

The Cognitive Neuroscience of True and False Memories*

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Abstract Of central relevance to the recovered/false memory debate is understanding the factors that cause us to *believe that a mental experience is a memory of an actual past experience*. According to the source monitoring framework (SMF), memories are attributions that we make about our mental experiences based on their subjective qualities, our prior knowledge and beliefs, our motives and goals, and the social context. From this perspective, we discuss cognitive behavioral studies using both objective (e.g., recognition, source memory) and subjective (e.g., ratings of memory characteristics) measures that provide much information about the encoding, revival and monitoring processes that yield both true and false memories. The chapter also considers how neuroimaging findings, especially from functional magnetic resonance imaging studies, are contributing to our understanding of the relation between memory and reality.

Keywords False memories • Functional magnetic resonance imaging (fMRI) • Neuroimaging and memory • Source monitoring framework (SMF)

The recovered/false memory debate has centered around two main issues: Can traumatic events be forgotten for many years and then remembered? Are memories of trauma, including recovered memories, susceptible to memory distortion? Our perspective on these issues does not require taking sides: (1) Important events (even events that are highly emotionally charged at the time) can be forgotten; and previously forgotten events (even those long forgotten) sometimes may be remembered

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under appropriate cuing conditions. (2) Memories (even for highly emotional and significant events) can be inaccurate in consequential ways, but they sometimes can be quite accurate. The relative likelihood of each of these phenomena in everyday life, or their likelihood as sequelae to trauma, are methodologically challenging questions with important implications, for example, for legal and clinical practice. However, our lab has had a more specific focus relevant to the recovered/false memory debate: understanding the factors that cause us to *believe that a mental experience is a memory*.

With respect to this question, efforts from many labs have yielded much progress in the cognitive analysis of remembering. At a rapid pace, cognitive behavioral insights are being followed and extended by evidence from cognitive neuroscience. This chapter provides an overview of a theoretical framework that we believe is useful for thinking about memory, along with associated cognitive/behavioral findings, and an overview of some recent neuroimaging work related to issues of true and false memory.

Remembering

Remembering is a subjective mental experience. To provide context for the concept of remembering, it can be contrasted with forgetting and with forms of memory that do not involve the subjective sense of remembering.

Forgetting

Forgetting happens for many reasons: poor encoding; a failure to consolidate or to keep memories accessible through mechanisms like reactivation or rehearsal; absence of appropriate cues for remembering; interference when cues associated with the target information have become associated with other information (perhaps cuing memory for an entirely different event, or a reinterpretation of the original event). Furthermore, all of these factors are subject to motivational influences. For example, encoding of traumatic events may be poor because of avoidance (e.g., self-distraction, dissociation), or because reactivation or rehearsal of traumatic events is actively inhibited. Cues triggering memories of traumatic events may be deliberately avoided, or a less disturbing interpretation may be sought. Given the many reasons and ways (both incidental and deliberate) to forget, it is perhaps not surprising that we forget much of what we experience. Chapters in this volume discuss evidence concerning potential mechanisms of motivated forgetting, including inhibition (Anderson & Huddleston, 2012) and repression (McNally, 2012), as well as potential differences in the types of trauma that might induce motivated attempts to forget (DePrince et al., 2012) and individual differences in propensity to forget in populations reporting recovered memories (Geraerts, 2012).

Multiple Forms of Memory

Although there is relatively little of the totality of our experience that we can deliberately remember, this does not mean that all our “forgotten” experiences have no impact on us. As William James (1892) noted, “nothing we ever do is, in strict scientific literalness, wiped out” (see also Johnson, 1977, 1983). This general idea is reflected in many modern multiple memory system, or multiple representation, theories, which emphasize that there are manifestations of memory that do not necessarily involve or require conscious remembering (e.g., *habits, skills, procedures, implicit memories, priming, perceptual learning, semantic memory*, etc.). For example, Johnson and colleagues proposed a multiple-entry modular cognitive system (*MEM*) that supports different types of memory (Johnson, 1983; Johnson & Hirst, 1993), different aspects of consciousness (Johnson & Reeder, 1997), and different emotional experiences (Johnson & Multhaup, 1992). The idea that different aspects of experiences are processed by different mechanisms or subsystems can account for many observed phenomena, including acquisition of affective responses to stimuli even when the reasons for these affective responses are not consciously available, as in amnesia (Johnson, Kim, & Risse, 1985), or when vivid perceptual fragments are unexpectedly cued despite poorly integrated narrative accounts of events, such as occurs in individuals with PTSD (Brewin, 2012; Brewin, Gregory, Lipton, & Burgess, 2010; see also, e.g., Verwoerd, Wessel, de Jong, & Nieuwenhuis, 2009 for relevant evidence).

Forgetting and non-conscious forms of memory are clearly central to some of the main themes of the 58th Nebraska Symposium. However, we focus on another key and intriguing issue—the experience of remembering. The question under consideration in this chapter is what accounts for the phenomenal experience of having in mind a representation of a specific event that is believed to have actually taken place in our personal past. In particular, our lab has been interested for many years in the mechanisms of a cognitive system that yields both veridical and distorted memories. That is, how should we understand the formation, revival, and evaluation of true and false memories of specific autobiographical events? Theoretical ideas and empirical findings from laboratory studies of cognitive psychology and cognitive neuroscience are directly relevant to these questions. Of course, no single laboratory study embodies all the factors that occur in real life events. Laboratories are highly simplified contexts and we may as yet be missing some important factors, and undoubtedly we have an incomplete theoretical understanding about how some mechanisms work or interact. But there is no reason to believe that the relationships demonstrated in laboratory studies are not relevant to real life (Banaji & Crowder, 1989; Henkel & Coffman, 2004; Lindsay & Read, 1994; Wade et al., 2007).

What is a “Memory”?

Before attacking questions surrounding “memories” we could ask, what are “events” in the first place? An event is a collection of features (persons, objects, location,

Fig. 1 Possible interpretations of the ambiguous duck/rabbit figure. What one perceives and/or later remembers can vary both between people and within a person at different times (From Johnson, M.K. [1996]. Adapted from author's original.). For an interesting historical discussion of the duck/rabbit figure see <http://socrates.berkeley.edu/~kihlstrm/JastrowDuck.htm>



time, colors, tastes, semantics, actions, emotions, etc.) that are experienced as occurring in relation to each other (e.g., *the blue pen is on the table and George is reaching for it to sign the divorce papers*). Like the Duck/Rabbit in Fig. 1, the same person may see an event differently, depending on set or context and, of course, different people may see the same event differently, or even disagree on event boundaries. Encodings of events are not perfect representations of the “actual” event, but rather reflect an individual’s prior knowledge, focus of attention, interests, motives, comprehension, and so on. Not only do we not expect memory of an event to be a perfect representation of the “actual” event, we do not even necessarily expect it to be a perfect representation of an individual’s initial encoding of it. For example, at any point in time, set or context can change and appropriate cues may or may not be available, or new information may be incorporated into our interpretation of what happened. In short, encoding and remembering are the outcome of constructive and reconstructive processes—the processes that create both true and false memories (e.g., Barlett, 1932; Bransford & Johnson, 1972, 1973).

What is a “False” Memory?

