2004;42:855–863. [PubMed: 15182723]
- Dolcos F, LaBar KS, Cabeza R. Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proceedings for the National Academy of Sciences of the United States of America* 2005;102:2626–2631.
- Dolcos, F.; LaBar, KS.; Cabeza, R. The memory enhancing effect of emotion: Functional neuroimaging evidence. In: Uttl, B.; Ohta, H.; Seigenthaler, AL., editors. *Memory and emotion: Interdisciplinary perspectives*. Malden, MA: Blackwell Publishing; 2006. p. 107-133.
- Dougal S, Phelps EA, Davachi L. The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cognitive, Affective, & Behavioral Neuroscience* 2007;7:233–242.
- Driscoll I, Hamilton DA, Petropoulos H, Yeo RA, Brooks WM, Baumgartner RN, Sutherland RJ. The aging hippocampus: Cognitive, biochemical and structural findings. *Cerebral Cortex* 2003;13:1344–1351. [PubMed: 14615299]
- Duarte A, Henson RN, Graham KS. The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex* 2008;18:2169–2180. [PubMed: 18165281]
- Duarte A, Ranganath C, Knight RT. Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *Journal of Neuroscience* 2005;25:8333–8337. [PubMed: 16148241]
- Dudukovic NM, Wagner AD. Goal-dependent modulation of declarative memory: Neural correlates of temporal recency decisions and novelty detection. *Neuropsychologia* 2007;45:2608–2620. [PubMed: 17499318]
- Durso FT, Johnson MK. The effects of orienting tasks on recognition, recall, and modality confusion of pictures and words. *Journal of Verbal Learning and Verbal Behavior* 1980;19:416–429.
- Duverne S, Habibi A, Rugg MD. Regional specificity of age effects on the neural correlates of episodic retrieval. *Neurobiology of Aging* 2008;29:1902–1916. [PubMed: 17560691]
- Dywan J, Segalowitz SJ, Arsenault A. Electrophysiological response during source memory decisions in older and younger adults. *Brain and Cognition* 2002;49:322–340. [PubMed: 12139957]

- Easterbrook JA. The effect of emotion on cue utilization and the organization of behavior. *Psychological Review* 1959;66:183–201. [PubMed: 13658305]
- Eich, E.; Geraerts, E.; Schooler, JW.; Forgas, JP. Memory in and about affect. In: Byrne, J.; Roediger, HL., III, editors. *Cognitive psychology of memory. Learning and memory: A comprehensive reference*. Vol. Vol. 2. Oxford: Elsevier; 2008. p. 239-260.(Series Ed.) (Vol. Ed.)
- Eichenbaum, H. The hippocampal system and declarative memory in humans and animals: Experimental analysis and historical origins. In: Schacter, DL.; Tulving, E., editors. *Memory systems*. Cambridge, MA: MIT Press; 1994. p. 147-202.
- Eichenbaum, H.; Fortin, N.; Ergorul, C.; Robitsek, J. Toward a neurobiology of episodic memory. In: Huston, JP.; Dere, E.; Easton, A.; Nadel, L.; Huston, JP., editors. *Handbook of behavioral neuroscience, Vol. 18, Handbook of episodic memory*. The Netherlands: Elsevier; 2008. p. 283-300.(Series Ed.) (Vol. Eds.)
- Eichenbaum H, Lipton PA. Towards a functional organization of the medial temporal lobe memory system: Role of the parahippocampal and medial entorhinal cortical areas. *Hippocampus* 2008;18:1314–1324. [PubMed: 19021265]
- Eichenbaum H, Yonelinas AP, Ranganath C. The medial temporal lobe and recognition memory. *Annual Review of Neuroscience* 2007;30:123–152.
- Eldridge LL, Engel SA, Zeineh MM, Bookheimer SY, Knowlton BJ. A dissociation of encoding and retrieval processes in the human hippocampus. *The Journal of Neuroscience* 2005;25:3280–3286. [PubMed: 15800182]
- Elfman KW, Parks CM, Yonelinas AP. Testing a neurocomputational model of recollection, familiarity, and source recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:752–768.
- Epstein R, Kanwisher N. A cortical representation of the local visual environment. *Nature* 1998;392:598–601. [PubMed: 9560155]
- Erk S, Martin S, Walter H. Emotional context during encoding of neutral items modulates brain activation not only during encoding but also during recognition. *NeuroImage* 2005;26:829–838. [PubMed: 15955493]
- Fenker DB, Schott BH, Richardson-Klavehn A, Heinze H-J, Duzel E. Recapitulating emotional context: activity of amygdala, hippocampus and fusiform cortex during recollection and familiarity. *European Journal of Neuroscience* 2005;21:1993–1999. [PubMed: 15869492]
- Fichtenholtz, H.; Qin, JJ.; Mitchell, KJ.; Johnson, DC.; Southwick, SM.; Johnson, MK., et al. PTSD patients' memory for neutral pictures in blocked and intermixed lists. Presented at the Annual Meeting of the Association for Psychological Science; Chicago, IL. 2008 May.
- Finke RA, Johnson MK, Shyi GC-W. Memory confusions for real and imagined completions of symmetrical visual patterns. *Memory & Cognition* 1988;16:133–137.
- Fleck MS, Daselaar SM, Dobbins IG, Cabeza R. Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cerebral Cortex* 2006;16:1623–1630. [PubMed: 16400154]
- Fotopoulou A, Conway MA, Solms M. Confabulation: Motivated reality monitoring. *Neuropsychologia* 2007;45:2180–2190. [PubMed: 17428509]
- Friedman D, Johnson RJ. Event-Related Potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique* 2000;51:6–28. [PubMed: 11002349]
- Gallo DA, Weiss JA, Schacter DL. Reducing false recognition with criterial recollection tests: Distinctiveness heuristic versus criterion shifts. *Journal of Memory and Language* 2004;51:473–493.
- Ganis G, Thompson WL, Kosslyn SM. Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cognitive Brain Research* 2004;20:226–241. [PubMed: 15183394]
- Gardiner, JM. Remembering and knowing. In: Byrne, J.; Roediger, HL., III, editors. *Cognitive psychology of memory. Learning and memory: A comprehensive reference*. Vol. Vol. 2. Oxford: Elsevier; 2008. p. 285-306.(Series Ed.) (Vol. Ed.)
- Gardiner, JM.; Richardson-Klavehn, A. Remembering and knowing. In: Tulving, E.; Craik, FIM., editors. *The Oxford handbook of memory*. New York: Oxford University Press; 2000. p. 229-244.

- Garoff RJ, Slotnick SD, Schacter DL. The neural origins of specific and general memory: the role of the fusiform cortex. *Neuropsychologia* 2005;43:847–859. [PubMed: 15716157]
- Garoff-Eaton RJ, Kensinger EA, Schacter DL. The neural correlates of conceptual and perceptual false recognition. *Learning & Memory* 2007;14:684–692. [PubMed: 17911372]
- Garoff-Eaton RJ, Slotnick SD, Schacter DL. Not all false memories are created equal: The neural basis of false recognition. *Cerebral Cortex* 2006;16:1645–1652. [PubMed: 16400158]
- Geuze E, Vermetten E, Ruf M, de Kloet CS, Westenberg HGM. Neural correlates of associative learning and memory in veterans with posttraumatic stress disorder. *Journal of Psychiatric Research* 2008;42:659–669. [PubMed: 17698081]
- Gilboa A, Winocur G, Grady CL, Hevenor SJ, Moscovitch M. Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex* 2004;14:1214–1225. [PubMed: 15166099]
- Giovanello KS, Schnyer D, Verfaellie M. Distinct hippocampal regions make unique contributions to relational memory. *Hippocampus* 2009;19:111–117. [PubMed: 18727049]
- Giovanello KS, Verfaellie M, Keane MM. Disproportionate deficit in associative recognition relative to item recognition in global amnesia. *Cognitive, Affective, & Behavioral Neuroscience* 2003;3:186–194.
- Glanzer M, Hilford A, Kim K. Six regularities of source recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2004;30:1176–1195.
- Glisky EL, Kong LL. Do young and older adults rely on different processes in source memory tasks? A neuropsychological study. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:809–822.
- Glisky EL, Polster MR, Routhieaux BC. Double dissociation between item and source memory. *Neuropsychology* 1995;9:229–235.
- Glisky EL, Rubin SR, Davidson PSR. Source memory in older adults: An encoding or retrieval problem? *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2001;27:1131–1146.
- Gold JJ, Hopkins RO, Squire LR. Single-item memory, associative memory, and the human hippocampus. *Learning & Memory* 2006;13:644–649. [PubMed: 16980546]
- Gold JJ, Smith CN, Bayley PJ, Shrager Y, Brewer JB, Stark CEL, et al. Item memory, source memory, and the medial temporal lobe: Concordant findings from fMRI and memory-impaired patients. *Proceedings of the National Academy of Sciences* 2006;103:9351–9356.
- Goldin PR, McRae K, Ramel W, Gross JJ. The neural bases of emotion regulation: Reappraisal and suppression of negative emotion. *Biological Psychiatry* 2008;63:577–586. [PubMed: 17888411]
- Golier J, Harvey P, Steiner A, Yehuda R. Source monitoring in PTSD. *Annals of the New York Academy of Science* 1997;821:472–475.
- Golomb J, Kluger A, de Leon MJ, Ferris SH, Mittelman M, Cohen J, et al. Hippocampal formation size predicts declining memory performance in normal aging. *Neurology* 1996;47:810–813. [PubMed: 8797485]
- Gonsalves B, Reber PJ, Gitelman DR, Parrish TB, Mesulam M-M, Paller KA. Neural evidence that vivid imagining can lead to false remembering. *Psychological Science* 2004;15:655–660. [PubMed: 15447635]
- Gordon R, Franklin N, Beck J. Wishful thinking and source monitoring. *Memory & Cognition* 2005;33:418–429.
- Grady CL. Cognitive neuroscience of aging. *Annals of the New York Academy of Sciences* 2008;1124:127–144. [PubMed: 18400928]
- Grady CL, McIntosh AR, Horwitz B, Maisog JM, Ungerleider LG, Mentis MJ, et al. Age-related reductions in human recognition memory due to impaired encoding. *Science* 1995;269:218–221. [PubMed: 7618082]
- Grady CL, Yu H, Alain C. Age-related differences in brain activity underlying working memory for spatial and nonspatial auditory information. *Cerebral Cortex* 2008;18:189–199. [PubMed: 17494060]

- Greenberg DL, Rice HJ, Cooper JJ, Cabeza R, Rubin DC, LaBar KS. Co-activation of the amygdala, hippocampus and inferior frontal gyrus during autobiographical memory retrieval. *Neuropsychologia* 2005;43:659–674. [PubMed: 15721179]
- Gronlund SD, Edwards MB, Ohrt DD. Comparison of the retrieval of item versus spatial position information. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1997;23:1261–1274.
- Gruppuso V, Lindsay DS, Kelley CM. The process-dissociation procedure and similarity: Defining and estimating recollection and familiarity in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1997;23:259–278.
- Gutchess AH, Welsh RC, Hedden T, Bangert A, Minear M, Liu LL, et al. Aging and the neural correlates of successful picture encoding: Frontal activations compensate for decreased medial-temporal activity. *Journal of Cognitive Neuroscience* 2005;17:84–96. [PubMed: 15701241]
- Guerin SA, Miller MB. Semantic organization of study materials has opposite effects on recognition and recall. *Psychonomic Bulletin & Review* 2008;15:302–308. [PubMed: 18488644]
- Haas BW, Canli T. Emotional memory function, personality structure and psychopathology: A neural system approach to the identification of vulnerability markers. *Brain Research Reviews* 2008;58:71–84. [PubMed: 18359090]
- Habib R, Nyberg L, Tulving E. Hemispheric asymmetries of memory: the HERA model revisited. *Trends in Cognitive Sciences* 2003;7:241–245. [PubMed: 12804689]
- Hadjikhani N, Roland PE. Cross-modal transfer of information between the tactile and the visual representations in the human brain: A positron emission tomographic study. *The Journal of Neuroscience* 1998;18:1072–1084. [PubMed: 9437027]
- Hamann S, Canli T. Individual differences in emotion processing. *Current Opinions in Neurobiology* 2004;14:233–238.
- Hamann SB, Ely TD, Grafton ST, Kilts CD. Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience* 1999;2:289–293.
- Hamilton JP, Gotlib IH. Neural substrates of increased memory sensitivity for negative stimuli in major depression. *Society of Biological Psychiatry* 2008;63:1155–1162.
- Hannula DE, Tranel D, Cohen NJ. The long and the short of it: Relational memory impairments in amnesia, even at short lags. *The Journal of Neuroscience* 2006;26:8352–8359. [PubMed: 16899730]
- Hasher, L.; Lustig, C.; Zacks, R. Inhibitory mechanisms and the control of attention. In: Conway, ARA.; Jarrold, C.; Kane, MJ.; Miyake, A.; Towse, JN., editors. *Variation in working memory*. New York: Oxford University Press; 2007. p. 227-249.
- Hasher, L.; Zacks, RT. Working memory, comprehension, and aging: A review and a new view. In: Bower, GH., editor. *The psychology of learning and motivation*. Vol. Vol. 22. New York: Academic Press; 1988. p. 193-225.
- Hashtroudi S, Johnson MK, Chrosniak LD. Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology and Aging* 1990;5:119–126. [PubMed: 2317290]
- Haskins AL, Yonelinas AP, Quamme JR, Ranganath C. Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron* 2008;59:554–560. [PubMed: 18760692]
- Hassabis D, Maguire EA. Deconstructing episodic memory with construction. *Trends in Cognitive Sciences* 2007;11:299–306. [PubMed: 17548229]
- Hayama HR, Johnson JD, Rugg MD. The relationship between the right frontal old/new ERP effect and post-retrieval monitoring: Specific or non-specific? *Neuropsychologia* 2008;46:1211–1223. [PubMed: 18234241]
- Healy MR, Light LL, Chung C. Dual-process models of associative recognition in young and older adults: Evidence from receiver operating characteristics. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2005;31:768–788.
- Hekkanen ST, McEvoy C. False memories and source-monitoring problems: Criterion differences. *Applied Cognitive Psychology* 2002;16:73–85.

