Psychological Bulletin
2009, Vol. 135, No. 4, 638–677

0033-2909/09/$12.00 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

Focusing primarily on functional magnetic resonance imaging (fMRI), this article reviews evidence regarding the roles of subregions of the medial temporal lobes, prefrontal cortex, posterior representational areas, and parietal cortex in source memory. In addition to evidence from standard episodic memory tasks assessing accuracy for neutral information, the article considers studies assessing the qualitative characteristics of memories, the encoding and remembering of emotional information, and false memories, as well as evidence from 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, fMRI is advancing understanding of source memory and highlighting unresolved issues. A continued 2-way interaction between cognitive theory, as illustrated by the source monitoring framework (M. K. Johnson, S. Hashtroudi, & D. S. Lindsay, 1993), and evidence from cognitive neuroimaging studies should clarify 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.

Keywords: source memory, prefrontal cortex (PFC), medial temporal lobes (MTL), parietal

In 1993, *Psychological Bulletin* published an article 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 article, 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 understanding (p. 19). The current article 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; Schnider, 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). Evidence and insights also come from neurocomputational modeling (Elfman, Parks, & Yonelinas, 2008; Li, Naveh-Benjamin, & Lindenberger, 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).

Karen J. Mitchell and Marcia K. Johnson, Department of Psychology, Yale University.

Preparation of this review was supported by National Institute of Aging 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 version of this article. We thank Kathleen Muller for help in organizing the references.

Correspondence concerning this article should be addressed to Karen J. Mitchell, Department of Psychology, Yale University, Box 208205, New Haven, CT 06520-8205. E-mail: karen.mitchell@yale.edu

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 et al., 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).

Findings from fMRI studies 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 have drawn 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 in 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 understanding 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 with 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 of the preferred model.

According to the SMF, mental experiences are attributed to source categories, such as perception, memory, dreaming, imagination, belief, and so forth, and to more specific sources (e.g., "Joe said it"; "It was a blue word on the list"; "It happened yesterday"), according to 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. However, active information (including a single feature) that does not cohere into fully formed representations can nevertheless affect perception and thought (e.g., masked priming; Marcel, 1983). In short, some source attributions are relatively nonspecific ("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. However, according to the SMF, exactly which processes are involved and the specificity of the information on which they work 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 how it is combined and evaluated during the attribution process. For example, given identical encoding, later asking a participant "Did you generate this item?" would lead to an emphasis (heavier weighting) on cognitive operations information, whereas asking the participant "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 the information is required to be (Johnson & Raye, 2000). A person would likely require less specific detail to attribute a comment to someone when reminiscing with friends than when testifying in court; he or she may have more confidence in a fairly vague recollection when attributing an action to something a colleague did at a conference last year versus 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). People *take as episodic memories* those mental experiences for which they have encoded, bound, revived, and evaluated features that induce (and sometimes seduce) them to attribute the source of the experience as a unique event that occurred in their 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); criterial recollection tasks, which encourage participants to base their memory judgment on whether a certain (criterial) 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 nonpresented 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), much overlap also would be expected in underlying processes (Steffens, Buchner, Martensen, & Erdfelder, 2000; Yu & Bellezza, 2000), and presumably then, 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 Versus Dual-Process Models

A complete review of dual-process models is beyond the scope of this article, 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 showing a disproportionate disruption in remember responses in older adults (Jacoby, Bishara, Hessels, & Toth, 2005; Jennings & Jacoby, 1997) and amnesiacs (Quamme, Yonelinas, & Norman, 2007; see Kensinger & Corkin, 2008, for a review, but see also 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, 1999, 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 (i.e., recollection can succeed or fail) and not necessarily that one will remember all features of a memory or none at all (Parks & Yonelinas, 2007). 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 in which 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 previously, 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, and 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

---

[1] From this perspective, memory strength is orthogonal to recollection and familiarity (e.g., one 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 versus 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, 2008; Wixted, 2007, for further discussion).

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 thus similar brain mechanisms should be expected 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). 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 et al., 2004), 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 versus 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 region is composed of the hippocampal formation (dentate gyrus, hippocampus proper [including the cornu ammonis, or CA, fields], subicular complex, and entorhinal cortex), as well as the perirhinal and parahippocampal cortices. In a later section on emotion and source memory, we 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, Yonelinas, & Ranganath, 2007; Eichenbaum et al., 2007; Mayes, Montaldi, & Migo, 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; Bunsey & Eichenbaum, 1996) and patient (Gold, Smith, 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 in associative or relational remembering (see Aggleton & Brown, 1999; Burgess, Maguire, & O'Keefe, 2002; Cohen & Eichenbaum, 1993; Eichenbaum et al., 2007, 2008; Kensinger & Corkin, 2008; Squire & Zola-Morgan, 1991, for reviews). Furthermore, there is evidence that amnesiacs with hippocampal damage show greater deficits in source than in item memory (Giovanello, Verfaellie, & Keane, 2003; Yonelinas et al., 2002; see Mayes et al., 2007, for a review), though this remains controversial (Gold, Hopkins, &

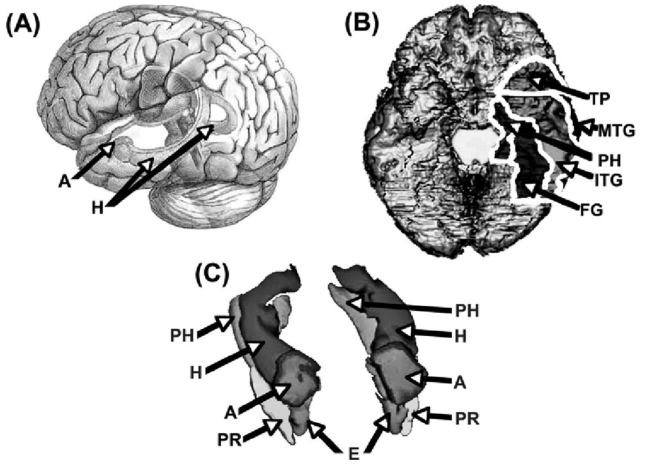


Figure 1. Anatomical relationships between various temporal regions. Panel A. Three-dimensional figure of the human brain (frontal lobes are to the left), with amygdala (A) and hippocampus (H) indicated. Panel B. View of temporal regions from below; top of the figure is the front of the brain. Panel C. Cut-away of medial temporal lobe structures as viewed from the front. E = entorhinal cortex; FG = fusiform gyrus; 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. Panel C from "Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events," by F. Dolcos, K. S. LaBar, and R. Cabeza, 2004, *Neuron, 42,* 855–863. Copyright 2004 by Cell Press. Adapted with permission.

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 et al., 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 with 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. nonassociative 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) proposed 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 thus far, as well as with 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).

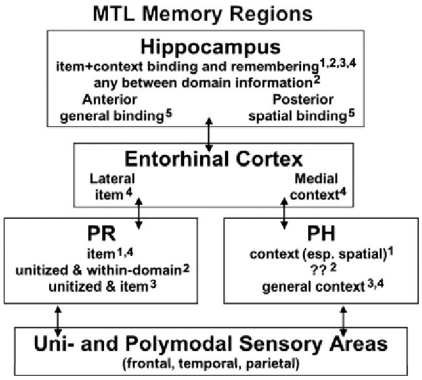


Figure 2. Schematic of the relationship between MTL regions with summary of several current hypotheses regarding their functions. MTL = medial temporal lobes; PR = perirhinal cortex; PH = parahippocampal cortex. Footnotes: [1]Davachi (2006); [2]Mayes et al. (2007); [3]Diana et al. (2007); [4]Eichenbaum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

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. On the basis of 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) proposed 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 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) proposed that parahippocampal activity is engaged for contextual information more generally (see also Bar, Aminoff, & Schacter, 2008), and Mayes et al. (2007) noted 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) suggested that activity in perirhinal cortex reflects familiarity processes and that 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. suggested, hippocampus may always be activated for recollection of interitem 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). 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) argued 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 et al. (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 that were judged to be 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 or 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 1 and given an incorrect source attribution at Stage 2 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. noted this possibility and dismissed 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 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 nonlinear 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 versus novel information, or rather reflects something related to the subjective memorial experiences associated with recollection versus 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) versus 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 Figures 3 and 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 et al., 1984; Shimamura & Squire, 1987; Simons et al., 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, 1997b).[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 for old–new recognition. Since then, a large number of fMRI studies have found that source memory judgments, relative to old–new recognition, are associated with increased activity in left lateral PFC, including superior, middle, and

---

[2] An influential hypothesis based on early neuroimaging studies of episodic memory was the hemispheric encoding/retrieval asymmetry [HERA] model, which proposed that left PFC is engaged more than right in episodic *encoding* and right PFC is engaged more than left in episodic *retrieval* (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994; also Habib, Nyberg, & Tulving, 2003; Shallice et al., 1994). Lepage et al. (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 would be expected to operate across various memory tasks.

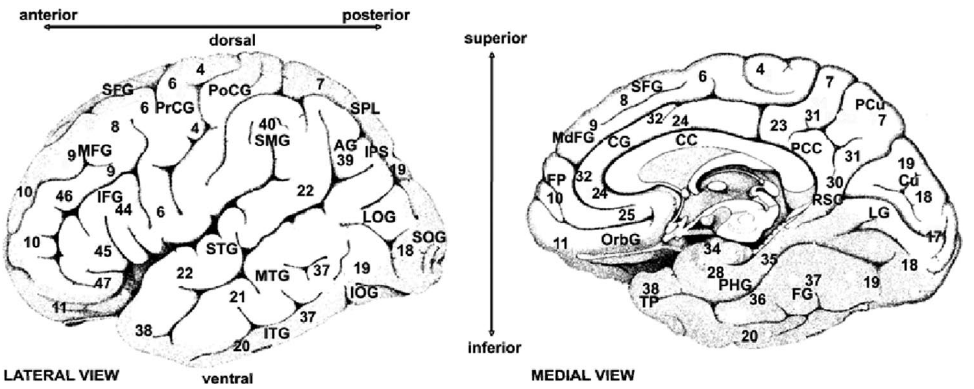


Figure 3. Lateral (left) and medial (right) views of the cortex. Numbers indicate approximate Brodmann areas (BA). Areas are approximate. AG = angular gyrus; CC = corpus collosum; CG = cingulate gyrus; Cu = cuneus; FG = fusiform gyrus; FP = frontal pole; IFG = inferior frontal gyrus; IOG = inferior occipital 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 is composed of BA 35, 36.

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 et al., 2002; Mitchell, Johnson, Raye, & Greene, 2004; Mitchell et al., 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- versus less-differentiated information (Nolde, Johnson, & Raye, 1998; see also, e.g., Suzuki et al., 2002).

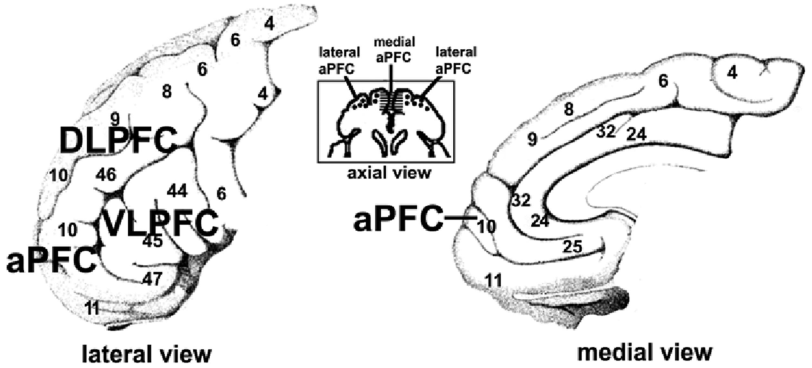
Two notable alternatives to the systematic–heuristic characterization of left and right PFC activity during tests of episodic memory have been proposed. The *production-monitoring hypothesis* suggests that left PFC is involved in production or generation during memory retrieval and right PFC is involved in memory monitoring (Cabeza, Locantore, & Anderson, 2003). The systematic–heuristic 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 and evaluation of more specific information, while the production-monitoring hypothesis predicts monitoring of all types to be right based. Rugg and his colleagues argued, as well, that monitoring generally is associated with right PFC and noted 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 postretrieval evaluation, per se; see also Dobbins & Han, 2006; Fleck, Daselaar, Dobbins, & Cabeza, 2006, for similar ideas). Rugg and colleagues also acknowledged 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).

LEFT/RIGHT PFC
systematic/heuristic processing[11]
monitoring more/less differentiated information [9, 11]
production-generation/monitoring[3]
yet-to-be-specified retrieval processes/monitoring[15]

DLPFC
encoding: elaborative & organizational processes [1, 13]
remembering:
evaluation (left more-, right less-differentiated)[9, 10]
mid: online monitoring & manipulation[12]
posterior: monitoring[4]

aPFC
lateral: pre-retrieval control processes[16]
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 frontopolar 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). Footnotes: [1]Blumenfeld and Ranganath (2007); [2]Buckner and Wheeler (2001); [3]Cabeza et al. (2003); [4]Dobbins and Han (2006); [5]Dobbins and Wagner (2005); [6]Kelley et al. (1998); [7]Lepage et al. (2000); [8]McDermott et al. (1999); [9]Mitchell et al., 2004; [10]Mitchell et al. (2008); [11]Nolde, Johnson, and Raye, (1998); [12]Petrides (2002); [13]Ranganath and Blumenfeld, 2008; [14]Raye et al. (2000); [15]Rugg et al. (2002; see also Hayama et al., 2008); [16]Simons et al. (2008); [17]Simons, Gilbert, et al., (2005); [18]Vinogradov et al. (2006; see also Vinogradov, Luks, Schulman, & Simpson, 2008); [19]Wagner, Poldrack, et al. (1998).