As generally understood, errors of commission are *false memories* and errors of omission are *memory failures* or *forgetting*. Commission errors (distortions) have long been of interest (Barlett, 1932; Carmichael, Hogan, & Walter, 1932), including the mechanisms of “false recognition” of words (Anisfeld & Knapp, 1968; Cramer, 1970; Deese, 1959; Underwood, 1965) and of tacit implications of prose (e.g., Bransford &

Franks, 1971; Johnson, Bransford, & Solomon, 1973) and, more generally, constructive processes of memory (e.g., Bransford & Johnson, 1973; Loftus & Palmer, 1974). The similarities and differences among false perceptions, false memories, and false beliefs have also been of interest (e.g., in discussions of delusions, Johnson, 1988; see Wade et al., 2007, for a review of other early uses of the term “false memory”). As the term “false memory” became more widely used, and as issues of recovered memories of traumatic events increasingly raised clinical and legal issues that received a great deal of attention in the press, the term itself became a source of controversy. Some questioned the appropriateness of using the same term for relatively benign intrusions and false recognitions in tests of lists learned in the laboratory as for more consequential errors in memory for actual autobiographical events, especially for traumatic events (e.g., DePrince, Allard, Oh, & Freyd, 2004; Pezdek & Lam, 2007). Of course it is important to consider whether theoretical explanations or interpretations are being over-generalized and to be appropriately cautious in our claims of understanding. However, the term “false memory” is not a theoretical construct or an explanation. Rather, it refers to the fact of (or the presumption of) a commission error. If it is appropriate to use the terms “memory” and “forgetting” in both laboratory and real world contexts, then it is appropriate to use the term “false memory” in both contexts. Furthermore, there are a number of commonly used terms that are conceptually equivalent to “false memory” (*false recognition, intrusion, source memory error*) that refer to observed behavior in a variety of experimental paradigms (source memory tasks, misinformation paradigms, the Deese-Roediger-McDermott [DRM] semantic associates paradigm, exclusion paradigms, associative recognition paradigms, induced autobiographical memory paradigms, imagination inflation paradigms, unconscious plagiarism paradigms, etc.). It seems unlikely that we need completely different theoretical concepts to explain findings from each experimental paradigm or, as noted above, to explain laboratory vs. naturalistic phenomena.

Terms such as *reality monitoring failure, source confusion, or source misattribution*, on the other hand, tend to be used in a more theoretical (explanatory) way to connote the operation of specific factors in creating memory distortions, as outlined in the next section.

A Source Monitoring Framework

Within a general constructive/reconstructive view of cognition and memory, the Source Monitoring Framework (SMF, Johnson & Raye, 1981, 2000; Johnson, Hashtroudi, & Lindsay, 1993; Johnson, 2006; Mitchell & Johnson, 2000, 2009) has served as a guide for investigating memory for events (including imagined events), interpreting empirical findings, and highlighting similarities among different theoretical ideas. The constructs outlined in the SMF are probably among the most frequently invoked in discussions of the potential mechanisms of false memories (Belli & Loftus, 1994; Lindsay, 2008; Lindsay & Read, 1994; Loftus & Davis, 2006; Thomas, Hannula, & Loftus, 2007; Zaragoza, Belli, & Payment, 2006).

Briefly, the SMF posits that the sense that one is remembering is an attribution about a current mental experience which is based on features that seem to have been (and often, in fact, were) bound together during a specific event. The qualities of these mental experiences include perceptual information (e.g., color, sound), contextual information (e.g., spatial and temporal features), semantic concepts, emotion (either our own affective reaction or as a feature of an event, item, or other person), and information about cognitive operations (i.e., cognitive activities engaged such as imaging, noting relations, retrieving additional information), as well as less specific qualities such as familiarity and recency. These qualities guide judgments about the origin of a mental experience because, on average, different sources differ on these dimensions. For example, the content of dreams is often more bizarre than real life; events experienced perceptually may be associated with more egocentric spatial detail while imagined events may be more likely to contain allocentric spatial information. But, because the distributions of qualities from different sources often overlap, misattributions occur (e.g., when a particularly vivid previous imagination is claimed to have been a previous perception).

Memory attributions are the result of a source monitoring process that cumulates “evidence” across different features of mental experiences, but how each type of information or feature is weighted varies depending on past experience, task context, motives, etc. In addition to a relatively heuristic assessment of qualities of mental experiences, the cognitive system can engage in additional, more systematic processes such as retrieving additional information, examining internal consistency of a memory narrative, evaluating plausibility given prior knowledge, etc. Such heuristic and systematic processes are mutually correcting, helping to create doubt about vivid but implausible “memories” or about plausible but sketchy “memories.” Doubt is extremely functional in that it may be the cue for further efforts at remembering, seeking corroboration, reserving judgment, or deciding to live with ambiguity. Both heuristic and systematic source monitoring processes are affected by prior knowledge and beliefs (e.g., What qualities should a memory from this source have?) and the social and cultural context in which memories are evaluated and consulted. Social/cultural context affects what kinds of things we remember, how often we do so, and what we take to be appropriate evidence of remembering an event. For example, someone giving testimony in court about what *did happen* might be expected to have an accuracy-driven agenda during remembering. They may therefore focus on specific details of the defendant’s appearance, where and when they saw the defendant, and they may consult other information such as plausibility to corroborate their memory. On the other hand, someone encouraged in therapy to consider *possible* scenarios in which they *could* have encountered a person, might focus less on specific perceptual and temporal details and more on familiarity and emotional details. Even if the details initially encoded were the same in both cases, the extent to which different features (e.g., perceptual details vs. feelings) are weighted, and the extent to which heuristic vs. more systematic processing are brought to bear, would likely be different depending on the currently activated agenda and the social context (e.g., being cross-examined vs. being supported).

Many laboratory studies, using many paradigms (source identification, eyewitness testimony, unconscious plagiarism, etc.) have yielded evidence consistent with

the SMF (see, Johnson, 2006; Lindsay, 2008; Mitchell & Johnson, 2009 for reviews). Imagined words (Foley, Johnson, & Raye, 1983), pictures (Durso & Johnson, 1980), actions (Anderson, 1984; Foley & Johnson, 1985; McDaniel, Lyle, Butler, & Dornburg, 2008), and complex events (Hashtroudi, Johnson, & Chrosniak, 1990; Loftus & Pickrell, 1995; Loftus, 2005; Zaragoza & Koshmider, 1989) can be misattributed to perception or action. Furthermore, perceptual and semantic similarity can increase source errors (Johnson, Raye, Wang, & Taylor, 1979; Johnson, Foley, & Leach, 1988; Lindsay, Johnson, & Kwon, 1991; Mitchell & Zaragoza, 2001; Roediger & McDermott, 1995; Mather, Henkel, & Johnson, 1997). Repeatedly imagining events increases their vividness (Suengas & Johnson, 1988), increases the likelihood they will be judged to have actually happened (Goff & Roediger, 1998; Henkel, 2004), and increases people's confidence that they did happen (Garry, Manning, Loftus, & Sherman, 1996). Of course, thinking about an actual event in ways that reactivate accurate details of the event can help consolidate and sustain an accurate memory (Hashtroudi et al.; Henkel, 2004). And thinking and talking about an event helps construct a narrative (Nelson, 1993; Nelson & Fivush, 2004) that itself may be less subject to distortion/suggestion (Henkel, 2008).