- Henke K, Buck A, Weber B, Wieser HG. Human hippocampus establishes associations in memory. *Hippocampus* 1997;7:249–256. [PubMed: 9228523]
- Henke K, Weber B, Kneifel S, Wieser HG, Buck A. Human hippocampus associates information in memory. *Proceedings of the National Academy of Sciences of the United States of America* 1999;96:5884–5889. [PubMed: 10318979]
- Henkel LA, Franklin N, Johnson MK. Cross-modal source monitoring confusions between perceived and imagined events. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2000;26:321–335.
- Henkel LA, Johnson MK, De Leonardis DM. Aging and source monitoring: Cognitive processes and neuropsychological correlates. *Journal of Experimental Psychology: General* 1998;127:251–268. [PubMed: 9742716]
- Henson R. A mini-review of fMRI studies of human medial temporal lobe activity associated with recognition memory. *The Quarterly Journal of Experimental Psychology* 2005;58B:340–360. [PubMed: 16194973]
- Henson RNA, Shallice T, Dolan RJ. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. *Brain* 1999;122:1367–1381. [PubMed: 10388802]
- Hertel, PT. Emotion, mood and memory. In: Squire, L., editor. *Encyclopedia of learning and memory*. New York: Macmillan; 1992. p. 157-161.
- Hertel, PT. The cognitive-initiative account of depression-related impairments in memory. In: Medin, D., editor. *The psychology of learning and motivation: Advances in research theory*. Vol. Vol. 39. San Diego: Academic Press; 2000. p. 47-71.
- Higgins, JA.; Johnson, MK. Unconscious competition can impair basic reflective processing of consciously experienced items. Yale University; 2008. Manuscript in preparation
- Hilford A, Glanzer M, Kim K, DeCarlo LT. Regularities of source recognition: ROC analysis. *Journal of Experimental Psychology: General* 2002;131:494–510. [PubMed: 12500860]
- Hintzman DL, Caulton DA, Levitin DJ. Retrieval dynamics in recognition and list discrimination: Further evidence of separate processes of familiarity and recall. *Memory & Cognition* 1998;26:449–462.
- Hoffman RE. Auditory/verbal hallucinations, speech perception neurocircuitry, and the social deafferentation hypothesis. *Clinical EEG & Neuroscience: Official Journal of the EEG & Clinical Neuroscience Society (ENCS)* 2008;39:87–90. [PubMed: 18450175]
- Hoffman RE, Hampson M, Wu K, Anderson AW, Gore JC, Buchanan RJ, et al. Probing the pathophysiology of auditory/verbal hallucinations by combining functional magnetic resonance imaging and transcranial magnetic stimulation. *Cerebral Cortex* 2007;17:2733–2743. [PubMed: 17298962]
- Hornberger M, Rugg MD, Henson RNA. fMRI correlates of retrieval orientation. *Neuropsychologia* 2006;44:1425–1436. [PubMed: 16480749]
- Hyman IE, Pentland J. The role of mental imagery in the creation of false childhood memories. *Journal of Memory and Language* 1996;35:101–117.
- Jacoby LL. A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language* 1991;30:513–541.
- Jacoby LL, Bishara AJ, Hessels S, Toth JP. Aging, subjective experience, and cognitive control: Dramatic false remembering by older adults. *Journal of Experimental Psychology: General* 2005;134:131–148. [PubMed: 15869342]
- Jacoby LL, Kelley C, Brown J, Jasechko J. Becoming famous overnight: Limits on the ability to avoid unconscious influences of the past. *Journal of Personality and Social Psychology* 1989;56:326–338.
- Jennings JM, Jacoby LL. An opposition procedure for detecting age-related deficits in recollection: Telling effects of repetition. *Psychology and Aging* 1997;12:352–361. [PubMed: 9189995]
- Johnson JD, Rugg MD. Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex* 2007;17:2507–2515. [PubMed: 17204822]
- Johnson, MK. Discriminating the origin of information. In: Oltmanns, TF.; Maher, BA., editors. *Delusional beliefs*. New York: John Wiley & Sons; 1988. p. 34-65.

- Johnson, MK. Reality monitoring: Evidence from confabulation in organic brain disease patients. In: Prigatano, GP.; Schacter, DL., editors. *Awareness of deficit after brain injury*. New York: Oxford University Press; 1991. p. 176-197.
- Johnson MK. MEM: Mechanisms of recollection. *Journal of Cognitive Neuroscience* 1992;4:268–280.
- Johnson, MK. Identifying the origin of mental experience. In: Myslobodsky, MS., editor. *The mythomanias: The nature of deception and self-deception*. Mahwah, NJ: Erlbaum; 1997a. p. 133-180.
- Johnson MK. Source monitoring and memory distortion. *Philosophical Transactions of the Royal Society of London* 1997b;352:1733–1745. [PubMed: 9415926]
- Johnson MK. The relation between source memory and episodic memory: Comment on Siedlecki et al. (2005). *Psychology and Aging* 2005;20:529–531. [PubMed: 16248712]
- Johnson MK. Memory and Reality. *American Psychologist* 2006;61:760–771. [PubMed: 17115808]
- Johnson MK, Bransford JD, Solomon SK. Memory for tacit implications of sentences. *Journal of Experimental Psychology* 1973;98:203–205.
- Johnson, MK.; Chalfonte, BL. Binding complex memories: The role of reactivation and the hippocampus. In: Schacter, DL.; Tulving, E., editors. *Memory systems 1994*. Cambridge, MA: MIT Press; 1994. p. 311-350.
- Johnson MK, Foley MA, Suengas AG, Raye CL. Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General* 1988;117:371–376. [PubMed: 2974863]
- Johnson MK, Hashtroudi S, Lindsay DS. Source Monitoring. *Psychological Bulletin* 1993;114:3–28. [PubMed: 8346328]
- Johnson, MK.; Hayes, SM.; D'Esposito, M.; Raye, CL. Confabulation. In: Boller, F.; Grafman, J., editors. *Handbook of neuropsychology. Memory and its disorders*. 2nd ed.. Vol. Vol. 2. Amsterdam: Elsevier Science; 2000. p. 383-407.
- Johnson, MK.; Hirst, W. MEM: Memory subsystems as processes. In: Collins, AF.; Gathercole, SE.; Conway, MA.; Morris, PE., editors. *Theories of memory*. East Sussex England: Lawrence Erlbaum Associates; 1993. p. 241-286.
- Johnson MK, Kounios J, Nolde SF. Electrophysiological brain activity and memory source monitoring. *NeuroReport* 1997;7:2929–2932. [PubMed: 9116212]
- Johnson MK, Kounios J, Reeder JA. Time-course studies of reality monitoring and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1994;20:1409–1419.
- Johnson MK, Mitchell KJ, Raye CL, McGuire JT, Sanislow CA. Mental rubbernecking to negative information depends on task context. *Psychonomic Bulletin & Review* 2006;13:614–618. [PubMed: 17201360]
- Johnson, MK.; Multhaup, KS. Emotion and MEM. In: Christianson, S-A., editor. *The handbook of emotion and memory: Current research and theory*. Hillsdale, NJ: Lawrence Erlbaum Associates; 1992. p. 33-66.
- Johnson MK, Nolde SF, De Leonardis DM. Emotional focus and source monitoring. *Journal of Memory and Language* 1996;35:135–156.
- Johnson MK, Nolde SF, Mather M, Kounios J, Schacter DL, Curran T. The similarity of brain activity associated with true and false recognition depends on test format. *Psychological Science* 1997;8:250–257.
- Johnson MK, O'Connor M, Cantor J. Confabulation, memory deficits, and frontal dysfunction. *Brain and Cognition* 1997;34:189–206. [PubMed: 9220085]
- Johnson MK, Raye CL. Reality monitoring. *Psychological Review* 1981;88:67–85.
- Johnson, MK.; Raye, CL. Cognitive and brain mechanisms of false memories and beliefs. In: Schacter, DL.; Scarry, E., editors. *Memory and belief*. Cambridge, MA: Harvard University Press; 2000. p. 35-86.
- Johnson MK, Raye CL, Mitchell KJ, Greene EJ, Cunningham WA, Sanislow CA. Using fMRI to investigate a component process of reflection: Prefrontal correlates of refreshing a just-activated representation. *Cognitive, Affective, & Behavioral Neuroscience* 2005;5:339–361.

- Johnson MK, Raye CL, Mitchell KJ, Touryan SR, Greene EJ, Nolen-Hoeksema S. Dissociating medial frontal and posterior cingulate activity during self-reflection. *Social Cognitive and Affective Neuroscience* 2006;1:56–64. [PubMed: 18574518]
- Johnson MK, Verfaellie M, Dunlosky J. Introduction to the special section on integrative approaches to source memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition* 2008;34:727–729.
- Jonides J, Lewis RL, Nee DE, Lustig CA, Berman MG, Moore KS. The mind and brain of short-term memory. *Annual Review of Psychology* 2008;59:193–224.
- Kahn I, Andrews-Hanna JR, Vincent JL, Snyder AZ, Buckner RL. Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *Journal of Neurophysiology* 2008;100:129–139. [PubMed: 18385483]
- Kahn I, Davachi L, Wagner AD. Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *The Journal of Neuroscience* 2004;24:4172–4180. [PubMed: 15115812]
- Kanwisher N, McDermott J, Chun MM. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience* 1997;17:4302–4311. [PubMed: 9151747]
- Karpel ME, Hoyer WJ, Toglia MP. Accuracy and qualities of real and suggested memories: Nonspecific age differences. *Journals of Gerontology Series B-Psychological Sciences & Social Sciences* 2001;56B:103–110.
- Kaszniak, AW.; Newman, MC. Toward a neuropsychology of cognitive aging. In: Qualls, SH.; Abeles, N., editors. *Psychology and the aging revolution: How we adapt to longer life*. Washington, DC, US: American Psychological Association; 2000. p. 43-67.
- Kelley, CM.; Jacoby, LL. Recollection and familiarity: Process-dissociation. In: Tulving, E.; Craik, FIM., editors. *The Oxford handbook of memory*. New York: Oxford University Press; 2000. p. 215-228.
- Kelley CM, Sahakyan L. Memory, monitoring, and control in the attainment of memory accuracy. *Journal of Memory and Language* 2003;48:704–721.
- Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF. Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience* 2002;14:785–794. [PubMed: 12167262]
- Kelley WL, Miezin FM, McDermott K, Buckner RL, Raichle ME, Cohen NJ, Petersen SE. Hemispheric specialization in human dorsal frontal cortex and medial temporal lobes for verbal and nonverbal memory encoding. *Neuron* 1998;20:927–936. [PubMed: 9620697]
- Kensinger EA. Negative emotion enhances memory: Accuracy behavioral and neuroimaging evidence. *Current Directions in Psychological Science* 2007;16:213–218.
- Kensinger EA. How emotion affects older adults' memories for event details. *Memory*. (in press).
- Kensinger EA, Clarke RJ, Corkin S. What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience* 2003;23:2407–2415. [PubMed: 12657700]
- Kensinger EA, Corkin S. Two routes to emotional memory: Distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences* 2004;101:3310–3315.
- Kensinger, EA.; Corkin, S. Amnesia: point and counterpoint. In: Byrne, J.; Menzel, R., editors. *Learning theory and behavior. Learning and memory: A comprehensive reference. Vol. Vol. 1*. Oxford: Elsevier; 2008. p. 259-286.(Series Ed.) (Vol. Ed.)
- Kensinger EA, Garoff-Eaton RJ, Schacter DL. How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience* 2007;19:1872–1887. [PubMed: 17958489]
- Kensinger EA, Schacter DL. Retrieving accurate and distorted memories: Neuroimaging evidence for effects of emotion. *NeuroImage* 2005a;27:167–177. [PubMed: 15919215]
- Kensinger EA, Schacter DL. Emotional content and reality-monitoring ability: fMRI evidence for the influences of encoding processes. *Neuropsychologia* 2005b;43:1429–1443. [PubMed: 15989934]
- Kensinger EA, Schacter DL. Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *The Journal of Neuroscience* 2006;26:2564–2570. [PubMed: 16510734]