For example, on the basis of 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, Staresina 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 dorsal versus ventral fractionation has been proposed with respect to *remembering*, as well. For example, Petrides proposed that whereas mid-ventrolateral prefrontal cortex is 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 previously 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 these processes would be expected to have different neural correlates. However, 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, and 45), and a smaller region of right as well when participants tried to remember in which format (picture vs. word) or location (left vs. right) one of four items had appeared 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 with 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- or less-differentiated information, respectively) and/or on 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, et al., 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 et al., 1993; Johnson & Raye, 1981). 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 with 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- versus other-generated information (Simons, Henson, Gilbert, & Fletcher, 2008; Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vinogradov et al., 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 versus 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, Kounios, & Nolde, 1997; Johnson, Nolde, et al., 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 seeks;[3] on 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 preretrieval 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 preretrieval processes in the service of source memory that lateral anterior PFC is involved in identifying and maintaining memory-relevant goals, the set to remember, or specific source monitoring agendas (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 previously, making source memory decisions about encoding tasks 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 *refreshing* (foregrounding) 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 anterior cingulate cortex, 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.

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 versus 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 PFC 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 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 there is a full understanding of PFC specificity with respect to source memory. This understanding will be furthered by investigations into 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 results, to examine causal relationships, or to use ERP to examine the time course 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

---

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

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], and words [Wagner, Poldrack, 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 occipitotemporal 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 of 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 left dorsolateral PFC 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 previously, activity in intraparietal sulcus (as well as in 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 multifeatural 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 for 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 versus 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 versus 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 familiarity.[4] 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 also discussion in later section of attentional accounts, but see Vilberg & Rugg, in press). They also argued that inferior parietal cortex appears to be more directly involved in recollection, and they suggested 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 data from patients with lesions, 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

---

[4] It 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.

picture the participant made), but they were less confident in their source judgments. Of note, they did not differ from controls in old–new recognition or their confidence in their old–new judgments. It is interesting that 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 et al., 2007; Raye, Johnson, Mitchell, Reeder, & Greene, 2002). 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 BA 19) are involved in top-down modulation of memory retrieval, and more inferior posterior parietal regions (BAs 40 and 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) referred to the relevant areas as superior parietal lobe (SPL) and inferior parietal lobe (IPL) in their *attention to memory (AtoM)* hypothesis, whereas Cabeza (2008) referred to essentially these same areas as dorsal parietal cortex (DPC) and ventral parietal cortex (VPC), respectively, in his *dual attentional* (*DAP*) hypothesis. 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 hypotheses 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 earlier, 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) pointed out that whereas this approach would predict both IPL and SPL activity associated with source memory compared with item memory (IPL activity associated with processing specific active source detail and SPL activity associated with greater need for controlled search in source than in 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 in source identification tasks, participants are asked 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 much overlap should be expected in underlying processes among various episodic memory tasks, and thus 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 lead to significant advances 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 in which 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, few neuroimaging studies have used 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 task 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 et al., 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 postscan, 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 time course 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, and 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). Daselaar et al. suggested 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 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 and positive words [e.g., rape, slime, joy, peace], pictures [e.g., of accidents, war, babies, puppies, faces expressing emotion], and emotive film clips). We will not discuss, for example, mood induction studies (see, e.g., Eich et al., 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 et al., 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 of 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 of 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, that 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–hippocampus 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 with a 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 with 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 nonarousing 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 versus 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 earlier) and more accurate source memory (see later discussion). What has received less attention is the idea that emotion also can serve as a feature of the event that 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 one (or someone else) felt would be expected to lead to more vivid memories attributed with higher confidence.

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 one feels again years later the pain of losing a loved one, or more cognitively (i.e., *cold cognition*, perhaps reflecting PFC–hippocampus connectivity), as when one factually remembers finding 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, LaBar, & Cabeza, 2005; see also, e.g., Kensinger & Schacter, 2005b; Mickley & 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 participants had to remember four pictures and corresponding locations 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 with 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 for 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 (2005a) 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 for 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 for 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 intraobject 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 earlier section on MTL), 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. A review of existing literature has 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 versus 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 from the use of paradigms designed to provoke errors. Source errors can be introduced when a memory is initially created (encoded) or when 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 similar[5] (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), when features are weighted inappropriately, or when time available to make a source judgment is limited (Benjamin & 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 participants later erroneously claimed to have seen showed greater activity in precuneus during encoding than imagined items later correctly identified as 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 of having seen the imagined items. Of note, 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 that participants identified as seen resulted in greater activity than imagined items identified as new, which produced greater activity than unseen items identified as 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 that were called seen and imagined items that were 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 activity 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

---

[5] Source 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. Often the base rate occurrence of a feature is not taken into account when it is used as evidence for a source attribution. For example, when attributing an idea to colleague A (someone well-known) rather than to colleague B (someone one less well-known), one is likely to be satisfied that A came to mind as the source of the idea without considering that the probability was higher that colleague A would come to mind, independent of his or her connection to the idea.

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 such as BA 17, 18) differentiate true and false visual memories, whereas other posterior areas show similar activity (e.g., later visual processing areas such as 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 previously noted in which participants are asked about specific qualitative features of their memory (see section on assessing qualitative characteristics), rather than just to judge 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 older adults, relative to young adults, show memory binding deficits (Chalfonte & Johnson, 1996; Glisky, Rubin, & Davidson, 2001; Mitchell, Johnson, Raye, Mather, et al., 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 found (Golomb et al., 1996; O'Brien, Desmond, Ames, Schweitzer, & Tress, 1997; Raz, 2000; Raz et al., 2005; Small, Tsai, De La Paz, 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), the relationships 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 et al., 1995; Henkel et al., 1998; Mather et al., 1999) have been variable.

Aging disproportionately affects the PFC, compared with 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 or source memory (see Cabeza, 2006, for a review). The findings to

Table 1

Summary of Some Source Monitoring–Related Behavioral and Brain Activity Differences in Populations Exhibiting Behavioral Source Memory Deficits

Older adults
Behavioral findings
Memory binding deficit (feature combination deficit > item deficit)
Source monitoring deficits > item deficits
Recollection (Remember) deficits > Familiarity (Know) deficits
Poor calibration of responses on subjective (e.g., confidence) vs. objective (e.g., accuracy) memory measures
Overweighting of semantic information
Preserved source monitoring for affective information (and maybe overweighting)
Increased false memory
Imaging findings
Some MTL atrophy, dysfunction (especially in hippocampus) in binding and episodic encoding tasks
PFC atrophy disproportionate to other brain areas, dysfunction (especially in dorsolateral PFC); source monitoring–related left lateral PFC deficit related to evaluating specific information
Reduced PFC activity for source monitoring 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 source monitoring tasks
Individuals with 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 in 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, and STG during encoding
Attenuated difference between activity for associative vs. item memory in left DLPFC, right inferior PFC, medial PFC, and superior parietal cortex at test
Deficits in medial anterior PFC during reality monitoring tasks
Hallucinating patients:
More widespread 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
Individuals with posttraumatic stress disorder
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 recollection (Remember) responses
Source monitoring 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, dysfunction
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 and hippocampal activity during exposure to emotional stimuli
Individuals with depression
Behavioral findings
Overly general episodic memories
Source monitoring 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

Note. ACC = anterior cingulate cortex; BA = Brodmann areas; DLPFC = dorsolateral prefrontal cortex; MTL = medial temporal lobes; PFC = prefrontal cortex; STG = superior temporal gyrus.

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 with 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, Johnson, Raye, and D'Esposito (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 showing 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. Of note, the hippocampal–PFC connectivity was stronger in older than in 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 aging 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 later section 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 or 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 with 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 earlier 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 in addition to 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 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 et al., 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 et al., 2005; Rubin & Schulkind, 1997) those given by young adults. As Bloise (2008) noted, the different relation between age and subjective memory obtained with different measures (e.g., Remember/Know vs. MCQ) and the sometimes lack of correspondence between age differences on subjective and objective measures suggest 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 MRI 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) found that older adults showed 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 with 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 five 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 earlier 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 with, for example, perceptual information (see, e.g., Kensinger, 2009, 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 versus 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 that they 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, et al., 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 or emotional reactions during encoding enhance or detract from encoding perceptual and other details, and (b) specifying the conditions under which personal relevance or 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, 2009; 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 their recognition memory for pictures that were exactly the same as, similar to, or different than pictures they had 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 for which older adults showed more activity in the medial prefrontal cortex and cingulate gyrus than did 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 & Hrubi-Bopp, 2000; see, e.g., Schacter, Koutstaal, & Norman, 1997, for a review). For example, perceptual similarity between an imagined item and a perceived item increases the proportion of imagined objects erroneously called seen, 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 earlier (see also Roediger & Geraci, 2007).

A pair of articles 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 with 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 nonpresented items, older adults showed relatively greater activity in lateral temporal cortex (Dennis et al., 2008). The authors interpreted this overall pattern as being 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 research on 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.

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 with 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/or 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 subregions 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, Hayes, D'Esposito, & Raye, 2000; Metcalf, 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 or disconfirming information, and failure to access and/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, posttraumatic 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, Grangé, & 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). However, 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).

Results of 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 with the item memory condition, relative to the patient group (and, in the STG, as well, a point we will return to later). 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 in 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 (Õngur et al., 2006; 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 the left STG is in patients with schizophrenia, 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 results of Mather et al. (2006), remains to be seen.

Of interest, in a study in which schizophrenia patients who did or 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 and 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 schizophrenia patients with a history of auditory hallucinations (Shergill et al., 2003). One recent study in which participants with schizophrenia were scanned as they experienced auditory hallucinations versus 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- versus other-generated information (Simons et al., 2006; Simons, Gilbert, et al., 2005; Simons, Henson, et al., 2008; 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, Loughead, Gur, & Gur, 2006). A recent study showed that schizophrenia patients were slower and less accurate than control participants at a reality-monitoring task requiring them to differentiate between words that were self-generated or read during encoding; moreover, the schizophrenia 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 in 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 or monitoring internally generated information (see, e.g., Allen, Larøi, McGuire, & Aleman, 2008, for further review).

Posttraumatic 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 decontextualized) 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 fMRI studies of PTSD 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 who had experienced trauma and who either 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 groups (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, and right parahippocampal gyrus. Of note, 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 activity,[6] the functional 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 with 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 to less diagnostic or specific information, being encoded, and 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 remember source information, perhaps after a longer delay (Qin et al., 2003).

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 with control participants (see Bremner, 2007, for a review). Within the range of normal reactions to emotional information that were discussed previously in the section on emotion, increased amygdala activity modulates the hippocampus and is associated with better memory. The amygdala hyper-reactivity of PTSD patients, on the other hand, appears 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 versus neutral contexts. In one event-related fMRI study, investigators 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, 2009). There were no differences in old–new recognition performance for the items encoded in emotional versus 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 with neutral, contexts in several areas associated with successful episodic memory including insula, hippocampus, precuneus/posterior cingulate, and 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

---

[6] This apparent anterior-to-posterior shift stands in contrast to the posterior-to-anterior shift associated with aging noted earlier, 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).

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 overly general, memories compared with 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, Siegle 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 with non-depressed individuals, depressed participants showed greater sustained amygdala response for negative but not for positive items. The time course of the activity suggested that it was sustained for up to 30 s 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. Of note, 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 shown 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 et al., 2004). Using a blocked design, Siegle et al. (2007) had depressed and non-depressed participants perform 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; BA 9, 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. 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 for neutral or positive information. A recent fMRI study (Hamilton & Gotlib, 2008) confirmed such a bias for negative, compared with 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 have 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 versus 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 previously), 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 for it 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 disorders need to be considered to allow development of 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 schizophrenia patients with greater negative symptoms compared with both controls and schizophrenia patients with less negative symptoms. On the basis of 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 symptomatology and episodic memory (see Thoma et al., 2006 for their evidence). However, this hypothesis remains to be directly tested. As another example, a recent meta-analysis of behavioral studies of 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 participants with schizophrenia hallucinated, citing too few studies of each type and high variability within type as limiting factors in conducting such a comparison. Given the previously discussed evidence 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 article, 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 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 (e.g., semantic, perceptual, spatial, temporal, emotional) 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 application 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.

Results of fMRI studies also are prompting investigators to articulate theoretical assumptions (whether explicitly or tacitly held) with greater specificity. For example, as discussed earlier, 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 compose 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). Of note, 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 versus 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., Kirwan et al., 2008, and discussion in the section on MTL).

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 that 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 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, and 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) (e.g., semantic, perceptual, emotional), 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 or 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-featural 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 with recollection), either may have functional consequences. The first kind of familiarity provides a rapid signal that can help guide orientation toward 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 initiate a 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 earlier, 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, in drawing conclusions about brain regions associated with familiarity and recollection, one needs 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 subregions within MTL, PFC, and posterior cortex are involved in representing or processing specific source features, whereas other subregions 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). The neuroscience of source memory (see Table 2) will be advanced by (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 are related to subjective reports of strength of familiarity and vividness of recollection; and (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 further specify representational and binding regions (and networks), but also clarify whether familiarity arises from activity

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 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: (a) setting and implementing agendas (e.g., for organization, feature binding) during the encoding of events; (b) 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: (a) groups showing source memory deficits (e.g., older adults, individuals with schizophrenia, PTSD, or depression); (b) individual differences related to errors in source memory (e.g., imagery ability, suggestibility, anxiety)

Note. MCQ = Memory Characteristics Questionnaire; PTSD = posttraumatic stress disorder.