Thoughts and images that are created deliberately (compared to those that occur spontaneously or simply more easily), are less likely later to be misattributed to a perceptual (external) source, consistent with the idea that cognitive operations are encoded and can later be cues to source (Durso & Johnson, 1980; Finke, Johnson, & Shyi, 1988). In fact, it is perhaps the absence of cognitive operations information in certain mental experiences, for example, dreams (Johnson, Kahan, & Raye, 1984) or PTSD "flashbacks" (Brewin, 2012), that makes them feel like an external reality. Even when cognitive operations information is quite salient at encoding, it may not be available or considered later. For example, if people are forced to generate information that they know to be false in response to forced-recall questions, they sometimes later come to misremember their own deliberate confabulations as part of the witnessed event (Ackil & Zaragoza, 1998; see Chrobak & Zaragoza, 2009, for a review).

Information from an irrelevant modality (e.g., auditory) can influence judgments about whether we experienced an event in another, relevant, modality (e.g., visual). For example, participants may be more likely to claim to have seen an item (e.g., a dog) they imagined visually if they heard a sound associated with that item (e.g., barking, Henkel, Franklin, & Johnson, 2000; see Fig. 2). In addition, once an irrelevant memory is activated based on some feature-similarity with a target memory, other features from the irrelevant memory can be incorporated into the target memory (Lyle & Johnson, 2006). For example, people sometimes misattribute an imagined item (e.g., *ice cream cone*, *bowling pin*) to perception based on physical similarity (e.g., shape) with an actually seen item (e.g., *funnel*, *wine bottle*, respectively), and then also claim to have seen the imagined item in the location or color of the similar item that they did see. That is, similarity in one feature causes other features to be imported, or "borrowed" (Lampinen, Neuschatz, & Payne, 1999). Feature importing is an especially potent source of vivid false memories that can generate high confidence because memories constructed from bits and pieces of actual events are more compelling (seem more vivid and detailed, i.e., "real") than those constructed from

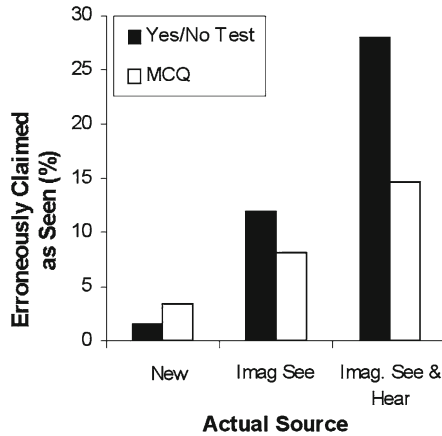


Fig. 2 Hearing the sound of an item that was only imagined (e.g., imagining seeing a basketball and actually hearing a bouncing ball) increases the rate of saying the item was seen. Note that the rate of false memories was reduced when participants rated memories on a memory characteristics questionnaire (MCQ) compared to when they simply indicated whether an item had been seen (Yes/No) (Adapted with permission from Henkel, et al., 2000)

imagination alone (Lyle &, Johnson). It should be noted that importing features from similar memories can also enhance accurate memories by increasing their vividness and detail (Lyle & Johnson, 2007).

Another important aspect of source monitoring is that the criteria used to make source attributions are flexible (Henkel et al., 2000; Lindsay & Johnson, 1989; Marsh & Hicks, 1998; Mather et al., 1997; Parker, Garry, Engle, Harper, & Clifasefi, 2008). Source misattributions are less likely if people are induced to examine their memories more carefully, for example, by asking specific questions about perceptual and affective detail (Henkel et al.; see Fig. 2). Interestingly, giving participants a placebo “drug” before a memory test and suggesting it will improve their memory also reduces source misattributions (Parker et al), presumably because the suggestion encourages a stricter criterion and/or more systematic processing.

The impact of emotion on source memory is, of course, especially important in the context of the recovered/false memory debate. Here we highlight just a few central issues. In general, if only item memory is considered, emotional items (e.g., words, stories, pictures) are recalled and recognized better than neutral items. The effect of emotion on source memory is more complex, depending on its role. Emotion can be a compelling feature in making source attributions, fostering a greater sense of recollection or confidence, even when it is not associated with greater accuracy (Dougal & Rotello, 2007; Ochsner, 2000; Sharot & Yonelinas, 2008; Talarico & Rubin, 2003). Emotional focus on oneself (e.g., how one feels about what two speakers are saying, in contrast to focusing on how the speakers are feeling), increases old/new recognition but decreases source memory (e.g., for who made which statement; Johnson, Nolde, & De Leonardis, 1996). Also, in a short-term memory

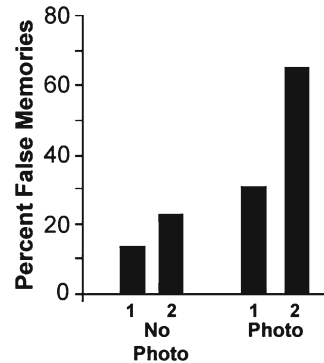
task, people better remembered the location of neutral than emotional pictures (Mather et al., 2006). At the same time, some studies find better long-term source memory for emotional than neutral information (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003). Mather (2007) has suggested that arousal enhances within-object binding of features but it also impairs (or does not affect) associations between an object and other objects or between an object and its broader context (see also Kensinger, 2007). Differences in the impact of emotion on within-object and between-object binding could explain some inconsistencies in the literature.

Motivation can affect all of the aspects of source memory discussed above— influencing, for example, the kinds of events or features of events that are attended to initially, are thought or talked about after an event, and are accessed or given the most weight later during remembering. For example, people may selectively attend to or remember positive rather than negative information to regulate mood (e.g., Carstensen & Mikels, 2005; Mather & Carstensen, 2005), or misattribute information to sources based on desired outcomes (e.g., Barber, Gordon, & Franklin, 2009; Gordon, Franklin, & Beck, 2005).

Do the laboratory findings we have been discussing generalize to real life? Several lines of evidence suggest that they do. First, memories for highly emotional or traumatic public events like the Challenger explosion or the 9/11 terrorist attacks show source misattributions on delayed tests and confidence that may be out of line with accuracy (e.g., Greenberg, 2004; Hirst et al., 2009; Neisser & Harsch, 1992; Schmolck, Buffalo, & Squire, 2000; Talarico & Rubin, 2003). Also, investigators are able to induce participants to construct false autobiographical memories of reasonably complex, emotionally significant events (e.g., being taken to the hospital or being lost in a shopping mall; Ceci, Huffman, Smith, & Loftus, 1994; Hyman & Billings, 1998; Lindsay, Hagen, Read, Wade, & Garry, 2004; Loftus, 2005; Loftus & Pickrell, 1995; Porter, Yuille, & Lehman, 1999; see also Thomas et al., 2007). Researchers are able to induce false memories for complex autobiographical events using combinations of the same factors that work for words, lists, and stories—namely, encouraging imagination, repeated questioning (rehearsal), encouraging participants to relate a false target event to real events in their lives, and so on. For example, Lindsay et al. were able to greatly increase false memories of a childhood event that supposedly occurred at school by showing participants a class photo from the general period of the alleged event (see Fig. 3). Compared to those not seeing a photo, participants who saw the photo later presumably mistook the primed and readily available perceptual information about themselves, their friends, and their teacher as evidence that they had experienced the event. Moreover, studies of induced autobiographical memories further support previous suggestions (e.g., Dobson & Markham, 1993; Johnson et al., 1979) that individual differences in imagery, hypnotizability, and suggestibility, or high scores on a dissociative experiences scale, are associated with increased rates of false memories (Hyman & Pentland, 1996; Porter, Birt, Yuille, & Lechman, 2000).