- Kensinger EA, Schacter DL. Remembering the specific visual details of presented objects: Neuroimaging evidence for effects of emotion. *Neuropsychologia* 2007;45:2951–2962. [PubMed: 17631361]
- Kensinger, EA.; Schacter, DL. Memory and emotion. In: Lewis, M.; Haviland-Jones, JM.; Barrett, LF., editors. *The handbook of emotions*, 3rd Edition. New York: Guilford; 2008a. p. 601-617.
- Kensinger EA, Schacter DL. Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience* 2008b;20:1161–1173. [PubMed: 18284340]
- Kim H, Cabeza R. Differential contributions of prefrontal, medial temporal, and sensory-perceptual regions to true and false memory formation. *Cerebral Cortex* 2007a;17:2143–2150. [PubMed: 17110592]
- Kim H, Cabeza R. Trusting our memories: Dissociating the neural correlates of confidence in veridical versus illusory memories. *The Journal of Neuroscience* 2007b;27:12190–12197. [PubMed: 17989285]
- Kintsch W. Recognition and free recall of organized lists. *Journal of Experimental Psychology* 1968;78:481–487.
- Kirchhoff BA, Wagner AD, Maril A, Stern CE. Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *The Journal of Neuroscience* 2000;20:6173–6180. [PubMed: 10934267]
- Kirwan CB, Jones CK, Miller MI, Stark CEL. High-resolution fMRI investigation of the medial temporal lobe. *Human Brain Mapping* 2007;28:959–966. [PubMed: 17133381]
- Kirwan CB, Stark CEL. Overcoming interference: An fMRI investigation of pattern separation in the medial temporal lobe. *Learning & Memory* 2007;14:625–633. [PubMed: 17848502]
- Kirwan CB, Wixted JT, Squire LR. Activity in the medial temporal lobe predicts memory strength, whereas activity in the prefrontal cortex predicts recollection. *The Journal of Neuroscience* 2008;28:10541–10548. [PubMed: 18923030]
- Knight M, Seymour TL, Gaunt JT, Baker C, Nesmith K, Mather M. Aging and goal-directed emotional attention: Distraction reverses emotional biases. *Emotion* 2007;7:705–714. [PubMed: 18039037]
- Kohler S, Paus T, Buckner RL, Milner B. Effects of left inferior prefrontal stimulation on episodic memory formation: A two-stage fMRI–rTMS Study. *Journal of Cognitive Neuroscience* 2004;16:178–188. [PubMed: 15068590]
- Konishi S, Uchida I, Okuaki T, Machida T, Shirouzu I, Miyashita Y. Neural correlates of recency judgment. *The Journal of Neuroscience* 2002;22:9549–9555. [PubMed: 12417679]
- Kroll NEA, Knight RT, Metcalfe J, Wolf ES, Tulving E. Cohesion failure as a source of memory illusions. *Journal of Memory and Language* 1996;35:176–196.
- Kumaran D, Maguire EA. Novelty signals: a window into hippocampal information processing. *Trending in Cognitive Sciences* 2009;13:47–54.
- Kuskowski MA, Pardo JV. The role of the fusiform gyrus in successful encoding of face stimuli. *NeuroImage* 1999;9:599–610. [PubMed: 10334903]
- Lampinen JM, Meier CR, Arnal JD, Leding JK. Compelling untruths: Content borrowing and vivid false memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2005;31:954–963.
- Lepage M, Ghaffar O, Nyberg L, Tulving E. Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences of the United States of America* 2000;97:506–511. [PubMed: 10618448]
- Lepage M, Habib R, Tulving E. Hippocampal PET activations of memory encoding and retrieval: The HIPER model. *Hippocampus* 1998;8:313–322. [PubMed: 9744418]
- Lepage M, Montoya A, Pelletier M, Achim AM, Menear M, Lal S. Associative memory encoding and recognition schizophrenia: An event-related fMRI study. *Biological Psychiatry* 2006;60:1215–1223. [PubMed: 16814264]
- Leynes PA, Phillips MC. Event-related Potential (ERP) evidence for varied recollection during source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:741–751.

- Li S-C, Naveh-Benjamin M, Lindenberger U. Aging neuromodulation impairs associative binding: A neurocomputational account. *Psychological Science* 2005;16:445–450. [PubMed: 15943670]
- Liberzon I, Sripada CS. The functional neuroanatomy of PTSD: a critical review. *Progress in Brain Research* 2008;167:151–169. [PubMed: 18037013]
- Liberzon I, Taylor SF, Amdur R, Jung TD, Chamberlain KR, Minoshima S, et al. Brain activation in PTSD in response to trauma-related stimuli. *Biological Psychiatry* 1999;45:817–826. [PubMed: 10202568]
- Light, LL.; Prull, MW.; La Voie, DJ.; Healy, MR. Dual process theories of memory in old age. In: Perfect, TJ.; Maylor, EA., editors. *Models of cognitive aging*. Oxford: Oxford University Press; 2000. p. 238-300.
- Lindsay, DS. Source Monitoring. In: Byrne, J.; Roediger, HL., III, editors. *Cognitive psychology of memory. Learning and memory: A comprehensive reference*. Vol. Vol. 2. Oxford: Elsevier; 2008. p. 325-348.(Series Ed.) (Series Ed.)
- Lindsay DS, Hagen L, Read JD, Wade KA, Garry M. True photographs and false memories. *Psychological Science* 2004;15:149–154. [PubMed: 15016285]
- Lindsay DS, Johnson MK. The eyewitness suggestibility effect and memory for source. *Memory & Cognition* 1989;17:349–358.
- Lindsay DS, Johnson MK, Kwon P. Developmental changes in memory source monitoring. *Journal of Experimental Child Psychology* 1991;52:297–318. [PubMed: 1770330]
- Lindsay DS, Read JD. Psychotherapy and memories of childhood sexual abuse: A cognitive perspective. *Applied Cognitive Psychology* 1994;8:281–338.
- Lipton PA, Eichenbaum H. Complementary roles of hippocampus and medial entorhinal cortex in episodic memory. *Neural Plasticity* 2008;Vol. 2008:1–8.
- Loftus, EF. *Eyewitness testimony*. Cambridge, MA: Harvard University Press; 1979.
- Loftus EF, Pickrell JE. The formation of false memories. *Psychiatric Annals* 1995;25:720–725.
- Lyle KB, Bloise SM, Johnson MK. Age-related binding deficits and the content of false memories. *Psychology and Aging* 2006;21:86–95. [PubMed: 16594794]
- Lyle KB, Johnson MK. Importing perceived features into false memories. *Memory* 2006;14:197–213. [PubMed: 16484110]
- Lyle KB, Johnson MK. Source misattributions may increase the accuracy of source judgments. *Memory & Cognition* 2007;35:1024–1033.
- MacPherson SE, Phillips LH, Della Sala S. Age, executive function, and social decision making: A dorsolateral prefrontal theory of cognitive aging. *Psychology & Aging* 2002;17:598–609. [PubMed: 12507357]
- Macrae CN, Moran JM, Heatherton TF, Banfield JF, Kelley WM. Medial prefrontal activity predicts memory for self. *Cerebral Cortex* 2004;14:647–654. [PubMed: 15084488]
- Maratos EJ, Dolan RJ, Morris JS, Henson RNA, Rugg MD. Neural activity associated with episodic memory for emotional context. *Neuropsychologia* 2001;39:910–920. [PubMed: 11516444]
- Marcel AJ. Conscious and unconscious perception: Experiments on visual masking and word recognition. *Cognitive Psychology* 1983;15:197–237. [PubMed: 6617135]
- Maril A, Simons JS, Weaver JJ, Schacter DL. Graded recall success: an event-related fMRI comparison of tip of the tongue and feeling of knowing. *NeuroImage* 2005;24:1130–1138. [PubMed: 15670690]
- Marsh, EJ.; Eslick, AN.; Fazio, LK. False memories. In: Byrne, J.; Roediger, HL., III, editors. *Cognitive psychology of memory. Learning and memory: A comprehensive reference*. Vol. Vol. 2. Oxford: Elsevier; 2008. p. 221-238.
- Marsh RL, Hicks JL. Test formats change source-monitoring decision processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1998;24:1137–1151.
- Mather, M. Aging and emotional memory. In: Reisberg, D.; Hertel, P., editors. *Memory and emotion*. New York: Oxford University Press; 2004. p. 272-307.
- Mather, M. Why memories may become more positive with age. In: Uttl, B.; Ohta, N.; Siegenthaler, AL., editors. *Memory and emotion: Interdisciplinary perspectives*. Boston: Blackwell Publishing; 2006. p. 135-159.

- Mather M. Emotional arousal and memory binding: An object-based framework. *Perspectives on Psychological Science* 2007;2:33–52.
- Mather M, Henkel LA, Johnson MK. Evaluating characteristics of false memories: Remember/know judgments and memory characteristics questionnaire compared. *Memory & Cognition* 1997;25:826–837.
- Mather M, Johnson MK, De Leonardis DM. Stereotype reliance in source monitoring: Age differences and neuropsychological test correlates. *Cognitive Neuropsychology* 1999;16:437–458.
- Mather M, Mitchell KJ, Raye CL, Novak DL, Greene EJ, Johnson MK. Emotional arousal can impair feature binding in working memory. *Journal of Cognitive Neuroscience* 2006;18:614–625. [PubMed: 16768364]
- May CP, Rahhal T, Berry EM, Leighton EA. Aging, source memory, and emotion. *Psychology and Aging* 2005;20:571–578. [PubMed: 16420132]
- Mayes A, Montaldi D, Migo E. Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences* 2007;11:126–135. [PubMed: 17270487]
- McCandliss BD, Cohen L, Dehaene S. The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences* 2003;7:293–299. [PubMed: 12860187]
- McDermott KB, Buckner RL, Petersen SE, Kelley WM, Sanders AL. Set- and code-specific activation in the frontal cortex: an fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience* 1999;11:631–640. [PubMed: 10601744]
- McDuff, S.; Frankel, HC.; Norman, KA. Many roads to the source: Tracking differences in memory retrieval strategies using multi-voxel pattern analysis. Princeton University; 2008. Manuscript under review
- McElree B, Dolan PO, Jacoby LL. Isolating the contributions of familiarity and source information to item recognition: A time course analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1999;25:563–582.
- McGinnis D, Roberts P. Qualitative characteristics of vivid memories attributed to real and imagined experiences. *American Journal of Psychology* 1996;109:59–77.
- McGuire PK, Silbersweig DA, Wright I, Murray RM, David AS, Frackowiak RSJ, et al. Abnormal monitoring of inner speech: a physiological basis for auditory hallucinations. *Lancet* 1995;346:596–600. [PubMed: 7651003]
- McNally RJ. Cognitive abnormalities in post-traumatic stress disorder. *Trends in Cognitive Sciences* 2006;10:271–277. [PubMed: 16697695]
- Meiser T, Broder A. Memory for multidimensional source information. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2002;28:116–137.
- Meiser T, Sattler C. Boundaries of the relation between conscious recollection and source memory for perceptual details. *Consciousness and Cognition* 2007;16:189–210. [PubMed: 16725348]
- Metcalfe K, Langdon R, Coltheart M. Models of confabulation: A critical review and a new framework. *Cognitive Neuropsychology* 2007;24:23–47. [PubMed: 18416482]
- Meyer-Lindenberg AS, Olsen RK, Kohn PD, Brown T, Egan MF, Weinberger DR, et al. Regionally specific disturbance of dorsolateral prefrontal-hippocampal connectivity in schizophrenia. *Archives of General Psychiatry* 2005;62:379–386. [PubMed: 15809405]
- Mickley KR, Kensinger EA. Emotional valence influences the neural correlates associated with remembering and knowing. *Cognitive, Affective, & Behavioral Neuroscience* 2008;8:143–152.
- Mikels JA, Larkin GR, Reuter-Lorenz PA, Carstensen LL. Divergent trajectories in the aging mind: Changes in working memory for affective versus visual information with age. *Psychology and Aging* 2005;20:542–553. [PubMed: 16420130]
- Mitchell, KJ.; Johnson, MK. Source monitoring: Attributing mental experiences. In: Tulving, E.; Craik, FIM., editors. *The Oxford handbook of memory*. New York: Oxford University Press; 2000. p. 179-195.
- Mitchell, KJ.; Johnson, MR.; Higgins, JA.; Johnson, MK. Effects of age on modulation of posterior category-specific activity during reflective attention. Yale University; 2009. Manuscript in preparation
- Mitchell KJ, Johnson MK, Mather M. Source monitoring and suggestibility to misinformation: Adult age-related differences. *Applied Cognitive Psychology* 2003;17:107–119.