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 to further distinguish the brain regions (networks) in which activity is related to the representation, or processing, of different types of information from regions in which 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 the 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.

References

Achim, A. M., & Weiss, A. P. (2008). No evidence for a differential deficit of reality monitoring in schizophrenia: A meta-analysis of the associative memory literature. *Cognitive Neuropsychiatry, 13,* 369–384.

Ackil, J. K., & Zaragoza, M. S. (1998). Memorial consequences of forced confabulation: Age differences in susceptibility to false memories. *Developmental Psychology, 34,* 1358–1372.

Addis, D. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus, 14,* 752–762.

Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences, 22,* 425–489.

Aleman, A., Hijman, R., De Haan, E. H. F., & Kahn, R. S. (1999). Memory impairment in schizophrenia: A meta-analysis. *American Journal of Psychiatry, 156,* 1358–1366.

Allen, P., Larøi, F., McGuire, P. K., & Aleman, A. (2008). The hallucinating brain: A review of structural and functional neuroimaging studies of hallucinations. *Neuroscience and Biobehavioral Reviews, 32,* 175–191.

Anastasi, J. S., Rhodes, M. G., & Burns, M. C. (2000). Distinguishing between memory illusions and actual memories using phenomenological measurements and explicit warnings. *American Journal of Psychology, 113,* 1–26.

Anderson, N. D., Ebert, P. L., Jennings, J. M., Grady, C. L., Cabeza, R., & Graham, S. J. (2008). Recollection- and familiarity-based memory in healthy aging and amnestic mild cognitive impairment. *Neuropsychology, 22,* 177–187.

Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. M. (2000). The effects of divided attention on encoding- and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience, 12,* 775–792.

Awipi, T., & Davachi, L. (2008). Content-specific source encoding in human medial temporal lobe. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 769–779.

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4,* 417–423.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47,* 907–918.

Banks, W. P. (2000). Recognition and source memory as multivariate decision processes. *Psychological Science, 11,* 267–273.

Bar, M., Aminoff, E., & Schacter, D. L. (2008). Scenes unseen: The parahippocampal cortex intrinsically subserves contextual associations, not scenes or places per se. *The Journal of Neuroscience, 28,* 8539–8544.

Bartlett, F. C. (1932). *Remembering: A study in experimental and social psychology.* Cambridge, England: Cambridge University Press.

Batchelder, W. H., & Riefer, D. M. (1990). Multinomial processing models of source monitoring. *Psychological Review, 97,* 548–564.

Bayen, U. J., Murnane, K., & Erdfelder, E. (1996). Source discrimination, item detection and multinomial models of source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 22,* 197–215.

Benjamin, A. S., & Craik, F. I. M. (2001). Parallel effects of aging and time pressure on memory for source: Evidence from the spacing effect. *Memory & Cognition, 29,* 691–697.

Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience, 27,* 14415–14423.

Bird, C. M., & Burgess, N. (2008). The hippocampus and memory: Insights from spatial processing. *Nature Reviews Neuroscience, 9,* 182–194.

Bleich, A., Attias, J., & Furman, V. (1996). Effect of repeated visual traumatic stimuli on the event related P3 brain stress disorder potential in post-traumatic stress disorder. *International Journal Neuroscience, 85,* 45–55.

Bloise, S. (2008). *Aging and the subjective experience of remembering.* Unpublished doctoral dissertation, Yale University, New Haven, Connecticut.

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

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences, 8,* 539–546.

Botzung, A., Denkova, E., Ciuciu, P., Scheiber, C., & Manning, L. (2008). The neural bases of the constructive nature of autobiographical memories studied with a self-paced fMRI design. *Memory, 16,* 351–363.

Boyer, P. A., Phillips, J. L., Rousseau, F. L., & Ilivitsky, S. (2007). Hippocampal abnormalities and memory deficits: New evidence of a strong pathophysiological link in schizophrenia. *Brain Research Reviews, 54,* 92–112.

Bransford, J. D., & Johnson, M. K. (1973). Considerations of some problems of comprehension. In W. Chase (Ed.), *Visual information processing* (pp. 383–438). New York: Academic Press.

Brasted, P. J., Bussey, T. J., Murray, E. A., & Wise, S. P. (2003). Role of the hippocampal system in associative learning beyond the spatial domain. *Brain, 126,* 1202–1223.

Braver, T. S., Barch, D. M., Kelley, W. M., Buckner, R. L., Cohen, N. J., Miezin, F. M., et al. (2001). Direct comparison of prefrontal cortex regions engaged by working and long-term memory tasks. *NeuroImage, 14,* 48–59.

Bremner, J. D. (2007). Neuroimaging in posttraumatic stress disorder and other stress-related disorders. *Neuroimaging Clinics of North America, 17,* 523–538.

Bremner, J. D., Krystal, J. H., Southwick, S. M., & Charney, D. S. (1995). Functional neuroanatomical correlates of the effects of stress on memory. *Journal of Traumatic Stress, 8,* 527–553.

Bremner, J. D., & Narayan, M. (1998). The effects of stress on memory and the hippocampus throughout the life cycle: Implications for childhood development and aging. *Development and Psychopathology, 10,* 871–885.

Bremner, J. D., Vythilingam, M., Vermetten, E., Southwick, S. M., McGlashan, T., Nazeer, A., et al. (2003). 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, 160,* 924–932.

Brewin, C. R., Kleiner, J. S., Vasterling, J. J., & Field, A. P. (2007). Memory for emotionally neutral information in posttraumatic stress disorder: A meta-analytic investigation. *Journal of Abnormal Psychology, 116,* 448–463.

Brunelin, J., Combris, M., Poulet, E., Kallel, L., D'Amato, T., Dalery, J., & Saoud, M. (2006). Source monitoring deficits in hallucinating compared to non-hallucinating patients with schizophrenia. *European Psychiatry, 21,* 259–261.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11,* 49–57.

Buckner, R. L., & Wheeler, M. E. (2001). The cognitive neuroscience of remembering. *Nature Reviews Neuroscience, 2,* 624–634.

Budson, A. E., Sullivan, A. L., Daffner, K. R., & Schacter, D. L. (2003). Semantic versus phonological false recognition in aging and Alzheimer's disease. *Brain & Cognition, 51,* 251–261.

Bunce, D. (2003). Cognitive support at encoding attenuates age differences in recollective experience among adults of lower frontal lobe function. *Neuropsychology, 17,* 353–361.

Bunsey, M., & Eichenbaum, H. (1996). Conservation of hippocampal memory function in rats and humans. *Nature, 379,* 255–257.

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron, 35,* 625–641.

Burgess, P. W., & Shallice, T. (1996). Confabulation and the control of recollection. *Memory, 4,* 359–411.

Burglen, F., Marczewski, P., Mitchell, K. J., van der Linden, M., Johnson, M. K., Danion, J.-M., & Salamé, P. (2004). Impaired performance in a working memory binding task in patients with schizophrenia. *Psychiatry Research, 125,* 247–255.

Burianova, H., & Grady, C. L. (2007). Common and unique neural activations in autobiographical, episodic, and semantic retrieval. *Journal of Cognitive Neuroscience, 19,* 1520–1534.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging, 17,* 85–100.

Cabeza, R. (2006). Prefrontal and medial temporal lobe contributions to relational memory in young and older adults. In D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Binding in human memory: A neurocognitive approach* (pp. 595–626). New York: Oxford University Press.

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

Cabeza, R., Anderson, N. D., Houle, S., Mangels, J. A., & Nyberg, L. (2000). Age-related differences in neural activity during item and temporal-order memory retrieval: A positron emission tomography study. *Journal of Cognitive Neuroscience, 12,* 197–206.

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage, 17,* 1394–1402.

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

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

Cabeza, R., Mangels, J., Nyberg, L., Habib, R., Houle, S., McIntosh, A. R., & Tulving, E. (1997). Brain regions differentially involved in remembering what and when: A PET study. *Neuron, 19,* 863–870.

Cabeza, R., Prince, S. E., Daselaar, S. M., Greenberg, D. L., Budde, M., Dolcos, F., et al. (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience, 16,* 1583–1594.

Cabeza, R., Rao, S. M., Wagner, A. D., Mayer, A. R., & Schacter, D. L. (2001). 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 of the United States of America, 98,* 4805–4810.

Cabeza, R., & St. Jacques, P. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences, 11,* 219–227.

Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., et al. (1996). 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, 93,* 8016–8021.

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D. E., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *The Journal of Neuroscience, 20*(RC99), 1–5.

Canli, T., Zhao, Z., Desmond, J. E., Glover, G., & Gabrieli, J. D. E. (1999). fMRI identifies a network of structures correlated with retention of positive and negative emotional memory. *Psychobiology, 27,* 441–452.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex, 12,* 1049–1056.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain, 129,* 564–583.

Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults. *Memory & Cognition, 24,* 403–416.

Chee, M. W. L., Goh, J. O. S., Venkatraman, V., Tan, J. C., Gutchess, A., Sutton, B., et al. (2006). Age-related changes in object processing and contextual binding revealed using fMRI adaptation. *Journal of Cognitive Neuroscience, 18,* 495–507.

Christianson, S.-Å. (Ed.). (1992). *The handbook of emotion and memory: Research and theory.* Hillsdale, NJ: Erlbaum.

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

Ciaramelli, E., & Spaniol, J. (2008). *Ventromedial prefrontal damage and confabulation impair source but not associative memory.* Manuscript submitted for publication.

Cohen, N. J., & Eichenbaum, H. (1993). *Memory, amnesia, and the hippocampal system.* Cambridge, MA: MIT Press.

Comblain, C., D'Argembeau, A., & Van der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research, 31,* 173–189.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3,* 201–215.

Craik, F. I. M., Morris, L. W., Morris, R. G., & Loewen, E. R. (1990). Relations between source amnesia and frontal lobe functioning in older adults. *Psychology and Aging, 5,* 148–151.

Cunningham, W. A., Johnson, M. K., Raye, C. L., Gatenby, J. C., Gore, J. C., & Banaji, M. R. (2004). Separable neural components in the processing of black and white faces. *Psychological Science, 15,* 806–813.

Danion, J.-M., Huron, C., Vidailhet, P., & Berna, F. (2007). Functional mechanisms of episodic memory impairment in schizophrenia. *Canadian Journal of Psychiatry, 52,* 693–701.

Danion, J.-M., Rizzo, L., & Bruant, A. (1999). Functional mechanisms underlying impaired recognition memory and conscious awareness in patients with schizophrenia. *Archives of General Psychiatry, 56,* 639–644.

Daselaar, S., & Cabeza, R. (2008). Episodic memory decline and healthy aging. In J. Byrne (Series Ed.) & H. Eichenbaum (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 3: Memory systems* (pp. 577–599). Oxford, England: Elsevier.

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

Daselaar, S. M., Rice, H. J., Greenberg, D. L., Cabeza, R., LaBar, K. S., & Rubin, D. C. (2008). The spatiotemporal dynamics of autobiographical memory: Neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex, 18,* 217–229.

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

Davachi, L., & Dobbins, I. G. (2008). Declarative memory. *Current Directions in Psychological Science, 17,* 112–118.

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior–anterior shift in aging. *Cerebral Cortex, 18,* 1201–1209.

Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology, 58,* 17–22.

Degl'Innocenti, A., & Backman, L. (1999). Source memory in major depression. *Journal of Affective Disorders, 54,* 205–209.

Dennis, N. A., & Cabeza, R. (2008). Neuroimaging of healthy cognitive aging. In F. I. M. Craik & T. A. Salthouse (Eds.), *Handbook of aging and cognition* (3rd ed., pp. 1–54). Mahwah, NJ: Erlbaum.

Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 791–808.

Dennis, N. A., Kim, H., & Cabeza, R. (2007). Effects of aging on true and false memory formation: An fMRI study. *Neuropsychologia, 45,* 3157–3166.

Dennis, N. A., Kim, H., & Cabeza, R. (2008). Age-related differences in brain activity during true and false memory retrieval. *Journal of Cognitive Neuroscience, 20,* 1390–1402.

Dewhurst, S. A., Holmes, S. J., Brandt, K. R., & Dean, G. M. (2006). Measuring the speed of the conscious components of recognition memory: Remembering is faster than knowing. *Consciousness and Cognition, 15,* 147–162.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences, 11,* 379–386.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2008). 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, 34,* 730–740.

Ditman, T., & Kuperberg, G. R. (2005). A source-monitoring account of auditory verbal hallucinations in patients with schizophrenia. *Harvard Review of Psychiatry, 13,* 280–299.

Dobbins, I. G., Foley, H., Schacter, D. L., & Wagner, A. D. (2002). Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron, 35,* 989–996.

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

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

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

Dodson, C. S., Holland, P. W., & Shimamura, A. P. (1998). On the recollection of specific-and partial-source information. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 24,* 1121–1136.

Dodson, C. S., & Schacter, D. L. (2001). "If I had said it I would have remembered it": Reducing false memories with a distinctiveness heuristic. *Psychonomic Bulletin & Review, 8,* 155–161.

Dolan, R. J., Lane, R., Chua, P., & Fletcher, P. (2000). Dissociable temporal lobe activations during emotional episodic memory retrieval. *NeuroImage, 11,* 203–209.