These are the types of findings that fuel concerns about the uncritical use of memory-recovery practices that involve repeated suggestive questions, guided imagery, photos, hypnosis or sodium amytal, exposing individuals to accounts of sexual abuse in support

Fig. 3 Viewing a class picture increased adults' false memories of a childhood classroom event that never happened, both at session 1 and, especially, at session 2 (1 week later) (Adapted with permission of SAGE Publications from Lindsay et al., 2004, copyright © 2004 Association for Psychological Science)



groups, or popular self-help books that encourage lax criteria for attributing a mental experience to memory (Kihlstrom, 2004; Lindsay & Read, 1994, 1995; Loftus, 2004; Loftus & Davis, 2006; McNally, 2003). Such practices are surprisingly common. A survey of therapists in the US and UK conducted by Poole, Lindsay, Memon, and Bull (1995) found that 25% of the therapists responding thought recovering memories is important, believed that they could identify clients with hidden memories in the first therapy session, and reported using two or more memory recovery techniques that could be suggestive (see also, Polusny & Follette, 1996). A more recent survey of Canadian social workers, psychologists, and psychiatrists (Legault & Laurence, 2007), found that although 94% of respondents agreed that post-event information can interfere with a person's recall of an event, 53% also endorsed the idea that hypnosis can be used to recover memories of actual events from as far back as birth. In addition, respondents indicated that they use in their practice, on average, 2–3 “memory recovery techniques” to help their clients remember childhood events; hypnosis, age-regression, guided imagery, and imagination work were all endorsed at >20%; and 55% of those who responded to a question about childhood sexual abuse said that at least one of their clients had recovered such memories. These findings suggest that in spite of increased attention to research related to mechanisms of memory distortion, a substantial proportion of surveyed therapists still support the use of risky memory recovery practices.¹

Of course, we are not the first to note that because some recovered memories may be false does not mean that all recovered memories are false. Corroborative evidence has been found for some reports of recovered memories (e.g., Schooler, Ambadar, & Bendiksen, 1997; Schooler, Bendiksen, & Ambadar, 1997; Shobe &

¹Note that there were differences among professional groups in the level of endorsement of memory recovery work. In general, the psychiatrists were most likely to endorse the idea of memory fallibility and social workers the least likely. The reverse was true for endorsing the validity of recovered memories, with social workers being most likely to believe in the validity of such memories and psychiatrist the most skeptical. Respondents were also asked to indicate which, of a list of 13 memory recovery techniques, they either use or suggest clients use to “help them remember childhood events”. Social workers and psychologists endorsed more of these techniques (M 's=3) than did psychiatrists (M =2), and they also rejected fewer as totally inappropriate (M 's: social workers=1, psychologists=2) than did psychiatrists (M =4).

Schooler, 2001). Geraerts et al. (2007) found that memories of childhood sexual abuse that were recovered spontaneously outside of therapy were more likely to be corroborated than those recovered as a consequence of therapy (see also Clancy, McNally, Schacter, Lenzenweger, & Pitman, 2002 and Loftus & Davis, 2006 for discussions of the “recovery” of highly implausible “memories”). Furthermore, compared to individuals who report spontaneous recovery of memories of childhood sexual abuse, individuals who report that they recovered memories of childhood sexual abuse during therapy make more intrusions of semantically related items in laboratory tests of word list memory (Geraerts et al., 2009; Geraerts, 2012). Such findings further highlight the interaction of individual difference variables (imagery ability, suggestibility, prior beliefs) with potentially suggestive therapy practices. It should be noted that recovery of childhood memories is by no means thought by all therapists to be central to the success of therapy (DePrince et al., 2012; Polusny & Follette, 1996), providing an additional reason to be cautious about suggestive practices.

Interestingly, Geraerts et al. (2009, 2012) tested the same participants using a forgot-it-all-along paradigm (FIA, Arnold & Lindsay, 2002). In this procedure, participants learn items in one context (e.g., hand-*palm*) and then are later tested with cues reinstating the same (hand-*p**m*) or a different (tree-*p**m*) context. On a final test using only original first context cues, participants are asked if they previously recalled the item. Geraerts et al. found that participants who had recovered memories of childhood sexual abuse spontaneously were less likely than those who recovered memories in therapy to remember that they had previously remembered an item on the first test when the test context had changed but not when it remained the same. These findings suggest that those who forget (or believe they have forgotten) traumatic events may be particularly dominated by current context. If so, shifts in context may provide them greater “protection” against the cuing of previous events, and hence poorer memory for prior recall of those events. These findings highlight that forgetting, just like remembering, is an attribution based on the qualities of current mental experiences. Consistent with the idea that forgetting is an attribution, Belli, Winkielman, Read, Schwarz, and Lynn (1998) found that asking people to recall more events from childhood can lead them to judge their memory to be poorer than people asked to recall less.

Cognitive Neuroscience of Memory

Attempts to link the cognitive processes involved in memory to brain mechanisms have increased substantially in recent years as a result of developments in neuroimaging, especially functional magnetic resonance imaging (fMRI; for reviews see Davachi, 2006; Davachi & Dobbins, 2008; Mitchell & Johnson, 2009; Ranganath, 2010; Skinner & Fernandez, 2007). What follows is a brief overview of some relevant findings from a cognitive neuroscience approach to understanding memory.

MTL and memory. The importance of the medial temporal lobes (MTL) for memory, especially the hippocampus, has long been recognized because of the profound amnesia that results from bilateral hippocampal damage (e.g., Eichenbaum & Cohen, 2001;

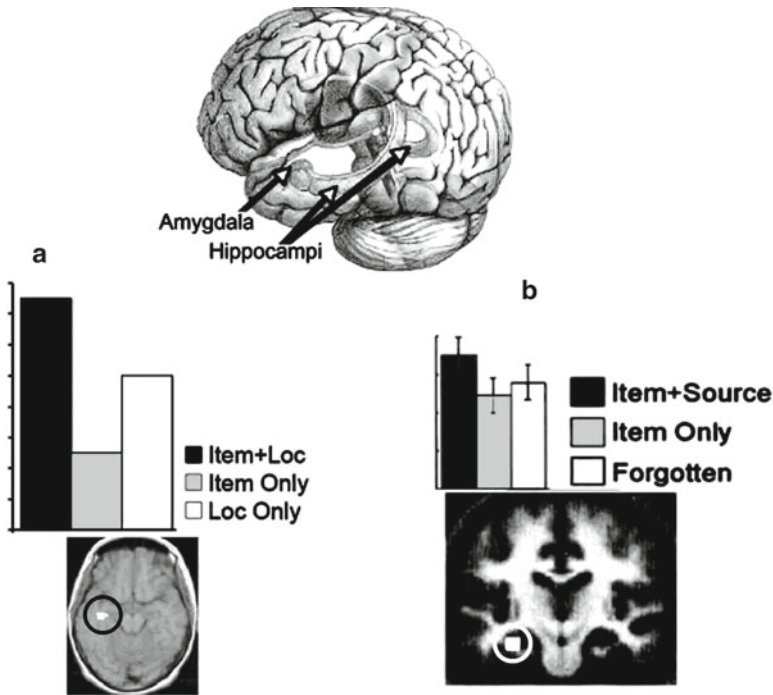


Fig. 4 Anterior hippocampus is associated with memory binding: (a) Greater activity during encoding when people were asked to remember items and locations, compared to just items or locations (Adapted with permission from Mitchell et al., 2000, copyright © 2000 Elsevier Science B.V.). (b) Greater activity at encoding associated with subsequent accurate source memory, compared to item memory or items that were forgotten (Adapted with permission from Davachi et al., 2003, copyright © 2003 National Academy of Sciences, U.S.A.). The schematic at the top shows the relationship of the hippocampus and amygdala within the MTL (Adapted with permission from Mitchell et al., 2009)