- Mitchell KJ, Johnson MK, Raye CL, D'Esposito M. fMRI evidence of age-related hippocampal dysfunction in feature binding in working memory. *Cognitive Brain Research* 2000;10:197–206. [PubMed: 10978709]
- Mitchell KJ, Johnson MK, Raye CL, Greene EJ. Prefrontal cortex activity associated with source monitoring in a working memory task. *Journal of Cognitive Neuroscience* 2004;16:921–934. [PubMed: 15298780]
- Mitchell KJ, Johnson MK, Raye CL, Mather M, D'Esposito M. Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging* 2000;15:527–541. [PubMed: 11014715]
- Mitchell KJ, Mather M, Johnson MK, Raye CL, Greene EJ. A functional magnetic resonance imaging investigation of short-term source and item memory for negative pictures. *NeuroReport* 2006;17:1543–1547. [PubMed: 16957605]
- Mitchell, KJ.; Nolen-Hoeksema, S.; Johnson, MK. The effects of dysphoria on brain activity associated with source memory for emotional information. Yale University; 2009. Manuscript in preparation
- Mitchell KJ, Raye CL, Johnson MK, Greene EJ. An fMRI investigation of short-term source memory in young and older adults. *NeuroImage* 2006;30:627–633. [PubMed: 16256377]
- Mitchell KJ, Raye CL, McGuire JT, Frankel H, Greene EJ, Johnson MK. Neuroimaging evidence for agenda-dependent monitoring of different features during short-term source memory tests. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2008;34:780–790.
- Mitchell KJ, Zaragoza MS. Contextual overlap and eyewitness suggestibility. *Memory & Cognition* 2001;29:616–626.
- Morcom AM, Li J, Rugg MD. Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cerebral Cortex* 2007;17:2491–2506. [PubMed: 17204820]
- Morris CD, Bransford JD, Franks JJ. Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior* 1977;16:519–533.
- Moscovitch M. Memory and working-with-memory: A component process model based on modules and central systems. *Journal of Cognitive Neuroscience* 1992;4:257–267.
- Moscovitch, M. Confabulation. In: Schacter, DL., editor. *Memory distortion: How minds, brains, and societies reconstruct the past*. Cambridge, MA: Harvard University Press; 1995. p. 226-251.
- Moscovitch M, Winocur G. Frontal lobes, memory, and aging. *Annals of the New York Academy of Sciences* 1995;769:119–150. [PubMed: 8595020]
- Most SB, Chun MM, Widders DM, Zald DH. Attentional rubbernecking: Cognitive control and personality in emotion-induced blindness. *Psychonomic Bulletin & Review* 2005;12:654–661. [PubMed: 16447378]
- Multhaup KS, De Leonardis DM, Johnson MK. Source memory and eyewitness suggestibility in older adults. *Journal of General Psychology* 1999;126:74–84. [PubMed: 10216970]
- Myers CE, Shohamy D, Gluck MA, Grossman S, Kluger A, Ferris S, et al. Dissociating hippocampal versus basal ganglia contributions to learning and transfer. *Journal of Cognitive Neuroscience* 2003;15:185–193. [PubMed: 12676056]
- Nadel L, Hardt O. The spatial brain. *Neuropsychology* 1994;18:473–476. [PubMed: 15291725]
- Naveh-Benjamin M. Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2000;26:1170–1187.
- Naveh-Benjamin M, Brav TK, Levy O. The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging* 2007;22:202–208. [PubMed: 17385995]
- Naveh-Benjamin, M.; Old, SR. Aging and memory. In: Byrne, J.; Roediger, HL., III, editors. *Cognitive psychology of memory. Learning and memory: A comprehensive reference*. Vol. Vol. 2. Oxford: Elsevier; 2008. p. 787-808.(Series Ed.) (Vol. Ed.)
- Neisser U. John Dean's memory: A case study. *Cognition* 1981;9:1–22. [PubMed: 7196816]
- Newcombe, NS.; Lloyd, ME.; Ratliff, KR. Development of episodic and autobiographical memory: A cognitive neuroscience perspective. In: Kail, RV., editor. *Advances in child development and behavior*. Vol. Vol. 35. San Diego, CA: Elsevier; 2007. p. 37-85.

- Nolde SF, Johnson MK, D'Esposito M. Left prefrontal activation during episodic remembering: an event-related fMRI study. *NeuroReport* 1998;9:3509–3514. [PubMed: 9855308]
- Nolde SF, Johnson MK, Raye CL. The role of the prefrontal cortex during tests of episodic memory. *Trends in Cognitive Sciences* 1998;2:399–406.
- Norman, KA.; Detre, G.; Polyn, SM. Computational models of episodic memory. In: Sun, R., editor. *The Cambridge handbook of computational cognitive modeling*. New York: Cambridge University Press; 2008. p. 189-225.
- Norman KA, O'Reilly RC. Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review* 2003;110:611–646. [PubMed: 14599236]
- Norman KA, Schacter DL. False recognition in younger and older adults: Exploring the characteristics of illusory memories. *Memory & Cognition* 1997;25:838–848.
- Northoff G, Heinzl A, de Greck M, Bermpohl F, Dobrowolny H, Panksepp J. Self-referential processing in our brain-A meta-analysis of imaging studies on the self. *NeuroImage* 2006;31:440–457. [PubMed: 16466680]
- O'Brien JT, Desmond P, Ames D, Schweitzer I, Tress B. Magnetic resonance imaging correlates of memory impairment in the healthy elderly: Association with medial temporal lobe atrophy but not white matter lesions. *International Journal of Geriatric Psychiatry* 1997;12:369–374. [PubMed: 9152723]
- Ochsner KN, Beer JS, Robertson ER, Cooper JC, Gabrieli JDE, Kihlstrom JF, et al. The neural correlates of direct and reflected self-knowledge. *NeuroImage* 2005;28:797–814. [PubMed: 16290016]
- Ochsner KN, Knierim K, Ludlow DH, Hanelin J, Ramachandran T, Glover G, et al. Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience* 2004;16:1746–1772. [PubMed: 15701226]
- O'Hanlon L, Wilcox KA, Kemper S. Age differences in implicit and explicit associative memory: Exploring elaborative processing effects. *Experimental Aging Research* 2001;27:341–359. [PubMed: 11681197]
- Okado Y, Stark C. Neural processing associated with true and false memory retrieval. *Cognitive, Affective, & Behavioral Neuroscience* 2003;3:323–334.
- Old SR, Naveh-Benjamin M. Differential effects of age on item and associative measures of memory: A meta-analysis. *Psychology and Aging* 2008;23:104–118. [PubMed: 18361660]
- Olson IR, Berryhill M. Some surprising findings on the involvement of the parietal lobe in human memory. *Neurobiology of Learning and Memory*. (in press).
- Olson IR, Page K, Moore KS, Chatterjee A, Verfaellie M. Working memory for conjunctions relies on the medial temporal lobe. *The Journal of Neuroscience* 2006;26:4596–4601. [PubMed: 16641239]
- Olson IR, Plotzker A, Ezzyat Y. The enigmatic temporal pole: a review of findings on social and emotional processing. *Brain* 2007;130:1718–1731. [PubMed: 17392317]
- Öngür D, Cullen TJ, Wolf DH, Rohan M, Barreira P, Zalesak M, et al. The neural basis of relational memory deficits in schizophrenia. *Archives of General Psychiatry* 2006;63:356–365. [PubMed: 16585464]
- Onitsuka T, Shenton ME, Salisbury DF, Dickey CC, Kasai K, Toner SK, et al. Middle and inferior temporal gyrus gray matter volume abnormalities in chronic schizophrenia: An MRI study. *American Journal of Psychiatry* 2004;161:1603–1611. [PubMed: 15337650]
- Otten LJ. Fragments of a larger whole: Retrieval cues constrain observed neural correlates of memory encoding. *Cerebral Cortex* 2007;17:2030–2038. [PubMed: 17088375]
- Paller KA. Electrical signals of memory and of the awareness of remembering. *Current Directions in Psychological Science* 2004;13:49–55.
- Paller KA, Voss JL, Boehm SG. Validating neural correlates of familiarity. *Trends in Cognitive Sciences* 2007;11:243–250. [PubMed: 17475539]
- Park DC, Polk TA, Park R, Minear M, Savage A, Smith MR. Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences* 2004;101:13091–13095.

- Parkin A. The neuropsychology of false memory. *Learning and Individual Differences* 1997;9:341–357.
- Parkin AJ, Walter BM. Recollective experience, normal aging, and frontal dysfunction. *Psychology and Aging* 1992;7:290–298. [PubMed: 1610518]
- Parks CM, Yonelinas AP. Moving beyond pure signal-detection models: Comment on Wixted (2007). *Psychological Review* 2007;114:188–202. [PubMed: 17227187]
- Payer D, Marshuetz C, Sutton B, Hebrank A, Welsh RC, Park DC. Decreased neural specialization in old adults on a working memory task. *NeuroReport* 2006;17:487–491. [PubMed: 16543812]
- Persson, J.; Nyberg, L. Altered brain activity in healthy seniors: what does it mean?. In: Møller, A., editor. *Reprogramming the human brain. Progress in Brain Research. Vol. Vol. 157. The Netherlands: Elsevier; 2006. p. 45-56.*
- Peters J, Koch B, Schwarz M, Daum I. Domain-specific impairment of source memory following a right posterior medial temporal lobe lesion. *Hippocampus* 2007;17:505–509. [PubMed: 17476681]
- Peters J, Suchan B, Köster O, Daum I. Domain-specific retrieval of source information in the medial temporal lobe. *European Journal of Neuroscience* 2007;26:1333–1343. [PubMed: 17767510]
- Petrides M. The mid-ventrolateral prefrontal cortex and active mnemonic retrieval. *Neurobiology of Learning and Memory* 2002;78:528–538. [PubMed: 12559832]
- Phan KL, Wager T, Taylor SF, Liberzon I. Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage* 2002;16:331–348. [PubMed: 12030820]
- Phelps EA. Emotion and cognition: Insights from studies of the human amygdala. *Annual Review of Psychology* 2006;57:27–53.
- Phelps EA, Ling S, Carrasco M. Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science* 2006;17:292–299. [PubMed: 16623685]
- Phelps EA, Sharot T. How (and why) emotion enhances the subjective sense of recollection. *Current Directions in Psychological Science* 2008;17:147–152.
- Prabhakaran V, Narayanan K, Zhao Z, Gabrieli JDE. Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience* 2000;3:85–90.
- Preston AR, Gabrieli JDE. Dissociation between explicit memory and configural memory in the human medial temporal lobe. *Cerebral Cortex* 2008;18:2192–2207. [PubMed: 18234685]
- Protzner AB, McIntosh AR. Modulation of ventral prefrontal cortex functional connections reflects the interplay of cognitive processes and stimulus characteristics. *Cerebral Cortex*. 2008
- Prull MW, Dawes LLC, Martin AM III, Rosenberg HF, Light LL. Recollection and familiarity in recognition memory: Adult age differences and neuropsychological test correlates. *Psychology and Aging* 2006;21:107–118. [PubMed: 16594796]
- Puce A, Allison T, Gore JC, McCarthy G. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology* 1995;74:1192–1199. [PubMed: 7500143]
- Qin J, Mitchell KJ, Johnson MK, Krystal JH, Southwick SM, Rasmusson AM, et al. Reactions to and memories for the September 11, 2001 terrorist attacks in adults with posttraumatic stress disorder. *Applied Cognitive Psychology* 2003;17:1081–1097.
- Qin J, Raye CL, Johnson MK, Mitchell KJ. Source ROCs are (typically) curvilinear: Comment on Yonelinas (1999). *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2001;27:1110–1115.
- Quamme JR, Yonelinas AP, Norman KA. Effect of unitization on associative recognition in amnesia. *Hippocampus* 2007;17:192–200. [PubMed: 17203466]
- Ragland JD, Valdez JN, Loughhead J, Gur RC, Gur RE. Functional magnetic resonance imaging of internal source monitoring in schizophrenia: Recognition with and without recollection. *Schizophrenia Research* 2006;87:160–171. [PubMed: 16814525]
- Rahhal TA, May CP, Hasher L. Truth and character: Sources that older adults can remember. *Psychological Science* 2002;13:101–105. [PubMed: 11933991]