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.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2005). 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, 102,* 2626–2631.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2006). The memory enhancing effect of emotion: Functional neuroimaging evidence. In B. Uttl, H. Ohta & A. L. Seigenthaler (Eds.), *Memory and emotion: Interdisciplinary perspectives* (pp. 107–133). Malden, MA: Blackwell.

Dougal, S., Phelps, E. A., & Davachi, L. (2007). The role of medial temporal lobe in item recognition and source recollection of emotional stimuli. *Cognitive, Affective, & Behavioral Neuroscience, 7,* 233–242.

Driscoll, I., Hamilton, D. A., Petropoulos, H., Yeo, R. A., Brooks, W. M., Baumgartner, R. N., & Sutherland, R. J. (2003). The aging hippocampus: Cognitive, biochemical and structural findings. *Cerebral Cortex, 13,* 1344–1351.

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

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

Dudukovic, N. M., & Wagner, A. D. (2007). Goal-dependent modulation of declarative memory: Neural correlates of temporal recency decisions and novelty detection. *Neuropsychologia, 45,* 2608–2620.

Durso, F. T., & Johnson, M. K. (1980). The effects of orienting tasks on recognition, recall, and modality confusion of pictures and words. *Journal of Verbal Learning and Verbal Behavior, 19,* 416–429.

Duverne, S., Habibi, A., & Rugg, M. D. (2008). Regional specificity of age effects on the neural correlates of episodic retrieval. *Neurobiology of Aging, 29,* 1902–1916.

Dywan, J., Segalowitz, S. J., & Arsenault, A. (2002). Electrophysiological response during source memory decisions in older and younger adults. *Brain and Cognition, 49,* 322–340.

Easterbrook, J. A. (1959). The effect of emotion on cue utilization and the organization of behavior. *Psychological Review, 66,* 183–201.

Eich, E., Geraerts, E., Schooler, J. W., & Forgas, J. P. (2008). Memory in and about affect. In J. Byrne (Series Ed.) & H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 2: Cognitive psychology of memory.* (pp. 239–260). Oxford, England: Elsevier.

Eichenbaum, H. (1994). The hippocampal system and declarative memory in humans and animals: Experimental analysis and historical origins. In D. L. Schacter & E. Tulving (Eds.), *Memory systems.* (pp. 147–202). Cambridge, MA: MIT Press.

Eichenbaum, H., Fortin, N., Ergorul, C., & Robitsek, J. (2008). Toward a neurobiology of episodic memory. In J. P. Huston (Series Ed.) & E. Dere, A. Easton, L. Nadel, & J. P. Huston (Vol. Eds.), *Handbook of behavioral neuroscience: Vol. 18. Handbook of episodic memory,* (pp. 283–300). Amsterdam: Elsevier.

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

Eldridge, L. L., Engel, S. A., Zeineh, M. M., Bookheimer, S. Y., & Knowlton, B. J. (2005). A dissociation of encoding and retrieval processes in the human hippocampus. *The Journal of Neuroscience, 25,* 3280–3286.

Elfman, K. W., Parks, C. M., & Yonelinas, A. P. (2008). Testing a neurocomputational model of recollection, familiarity, and source recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 752–768.

Epstein, R., & Kanwisher, N. (1998, April 9). A cortical representation of the local visual environment. *Nature, 392,* 598–601.

Erk, S., Martin, S., & Walter, H. (2005). Emotional context during encoding of neutral items modulates brain activation not only during encoding but also during recognition. *NeuroImage, 26,* 829–838.

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

Fichtenholtz, H., Qin, J. J., Mitchell, K. J., Johnson, D. C., Southwick, S. M., Johnson, M. K., et al. (2008, May), *PTSD patients' memory for neutral pictures in blocked and intermixed lists.* Paper presented at the annual meeting of the Association for Psychological Science, Chicago.

Finke, R. A., Johnson, M. K., & Shyi, G. C.-W. (1988). Memory confusions for real and imagined completions of symmetrical visual patterns. *Memory & Cognition, 16,* 133–137.

Fleck, M. S., Daselaar, S. M., Dobbins, I. G., & Cabeza, R. (2006). Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cerebral Cortex, 16,* 1623–1630.

Fotopoulou, A., Conway, M. A., & Solms, M. (2007). Confabulation: Motivated reality monitoring. *Neuropsychologia, 45,* 2180–2190.

Friedman, D., & Johnson, R. J. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique, 51,* 6–28.

Gallo, D. A., Weiss, J. A., & Schacter, D. L. (2004). Reducing false recognition with criterial recollection tests: Distinctiveness heuristic versus criterion shifts. *Journal of Memory and Language, 51,* 473–493.

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research, 20,* 226–241.

Gardiner, J. M. (2008). Remembering and knowing. In J. Byrne (Series Ed.) & H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference*. *Vol. 2: Cognitive psychology of memory* (pp. 285–306). Oxford, England: Elsevier.

Gardiner, J. M., & Richardson-Klavehn, A. (2000). Remembering and knowing. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 229–244). New York: Oxford University Press.

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

Garoff-Eaton, R. J., Kensinger, E. A., & Schacter, D. L. (2007). The neural correlates of conceptual and perceptual false recognition. *Learning & Memory, 14,* 684–692.

Garoff-Eaton, R. J., Slotnick, S. D., & Schacter, D. L. (2006). Not all false memories are created equal: The neural basis of false recognition. *Cerebral Cortex, 16,* 1645–1652.

Geuze, E., Vermetten, E., Ruf, M., de Kloet, C. S., & Westenberg, H. G. M. (2008). Neural correlates of associative learning and memory in veterans with posttraumatic stress disorder. *Journal of Psychiatric Research, 42,* 659–669.

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

Giovanello, K. S., Schnyer, D., & Verfaellie, M. (2009). Distinct hippocampal regions make unique contributions to relational memory. *Hippocampus, 19,* 111–117.

Giovanello, K. S., Verfaellie, M., & Keane, M. M. (2003). Disproportionate deficit in associative recognition relative to item recognition in global amnesia. *Cognitive, Affective, and Behavioral Neuroscience, 3,* 186–194.

Glanzer, M., Hilford, A., & Kim, K. (2004). Six regularities of source recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 30,* 1176–1195.

Glisky, E. L., & Kong, L. L. (2008). Do young and older adults rely on different processes in source memory tasks? A neuropsychological study. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 809–822.

Glisky, E. L., Polster, M. R., & Routhieaux, B. C. (1995). Double dissociation between item and source memory. *Neuropsychology, 9,* 229–235.

Glisky, E. L., Rubin, S. R., & Davidson, P. S. R. (2001). Source memory in older adults: An encoding or retrieval problem? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27,* 1131–1146.

Gold, J. J., Hopkins, R. O., & Squire, L. R. (2006). Single-item memory, associative memory, and the human hippocampus. *Learning & Memory, 13,* 644–649.

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

Goldin, P. R., McRae, K., Ramel, W., & Gross, J. J. (2008). The neural bases of emotion regulation: Reappraisal and suppression of negative emotion. *Biological Psychiatry, 63,* 577–586.

Golier, J., Harvey, P., Steiner, A., & Yehuda, R. (1997). Source monitoring in PTSD. *Annals of the New York Academy of Science, 821,* 472–475.

Golomb, J., Kluger, A., de Leon, M. J., Ferris, S. H., Mittelman, M., Cohen, J., et al. (1996). Hippocampal formation size predicts declining memory performance in normal aging. *Neurology, 47,* 810–813.

Gonsalves, B., Reber, P. J., Gitelman, D. R., Parrish, T. B., Mesulam, M.-M., & Paller, K. A. (2004). Neural evidence that vivid imagining can lead to false remembering. *Psychological Science, 15,* 655–660.

Gordon, R., Franklin, N., & Beck, J. (2005). Wishful thinking and source monitoring. *Memory & Cognition, 33,* 418–429.

Grady, C. L. (2008). Cognitive neuroscience of aging. *Annals of the New York Academy of Sciences, 1124,* 127–144.

Grady, C. L., McIntosh, A. R., Horwitz, B., Maisog, J. M., Ungerleider, L. G., Mentis, M. J., et al. (1995, July 14). Age-related reductions in human recognition memory due to impaired encoding. *Science, 269,* 218–221.

Grady, C. L., Yu, H., & Alain, C. (2008). Age-related differences in brain activity underlying working memory for spatial and nonspatial auditory information. *Cerebral Cortex, 18,* 189–199.

Greenberg, D. L., Rice, H. J., Cooper, J. J., Cabeza, R., Rubin, D. C., & LaBar, K. S. (2005). Co-activation of the amygdala, hippocampus, and inferior frontal gyrus during autobiographical memory retrieval. *Neuropsychologia, 43,* 659–674.

Gronlund, S. D., Edwards, M. B., & Ohrt, D. D. (1997). Comparison of the retrieval of item versus spatial position information. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23,* 1261–1274.

Gruppuso, V., Lindsay, D. S., & Kelley, C. M. (1997). The process-dissociation procedure and similarity: Defining and estimating recollection and familiarity in recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23,* 259–278.

Guerin, S. A., & Miller, M. B. (2008). Semantic organization of study materials has opposite effects on recognition and recall. *Psychonomic Bulletin & Review, 15, 302*–308.

Gutchess, A. H., Welsh, R. C., Hedden, T., Bangert, A., Minear, M., Liu, L. L., et al. (2005). Aging and the neural correlates of successful picture encoding: Frontal activations compensate for decreased medial-temporal activity. *Journal of Cognitive Neuroscience, 17,* 84–96.

Haas, B. W., & Canli, T. (2008). Emotional memory function, personality structure, and psychopathology: A neural system approach to the identification of vulnerability markers. *Brain Research Reviews, 58,* 71–84.

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

Hadjikhani, N., & Roland, P. E. (1998). 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, 18,* 1072–1084.

Hamann, S., & Canli, T. (2004). Individual differences in emotion processing. *Current Opinions in Neurobiology, 14,* 233–238.

Hamann, S. B., Ely, T. D., Grafton, S. T., & Kilts, C. D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience, 2,* 289–293.

Hamilton, J. P., & Gotlib, I. H. (2008). Neural substrates of increased memory sensitivity for negative stimuli in major depression. *Society of Biological Psychiatry, 63,* 1155–1162.

Hannula, D. E., Tranel, D., & Cohen, N. J. (2006). The long and the short of it: Relational memory impairments in amnesia, even at short lags. *The Journal of Neuroscience, 26,* 8352–8359.

Hasher, L., Lustig, C., & Zacks, R. (2007). Inhibitory mechanisms and the control of attention. In A. R. A. Conway, C. Jarrold, M. J. Kane, A. Miyake, & J. N. Towse (Eds.), *Variation in working memory* (pp. 227–249). New York: Oxford University Press.

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *The psychology of learning and motivation*: *Advances in research and theory* (Vol. 22, pp. 193–225). New York: Academic Press.

Hashtroudi, S., Johnson, M. K., & Chrosniak, L. D. (1990). Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology and Aging, 5,* 119–126.

Haskins, A. L., Yonelinas, A. P., Quamme, J. R., & Ranganath, C. (2008). Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron, 59,* 554–560.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences, 11,* 299–306.

Hayama, H. R., Johnson, J. D., & Rugg, M. D. (2008). The relationship between the right frontal old/new ERP effect and post-retrieval monitoring: Specific or non-specific? *Neuropsychologia, 46,* 1211–1223.

Healy, M. R., Light, L. L., & Chung, C. (2005). Dual-process models of associative recognition in young and older adults: Evidence from receiver operating characteristics. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31,* 768–788.

Hekkanen, S. T., & McEvoy, C. (2002). False memories and source-monitoring problems: Criterion differences. *Applied Cognitive Psychology, 16,* 73–85.

Henke, K., Buck, A., Weber, B., & Wieser, H. G. (1997). Human hippocampus establishes associations in memory. *Hippocampus, 7,* 249–256.

Henke, K., Weber, B., Kneifel, S., Wieser, H. G., & Buck, A. (1999). Human hippocampus associates information in memory. *Proceedings of the National Academy of Sciences of the United States of America, 96,* 5884–5889.

Henkel, L. A., Franklin, N., & Johnson, M. K. (2000). Cross-modal source monitoring confusions between perceived and imagined events. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 321–335.

Henkel, L. A., Johnson, M. K., & De Leonardis, D. M. (1998). Aging and source monitoring: Cognitive processes and neuropsychological correlates. *Journal of Experimental Psychology: General, 127,* 251–268.

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

Henson, R. N. A., Shallice, T., & Dolan, R. J. (1999). Right prefrontal cortex and episodic memory retrieval: A functional MRI test of the monitoring hypothesis. *Brain, 122,* 1367–1381.

Hertel, P. T. (1992). Emotion, mood and memory. In L. Squire (Ed.), *Encyclopedia of learning and memory* (pp. 157–161). New York: Macmillan.

Hertel, P. T. (2000). The cognitive-initiative account of depression-related impairments in memory. In D. Medin (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 39, pp. 47–71). San Diego: Academic Press.

Hilford, A., Glanzer, M., Kim, K., & DeCarlo, L. T. (2002). Regularities of source recognition: ROC analysis. *Journal of Experimental Psychology: General, 131,* 494–510.

Hintzman, D. L., Caulton, D. A., & Levitin, D. J. (1998). Retrieval dynamics in recognition and list discrimination: Further evidence of separate processes of familiarity and recall. *Memory & Cognition, 26,* 449–462.