Milner et al., 1998; Squire & Knowlton, 2000). Although measures of hippocampal volume have been associated with measures of memory, findings are mixed, with some indication that the direction of the association depends on the specific populations studied (e.g., Bremner, Randall, Scott, et al., 1995, Bremner, Randall, Vermetten, et al., 1997; Duarte et al., 2006; Nestor et al., 2007; see Van Petten, 2004, for a review).

Our understanding of the role of MTL in memory is being expanded by functional neuroimaging studies. For example, as shown in Fig. 4, there is greater hippocampal activity when participants try to bind items together (e.g., a person and house, Henke, Buck, Weber, & Wieser, 1997; an object and location, Mitchell, Johnson, Raye, & D'Esposito, 2000) than when they simply try to encode individual items. Furthermore, greater hippocampal activity during encoding is associated with better source (but not necessarily better item) memory (Davachi, Mitchell, & Wagner,

2003; Kensinger & Schacter, 2006a; Ranganath et al., 2004). Darsaud et al. (2011) found greater hippocampal activity at encoding for those lists that later were less likely to produce false recognition of semantically related lures than lists which were more likely to produce semantically-related false positives. Presumably this activity was associated with the encoding/binding of source-specifying features that contributed to more accurate memory. With respect to brain activity during remembering, hippocampal activity is greater on test trials where participants remember the correct source than for trials on which they remember only the item (Cansino, Maquet, Dolan, & Rugg, 2002; Weis et al., 2004), for trials where they remember which two items went together compared to item recognition (Giovanello, Schnyer, & Verfaellie, 2004), and for items given “remember” vs. “know” responses (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000). Furthermore, hippocampal activity while remembering autobiographical events is positively correlated with rated memory for details (Addis, Moscovitch, Crawley, & McAndrews, 2004).

Although it is generally agreed that the hippocampus is critical for binding features together (i.e., relational memory), the relative roles of other MTL regions (e.g., the entorhinal cortex, perirhinal cortex, and parahippocampal cortex) are less clear. A number of findings point to the importance of the perirhinal cortex for item or object memory (Brown & Aggleton, 2001; Davachi et al., 2003), or situations where information seems familiar but specific source information is not available (Eichenbaum, Yonelinas, & Ranganath, 2007), and to the importance of the parahippocampal cortex for memory for spatial context. Whether regions of MTL have been adequately dissociated is the topic of ongoing debate (e.g., Squire, Stark, & Clark, 2004).

Cortical representational areas. Evidence is also accumulating about the brain regions/networks that are involved in the representation of different qualitative features of memories. For example, brain regions have been identified that play a critical role in the representation of faces (fusiform face area, FFA, Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995), places/scenes (parahippocampal place area, PPA, Aguirre, Detre, Alsop, & D’Esposito, 1996; Epstein & Kanwisher, 1998), bodies (right lateral occipitotemporal cortex [extrastriate body area], Downing, Jiang, Shuman, & Kanwisher, 2001), words (visual word form area, left posterior occipitotemporal sulcus, Cohen & Dehaene, 2004), semantic information (anterior temporal cortex, Martin & Chao, 2001; Rogers et al., 2006), colors (posterior inferior temporal cortex, Chao & Martin, 1999; Kellenbach, Brett, & Patterson, 2001), sounds (left superior temporal sulcus [STS], Goldberg, Perfetti, & Schneider, 2006), objects (lateral occipital complex [LOC], Grill-Spector, Kourtzi, & Kanwisher, 2001; Malach et al., 1995), and even the “self” (medial prefrontal cortex [mPFC], Kelley et al., 2002). Furthermore, different aspects of a given type of information (e.g., place) may be differentially represented in different parts of a network. For example, the PPA appears to represent relatively specific place information whereas the retrosplenial cortex (RSC) appears to be involved in placing that information in a broader spatial context (Aminoff, Schacter, & Bar, 2008; Epstein & Higgins, 2007; Park, Chun, & Johnson, 2010).

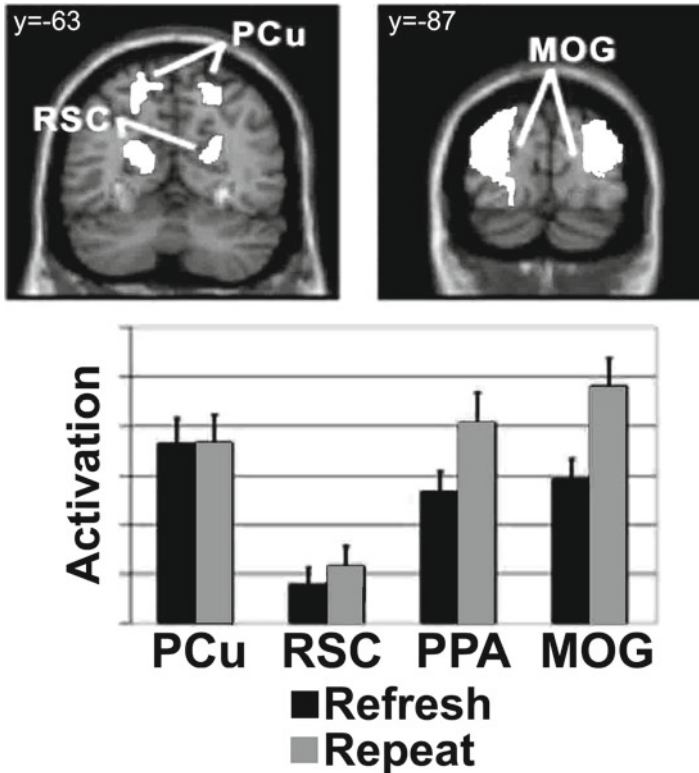


Fig. 5 Perceiving a scene (seeing it again, *Repeat*) and refreshing a scene (thinking of it again when it is no longer present but is still active, *Refresh*) resulted in activity in the same network of posterior scene-selective areas, but there was a gradient such that activity was more similar for perceiving and thinking in PCu than in MOG. See text for details. *MOG* medial occipital gyrus, *PCu* precuneus, *RSC* retrosplenial cortex (Adapted with permission from Johnson et al., 2007, copyright © 2007 Elsevier)

Importantly, the same regions that are involved in the perception of a particular type of information are also involved in thinking about such information (e.g., Ganis, Thompson, & Kosslyn, 2004; M. R. Johnson, Mitchell, Raye, D'Esposito, & Johnson, 2007; O'Craven & Kanwisher, 2000; Wheeler, Petersen, & Buckner, 2000). For example, Fig. 5 shows data from a study where, on each trial, participants saw a face and a scene and then either were shown one of the stimuli again or were cued with a location cue (a dot) to think back to (refresh) one of the items (M.R. Johnson et al.). Both seeing a scene again and refreshing a scene by thinking of it again resulted in activity in the same network of areas: middle occipital gyrus (MOG), PPA, RSC, and precuneus (PCu). In addition, there was a gradient such that activity was relatively greater in MOG for seeing compared to thinking and in PCu there was little difference. The fact that the relative similarity in levels of activation

during perception and reflection differs across brain regions may provide important clues about potential differences in the contributions of different brain regions to true and false memories (see, e.g., Slotnick & Schacter, 2004).