- Rajah MN, D'Esposito M. Region-specific changes in prefrontal function with age: a review of PET and fMRI studies on working and episodic memory. *Brain* 2005;128:1964–1983. [PubMed: 16049041]
- Rajarethinam R, Sahni S, Rosenberg DR, Keshavan MS. Reduced superior temporal gyrus volume in young offspring of patients with schizophrenia. *American Journal of Psychiatry* 2004;161:1121–1124. [PubMed: 15169705]
- Ranganath C, Blumenfeld RS. Doubts about double dissociations between short-and long-term memory. *Trends in Cognitive Sciences* 2005;9:374–380. [PubMed: 16002324]
- Ranganath, C.; Blumenfeld, RS. Prefrontal cortex and memory. In: Byrne, J.; Eichenbaum, H., editors. *Memory systems. Learning and memory: A comprehensive reference*. Vol. 3. Oxford: Elsevier; 2008. p. 261-280.(Series Ed.) (Vol. Ed.)
- Ranganath C, Johnson MK, D'Esposito M. Left anterior prefrontal activation increases with demands to recall specific perceptual information. *The Journal of Neuroscience* 2000;20:RC108:1–5. [PubMed: 10627575]
- Ranganath C, Minzenberg MJ, Ragland JD. The cognitive neuroscience of memory function and dysfunction in schizophrenia. *Biological Psychiatry* 2008;64:18–25. [PubMed: 18495087]
- Rauch SL, Whalen PJ, Shin LM, McInerney SC, Macklin ML, Lasko NB, et al. Exaggerated amygdala response to masked facial stimuli in posttraumatic stress disorder: A functional MRI study. *Biological Psychiatry* 2000;47:769–776. [PubMed: 10812035]
- Raye CL, Johnson MK, Mitchell KJ, Greene EJ, Johnson MR. Refreshing: A minimal executive function. *Cortex* 2007;43:135–145. [PubMed: 17334213]
- Raye C, Johnson MK, Mitchell KJ, Nolde SF, D'Esposito M. fMRI investigations of left and right PFC contributions to episodic remembering. *Psychobiology* 2000;28:197–206.
- Raye CL, Johnson MK, Mitchell KJ, Reeder JA, Greene EJ. Neuroimaging a single thought: Dorsolateral PFC activity associated with refreshing just-activated information. *NeuroImage* 2002;15:447–453. [PubMed: 11798278]
- Raz, N. Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In: Craik, FIM.; Salthouse, TA., editors. *Handbook of aging and cognition: Second edition*. Mahwah, NJ: Erlbaum; 2000. p. 1-90.
- Raz N, Lindenberger U, Rodrigue KM, Kennedy KM, Head D, Williamson A, et al. Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex* 2005;15:1676–1689. [PubMed: 15703252]
- Raz N, Rodrigue KM. Differential aging of the brain: Patterns, cognitive correlates and modifiers. *Neuroscience and Biobehavioral Reviews* 2006;30:730–748. [PubMed: 16919333]
- Raz N, Rodrigue KM, Head D, Kennedy KM, Acker JD. Differential aging of the medial temporal lobe: A study of a five-year change. *Neurology* 2004;62:433–438. [PubMed: 14872026]
- Reinartz MT, Verfaellie M, Milberg WP. Memory conjunction errors in normal and amnesic subjects. *Journal of Memory and Language* 1996;35:286–299.
- Reisberg, D.; Heuer, F. Memory for emotional events. In: Reisberg, D.; Hertel, P., editors. *Memory and emotion*. New York: Oxford University Press; 2004. p. 3-41.
- Reuter-Lorenz PA. New visions of the aging mind and brain. *Trends in Cognitive Sciences* 2002;6:394–400. [PubMed: 12200182]
- Riccio DC, Ackil J, Burch-Vernon A. Forgetting of stimulus attributes: Methodological implications for assessing associative phenomena. *Psychological Bulletin* 1992;112:433–445. [PubMed: 1438637]
- Richardson MP, Strange BA, Dolan RJ. Encoding of emotional memories depends on amygdala and hippocampus and their interactions. *Nature Neuroscience* 2004;7:278–285.
- Ritchey M, Dolcos F, Cabeza R. Role of amygdala connectivity in the persistence of emotional memories over time: An event-related fMRI investigation. *Cerebral Cortex* 2008;18:2494–2504. [PubMed: 18375529]
- Rizzo L, Danion J-M, Van der Linden M, Grange´ D, Rohmer J-G. Impairment of memory for spatial context in schizophrenia. *Neuropsychology* 1996;10:376–384.
- Roediger HL III, Geraci L. Aging and the misinformation effect: A neuropsychological analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2007;33:321–334.

- Roediger HL III, McDermott KB. Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1995;21:803–814.
- Ross, M. Validating memories. In: Stein, NL.; Ornstein, PA.; Tversky, B.; Brainerd, C., editors. *Memory for everyday and emotional events*. Mahwah, NJ: Erlbaum; 1997. p. 49-81.
- Rossi S, Pasqualetti P, Zito G, Vecchio F, Cappa SF, Miniussi C, et al. Prefrontal and parietal cortex in human episodic memory: an interference study by repetitive transcranial magnetic stimulation. *European Journal of Neuroscience* 2006;23:793–800. [PubMed: 16487159]
- Rotello CM, Macmillan NA, Reeder JA. Sum-difference theory of remembering and knowing: A two-dimensional signal-detection model. *Psychological Review* 2004;111:588–616. [PubMed: 15250777]
- Rubin DC, Feldman ME, Beckham JC. Reliving, emotions, and fragmentation in the autobiographical memories of veterans diagnosed with PTSD. *Applied Cognitive Psychology* 2004;18:17–35.
- Rubin DC, Schulkind MD. Distribution of important and word-cue autobiographical memories in 20-, 35-, and 70-year-old adults. *Psychology and Aging* 1997;12:524–535. [PubMed: 9308099]
- Rugg MD, Curran T. Event-related potentials and recognition memory. *Trends in Cognitive Sciences* 2007;11:251–257. [PubMed: 17481940]
- Rugg MD, Fletcher PC, Chua PM-L, Dolan RJ. The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage* 1999;10:520–529. [PubMed: 10547329]
- Rugg MD, Otten LJ, Henson RNA. The neural basis of episodic memory: evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society B* 2002;357:1097–1110.
- Rugg MD, Wilding EL. Retrieval processing and episodic memory. *Trends in Cognitive Sciences* 2000;4:108–115. [PubMed: 10689345]
- Ryan L, Nadel L, Keil K, Putnam K, Schnyer D, Trouard T, et al. Hippocampal complex and retrieval of recent and very remote autobiographical memories: Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus* 2001;11:707–714. [PubMed: 11811665]
- Rybash JM, Hruby-Bopp KL. Source monitoring and false recollection: A life span developmental perspective. *Experimental Aging Research* 2000;26:75–87. [PubMed: 10689557]
- Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. *Nature Reviews Neuroscience* 2007;8:657–661.
- Schacter DL, Harbluk JL, McLachlan DR. Retrieval without recollection: An experimental analysis of source amnesia. *Journal of Verbal Learning and Verbal Behavior* 1984;23:593–611.
- Schacter DL, Israel L, Racine C. Suppressing false recognition in younger and older adults: The distinctiveness heuristic. *Journal of Memory and Language* 1999;40:1–24.
- Schacter DL, Koutstaal W, Norman KA. False memories and aging. *Trends in Cognitive Sciences* 1997;1:229–236.
- Schacter DL, Osowiecki D, Kaszniak AW, Kihlstrom JF, Valdiserri M. Source memory: Extending the boundaries of age-related deficits. *Psychology and Aging* 1994;9:81–89. [PubMed: 8185872]
- Schacter DL, Reiman E, Curran T, Yun LS, Bandy D, McDermott KB, et al. Neuroanatomical correlates of veridical and illusory recognition memory: Evidence from positron emission tomography. *Neuron* 1996;17:267–274. [PubMed: 8780650]
- Schacter DL, Wagner AD. Perspectives: neuroscience. Remembrance of things past. *Science* 1999;285:1503–1504. [PubMed: 10498535]
- Schneider, A. *The confabulating mind: How the brain creates reality*. New York: Oxford University Press; 2008.
- Shallice T, Fletcher P, Frith CD, Grasby P, Frackowiak RSJ, Dolan RJ. Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* 1994;368:633–635. [PubMed: 8145849]
- Sharot T, Delgado MR, Phelps EA. How emotion enhances the feeling of remembering. *Nature Neuroscience* 2004;7:1376–1380.
- Sharot T, Yonelinas AP. Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition* 2008;106:538–547. [PubMed: 17451666]

- Shenton ME, Dickey CC, Frumin M, McCarley RW. A review of MRI findings in schizophrenia. *Schizophrenia Research* 2001;49:1–52. [PubMed: 11343862]
- Shergill SS, Brammer MJ, Fukuda H, Williams SCR, Murray RM, McGuire PK. Engagement of brain areas implicated in processing inner speech in people with auditory hallucinations. *British Journal of Psychiatry* 2003;182:525–531. [PubMed: 12777344]
- Shimamura, AP. Memory and the prefrontal cortex Structure and function of the human prefrontal cortex. In: Grafman, J.; Holyoak, KJ.; Boller, F., editors. *Annals of the New York Academy of Sciences*. Vol. Vol. 769. 1995. p. 151-159.
- Shimamura, AP. Relational binding theory and the role of consolidation in memory retrieval. In: Squire, LR.; Schacter, DL., editors. *Neuropsychology of memory*, 3rd Ed. New York: The Guilford Press; 2002. p. 61-72.
- Shimamura AP, Squire LR. A neuropsychological study of fact memory and source amnesia. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1987;13:464–473.
- Shin LM, Rauch SL, Pitman RK. Amygdala, medial prefrontal cortex, and hippocampal function in PTSD. *Annals of the New York Academy of Sciences* 2006;1071:67–79. [PubMed: 16891563]
- Shohamy D, Wagner AD. Integrating memories in the human brain: Hippocampal-midbrain encoding of overlapping events. *Neuron* 2008;60:378–389. [PubMed: 18957228]
- Siegle GJ, Steinhauer SR, Thase ME, Stenger VA, Carter CS. Can't shake that feeling: Event-related fMRI assessment of sustained amygdala activity in response to emotional information in depressed individuals. *Biological Psychiatry* 2002;51:693–707. [PubMed: 11983183]
- Siegle GJ, Thompson W, Carter CS, Steinhauer SR, Thase ME. Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: Related and independent features. *Biological Psychiatry* 2007;61:198–209. [PubMed: 17027931]
- Simons, JS. Constraints on cognitive theories from neuroimaging studies of source memory. In: Rösler, F.; Ranganath, C.; Röder, B.; Kluwe, RH., editors. *Neuroimaging and Psychological Theories of Human Memory*. Oxford: Oxford University Press; (in press).
- Simons JS, Davis SW, Gilbert SJ, Frith CD, Burgess PW. Discriminating imagined from perceived information engages brain areas implicated in schizophrenia. *NeuroImage* 2006;32:696–703. [PubMed: 16797186]
- Simons JS, Dodson CS, Bell D, Schacter DL. Specific-and partial-source memory: Effects of aging. *Psychology and Aging* 2004;19:689–694. [PubMed: 15584793]
- Simons JS, Gilbert SJ, Owen AM, Fletcher PC, Burgess PW. Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. *Journal of Neurophysiology* 2005;94:813–820. [PubMed: 15728761]
- Simons JS, Henson RNA, Gilbert SJ, Fletcher PC. Separable forms of reality monitoring supported by the anterior prefrontal cortex. *Journal of Cognitive Neuroscience* 2008;20:447–457. [PubMed: 18004946]
- Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter DL. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. *NeuroImage* 2003;19:613–626. [PubMed: 12880792]
- Simons JS, Owen AM, Fletcher PC, Burgess PW. Anterior prefrontal cortex and the recollection of contextual information. *Neuropsychologia* 2005;43:1774–1783. [PubMed: 16154453]
- Simons JS, Peers PV, Hwang DY, Ally BA, Fletcher PC, Budson AE. Is the parietal lobe necessary for recollection in humans? *Neuropsychologia* 2008;46:1185–1191. [PubMed: 17850832]
- Simons J, Peers P, Mazuz Y, Berryhill M, Olson I. Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. 2009 Manuscript under review.
- Simons JS, Verfaellie M, Galton CJ, Miller BL, Hodges JR, Graham KS. Recollection-based memory in frontotemporal dementia: implications for theories of long-term memory. *Brain* 2002;125:2523–2536. [PubMed: 12390977]
- Skinner EI, Fernandes MA. Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia* 2007;45:2163–2179. [PubMed: 17445844]
- Slotnick SD, Klein SA, Dodson CS, Shimamura AP. An analysis of signal detection and threshold models of source memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2000;26:1499–1517.