Hoffman, R. E. (2008). Auditory/verbal hallucinations, speech perception neurocircuitry, and the social deafferentation hypothesis. *Clinical EEG & Neuroscience: Official Journal of the EEG & Clinical Neuroscience Society (ENCS), 39,* 87–90.

Hoffman, R. E., Hampson, M., Wu, K., Anderson, A. W., Gore, J. C., Buchanan, R. J., et al. (2007). Probing the pathophysiology of auditory/verbal hallucinations by combining functional magnetic resonance imaging and transcranial magnetic stimulation. *Cerebral Cortex, 17,* 2733–2743.

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

Hyman, I. E., & Pentland, J. (1996). The role of mental imagery in the creation of false childhood memories. *Journal of Memory and Language, 35,* 101–117.

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

Jacoby, L. L., Bishara, A. J., Hessels, S., & Toth, J. P. (2005). Aging, subjective experience, and cognitive control: Dramatic false remembering by older adults. *Journal of Experimental Psychology: General, 134,* 131–148.

Jacoby, L. L., Kelley, C., Brown, J., & Jasechko, J. (1989). Becoming famous overnight: Limits on the ability to avoid unconscious influences of the past. *Journal of Personality and Social Psychology, 56,* 326–338.

Jennings, J. M., & Jacoby, L. L. (1997). An opposition procedure for detecting age-related deficits in recollection: Telling effects of repetition. *Psychology and Aging, 12,* 352–361.

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

Johnson, M. K. (1988). Discriminating the origin of information. In T. F. Oltmanns & B. A. Maher (Eds.), *Delusional beliefs* (pp. 34–65). New York: Wiley.

Johnson, M. K. (1991). Reality monitoring: Evidence from confabulation in organic brain disease patients. In G. P. Prigatano & D. L. Schacter (Eds.), *Awareness of deficit after brain injury* (pp. 176–197). New York: Oxford University Press.

Johnson, M. K. (1992). MEM: Mechanisms of recollection. *Journal of Cognitive Neuroscience, 4,* 268–280.

Johnson, M. K. (1997a). Identifying the origin of mental experience. In M. S. Myslobodsky (Ed.), *The mythomanias: The nature of deception and self-deception* (pp. 133–180). Mahwah, NJ: Erlbaum.

Johnson, M. K. (1997b). Source monitoring and memory distortion. *Philosophical Transactions of the Royal Society of London, 352,* 1733–1745.

Johnson, M. K. (2005). The relation between source memory and episodic memory: Comment on Siedlecki et al. (2005). *Psychology and Aging, 20,* 529–531.

Johnson, M. K. (2006). Memory and reality. *American Psychologist, 61,* 760–771.

Johnson, M. K., Bransford, J. D., & Solomon, S. K. (1973). Memory for tacit implications of sentences. *Journal of Experimental Psychology, 98,* 203–205.

Johnson, M. K., & Chalfonte, B. L. (1994). Binding complex memories: The role of reactivation and the hippocampus. In D. L. Schacter & E. Tulving (Eds.), *Memory systems 1994* (pp. 311–350). Cambridge, MA: MIT Press.

Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General, 117,* 371–376.

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin, 114,* 3–28.

Johnson, M. K., Hayes, S. M., D'Esposito, M., & Raye, C. L. (2000). Confabulation. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology. Memory and its disorders* (2nd ed., Vol. 2, pp. 383–407). Amsterdam: Elsevier Science.

Johnson, M. K., & Hirst, W. (1993). MEM: Memory subsystems as processes. In A. F. Collins, S. E. Gathercole, M. A. Conway, & P. E. Morris (Eds.), *Theories of memory* (pp. 241–286). East Sussex, England: Erlbaum.

Johnson, M. K., Kounios, J., & Nolde, S. F. (1997). Electrophysiological brain activity and memory source monitoring. *NeuroReport, 7,* 2929–2932.

Johnson, M. K., Kounios, J., & Reeder, J. A. (1994). Time-course studies of reality monitoring and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 20,* 1409–1419.

Johnson, M. K., Mitchell, K. J., Raye, C. L., McGuire, J. T., & Sanislow, C. A. (2006). Mental rubbernecking to negative information depends on task context. *Psychonomic Bulletin & Review, 13,* 614–618.

Johnson, M. K., & Multhaup, K. S. (1992). Emotion and MEM. In S.-A. Christianson (Ed.), *The handbook of emotion and memory: Current research and theory* (pp. 33–66). Hillsdale, NJ: Erlbaum.

Johnson, M. K., Nolde, S. F., & De Leonardis, D. M. (1996). Emotional focus and source monitoring. *Journal of Memory and Language, 35,* 135–156.

Johnson, M. K., Nolde, S. F., Mather, M., Kounios, J., Schacter, D. L., & Curran, T. (1997). The similarity of brain activity associated with true and false recognition depends on test format. *Psychological Science, 8,* 250–257.

Johnson, M. K., O'Connor, M., & Cantor, J. (1997). Confabulation, memory deficits, and frontal dysfunction. *Brain and Cognition, 34,* 189–206.

Johnson, M. K., & Raye, C. L. (1981). Reality monitoring. *Psychological Review, 88,* 67–85.

Johnson, M. K., & Raye, C. L. (2000). Cognitive and brain mechanisms of false memories and beliefs. In D. L. Schacter & E. Scarry (Eds.), *Memory and belief* (pp. 35–86). Cambridge, MA: Harvard University Press.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Greene, E. J., Cunningham, W. A., & Sanislow, C. A. (2005). Using fMRI to investigate a component process of reflection: Prefrontal correlates of refreshing a just-activated representation. *Cognitive, Affective, & Behavioral Neuroscience, 5,* 339–361.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Touryan, S. R., Greene, E. J., & Nolen-Hoeksema, S. (2006). Dissociating medial frontal and posterior cingulate activity during self-reflection. *Social Cognitive and Affective Neuroscience, 1,* 56–64.

Johnson, M. K., Verfaellie, M., & Dunlosky, J. (2008). Introduction to the special section on integrative approaches to source memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 34,* 727–729.

Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annual Review of Psychology, 59,* 193–224.

Kahn, I., Andrews-Hanna, J. R., Vincent, J. L., Snyder, A. Z., & Buckner, R. L. (2008). Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *Journal of Neurophysiology, 100,* 129–139.

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

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience, 17,* 4302–4311.

Karpel, M. E., Hoyer, W. J., & Toglia, M. P. (2001). Accuracy and qualities of real and suggested memories: Nonspecific age differences. *Journals of Gerontology, Series B: Psychological Sciences and Social Sciences, 56,* 103–110.

Kaszniak, A. W., & Newman, M. C. (2000). Toward a neuropsychology of cognitive aging. In S. H. Qualls & N. Abeles (Eds.), *Psychology and the aging revolution: How we adapt to longer life* (pp. 43–67). Washington, DC: American Psychological Association.

Kelley, C. M., & Jacoby, L. L. (2000). Recollection and familiarity: Process-dissociation. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 215–228). New York: Oxford University Press.

Kelley, C. M., & Sahakyan, L. (2003). Memory, monitoring, and control in the attainment of memory accuracy. *Journal of Memory and Language, 48,* 704–721.

Kelley, W. L., Miezin, F. M., McDermott, K., Buckner, R. L., Raichle, M. E., Cohen, N. J., & Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobes for verbal and nonverbal memory encoding. *Neuron, 20,* 927–936.

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience, 14,* 785–794.

Kensinger, E. A. (2007). Negative emotion enhances memory: Accuracy behavioral and neuroimaging evidence. *Current Directions in Psychological Science, 16,* 213–218.

Kensinger, E. A. (2009). How emotion affects older adults' memories for event details. *Memory, 17,* 208–219.

Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience, 23,* 2407–2415.

Kensinger, E. A., & Corkin, S. (2004). Two routes to emotional memory: Distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences of the United States of America, 101,* 3310–3315.

Kensinger, E. A., & Corkin, S. (2008). Amnesia: Point and counterpoint. In J. Byrne (Series Ed.) & R. Menzel (Vol. Ed.), *Learning and memory: A comprehensive reference*. Vol. 1: *Learning theory and behavior* (pp. 259–286). Oxford, England: Elsevier.

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience, 19,* 1872–1887.

Kensinger, E. A., & Schacter, D. L. (2005a). Emotional content and reality-monitoring ability: FMRI evidence for the influences of encoding processes. *Neuropsychologia, 43,* 1429–1443.

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

Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. *The Journal of Neuroscience, 26,* 2564–2570.

Kensinger, E. A., & Schacter, D. L. (2007). Remembering the specific visual details of presented objects: Neuroimaging evidence for effects of emotion. *Neuropsychologia, 45,* 2951–2962.

Kensinger, E. A., & Schacter, D. L. (2008a). Memory and emotion. In M. Lewis, J. M. Haviland-Jones, and L. F. Barrett (Eds.), *The handbook of emotions* (3rd ed., pp. 601–617). New York: Guilford.

Kensinger, E. A., & Schacter, D. L. (2008b). Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience, 20,* 1161–1173.

Kim, H., & Cabeza, R. (2007a). Differential contributions of prefrontal, medial temporal, and sensory-perceptual regions to true and false memory formation. *Cerebral Cortex, 17,* 2143–2150.

Kim, H., & Cabeza, R. (2007b). Trusting our memories: Dissociating the neural correlates of confidence in veridical versus illusory memories. *The Journal of Neuroscience, 27,* 12190–12197.

Kintsch, W. (1968). Recognition and free recall of organized lists. *Journal of Experimental Psychology, 78,* 481–487.

Kirchhoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *The Journal of Neuroscience, 20,* 6173–6180.

Kirwan, C. B., Jones, C. K., Miller, M. I., & Stark, C. E. L. (2007). High-resolution fMRI investigation of the medial temporal lobe. *Human Brain Mapping, 28,* 959–966.

Kirwan, C. B., & Stark, C. E. L. (2007). Overcoming interference: An fMRI investigation of pattern separation in the medial temporal lobe. *Learning & Memory, 14,* 625–633.

Kirwan, C. B., Wixted, J. T., & Squire, L. R. (2008). Activity in the medial temporal lobe predicts memory strength, whereas activity in the prefrontal cortex predicts recollection. *The Journal of Neuroscience, 28,* 10541–10548.

Knight, M., Seymour, T. L., Gaunt, J. T., Baker, C., Nesmith, K., & Mather, M. (2007). Aging and goal-directed emotional attention: Distraction reverses emotional biases. *Emotion, 7,* 705–714.

Köhler, S., Paus, T., Buckner, R. L., & Milner, B. (2004). Effects of left inferior prefrontal stimulation on episodic memory formation: A two-stage fMRI–rTMS study. *Journal of Cognitive Neuroscience, 16,* 178–188.

Konishi, S., Uchida, I., Okuaki, T., Machida, T., Shirouzu, I., & Miyashita, Y. (2002). Neural correlates of recency judgment. *The Journal of Neuroscience, 22,* 9549–9555.

Kroll, N. E. A., Knight, R. T., Metcalfe, J., Wolf, E. S., & Tulving, E. (1996). Cohesion failure as a source of memory illusions. *Journal of Memory and Language, 35,* 176–196.

Kuhl, B. A., & Wagner, A. D. (2009). Strategic control of memory. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (Vol. 9, pp. 437–444). Oxford, UK: Academic Press.

Kumaran, D., & Maguire, E. A. (2009). Novelty signals: A window into hippocampal information processing. *Trending in Cognitive Sciences, 13,* 47–54.

Kuskowski, M. A., & Pardo, J. V. (1999). The role of the fusiform gyrus in successful encoding of face stimuli. *NeuroImage, 9,* 599–610.

Lampinen, J. M., Meier, C. R., Arnal, J. D., & Leding, J. K. (2005). Compelling untruths: Content borrowing and vivid false memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31,* 954–963.

Lepage, M., Ghaffar, O., Nyberg, L., & Tulving, E. (2000). Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences of the United States of America, 97,* 506–511.

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

Lepage, M., Montoya, A., Pelletier, M., Achim, A. M., Menear, M., & Lal, S. (2006). Associative memory encoding and recognition schizophrenia: An event-related fMRI study. *Biological Psychiatry, 60,* 1215–1223.

Leynes, P. A., & Phillips, M. C. (2008). Event-related potential (ERP) evidence for varied recollection during source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 741–751.

Li, S.-C., Naveh-Benjamin, M., & Lindenberger, U. (2005). Aging neuromodulation impairs associative binding: A neurocomputational account. *Psychological Science, 16,* 445–450.

Liberzon, I., & Sripada, C. S. (2008). The functional neuroanatomy of PTSD: A critical review. *Progress in Brain Research, 167,* 151–169.

Liberzon, I., Taylor, S. F., Amdur, R., Jung, T. D., Chamberlain, K. R., Minoshima, S., et al. (1999). Brain activation in PTSD in response to trauma-related stimuli. *Biological Psychiatry, 45,* 817–826.

Light, L. L., Prull, M. W., La Voie, D. J., & Healy, M. R. (2000). Dual process theories of memory in old age. In T. J. Perfect & E. A. Maylor (Eds.), *Models of cognitive aging* (pp. 238–300). Oxford, England: Oxford University Press.

Lindsay, D. S. (2008). Source monitoring. In J. Byrne (Series Ed.) & H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 2: Cognitive psychology of memory* (pp. 325–348). Oxford, England: Elsevier.