Using a procedure similar to one used in behavioral studies investigating reality monitoring (e.g., Durso & Johnson, 1980) combined with fMRI, Gonsalves et al. (2004) assessed brain activity while participants saw and imagined pictures. They found that the activity was greater in PCu for imagined items that participants subsequently incorrectly called “seen” than for those subsequently correctly called “imagined” (see also Kensinger & Schacter, 2006b). This finding provides neural evidence that, as posited by the SMF, source attributions are made, in part, on the basis of the amount of activated perceptual information in mental representations.

The PCu is an area that frequently shows activity during episodic memory (Cavanna & Trimble, 2006; Lundstrom et al., 2003). The similarity in activity in PCu during perceiving and refreshing in the M.R. Johnson et al. (2007) study (see Fig. 5), along with the association of PCu activity with false memories in the Gonsalves et al. (2004) study, suggests that activity in this area is associated with a phenomenal experience of “perceptual” qualities that may contribute to the subjective experience of remembering, but alone may provide relatively poor evidence about the actual origin of mental experiences.

Consistent with behavioral findings that false memories tend to have less detail than true memories (e.g., Mather et al., 1997; Norman & Schacter, 1997; Schooler, Gerhard, & Loftus, 1986), several neuroimaging studies have found less activity for false than true memories in areas presumed to be involved in the encoding and/or retrieval of perceptual detail. Okado and Stark (2003) scanned participants during test trials for items that during encoding had been accompanied by an actual picture, or for which participants had imagined a picture. True memories for seen pictures showed greater activation in occipital cortex (primary visual cortex) than false memories (imagined items called seen). In a DRM study, Schacter et al. (1996) presented words auditorily, and found that later correct “yes” responses showed greater activity in an area associated with auditory processing (left temporoparietal cortex) than incorrect “yes” responses to semantically related distractors. Some differences between true and false memories in neural activity presumably correspond to differences in subjective experience that are detected in participants’ ratings of their memories (e.g., Mather et al., 1997; Norman & Schacter; Henkel et al., 2000). However, it should be noted that presenting the same item again can produce priming even when participants do not recognize the item as old (e.g., Spencer, Montaldi, Gong, Roberts, & Mayes, 2009), and sometimes there is no difference in activity in early perceptual regions between old items that are correctly recognized and old items that are missed (Schacter & Slotnick, 2004). Thus, some differences between true and false memories in neural activity may reflect sensory/perceptual records (e.g., Johnson, 1983; Tulving & Schacter, 1990) that do not necessarily affect conscious introspection and thus would not be reflected in participants’ ratings of their memories.

Also, when strong cues of one type are available, people may ignore other types of cues. For example, when participants are attempting to remember lists of related

items (e.g., *night*, *dream*, etc.), they may be more likely to assess semantic than perceptual information, leading to high rates of false recognition of semantically related lures (e.g., *sleep*, Deese, 1959; Roediger & McDermott, 1995). Interestingly, when repetitive transcranial magnetic stimulation (rTMS)² was administered to left anterior temporal cortex (an area associated with semantic memory) after such lists were learned but before a recognition test, the false alarms to semantically related distractors were reduced, with no reduction in correct recognition of words that had been presented (Gallate, Chi, Ellwood, & Snyder, 2009; see also Boggio et al., 2009). At least two possibilities, not mutually exclusive, would be consistent with the SMF and behavioral findings (e.g., Mather et al., 1997; Norman & Schacter, 1997). First, the activation of related lures during list presentation may result in relatively weak semantic representations which are more likely to be disrupted by TMS than stronger semantic representations for perceived items. Second, perceived items are more likely to be associated with features in addition to semantic information (e.g., more vivid perceptual information), and when semantic representations are disrupted via TMS this other information is more influential in source judgments.

Misinformation paradigms have been used extensively in behavioral studies investigating false memories (e.g., Loftus, Miller, & Burns, 1978; see also Loftus, 2005; Mitchell & Johnson, 2000; Zaragoza et al., 2006, for reviews). Generally, misinformation paradigms present an original event (movie, slides) and then follow it with a second phase which includes the suggestion that some information was present in the original event that was, in fact, not present. Source errors occur when participants subsequently falsely claim the misinformation was present in the original event. At least two studies have attempted to adapt a misinformation procedure to the scanner (Baym & Gonsalves, 2010; Okado & Stark, 2005). Okado and Stark assessed neural activity during both the original event and misinformation phases of the procedure and found that activity in the left hippocampus and left perirhinal cortex predicted whether the original or suggested information would be selected on a subsequent forced-choice test: Activity was greater in these regions during the original event for items participants would later be accurate about than items participants would later be misled about, but greater during the misinformation phase for items associated with subsequent false than true memories. Furthermore, Baym and Gonsalves found that activity in visual processing areas (occipital and temporal [fusiform gyrus] cortex) during an original event was greater for items for which participants subsequently chose the true response rather than the false alternative. These findings are consistent with behavioral evidence that information encoded during a misinformation phase has a better chance of being misattributed to the original event when the corresponding information from the original phase has been weakly encoded (Pezdek & Roe, 1995; Sutherland & Hayne, 2001). Baym and Gonsalves did not observe any differences in right hippocampus or bilateral parahippocampus during the original event between items that subsequently resulted in

²rTMS is a non-invasive method for stimulating specific clusters of neurons; it can serve as a temporary virtual “knockout” to investigate the causal role of particular brain areas, as described here.