- Slotnick SD, Moo LR, Segal JB, Hart J. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cognitive Brain Research* 2003;17:75–82. [PubMed: 12763194]
- Slotnick SD, Schacter DL. A sensory signature that distinguishes true from false memories. *Nature Neuroscience* 2004;7:664–672.
- Small GW, Bookheimer SY, Thompson PM, Cole GM, Huang S-C, Kepe V, et al. Current and future uses of neuroimaging for cognitively impaired patients. *Lancet Neurology* 2008;7:161–172. [PubMed: 18207114]
- Small SA, Tsai WY, DeLaPaz R, Mayeux R, Stern Y. Imaging hippocampal function across the human life span: Is memory decline normal or not? *Annals of Neurology* 2002;51:290–295. [PubMed: 11891823]
- Smith APR, Henson RNA, Dolan RJ, Rugg MD. fMRI correlates of the episodic retrieval of emotional contexts. *NeuroImage* 2004;22:868–878. [PubMed: 15193617]
- Smith APR, Henson RNA, Rugg MD, Dolan RJ. Modulation of retrieval processing reflects accuracy of emotional source memory. *Learning & Memory* 2005;12:472–479. [PubMed: 16204201]
- Sommer IEC, Diederer KMJ, Blom J-D, Willems A, Kushan L, Slotema K, et al. Auditory verbal hallucinations predominantly activate the *right* inferior frontal area. *Brain* 2008;131:3169–3177. [PubMed: 18854323]
- Spencer WD, Raz N. Differential effects of aging on memory for content and context: A meta-analysis. *Psychology and Aging* 1995;10:527–539. [PubMed: 8749580]
- Sperling RA, Bates JF, Chua EF, Cocchiarella AJ, Rentz DM, Rosen BR, et al. fMRI studies of associative encoding in young and elderly controls and mild Alzheimer's disease. *Journal of Neurology Neurosurgery and Psychiatry* 2003;74:44–50.
- Squire LR. Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory* 2004;82:171–177. [PubMed: 15464402]
- Squire, LR.; Knowlton, BJ. Memory, hippocampus, and brain systems. In: Gazzaniga, MS., editor. *The cognitive neurosciences*. Cambridge, MA: MIT Press; 1995. p. 825-837.
- Squire LR, Knowlton B, Musen G. The structure and organization of memory. *Annual Review of Psychology* 1993;44:453–495.
- Squire, LR.; Shragar, Y. Declarative memory system: amnesia. In: Byrne, J.; Eichenbaum, H., editors. *Memory systems. Learning and memory: A comprehensive reference*. Vol. Vol. 3. Oxford: Elsevier; 2008. p. 67-78.(Series Ed.) (Vol. Ed.)
- Squire LR, Stark CEL, Clark RE. The medial temporal lobe. *Annual Review of Neuroscience* 2004;27:279–306.
- Squire LR, Wixted JT, Clark RE. Recognition memory and the medial temporal lobe: a new perspective. *Nature Reviews Neuroscience* 2007;8:872–883.
- Squire LR, Zola-Morgan S. The medial temporal lobe memory system. *Science* 1991;253:1380–1386. [PubMed: 1896849]
- Staresina BP, Davachi L. Differential encoding mechanisms for subsequent associative recognition and free recall. *The Journal of Neuroscience* 2006;26:9162–9172. [PubMed: 16957073]
- Stark CEL, Bayley PJ, Squire LR. Recognition memory for single items and for associations is similarly impaired following damage to the hippocampal region. *Learning & Memory* 2002;9:238–242. [PubMed: 12359833]
- Stark CEL, Squire LR. Hippocampal damage equally impairs memory for single items and memory for conjunctions. *Hippocampus* 2003;13:281–292. [PubMed: 12699335]
- Starns JJ, Hicks JL. Source dimensions are retrieved independently in multidimensional monitoring tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2005;31:1213–1220.
- Starns JJ, Hicks JL, Brown NL, Martin BA. Source memory for unrecognized items: Predictions from multivariate signal detection theory. *Memory & Cognition* 2008;36:1–8.
- Steffens MC, Buchner A, Martensen H, Erdfelder E. Further evidence on the similarity of memory processes in the process dissociation procedure and in source monitoring. *Memory & Cognition* 2000;28:1152–1164.

- Stuss, DT.; Benson, DF. The frontal lobes. New York: Raven Press; 1986.
- Summerfield C, Greene M, Wager T, Egner T, Hirsch J, Mangels J. Neocortical connectivity during episodic memory formation. *PLoS Biology* 2006;4:855–864.
- Suzuki M, Fujii T, Tsukiura T, Okuda J, Umetsu A, Nagasaka T, et al. Neural basis of temporal context memory: A functional MRI study. *NeuroImage* 2002;17:1790–1796. [PubMed: 12498752]
- Swick D, Senkfor AJ, Van Petten C. Source memory retrieval is affected by aging and prefrontal lesions: Behavioral and ERP evidence. *Brain Research* 2006;1107:161–176. [PubMed: 16828722]
- Tapia G, Clarys D, El Hage W, Belzung C, Isingrini M. PTSD psychiatric patients exhibit a deficit in remembering. *Memory* 2007;15:145–153. [PubMed: 17534108]
- Thoma P, Zoppelt D, Wiebel B, Daum I. Recollection and familiarity in negative schizophrenia. *Neuropsychologia* 2006;44:430–435. [PubMed: 15993449]
- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences, USA* 1997;94:14792–14797.
- Tulving E, Kapur S, Craik FIM, Moscovitch M, Houle S. Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences of the United States of America* 1994;91:2016–2020. [PubMed: 8134342]
- Tulving E, Thomson DM. Encoding specificity and retrieval processes in episodic memory. *Psychological Review* 1973;80:352–373.
- Turner MS, Simons JS, Gilbert SJ, Frith CD, Burgess PW. Distinct roles for lateral and medial rostral prefrontal cortex in source monitoring of perceived and imagined events. *Neuropsychologia* 2008;46:1442–1453. [PubMed: 18294660]
- Uncapher MR, Otten LJ, Rugg MD. Episodic encoding is more than the sum of its parts: An fMRI investigation of multifeatured contextual encoding. *Neuron* 2006;52:547–556. [PubMed: 17088219]
- Uncapher MR, Rugg MD. Fractionation of the component processes underlying successful episodic encoding: A combined functional magnetic resonance imaging and divided-attention study. *Journal of Cognitive Neuroscience* 2008;20:240–254. [PubMed: 18275332]
- Valenzuela MJ, Breakspear M, Sachdev P. Complex mental activity and the aging brain: Molecular, cellular and cortical network mechanisms. *Brain Research Reviews* 2007;56:198–213. [PubMed: 17870176]
- Van Petten C. Relationship between hippocampal volume and memory ability in healthy individuals across the lifespan: review and meta-analysis. *Neuropsychologia* 2004;42:1394–1413. [PubMed: 15193947]
- Van Petten C, Luka BJ, Rubin SR, Ryan JP. Frontal brain activity predicts individual performance in an associative memory exclusion test. *Cerebral Cortex* 2002;12:1180–1192. [PubMed: 12379606]
- Velanova K, Lustig C, Jacoby LL, Buckner RL. Evidence for frontally mediated controlled processing differences in older adults. *Cerebral Cortex* 2007;17:1033–1046. [PubMed: 16774962]
- Viard A, Piolino P, Desgranges B, Chetelat G, Lebreton K, Landeau B, et al. Hippocampal activation for autobiographical memories over the entire lifetime in healthy aged subjects: An fMRI study. *Cerebral Cortex* 2007;17:2453–2467. [PubMed: 17204823]
- Vilberg KL, Rugg MD. Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia* 2007;45:2216–2225. [PubMed: 17449068]
- Vilberg KL, Rugg MD. Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia* 2008;46:1787–1799. [PubMed: 18343462]
- Vilberg KL, Rugg MD. An investigation of the effects of relative probability of old and new test items on neural correlates of successful and unsuccessful source memory. *Neuroimage*. (in press).
- Vinogradov S, Luks TL, Schulman BJ, Simpson GV. Deficit in a neural correlate of reality monitoring in schizophrenia patients. *Cerebral Cortex* 2008;18:2532–2539. [PubMed: 18321870]

- Vinogradov S, Luks TL, Simpson GV, Schulman BJ, Glenn S, Wong AE. Brain activation patterns during memory of cognitive agency. *NeuroImage* 2006;31:896–905. [PubMed: 16516497]
- Vogt, BA.; Laureys, S. Posterior cingulate, precuneal and retrosplenial cortices: cytology and components of the neural network correlates of consciousness. In: Layreys, S., editor. *Progress in brain research*. Vol. Vol. 150. The Netherlands: Elsevier; 2005. p. 205-217.
- Wagner AD. Working memory contributions to human learning and remembering. *Neuron* 1999;22:19–22. [PubMed: 10027285]
- Wagner AD, Poldrack RA, Eldridge LL, Desmond JE, Glover GH, Gabrieli JDE. Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport* 1998;9:3711–3717. [PubMed: 9858384]
- Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, et al. Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science* 1998;281:1188–1191. [PubMed: 9712582]
- Wagner AD, Shannon BJ, Kahn I, Buckner RL. Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences* 2005;9:445–453. [PubMed: 16054861]
- Wais PE. fMRI signals associated with memory strength in the medial temporal lobes: A meta-analysis. *Neuropsychologia* 2008;46:3185–3196. [PubMed: 18817791]
- Wais PE, Mickes L, Wixted JT. Remember/know judgments probe degrees of recollection. *Journal of Cognitive Neuroscience* 2008;20:400–405. [PubMed: 18004949]
- Wais PE, Squire LR, Wixted JT. In search of recollection and familiarity signals in the hippocampus. 2008 Manuscript under review.
- Waters FAV, Maybery MT, Badcock JC, Michie PT. Context memory and binding in schizophrenia. *Schizophrenia Research* 2004;68:119–125. [PubMed: 15099596]
- Weiss AP, Heckers S. Neuroimaging of declarative memory in schizophrenia. *Scandinavian Journal of Psychology* 2001;42:239–250. [PubMed: 11501738]
- Werner NS, Meindl T, Engel RR, Rosner R, Riedel M, Reiser M, et al. Hippocampal function during associative learning in patients with posttraumatic stress disorder. *Journal of Psychiatric Research* 2009;43:309–318. [PubMed: 18490028]
- West RL. An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin* 1996;120:272–292. [PubMed: 8831298]
- Whalley MG, Rugg MD, Smith APR, Dolan RJ, Brewin CR. Incidental retrieval of emotional contexts in post-traumatic stress disorder and depression: An fMRI study. *Brain and Cognition*. 2008
- Wheeler ME, Buckner RL. Functional-anatomic correlates of remembering and knowing. *NeuroImage* 2004;21:1337–1349. [PubMed: 15050559]
- Williams JMG, Barnhofer T, Crane C, Hermans D, Raes F, Watkins E, et al. Autobiographical memory specificity and emotional disorder. *Psychological Bulletin* 2007;133:122–148. [PubMed: 17201573]
- Wixted JT. Dual-process theory and signal-detection theory of recognition memory. *Psychological Review* 2007;114:152–176. [PubMed: 17227185]
- Woodruff CC, Johnson JD, Uncapher MR, Rugg MD. Content-specificity of the neural correlates of recollection. *Neuropsychologia* 2005;43:1022–1032. [PubMed: 15769488]
- Woodruff PWR, Wright IC, Bullmore ET, Brammer M, Howard RJ, Williams SCR, et al. Auditory hallucinations and the temporal cortical response to speech in schizophrenia: A functional magnetic resonance imaging study. *American Journal of Psychiatry* 1997;154:1676–1682. [PubMed: 9396945]
- Woodward TS, Weinstein S, Cairo TA, Metzack P, Ngan ETC, Kumar D. Hallucinations are associated with aberrant activation in inner speech regions during source monitoring [Abstract]. *Schizophrenia Research* 2008;102/1–3:96.
- Yonelinas AP. Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1994;20:1341–1354.
- Yonelinas AP. The contribution of recollection and familiarity to recognition and source-memory judgments: A formal dual-process model and an analysis of receiver operating characteristics. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1999;25:1415–1434.