Lindsay, D. S., Hagen, L., Read, J. D., Wade, K. A., & Garry, M. (2004). True photographs and false memories. *Psychological Science, 15,* 149–154.

Lindsay, D. S., & Johnson, M. K. (1989). The eyewitness suggestibility effect and memory for source. *Memory & Cognition, 17,* 349–358.

Lindsay, D. S., Johnson, M. K., & Kwon, P. (1991). Developmental changes in memory source monitoring. *Journal of Experimental Child Psychology, 52,* 297–318.

Lindsay, D. S., & Read, J. D. (1994). Psychotherapy and memories of childhood sexual abuse: A cognitive perspective. *Applied Cognitive Psychology, 8,* 281–338.

Lipton, P. A., & Eichenbaum, H. (2008). Complementary roles of hippocampus and medial entorhinal cortex in episodic memory. *Neural Plasticity, Vol. 2008,* 1–8.

Loftus, E. F. (1979). *Eyewitness testimony.* Cambridge, MA: Harvard University Press.

Loftus, E. F., & Pickrell, J. E. (1995). The formation of false memories. *Psychiatric Annals, 25,* 720–725.

Lyle, K. B., Bloise, S. M., & Johnson, M. K. (2006). Age-related binding deficits and the content of false memories. *Psychology and Aging, 21,* 86–95.

Lyle, K. B., & Johnson, M. K. (2006). Importing perceived features into false memories. *Memory, 14,* 197–213.

Lyle, K. B., & Johnson, M. K. (2007). Source misattributions may increase the accuracy of source judgments. *Memory & Cognition, 35,* 1024–1033.

MacPherson, S. E., Phillips, L. H., & Della Sala, S. (2002). Age, executive function, and social decision making: A dorsolateral prefrontal theory of cognitive aging. *Psychology & Aging, 17,* 598–609.

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

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

Marcel, A. J. (1983). Conscious and unconscious perception: Experiments on visual masking and word recognition. *Cognitive Psychology, 15,* 197–237.

Maril, A., Simons, J. S., Weaver, J. J., & Schacter, D. L. (2005). Graded recall success: An event-related fMRI comparison of tip of the tongue and feeling of knowing. *NeuroImage, 24,* 1130–1138.

Marsh, E. J., Eslick, A. N., & Fazio, L. K. (2008). False memories. In J. Byrne (Series Ed.) & H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 2: Cognitive psychology of memory* (pp. 221–238). Oxford, England: Elsevier.

Marsh, R. L., & Hicks, J. L. (1998). Test formats change source-monitoring decision processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 24,* 1137–1151.

Mather, M. (2004). Aging and emotional memory. In D. Reisberg & P. Hertel (Eds.), *Memory and emotion* (pp. 272–307). New York: Oxford University Press.

Mather, M. (2006). Why memories may become more positive with age. In B. Uttl, N. Ohta, & A. L. Siegenthaler (Eds.), *Memory and emotion: Interdisciplinary perspectives* (pp. 135–159). Boston: Blackwell.

Mather, M. (2007). Emotional arousal and memory binding: An object-based framework. *Perspectives on Psychological Science, 2,* 33–52.

Mather, M., Henkel, L. A., & Johnson, M. K. (1997). Evaluating characteristics of false memories: Remember/know judgments and memory characteristics questionnaire compared. *Memory & Cognition, 25,* 826–837.

Mather, M., Johnson, M. K., & De Leonardis, D. M. (1999). Stereotype reliance in source monitoring: Age differences and neuropsychological test correlates. *Cognitive Neuropsychology, 16,* 437–458.

Mather, M., Mitchell, K. J., Raye, C. L., Novak, D. L., Greene, E. J., & Johnson, M. K. (2006). Emotional arousal can impair feature binding in working memory. *Journal of Cognitive Neuroscience, 18,* 614–625.

May, C. P., Rahhal, T., Berry, E. M., & Leighton, E. A. (2005). Aging, source memory, and emotion. *Psychology and Aging, 20,* 571–578.

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

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences, 7,* 293–299.

McDermott, K. B., Buckner, R. L., Petersen, S. E., Kelley, W. M., & Sanders, A. L. (1999). Set- and code-specific activation in the frontal cortex: An fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience, 11,* 631–640.

McDuff, S., Frankel, H. C., & Norman, K. A. (2008). *Many roads to the source: Tracking differences in memory retrieval strategies using multi-voxel pattern analysis.* Manuscript submitted for publication.

McElree, B., Dolan, P. O., & Jacoby, L. L. (1999). Isolating the contributions of familiarity and source information to item recognition: A time course analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25,* 563–582.

McGinnis, D., & Roberts, P. (1996). Qualitative characteristics of vivid memories attributed to real and imagined experiences. *American Journal of Psychology, 109,* 59–77.

McGuire, P. K., Silbersweig, D. A., Wright, I., Murray, R. M., David, A. S., Frackowiak, R. S. J., et al. (1995). Abnormal monitoring of inner speech: A physiological basis for auditory hallucinations. *Lancet, 346,* 596–600.

McNally, R. J. (2006). Cognitive abnormalities in post-traumatic stress disorder. *Trends in Cognitive Sciences, 10,* 271–277.

Meiser, T., & Bröder, A. (2002). Memory for multidimensional source information. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28,* 116–137.

Meiser, T., & Sattler, C. (2007). Boundaries of the relation between conscious recollection and source memory for perceptual details. *Consciousness and Cognition, 16,* 189–210.

Metcalf, K., Langdon, R., & Coltheart, M. (2007). Models of confabulation: A critical review and a new framework. *Cognitive Neuropsychology, 24,* 23–47.

Meyer-Lindenberg, A. S., Olsen, R. K., Kohn, P. D., Brown, T., Egan, M. F., Weinberger, D. R., et al. (2005). Regionally specific disturbance of dorsolateral prefrontal-hippocampal functional connectivity in schizophrenia. *Archives of General Psychiatry, 62,* 379–386.

Mickley, K. R., & Kensinger, E. A. (2008). Emotional valence influences the neural correlates associated with remembering and knowing. *Cognitive, Affective, & Behavioral Neuroscience, 8,* 143–152.

Mikels, J. A., Larkin, G. R., Reuter-Lorenz, P. A., & Carstensen, L. L. (2005). Divergent trajectories in the aging mind: Changes in working memory for affective versus visual information with age. *Psychology and Aging, 20,* 542–553.

Mitchell, K. J., & Johnson, M. K. (2000). Source monitoring: Attributing mental experiences. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 179–195). New York: Oxford University Press.

Mitchell, K. J., Johnson, M. K., & Mather, M. (2003). Source monitoring and suggestibility to misinformation: Adult age-related differences. *Applied Cognitive Psychology, 17,* 107–119.

Mitchell, K. J., Johnson, M. K., Raye, C. L., & D'Esposito, M. (2000). fMRI evidence of age-related hippocampal dysfunction in feature binding in working memory. *Cognitive Brain Research, 10,* 197–206.

Mitchell, K. J., Johnson, M. K., Raye, C. L., & Greene, E. J. (2004). Prefrontal cortex activity associated with source monitoring in a working memory task. *Journal of Cognitive Neuroscience, 16,* 921–934.

Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., & D'Esposito, M. (2000). Aging and reflective processes of working memory: Binding and test load deficits. *Psychology and Aging, 15,* 527–541.

Mitchell, K. J., Johnson, M. R., Higgins, J. A., & Johnson, M. K. (2009). *Effects of age on modulation of posterior category-specific activity during reflective attention.* Manuscript in preparation.

Mitchell, K. J., Mather, M., Johnson, M. K., Raye, C. L., & Greene, E. J. (2006). A functional magnetic resonance imaging investigation of short-term source and item memory for negative pictures. *NeuroReport, 17,* 1543–1547.

Mitchell, K. J., Nolen-Hoeksema, S., & Johnson, M. K. (2009). *The effects of dysphoria on brain activity associated with source memory for emotional information.* Manuscript in preparation.

Mitchell, K. J., Raye, C. L., Johnson, M. K., & Greene, E. J. (2006). An fMRI investigation of short-term source memory in young and older adults. *NeuroImage, 30,* 627–633.

Mitchell, K. J., Raye, C. L., McGuire, J. T., Frankel, H., Greene, E. J., & Johnson, M. K. (2008). Neuroimaging evidence for agenda-dependent monitoring of different features during short-term source memory tests. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34,* 780–790.

Mitchell, K. J., & Zaragoza, M. S. (2001). Contextual overlap and eyewitness suggestibility. *Memory & Cognition, 29,* 616–626.

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

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior, 16,* 519–533.

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

Moscovitch, M. (1995). Confabulation. In D. L. Schacter (Ed.), *Memory distortion: How minds, brains, and societies reconstruct the past* (pp. 226–251). Cambridge, MA: Harvard University Press.

Moscovitch, M., & Winocur, G. (1995). Frontal lobes, memory, and aging. *Annals of the New York Academy of Sciences, 769,* 119–150.

Most, S. B., Chun, M. M., Widders, D. M., & Zald, D. H. (2005). Attentional rubbernecking: Cognitive control and personality in emotion-induced blindness. *Psychonomic Bulletin & Review, 12,* 654–661.

Multhaup, K. S., De Leonardis, D. M., & Johnson, M. K. (1999). Source memory and eyewitness suggestibility in older adults. *Journal of General Psychology, 126,* 74–84.

Myers, C. E., Shohamy, D., Gluck, M. A., Grossman, S., Kluger, A., Ferris, S., et al. (2003). Dissociating hippocampal versus basal ganglia contributions to learning and transfer. *Journal of Cognitive Neuroscience, 15,* 185–193.

Nadel, L., & Hardt, O. (1994). The spatial brain. *Neuropsychology, 18,* 473–476.

Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 1170–1187.

Naveh-Benjamin, M., Brav, T. K., & Levy, O. (2007). The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging, 22,* 202–208.

Naveh-Benjamin, M., & Old, S. R. (2008). Aging and memory. In J. Byrne (Series Ed.) & H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference*. *Vol. 2: Cognitive psychology of memory* (pp. 787–808). Oxford, England: Elsevier.

Neisser, U. (1981). John Dean's memory: A case study. *Cognition, 9,* 1–22.

Newcombe, N. S., Lloyd, M. E., & Ratliff, K. R. (2007). Development of episodic and autobiographical memory: A cognitive neuroscience perspective. In R. V. Kail (Ed.), *Advances in child development and behavior* (Vol. 35, pp. 37–85). San Diego, CA: Elsevier.

Nolde, S. F., Johnson, M. K., & D'Esposito, M. (1998). Left prefrontal activation during episodic remembering: An event-related fMRI study. *NeuroReport, 9,* 3509–3514.

Nolde, S. F., Johnson, M. K., & Raye, C. L. (1998). The role of the prefrontal cortex during tests of episodic memory. *Trends in Cognitive Sciences, 2,* 399–406.

Norman, K. A., Detre, G., & Polyn, S. M. (2008). Computational models of episodic memory. In R. Sun (Ed.), *The Cambridge handbook of computational cognitive modeling* (pp. 189–225). New York: Cambridge University Press.

Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review, 110,* 611–646.

Norman, K. A., & Schacter, D. L. (1997). False recognition in younger and older adults: Exploring the characteristics of illusory memories. *Memory & Cognition, 25,* 838–848.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain-A meta-analysis of imaging studies on the self. *NeuroImage, 31,* 440–457.

O'Brien, J. T., Desmond, P., Ames, D., Schweitzer, I., & Tress, B. (1997). 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, 12,* 369–374.

O'Hanlon, L., Wilcox, K. A., & Kemper, S. (2001). Age differences in implicit and explicit associative memory: Exploring elaborative processing effects. *Experimental Aging Research, 27,* 341–359.

Ochsner, K. N., Beer, J. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D. E., Kihlstrom, J. F., et al. (2005). The neural correlates of direct and reflected self-knowledge. *NeuroImage, 28,* 797–814.

Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., et al. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience, 16,* 1746–1772.

Okado, Y., & Stark, C. (2003). Neural processing associated with true and false memory retrieval. *Cognitive, Affective, & Behavioral Neuroscience, 3,* 323–334.

Old, S. R., & Naveh-Benjamin, M. (2008). Differential effects of age on item and associative measures of memory: A meta-analysis. *Psychology and Aging, 23,* 104–118.

Olson, I. R., & Berryhill, M. (in press). Some surprising findings on the involvement of the parietal lobe in human memory. *Neurobiology of Learning and Memory.*

Olson, I. R., Page, K., Moore, K. S., Chatterjee, A., & Verfaellie, M. (2006). Working memory for conjunctions relies on the medial temporal lobe. *The Journal of Neuroscience, 26,* 4596–4601.

Olson, I. R., Plotzker, A., & Ezzyat, Y. (2007). The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain, 130,* 1718–1731.

Õngur, D., Cullen, T. J., Wolf, D. H., Rohan, M., Barreira, P., Zalesak, M., et al. (2006). The neural basis of relational memory deficits in schizophrenia. *Archives of General Psychiatry, 63,* 356–365.

Onitsuka, T., Shenton, M. E., Salisbury, D. F., Dickey, C. C., Kasai, K., Toner, S. K., et al. (2004). Middle and inferior temporal gyrus gray matter volume abnormalities in chronic schizophrenia: An MRI study. *American Journal of Psychiatry, 161,* 1603–1611.

Otten, L. J. (2007). Fragments of a larger whole: Retrieval cues constrain observed neural correlates of memory encoding. *Cerebral Cortex, 17,* 2030–2038.