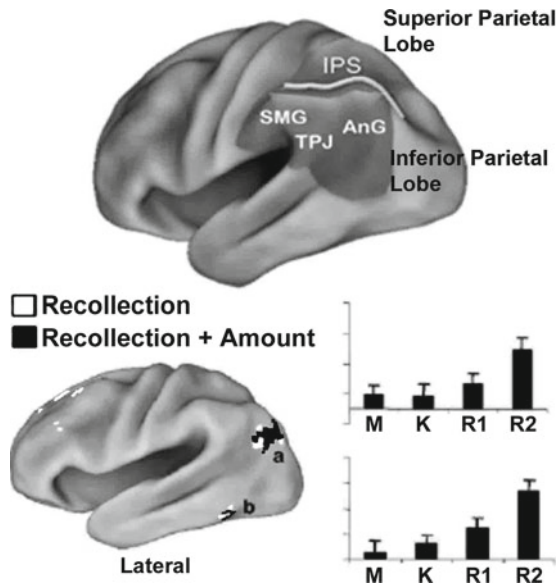


Fig. 6 Lateral parietal cortex, especially regions below the inferior parietal sulcus (IPS), is sensitive to the amount of information remembered (Adapted with permission from Uncapher and Wagner, 2009, copyright © 2009 Elsevier B.V.). The *lower figure* shows “recollection” responsive areas with greater activity for trials on which a “remember” response was given (i.e., R1 [a test picture was remembered but not the picture paired with it at study] or R2 [both test picture and paired picture remembered]) than a “know” response (K) (masked with $K > Miss$ [M]). The sub-regions of these recollection areas labeled “Recollection+ Amount” showed greater activity when more information was remembered ($R2 > R1$) (Adapted with permission from Vilberg & Rugg, 2007, copyright © 2007 Elsevier B.V.). *IPS* inferior parietal sulcus, *SMG* supramarginal gyrus, *TPJ* transparietal junction, *AnG* angular gyrus

true and false memories, but did observe more activity for these items than for subsequently forgotten items. They suggested that activity in these areas may reflect encoding of general contextual information and proposed that susceptibility to misleading information is most likely when general contextual information has been encoded but specific object details have not.

Parietal cortex and memory. Above we discussed precuneus, a medial part of the parietal cortex that is often activated during episodic remembering and imagery. But, there has been increasing interest in recent years about the role of various areas of lateral parietal cortex in episodic memory. Several studies have found activity in lateral parietal cortex (especially regions just below the inferior parietal sulcus [IPS], Brodmann Area [BA] 39; see Fig. 6) related to the number of features remembered, vividness, or for memories reported as a “recollection” (Uncapher, Otten, & Rugg, 2006; Vilberg & Rugg, 2007, 2008; Wagner, Shannon, Kahn, & Buckner, 2005; Wheeler & Buckner, 2004). Interestingly, when patients with bilateral parietal lesions are given

source memory tests, they do not show a deficit in source accuracy, but they do show reduced confidence in their source judgments (Simons, Peers, Mazuz, Berryhill, & Olson, 2010). Furthermore, if asked to remember autobiographical experiences, their reports include less detail than do autobiographical memories of controls (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). Simons et al. describe their patients as having “impaired subjective experience of rich episodic recollection” (p. 479). There are at least two ways such impairment in subjective experience might come about while not disrupting source memory for any particular individual feature when it is appropriately cued. Lateral parietal cortex may participate in the *integration* of multiple features, and such integration may contribute to a subjective sense of remembering. Alternatively, lateral parietal cortex may participate in iterative *attention* to different features. Thus, the parietal lobes may be where, as proposed in the SMF, evidence cumulates across different features of experience during source monitoring (Johnson & Raye, 1981; Johnson et al., 1993). A similar “accumulator” model was recently proposed by Donaldson, Wheeler, and Petersen (2010), who suggested that parietal cortex accumulates evidence for decision processes in memory (see also Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008 for related discussions of the functions of lateral parietal cortex).

Whether lateral parietal cortex subserves integration of or attention to multiple features during encoding and recollection of complex events, evidence indicates that for such functions, parietal cortex is part of a larger network involving frontal cortex.

Frontal cortex and memory. Key evidence of the importance of frontal cortex for memory comes from studies of patients with frontal damage (e.g., D’Esposito & Postle, 1999; Shallice & Burgess, 1991; Shimamura, 2000; Ranganath & Knight, 2003; Stuss & Levine, 2002). Frontal damage disrupts strategic search of memory. For example, it produces greater deficits in recall or source memory than old/new recognition memory (Mangels, Gershberg, Shimamura, & Knight, 1996; Shimamura, 1995). Furthermore, damage to frontal areas, especially ventromedial prefrontal cortex (VMPFC), can result in profound source misattributions that are clinically classified as *confabulations* (Damasio, Graff-Radford, Eslinger, Damasio, & Kassell, 1985; Johnson, 1991; Johnson, Hayes, D’Esposito, & Raye, 2000; Moscovitch, 1995; Schnider, 2008). Confabulations can range from the relatively trivial “filling in” of missing but highly likely information to quite bizarre “memories” of impossible events (e.g., having been a space pirate, Damasio et al.). Given that hallucinations and delusions—profound reality monitoring failures—are core cognitive problems in schizophrenia, it is not surprising that frontal dysfunction (Goldman-Rakic & Selemon, 1997; Weinberger, 1988) and disrupted source memory (Vinogradov, Luks, Schulman, & Simpson, 2008) are associated with the disorder. Frontal areas develop relatively slowly in children (Diamond, 2002; Fuster, 2002; Gogtay et al., 2004) and frontal areas also show evidence of neuropathology disproportionate to other brain regions in older adults (e.g., Raz & Rodrigue, 2006). Both children (e.g., Foley et al., 1983; Lindsay et al., 1991; see, Newcombe, Lloyd, & Ratliff, 2007, for a review) and older adults (Chalfonte & Johnson, 1996; Dehon & Bredart, 2004; Glisky & Kong, 2008; Hashtroudi, Johnson, & Chrosniak, 1989;

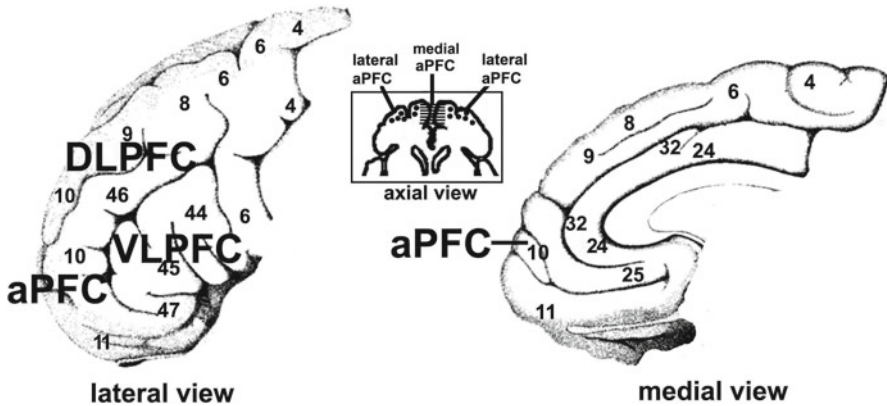


Fig. 7 Subregions of prefrontal cortex. *aPFC* anterior prefrontal cortex, *DLPFC* dorsolateral prefrontal cortex, *VLPFC* ventrolateral prefrontal cortex, the numbers are approximate Brodmann Areas (BA) (Adapted with permission from Mitchell and Johnson 2009)

Mitchell et al., 2000; see Mitchell & Johnson, 2009 for a review) show source memory deficits relative to young adults. (It should be noted that MTL may develop more slowly across childhood than has been assumed [Gogtay et al., 2006] and that normal aging is associated with some hippocampal dysfunction [e.g., Mitchell et al., 2000], thus some developmental effects may reflect MTL changes with age or a combination of MTL/PFC effects [see, e.g., Newcombe et al., 2007 for a discussion of consistent evidence in studies with children, Mitchell & Johnson, 2009 for evidence from aging studies]).