- Yonelinas AP. The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language* 2002;46:441–517.
- Yonelinas AP, Kroll NEA, Quamme JR, Lazzara MM, Sauve M-J, Widaman KF, et al. Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nature Neuroscience* 2002;5:1236–1241.
- Yonelinas AP, Parks CM. Receiver operating characteristics (ROCs) in recognition memory: A review. *Psychological Bulletin* 2007;133:800–832. [PubMed: 17723031]
- Yonelinas AP, Widaman K, Mungas D, Reed B, Weiner MW, Chui HC. Memory in the aging brain: Doubly dissociating the contribution of the hippocampus and entorhinal cortex. *Hippocampus* 2007;17:1134–1140. [PubMed: 17636547]
- Yu J, Bellezza FS. Process dissociation as source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 2000;26:1518–1533.
- Zacks, RT.; Hasher, L. Aging and long-term memory: Deficits are not inevitable. In: Bialystok, E.; Craik, FIM., editors. *Lifespan cognition: Mechanisms of change*. New York, NY: Oxford University Press; 2006. p. 162-177.
- Zaragoza MS, Koshmider JW III. Misled subjects may know more than their performance implies. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 1989;15:246–255.
- Zaragoza MS, Lane SM. Processing resources and eyewitness suggestibility. *Journal of Legal and Criminological Psychology* 1998;3:305–320.
- Zubieta J-K, Chinitz JA, Lombardi U, Fig LM, Cameron OG, Liberzon I. Medial frontal cortex involvement in PTSD symptoms: A SPECT study. *Journal of Psychiatric Research* 1999;33:259–264. [PubMed: 10367992]

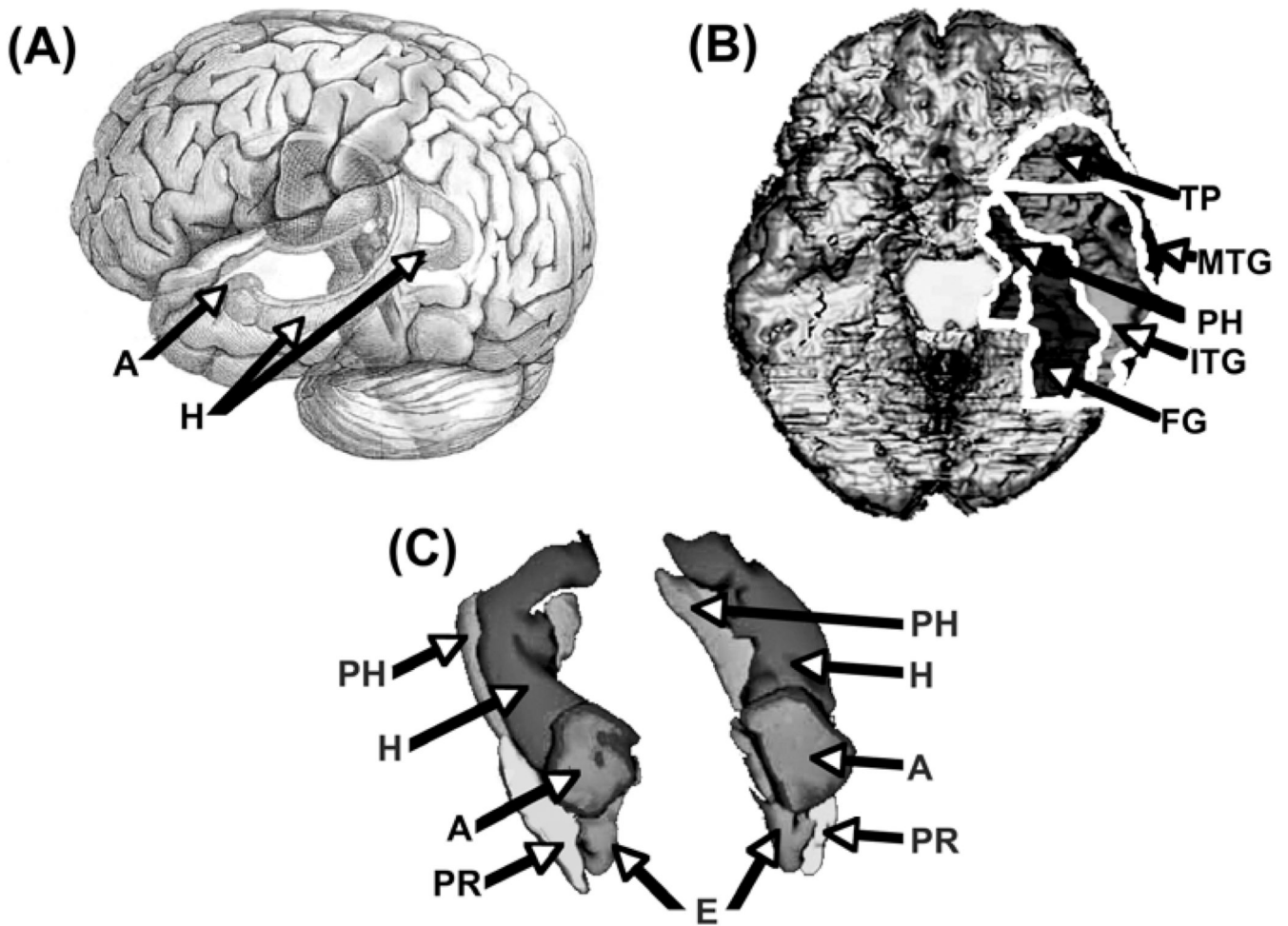


Figure 1.

Anatomical relationships between various temporal regions. (A) Three-D figure of the human brain (frontal lobes are to the left), with amygdala and hippocampus indicated. (B) View of temporal regions from below; top of the figure is the front of the brain. (C) Cut-away of medial temporal lobe structures as viewed from the front (adapted with permission from Figure 1A of Dolcos, F., LaBar, K. S., & Cabeza, R. [2004]. Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron*, 42, 855–863). A-amygdala, E-entorhinal cortex, FG-fusiform gyrus, H-hippocampus, ITG-inferior temporal gyrus, MTG-middle temporal gyrus, PR-perirhinal cortex (sometimes referred to in the literature as anterior parahippocampal gyrus), PH-parahippocampal cortex (sometimes referred to in the literature as posterior parahippocampal gyrus), TP-temporal pole.

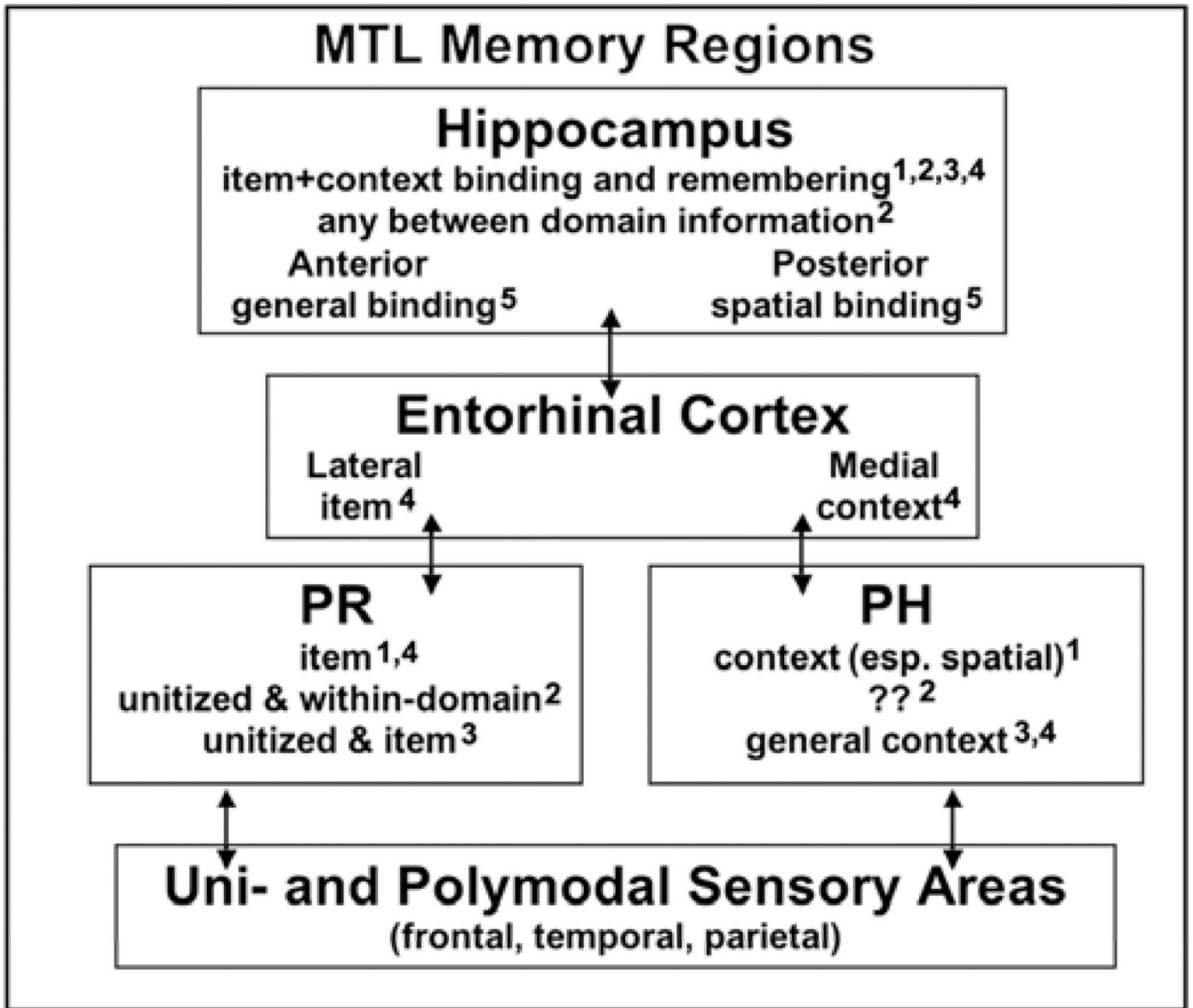


Figure 2. Schematic of the relationship between MTL regions with summary of several current hypotheses regarding their functions. MTL-medial temporal lobes; PR-perirhinal cortex; PH-parahippocampal cortex. Superscripts refer to: ¹Davachi (2006); ²Mayes et al. (2007); ³Diana et al. (2007); ⁴Eichenbaum et al. (2007); ⁵Awipi and Davachi (2008).