Paller, K. A. (2004). Electrical signals of memory and of the awareness of remembering. *Current Directions in Psychological Science, 13,* 49–55.

Paller, K. A., Voss, J. L., & Boehm, S. G. (2007). Validating neural correlates of familiarity. *Trends in Cognitive Sciences, 11,* 243–250.

Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 101,* 13091–13095.

Parkin, A. (1997). The neuropsychology of false memory. *Learning and Individual Differences, 9,* 341–357.

Parkin, A. J., & Walter, B. M. (1992). Recollective experience, normal aging, and frontal dysfunction. *Psychology and Aging, 7,* 290–298.

Parks, C. M., & Yonelinas, A. P. (2007). Moving beyond pure signal-detection models: Comment on Wixted (2007). *Psychological Review, 114,* 188–202.

Payer, D., Marshuetz, C., Sutton, B., Hebrank, A., Welsh, R. C., & Park, D. C. (2006). Decreased neural specialization in old adults on a working memory task. *NeuroReport, 17,* 487–491.

Persson, J., & Nyberg, L. (2006). Altered brain activity in healthy seniors: What does it mean? In A. Møller (Ed.), *Reprogramming the human brain. Progress in brain research* (Vol. 157, pp. 45–56). Amsterdam: Elsevier.

Peters, J., Koch, B., Schwarz, M., & Daum, I. (2007). Domain-specific impairment of source memory following a right posterior medial temporal lobe lesion. *Hippocampus, 17,* 505–509.

Peters, J., Suchan, B., Köster, O., & Daum, I. (2007). Domain-specific retrieval of source information in the medial temporal lobe. *European Journal of Neuroscience, 26,* 1333–1343.

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

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage, 16,* 331–348.

Phelps, E. A. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annual Review of Psychology, 57,* 27–53.

Phelps, E. A., Ling, S., & Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science, 17,* 292–299.

Phelps, E. A., & Sharot, T. (2008). How (and why) emotion enhances the subjective sense of recollection. *Current Directions in Psychological Science, 17,* 147–152.

Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. E. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience, 3,* 85–90.

Preston, A. R., & Gabrieli, J. D. E. (2008). Dissociation between explicit memory and configural memory in the human medial temporal lobe. *Cerebral Cortex, 18,* 2192–2207.

Protzner, A. B., & McIntosh, A. R. (2008). Modulation of ventral prefrontal cortex functional connections reflects the interplay of cognitive processes and stimulus characteristics. *Cerebral Cortex.* Advance online publication. Retrieved September, 11, 2008. doi: 10.1093/cercor/bhn146

Prull, M. W., Dawes, L. L. C., Martin, A. M. III, Rosenberg, H. F., & Light, L. L. (2006). Recollection and familiarity in recognition memory: Adult age differences and neuropsychological test correlates. *Psychology and Aging, 21,* 107–118.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology, 74,* 1192–1199.

Qin, J., Mitchell, K. J., Johnson, M. K., Krystal, J. H., Southwick, S. M., Rasmusson, A. M., et al. (2003). Reactions to and memories for the September 11, 2001 terrorist attacks in adults with posttraumatic stress disorder. *Applied Cognitive Psychology, 17,* 1081–1097.

Qin, J., Raye, C. L., Johnson, M. K., & Mitchell, K. J. (2001). Source ROCs are (typically) curvilinear: Comment on Yonelinas (1999). *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27,* 1110–1115.

Quamme, J. R., Yonelinas, A. P., & Norman, K. A. (2007). Effect of unitization on associative recognition in amnesia. *Hippocampus, 17,* 192–200.

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

Rahhal, T. A., May, C. P., & Hasher, L. (2002). Truth and character: Sources that older adults can remember. *Psychological Science, 13,* 101–105.

Rajah, M. N., & D'Esposito, M. (2005). Region-specific changes in prefrontal function with age: A review of PET and fMRI studies on working and episodic memory. *Brain, 128,* 1964–1983.

Rajarethinam, R., Sahni, S., Rosenberg, D. R., & Keshavan, M. S. (2004). Reduced superior temporal gyrus volume in young offspring of patients with schizophrenia. *American Journal of Psychiatry, 161,* 1121–1124.

Ranganath, C., & Blumenfeld, R. S. (2005). Doubts about double dissociations between short-and long-term memory. *Trends in Cognitive Sciences, 9,* 374–380.

Ranganath, C., & Blumenfeld, R. S. (2008). Prefrontal cortex and memory. In J. Byrne (Series Ed.) & H. Eichenbaum (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 3: Memory systems* (pp. 261–280). Oxford, England: Elsevier.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *The Journal of Neuroscience, 20*(RC108), 1–5.

Ranganath, C., Minzenberg, M. J., & Ragland, J. D. (2008). The cognitive neuroscience of memory function and dysfunction in schizophrenia. *Biological Psychiatry, 64,* 18–25.

Rauch, S. L., Whalen, P. J., Shin, L. M., McInerney, S. C., Macklin, M. L., Lasko, N. B., et al. (2000). Exaggerated amygdala response to masked facial stimuli in posttraumatic stress disorder: A functional MRI study. *Biological Psychiatry, 47,* 769–776.

Raye, C. L., Johnson, M. K., Mitchell, K. J., Greene, E. J., & Johnson, M. R. (2007). Refreshing: A minimal executive function. *Cortex, 43,* 135–145.

Raye, C. L., Johnson, M. K., Mitchell, K. J., Nolde, S. F., & D'Esposito, M. (2000). fMRI investigations of left and right PFC contributions to episodic remembering. *Psychobiology, 28,* 197–206.

Raye, C. L., Johnson, M. K., Mitchell, K. J., Reeder, J. A., & Greene, E. J. (2002). Neuroimaging a single thought: Dorsolateral PFC activity associated with refreshing just-activated information. *NeuroImage, 15,* 447–453.

Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. I. M. Craik & T. A. Salthouse (Eds.), *Handbook of aging and cognition* (2nd ed., pp. 1–90). Mahwah, NJ: Erlbaum.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., et al. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex, 15,* 1676–1689.

Raz, N., & Rodrigue, K. M. (2006). Differential aging of the brain: Patterns, cognitive correlates, and modifiers. *Neuroscience and Biobehavioral Reviews, 30,* 730–748.

Raz, N., Rodrigue, K. M., Head, D., Kennedy, K. M., & Acker, J. D. (2004). Differential aging of the medial temporal lobe: A study of a five-year change. *Neurology, 62,* 433–438.

Reinitz, M. T., Verfaellie, M., & Milberg, W. P. (1996). Memory conjunction errors in normal and amnesic subjects. *Journal of Memory and Language, 35,* 286–299.

Reisberg, D., & Heuer, F. (2004). Memory for emotional events. In D. Reisberg & P. Hertel (Eds.), *Memory and emotion* (pp. 3–41). New York: Oxford University Press.

Reuter-Lorenz, P. A. (2002). New visions of the aging mind and brain. *Trends in Cognitive Sciences, 6,* 394–400.

Riccio, D. C., Ackil, J., & Burch-Vernon, A. (1992). Forgetting of stimulus attributes: Methodological implications for assessing associative phenomena. *Psychological Bulletin, 112,* 433–445.

Richardson, M. P., Strange, B. A., & Dolan, R. J. (2004). Encoding of emotional memories depends on amygdala and hippocampus and their interactions. *Nature Neuroscience, 7,* 278–285.

Ritchey, M., Dolcos, F., & Cabeza, R. (2008). Role of amygdala connectivity in the persistence of emotional memories over time: An event-related fMRI investigation. *Cerebral Cortex, 18,* 2494–2504.

Rizzo, L., Danion, J.-M., Van der Linden, M., Grangé, D., & Rohmer, J.-G. (1996). Impairment of memory for spatial context in schizophrenia. *Neuropsychology, 10,* 376–384.

Roediger, H. L., III & Geraci, L. (2007). Aging and the misinformation effect: A neuropsychological analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33,* 321–334.

Roediger, H. L., III & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21,* 803–814.

Ross, M. (1997). Validating memories. In N. L. Stein, P. A. Ornstein, B. Tversky, & C. Brainerd (Eds.), *Memory for everyday and emotional events* (pp. 49–81). Mahwah, NJ: Erlbaum.

Rossi, S., Pasqualetti, P., Zito, G., Vecchio, F., Cappa, S. F., Miniussi, C., et al. (2006). Prefrontal and parietal cortex in human episodic memory: An interference study by repetitive transcranial magnetic stimulation. *European Journal of Neuroscience, 23,* 793–800.

Rotello, C. M., Macmillan, N. A., & Reeder, J. A. (2004). Sum-difference theory of remembering and knowing: A two-dimensional signal-detection model. *Psychological Review, 111,* 588–616.

Rubin, D. C., Feldman, M. E., & Beckham, J. C. (2004). Reliving, emotions, and fragmentation in the autobiographical memories of veterans diagnosed with PTSD. *Applied Cognitive Psychology, 18,* 17–35.

Rubin, D. C., & Schulkind, M. D. (1997). Distribution of important and word-cue autobiographical memories in 20-, 35-, and 70-year-old adults. *Psychology and Aging, 12,* 524–535.

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences, 11,* 251–257.

Rugg, M. D., Fletcher, P. C., Chua, P. M.-L., & Dolan, R. J. (1999). The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage, 10,* 520–529.

Rugg, M. D., Otten, L. J., & Henson, R. N. A. (2002). The neural basis of episodic memory: Evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society B: Biological Sciences, 357,* 1097–1110.

Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences, 4,* 108–115.

Ryan, L., Nadel, L., Keil, K., Putnam, K., Schnyer, D., Trouard, T., et al.

(2001). Hippocampal complex and retrieval of recent and very remote autobiographical memories: Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus, 11,* 707–714.

Rybash, J. M., & Hrubi-Bopp, K. L. (2000). Source monitoring and false recollection: A life span developmental perspective. *Experimental Aging Research, 26,* 75–87.

Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews Neuroscience, 8,* 657–661.

Schacter, D. L., Harbluk, J. L., & McLachlan, D. R. (1984). Retrieval without recollection: An experimental analysis of source amnesia. *Journal of Verbal Learning and Verbal Behavior, 23,* 593–611.

Schacter, D. L., Israel, L., & Racine, C. (1999). Suppressing false recognition in younger and older adults: The distinctiveness heuristic. *Journal of Memory and Language, 40,* 1–24.

Schacter, D. L., Koutstaal, W., & Norman, K. A. (1997). False memories and aging. *Trends in Cognitive Sciences, 1,* 229–236.

Schacter, D. L., Osowiecki, D., Kaszniak, A. W., Kihlstrom, J. F., & Valdiserri, M. (1994). Source memory: Extending the boundaries of age-related deficits. *Psychology and Aging, 9,* 81–89.

Schacter, D. L., Reiman, E., Curran, T., Yun, L. S., Bandy, D., McDermott, K. B., et al. (1996). Neuroanatomical correlates of veridical and illusory recognition memory: Evidence from positron emission tomography. *Neuron, 17,* 267–274.

Schacter, D. L., & Wagner, A. D. (1999, November 3). Perspectives: Neuroscience. Remembrance of things past. *Science, 285,* 1503–1504.

Schnider, A. (2008). *The confabulating mind: How the brain creates reality.* New York: Oxford University Press.

Shallice, T., Fletcher, P., Frith, C. D., Grasby, P., Frackowiak, R. S. J., & Dolan, R. J. (1994, April 14). Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature, 368,* 633–635.

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

Sharot, T., & Yonelinas, A. P. (2008). Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition, 106,* 538–547.

Shenton, M. E., Dickey, C. C., Frumin, M., & McCarley, R. W. (2001). A review of MRI findings in schizophrenia. *Schizophrenia Research, 49,* 1–52.

Shergill, S. S., Brammer, M. J., Fukuda, H., Williams, S. C. R., Murray, R. M., & McGuire, P. K. (2003). Engagement of brain areas implicated in processing inner speech in people with auditory hallucinations. *British Journal of Psychiatry, 182,* 525–531.

Shimamura, A. P. (1995). Memory and the prefrontal cortex. In J. Grafman, K. J. Holyoak, & F. Boller (Eds.), *Structure and function of the human prefrontal cortex*: *Annals of the New York Academy of Sciences, 769,* 151–159.

Shimamura, A. P. (2002). Relational binding theory and the role of consolidation in memory retrieval. In L. R. Squire & D. L. Schacter (Eds.), *Neuropsychology of memory* (3rd ed., pp. 61–72). New York: Guilford Press.

Shimamura, A. P., & Squire, L. R. (1987). A neuropsychological study of fact memory and source amnesia. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 13,* 464–473.

Shin, L. M., Rauch, S. L., & Pitman, R. K. (2006). Amygdala, medial prefrontal cortex, and hippocampal function in PTSD. In R. Yehuda (Ed.), *Psychobiology of posttraumatic stress disorder: A decade of progress. Annals of the New York Academy of Sciences, 1071,* 67–79.

Shohamy, D., & Wagner, A. D. (2008). Integrating memories in the human brain: Hippocampal-midbrain encoding of overlapping events. *Neuron, 60,* 378–389.

Siegle, G. J., Steinhauer, S. R., Thase, M. E., Stenger, V. A., & Carter, C. S. (2002). Can't shake that feeling: Event-related fMRI assessment of sustained amygdala activity in response to emotional information in depressed individuals. *Biological Psychiatry, 51,* 693–707.

Siegle, G. J., Thompson, W., Carter, C. S., Steinhauer, S. R., & Thase, M. E. (2007). Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: Related and independent features. *Biological Psychiatry, 61,* 198–209.

Simons, J. S. (in press). Constraints on cognitive theories from neuroimaging studies of source memory. In F. Rösler, C. Ranganath, B. Röder, & R. H. Kluwe (Eds.), *Neuroimaging and psychological theories of human memory.* Oxford, England: Oxford University Press.

Simons, J. S., Davis, S. W., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2006). Discriminating imagined from perceived information engages brain areas implicated in schizophrenia. *NeuroImage, 32,* 696–703.

Simons, J. S., Dodson, C. S., Bell, D., & Schacter, D. L. (2004). Specific- and partial-source memory: Effects of aging. *Psychology and Aging, 19,* 689–694.

Simons, J. S., Gilbert, S. J., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. *Journal of Neurophysiology, 94,* 813–820.

Simons, J. S., Henson, R. N. A., Gilbert, S. J., & Fletcher, P. C. (2008). Separable forms of reality monitoring supported by the anterior prefrontal cortex. *Journal of Cognitive Neuroscience, 20,* 447–457.

Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D., & Schacter, D. L. (2003). Neural mechanisms of visual object priming: Evidence for perceptual and semantic distinctions in fusiform cortex. *NeuroImage, 19,* 613–626.

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

Simons, J. S., Peers, P., Mazuz, Y., Berryhill, M., & Olson, I. (2009). *Dissociation between memory accuracy and memory confidence following bilateral parietal lesions.* Manuscript submitted for publication.

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

Simons, J. S., Verfaellie, M., Galton, C. J., Miller, B. L., Hodges, J. R., & Graham, K. S. (2002). Recollection-based memory in frontotemporal dementia: Implications for theories of long-term memory. *Brain, 125,* 2523–2536.

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

Slotnick, S. D., Klein, S. A., Dodson, C. S., & Shimamura, A. P. (2000). An analysis of signal detection and threshold models of source memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 1499–1517.

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

Slotnick, S. D., & Schacter, D. L. (2004). A sensory signature that distinguishes true from false memories. *Nature Neuroscience, 7,* 664–672.

Small, G. W., Bookheimer, S. Y., Thompson, P. M., Cole, G. M., Huang, S.-C., Kepe, V., et al. (2008). Current and future uses of neuroimaging for cognitively impaired patients. *Lancet Neurology, 7,* 161–172.

Small, S. A., Tsai, W. Y., De La Paz, R., Mayeux, R., & Stern, Y. (2002). Imaging hippocampal function across the human life span: Is memory decline normal or not? *Annals of Neurology, 51,* 290–295.

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

Smith, A. P. R., Henson, R. N. A., Rugg, M. D., & Dolan, R. J. (2005). Modulation of retrieval processing reflects accuracy of emotional source memory. *Learning & Memory, 12,* 472–479.

Sommer, I. E. C., Diederen, K. M. J., Blom, J.-D., Willems, A., Kushan, L., Slotema, K., et al. (2008). Auditory verbal hallucinations predominantly activate the *right* inferior frontal area. *Brain, 131,* 3169–3177.

Spencer, W. D., & Raz, N. (1995). Differential effects of aging on memory for content and context: A meta-analysis. *Psychology and Aging, 10,* 527–539.

Sperling, R. A., Bates, J. F., Chua, E. F., Cocchiarella, A. J., Rentz, D. M., Rosen, B. R., et al. (2003). fMRI studies of associative encoding in young and elderly controls and mild Alzheimer's disease. *Journal of Neurology Neurosurgery and Psychiatry, 74,* 44–50.

Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory, 82,* 171–177.

Squire, L. R., & Knowlton, B. J. (1995). Memory, hippocampus, and brain systems. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 825–837). Cambridge, MA: MIT Press.

Squire, L. R., Knowlton, B., & Musen, G. (1993). The structure and organization of memory. *Annual Review of Psychology, 44,* 453–495.

Squire, L. R., & Shrager, Y. (2008). Declarative memory system: Amnesia. In J. Byrne (Series Ed.) & H. Eichenbaum (Vol. Ed.), *Learning and memory: A comprehensive reference. Vol. 3: Memory systems* (pp. 67–78). Oxford, England: Elsevier.

Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience, 27,* 279–306.

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

Squire, L. R., & Zola-Morgan, S. (1991, September 20). The medial temporal lobe memory system. *Science, 253,* 1380–1386.

Staresina, B. P., & Davachi, L. (2006). Differential encoding mechanisms for subsequent associative recognition and free recall. *The Journal of Neuroscience, 26,* 9162–9172.

Stark, C. E. L., Bayley, P. J., & Squire, L. R. (2002). Recognition memory for single items and for associations is similarly impaired following damage to the hippocampal region. *Learning & Memory, 9,* 238–242.

Stark, C. E. L., & Squire, L. R. (2003). Hippocampal damage equally impairs memory for single items and memory for conjunctions. *Hippocampus, 13,* 281–292.

Starns, J. J., & Hicks, J. L. (2005). Source dimensions are retrieved independently in multidimensional monitoring tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31,* 1213–1220.

Starns, J. J., Hicks, J. L., Brown, N. L., & Martin, B. A. (2008). Source memory for unrecognized items: Predictions from multivariate signal detection theory. *Memory & Cognition, 36,* 1–8.

Steffens, M. C., Buchner, A., Martensen, H., & Erdfelder, E. (2000). Further evidence on the similarity of memory processes in the process dissociation procedure and in source monitoring. *Memory & Cognition, 28,* 1152–1164.

Stuss, D. T., & Benson, D. F. (1986). *The frontal lobes.* New York: Raven Press.

Summerfield, C., Greene, M., Wager, T., Egner, T., Hirsch, J., & Mangels, J. (2006). Neocortical connectivity during episodic memory formation. *PLoS Biology, 4,* 855–864.

Suzuki, M., Fujii, T., Tsukiura, T., Okuda, J., Umetsu, A., Nagasaka, T., et al. (2002). Neural basis of temporal context memory: A functional MRI study. *NeuroImage, 17,* 1790–1796.

Swick, D., Senkfor, A. J., & Van Petten, C. (2006). Source memory retrieval is affected by aging and prefrontal lesions: Behavioral and ERP evidence. *Brain Research, 1107,* 161–176.

Tapia, G., Clarys, D., El Hage, W., Belzung, C., & Isingrini, M. (2007). PTSD psychiatric patients exhibit a deficit in remembering. *Memory, 15,* 145–153.

Thoma, P., Zoppelt, D., Wiebel, B., & Daum, I. (2006). Recollection and familiarity in negative schizophrenia. *Neuropsychologia, 44,* 430–435.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences of the United States of America, 94,* 14792–14797.

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

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review, 80,* 352–373.

Turner, M. S., Simons, J. S., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2008). Distinct roles for lateral and medial rostral prefrontal cortex in source monitoring of perceived and imagined events. *Neuropsychologia, 46,* 1442–1453.

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

Uncapher, M. R., & Rugg, M. D. (2008). Fractionation of the component processes underlying successful episodic encoding: A combined functional magnetic resonance imaging and divided-attention study. *Journal of Cognitive Neuroscience, 20,* 240–254.

Valenzuela, M. J., Breakspear, M., & Sachdev, P. (2007). Complex mental activity and the aging brain: Molecular, cellular, and cortical network mechanisms. *Brain Research Reviews, 56,* 198–213.

Van Petten, C. (2004). Relationship between hippocampal volume and memory ability in healthy individuals across the lifespan: Review and meta-analysis. *Neuropsychologia, 42,* 1394–1413.

Van Petten, C., Luka, B. J., Rubin, S. R., & Ryan, J. P. (2002). Frontal brain activity predicts individual performance in an associative memory exclusion test. *Cerebral Cortex, 12,* 1180–1192.

Velanova, K., Lustig, C., Jacoby, L. L., & Buckner, R. L. (2007). Evidence for frontally mediated controlled processing differences in older adults. *Cerebral Cortex, 17,* 1033–1046.

Viard, A., Piolino, P., Desgranges, B., Chetelat, G., Lebreton, K., Landeau, B., et al. (2007). Hippocampal activation for autobiographical memories over the entire lifetime in healthy aged subjects: An fMRI study. *Cerebral Cortex, 17,* 2453–2467.

Vilberg, K. L., & Rugg, M. D. (in press). An investigation of the effects of relative probability of old and new test items on neural correlates of successful and unsuccessful source memory. *NeuroImage.*

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

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

Vinogradov, S., Luks, T. L., Schulman, B. J., & Simpson, G. V. (2008). Deficit in a neural correlate of reality monitoring in schizophrenia patients. *Cerebral Cortex, 18,* 2532–2539.

Vinogradov, S., Luks, T. L., Simpson, G. V., Schulman, B. J., Glenn, S., & Wong, A. E. (2006). Brain activation patterns during memory of cognitive agency. *NeuroImage, 31,* 896–905.

Vogt, B. A., & Laureys, S. (2005). Posterior cingulate, precuneal, and retrosplenial cortices: Cytology and components of the neural network correlates of consciousness. In S. Layreys (Ed.), *Progress in brain research,* (Vol. 150, pp. 205–217). Amsterdam: Elsevier.

Wagner, A. D. (1999). Working memory contributions to human learning and remembering. *Neuron, 22,* 19–22.

Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport, 9,* 3711–3717.

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences, 9,* 445–453.

Wais, P. E. (2008). fMRI signals associated with memory strength in the medial temporal lobes: A meta-analysis. *Neuropsychologia, 46,* 3185–3196.

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

Wais, P. E., Squire, L. R., & Wixted, J. T. (2008). *In search of recollection and familiarity signals in the hippocampus.* Manuscript in preparation.

Waters, F. A. V., Maybery, M. T., Badcock, J. C., & Michie, P. T. (2004). Context memory and binding in schizophrenia. *Schizophrenia Research, 68,* 119–125.

Weiss, A. P., & Heckers, S. (2001). Neuroimaging of declarative memory in schizophrenia. *Scandinavian Journal of Psychology, 42,* 239–250.

Werner, N. S., Meindl, T., Engel, R. R., Rosner, R., Riedel, M., Reiser, M., et al. (2009). Hippocampal function during associative learning in patients with posttraumatic stress disorder. *Journal of Psychiatric Research, 43,* 309–318.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120,* 272–292.

Whalley, M. G., Rugg, M. D., Smith, A. P. R., Dolan, R. J., & Brewin, C. R. (2009). Incidental retrieval of emotional contexts in post-traumatic stress disorder and depression: An fMRI study. *Brain and Cognition, 69,* 98–107.

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *NeuroImage, 21,* 1337–1349.

Williams, J. M. G., Barnhofer, T., Crane, C., Hermans, D., Raes, F., Watkins, E., et al. (2007). Autobiographical memory specificity and emotional disorder. *Psychological Bulletin, 133,* 122–148.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review, 114,* 152–176.

Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Content-specificity of the neural correlates of recollection. *Neuropsychologia, 43,* 1022–1032.

Woodruff, P. W. R., Wright, I. C., Bullmore, E. T., Brammer, M., Howard, R. J., Williams, S. C. R., et al. (1997). Auditory hallucinations and the temporal cortical response to speech in schizophrenia: A functional magnetic resonance imaging study. *American Journal of Psychiatry, 154,* 1676–1682.

Woodward, T. S., Weinstein, S., Cairo, T. A., Metzak, P., Ngan, E. T. C., & Kumar, D. (2008). *Hallucinations are associated with aberrant activation in inner speech regions during source monitoring* [Abstract]. *Schizophrenia Research, 102*(Suppl. 2), 96.

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

Yonelinas, A. P. (1999). 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, 25,* 1415–1434.

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

Yonelinas, A. P., Kroll, N. E. A., Quamme, J. R., Lazzara, M. M., Sauve, M.-J., Widaman, K. F., et al. (2002). Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nature Neuroscience, 5,* 1236–1241.

Yonelinas, A. P., & Parks, C. M. (2007). Receiver operating characteristics (ROCs) in recognition memory: A review. *Psychological Bulletin, 133,* 800–832.

Yonelinas, A. P., Widaman, K., Mungas, D., Reed, B., Weiner, M. W., & Chui, H. C. (2007). Memory in the aging brain: Doubly dissociating the contribution of the hippocampus and entorhinal cortex. *Hippocampus, 17,* 1134–1140.

Yu, J., & Bellezza, F. S. (2000). Process dissociation as source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 1518–1533.

Zacks, R. T., & Hasher, L. (2006). Aging and long-term memory: Deficits are not inevitable. In E. Bialystok & F. I. M. Craik (Eds.), *Lifespan cognition: Mechanisms of change* (pp. 162–177). New York: Oxford University Press.

Zaragoza, M. S., & Koshmider, J. W., III (1989). Misled subjects may know more than their performance implies. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15,* 246–255.

Zaragoza, M. S., & Lane, S. M. (1998). Processing resources and eyewitness suggestibility. *Journal of Legal and Criminological Psychology, 3,* 305–320.

Zubieta, J.-K., Chinitz, J. A., Lombardi, U., Fig, L. M., Cameron, O. G., & Liberzon, I. (1999). Medial frontal cortex involvement in PTSD symptoms: A SPECT study. *Journal of Psychiatric Research, 33,* 259–264.

Received November 3, 2008
Revision received November 3, 2008
Accepted January 9, 2009 ■