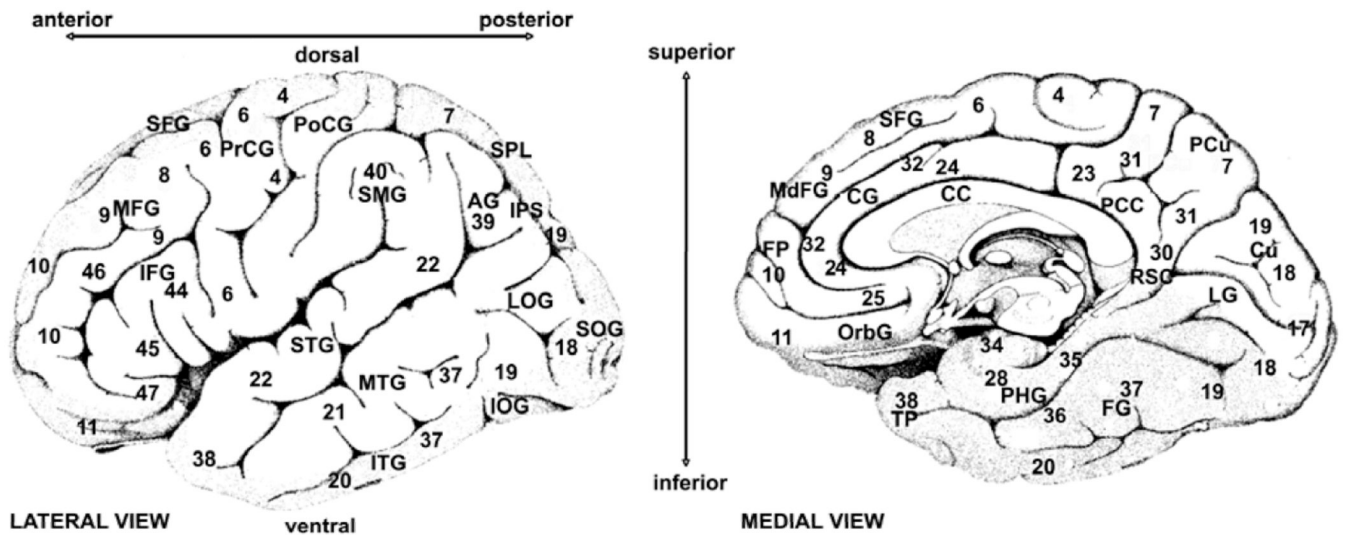
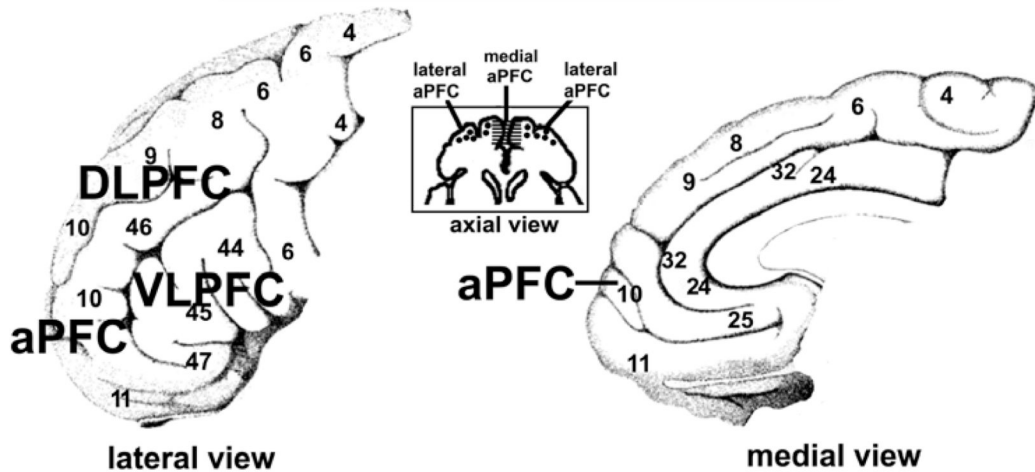


Figure 3. Lateral (left) and medial (right) views of the cortex. Numbers indicate approximate Brodmann Areas (BA). Abbreviations for regions (areas are approximate) are: AG-angular gyrus; CC-corpora collosa; CG-cingulate gyrus; Cu-cuneus; FG-fusiform gyrus; FP-frontal pole; IFG-inferior frontal gyrus; IOG-inferior occipital gyrus; IPS- intraparietal sulcus; ITG-inferior temporal gyrus; LG-lingual gyrus; LOG-lateral occipital gyrus; MdFG-medial frontal gyrus; MFG-middle frontal gyrus; MTG-middle temporal gyrus; OrbG-orbital gyrus; PCC-posterior cingulate cortex; PCu-precuneus; PHG-parahippocampal gyrus; PrCG-precentral gyrus; PoCG-postcentral gyrus; RSC-retrosplenial cortex; SFG-superior frontal gyrus; SOG-superior occipital gyrus; SMG-supramarginal gyrus; SPL-superior parietal lobule; STG-superior temporal gyrus; TP-temporal pole. In addition, entorhinal cortex (not labeled) is primarily comprised of BA 28, 34; perirhinal cortex-BA 35, 36.

LEFT / RIGHT PFC
 systematic / heuristic processing¹¹
 monitoring more / less differentiated information^{9, 11}
 production-generation / monitoring³
 yet-to-be-specified retrieval processes / monitoring¹⁵

DLPFC
 encoding: elaborative & organizational processes^{1, 13}
 remembering:
 evaluation (left more-, right less-differentiated)^{9, 10}
 mid: online monitoring & manipulation¹²
 posterior: monitoring⁴

aPFC
lateral: pre-retrieval control processes¹⁶
 selection/maintenance of goal, set, agenda^{7,8,13}
medial: monitoring self-generated information^{16 - 18}



VLPFC
 encoding: control processes to select specific features^{1, 13}
 remembering:
 mid: active retrieval/selection of information^{10, 12}
 left anterior: evaluating internally-generated information^{5, 10}
 left posterior: retrieval verbal information^{2, 6, 8, 14, 19}
 right posterior: focus on perceptual information^{5, 10}
 right posterior: retrieval non-verbal information^{2, 6, 8, 14, 19}

Figure 4. Summary of some hypotheses about functional specificity of prefrontal cortex (PFC) in source memory, and example references, as described in text. Nomenclature for anatomical regions varies historically and between labs, but generally, PFC areas involved in source memory include: Medial (hatch lines in axial view) and lateral (speckled in axial view) areas of anterior PFC (aPFC; primarily BA 10); aPFC is also sometimes referred to as fronto-polar cortex, or rostral PFC. Dorsolateral PFC (DLPFC = primarily dorsal BA 10, BAs 46, 9, but some investigators also include BA 8 and dorsal BA 6; mid-DLPFC = primarily BAs 9, 46; posterior DLPFC = primarily BA 9). Ventrolateral PFC (VLPFC = primarily BAs 47, 45, 44, but some investigators also include BAs 11 and ventral 6; anterior VLPFC = primarily

BA 47; mid-VLPFC = primarily BA 45; posterior VLPFC = primarily BA 44); VLPFC is also sometimes referred to as inferior frontal cortex (IFC). The inferior frontal sulcus is usually taken as the boundary between DLPFC and VLPFC (e.g., Kuhl & Wagner, 2009). Superscripts refer to: ¹Blumenfeld and Ranganath (2007); ²Buckner and Wheeler (2001); ³Cabeza et al. (2003); ⁴Dobbins and Han (2006); ⁵Dobbins and Wagner (2005); ⁶Kelley et al. (1998); ⁷Lepage et al. (2000); ⁸McDermott et al. (1999); ⁹Mitchell et al., 2004; ¹⁰Mitchell et al. (2008); ¹¹Nolde, Johnson, and Raye, (1998); ¹²Petrides (2002); ¹³Ranganath and Blumenfeld, 2008; ¹⁴Raye et al. (2000); ¹⁵Rugg et al. (2002; see also, Hayama et al., 2008); ¹⁶Simons et al. (2008); ¹⁷Simons, Gilbert, et al., (2005); ¹⁸Vinogradov et al. (2006; see also Vinogradov et al., 2008); ¹⁹Wagner, Poldrack, et al. (1998).

Table 1

Summary of SM-related behavioral and brain activity differences in populations that exhibit behavioral source memory deficits, as discussed in text.

Aging
Behavioral Findings

- Memory binding deficit (feature combination deficit > item deficit)
- SM deficits > item deficits
- R deficits > F deficits
- Poor calibration of responses on subjective (e.g., confidence) vs objective (e.g., accuracy) memory measures
- Overweighting of semantic information
- Preserved SM for affective information (and maybe overweighting)
- Increased false memory

Imaging Findings

- Some MTL atrophy, dysfunction (especially hippocampus) in binding and episodic encoding tasks
 - PFC atrophy disproportionate to other brain areas, dysfunction (especially dorsolateral PFC); SM-related left lateral PFC deficit related to evaluating specific information
 - Reduced PFC activity for SM in areas active in young adults, with sometimes greater activity in contralateral PFC, or other, areas in older adult “good performers” (compensatory?)
 - Changes in PFC-MTL (increase?) and MTL-posterior (decrease?) functional connectivity
 - Reduced specificity of activity in posterior regions (e.g., extrastriate cortex)
 - Relatively preserved amygdala and orbitofrontal cortex function in emotional SM tasks
-

Schizophrenia**Behavioral Findings**

- Memory binding deficit (feature combination deficit > item deficit)
- Hallucinations and deficits in laboratory reality monitoring tasks (e.g., *self vs other*)

Imaging Findings

- MTL structural changes (e.g., reduced volume), dysfunction (especially hippocampus?)
 - PFC structural changes, dysfunction
 - Abnormal PFC-hippocampus connectivity during working memory tasks
 - Reduced STG volume (related to severity of hallucinations), dysfunction (deficit when associating content of speech with source)
 - Attenuated difference between activity for associative vs item memory in left DLPFC, ACC, STG during encoding
 - Attenuated difference between activity for associative vs item memory in left DLPFC, right inferior PFC, medial PFC, superior parietal cortex at test
 - Deficits in medial anterior PFC during reality monitoring tasks
 - For hallucinating patients:
 - more wide-spread activity in left BA 40, 44 during reality monitoring judgments (*was the word said or heard?*)
 - disruption in modulatory relationship between speech generation (e.g., left inferior frontal cortex) and speech perception (e.g., temporal cortex) areas
-

PTSD**Behavioral Findings**

- Likely memory binding deficits (feature combination deficit > item deficit), but evidence not conclusive

- Increased attention to negative information
- Fragmented, impoverished episodic memory
- Reduced R responses
- SM deficits > item deficits (for both neutral and emotional information)

Imaging Findings

- Hippocampal structural changes (e.g., reduced volume), dysfunction (attenuated activity during encoding and remembering of emotional information)
- PFC structural changes
- Amygdala structural changes, dysfunction
- Attenuated PFC, middle temporal cortex, and precuneus activity, but greater superior temporal and parahippocampal activity during associative encoding; possible deficit in PFC-temporal functional connectivity during encoding
- Attenuated PFC and temporal cortex activity during test in associative tasks
- Exaggerated amygdala response, reduced medial PFC, hippocampal activity during exposure to emotional stimuli

Depression**Behavioral Findings**

- Over-general episodic memories
- SM deficits
- Rumination
- Memory bias for negative information

Imaging Findings

- Sustained amygdala activity, attenuated left DLPFC activity during processing of negative information
- Increased amygdala-hippocampal functional connectivity during encoding of negative information
- Increased activity in posterior “self” areas (posterior cingulate, inferior parietal lobes) when processing negative information
- Disruption of control circuit (cingulate, amygdala, DLPFC) involved in emotion regulation

Notes. ACC-anterior cingulate cortex; DLPFC-dorsolateral prefrontal cortex; F-familiarity (know); MTL-medial temporal lobes; PFC-prefrontal cortex; R-recollection (remember); SM-source memory/source monitoring; STG-superior temporal gyrus.

Table 2

Some continuing issues for a cognitive neuroscience of source memory.

-
- **Clarifying features**
 - Distinguishing between encoded features, activated/revived features, and used (weighted, evaluated) features
 - Differentiating the “self” as a feature, the originator, and the experiencer, of events
 - Assessing emotion as a feature of memory vs a modulator of other feature information
 - Clarifying how feature A may have an impact on judgments about feature B, and how information is imported (or cumulated) across representations
 - Characterizing the relation between information that yields a feeling of familiarity and information that yields a feeling of more specific recollection
 - Identifying the nature of the information (e.g., features, feature combinations) to which specific brain areas, or networks of areas, are sensitive
 - Specifying brain areas, and/or dynamic networks, associated with subjective ratings of vividness (e.g., MCQ)
 - **Clarifying processes**
 - Specifying the component processes recruited during source memory (e.g., *refreshing, rehearsing, noting, shifting, retrieving*) and how they are coordinated during encoding and remembering
 - Differentiating brain regions, networks, and temporal dynamics associated with
 - ◆ setting and implementing agendas (e.g., for organization, feature binding) during the encoding of events
 - ◆ making source attributions (e.g., retrieval orientation; looking for/weighting detail of type *X*; self-cuing; feature activation; evaluation/monitoring).
 - Identifying the conditions leading to, and functional significance of, increases/decreases of activity in a brain area vs increases/decreases in functional connectivity between areas
 - **Understanding disrupted source memory**
 - Capitalizing on advances on the issues noted above in the systematic study of
 - ◆ groups showing source memory deficits (e.g., older adults, individuals with schizophrenia, PTSD, depression)
 - ◆ individual differences related to errors in source memory (e.g., imagery ability, suggestibility, anxiety)