Along with other regions of the brain, frontal cortex is involved in both encoding and remembering. Frontally-mediated working memory/executive functions maintain agendas, refresh and rehearse relevant information, resist distraction, and direct attention to features, providing an opportunity for hippocampally-mediated feature binding. During remembering, frontal cortex is important for such functions as self-initiated cuing during effortful/strategic retrieval, assessing plausibility, and generating and comparing alternatives.

Differentiating among functions of various subregions of PFC is a major goal of cognitive neuroscience (see Fig. 7). Many studies have demonstrated that activity in ventrolateral PFC (VLPFC) during encoding is associated with subsequent memory (Blumenfeld & Ranganath, 2007; Ranganath & Blumenfeld, 2008; Staresina & Davachi, 2006; Wagner et al., 1998). In addition, encoding activity in VLPFC correlates with an index of later source memory (Staresina, Gray, & Davachi, 2008). Furthermore, different areas within VLPFC appear to play different roles. For example, anterior VLPFC (BA 47) is more active during semantic than nonsemantic encoding (Wagner et al.) and appears to be involved in a network with anterior temporal cortex in controlled semantic retrieval. Consistent with a role in semantic processing, Paz-Alonso, Ghetti, Donohue, Goodman, and Bunge (2008) found that,

for healthy young adults, activity in left VLPFC (BA 47) was similar for hits and false alarms to semantically related lures. Other areas of VLPFC are involved in selection and/or interference resolution (BA 45 [mid VLPFC] Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Jonides & Nee, 2006; Thompson-Schill et al., 1997) and rehearsal (BA 44 [posterior VLPFC], Awh et al., 1996; Smith & Jonides, 1999; Jonides & Nee, 2006).

There is greater activity in dorsolateral PFC (DLPFC) for relational encoding than for item encoding (Murray & Ranganath, 2007) or for sequences that can be “chunked” compared to those with less structure (Bor, Duncan, Wiseman, & Owen, 2003). Also, DLPFC activity during encoding is associated with subsequent memory for bound features (e.g., face-house pairs, Summerfield et al., 2006). Activity in both VLPFC and DLPFC (Ranganath, Cohen, & Brozinsky, 2005; see also Ranganath & D’Esposito, 2001) appears to modulate hippocampal activity, affecting which information will and will not (Anderson & Huddleston 2012) be remembered later.

During testing, there is greater activity in lateral PFC (often including both VLPFC and DLPFC regions) during source memory than item memory tests (Mitchell, Johnson, Raye, & Greene, 2004; Nolde, Johnson, & D’Esposito, 1998; Ranganath, Johnson, & D’Esposito, 2000; Raye, Johnson, Mitchell, Nolde, & D’Esposito, 2000). An age-related deficit in source memory, which is associated with reduced activity in lateral PFC (Mitchell, Raye, Johnson, & Greene, 2006), may reflect deficits in evaluation/monitoring processes, and/or strategic retrieval processes. PFC activity, especially in anterior PFC, appears to be involved in setting the agenda for the type of source information that is being looked for (Dobbins & Han, 2006; Lepage, Ghaffar, Nyberg, & Tulving, 2000). There is some evidence that left PFC may be more involved in monitoring more specific (differentiated) information or engaging more strategic processes (e.g., retrieval) whereas right PFC may be more involved in source memory judgments that are made more heuristically (Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins & Han; Kensinger, Clarke, & Corkin, 2003; Mitchell et al. 2004; Raye et al.), although this distinction may be too general to fully account for the findings (see Mitchell & Johnson, 2009 for further discussion and references).

Recently, investigators have focused attention on potential roles of anterior and medial PFC regions in source memory. These regions are found to be more active during self-referential tasks such as thinking about one’s traits (Macrae, Moran, Heatherton, Banfield, & Kelley, 2004) or one’s hopes and aspirations (Johnson et al., 2006) (see Amodio & Frith, 2006 and Van Overwalle, 2009 for reviews). They are also active during source decisions involving the self, for example, whether an item had been self- or other-generated (Simons, Henson, Gilbert, & Fletcher, 2008; Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vinogradov et al., 2006). Interestingly, schizophrenia patients show deficits in this area during source monitoring of self-generated information (Vinogradov et al.).

Amygdala and memory. The amygdala is a region of the limbic system that is located in the MTL, near the anterior hippocampus (see Fig. 4). Various lines of

evidence indicate that the amygdala is involved in the processing of emotion (e.g., LeDoux, 2000; McGaugh, 2004; Phelps, 2006). For example, bilateral amygdala damage eliminates the memory advantage for emotional over neutral items (Cahill, Babinsky, Markowitsch, & McGaugh, 1995; LaBar & Phelps, 1998). In healthy participants, during encoding, there is greater amygdala activity for emotional than neutral items (Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, Ely, Grafton, & Kilts, 1999), and greater amygdala activity at encoding for subsequently remembered than subsequently forgotten emotional items (Dolcos, LaBar, & Cabeza, 2004). There is also evidence that the amygdala may modulate activity in other MTL regions and the PFC (e.g., Dolcos & McCarthy, 2006; Kilpatrick & Cahill, 2003; Sharot, Verfaellie, & Yonelinas, 2007). For example, there is a larger correlation between activity in amygdala and other MTL regions for subsequently remembered emotional than neutral items (Dolcos et al.). The memory advantage for emotional items over neutral items is found for both positive and negative emotional items (e.g., Kensinger & Schacter, 2006a, 2008b). This is consistent with findings suggesting that the amygdala is more responsive to emotional intensity than valence (e.g., Anderson et al., 2003; Cunningham, Raye, & Johnson, 2004), but there is some controversy about the generality of this conclusion (Kensinger, 2009; Mather, 2007, 2009).

With respect to source memory, both behavioral and neuroimaging findings are mixed regarding the impact of emotion (see, e.g., Kensinger & Schacter, 2008a; Mather, 2007; Phelps & Sharot, 2008, for reviews). One under-investigated aspect proposed by the SMF that we would like to focus on here is that emotion can itself be a feature of a memory that contributes to the subjective sense of remembering (e.g., Johnson & Multhaup, 1992). For example, as in the behavioral studies discussed above, there is evidence that the subjective experience (sense of vividness or confidence) and amygdala activity are greater for emotional than neutral items even when memory for the emotional items is not more accurate (Phelps & Sharot; Sharot, Delgado, & Phelps, 2004). Interestingly, Qin et al. (2003) found that, compared to trauma-matched non-PTSD controls, participants who had PTSD prior to the 9/11 terrorists attacks had a tendency at 10 months after the attacks to remember their emotional response to the attacks as having been greater than they reported it to be 9 months earlier. One possibility is that individuals with PTSD may selectively rehearse or spontaneously experience reactivation of the most intense aspects of emotional experiences and thus memory for the “average” of the emotional experience may be inflated.

Rather than only an acute response to individual stimuli, emotion can also be a more sustained state (e.g., stress, depression, etc.). There is evidence that stress may enhance encoding of emotional but not neutral stimuli, but that it also may disrupt retrieval (Payne et al., 2007; see van Stegeren, 2009 for a review). In a situation where it is possible to induce very high levels of stress (i.e., military training), stress is associated with poorer memory (Morgan et al., 2004). Salivary cortisol level provides one index of stress and cortisol is associated with increased intrusions in memory for stories (Payne et al., 2007, see Fig. 8). Chronic stress (chronically increased cortisol levels) is associated with impaired PFC and hippocampal function (van

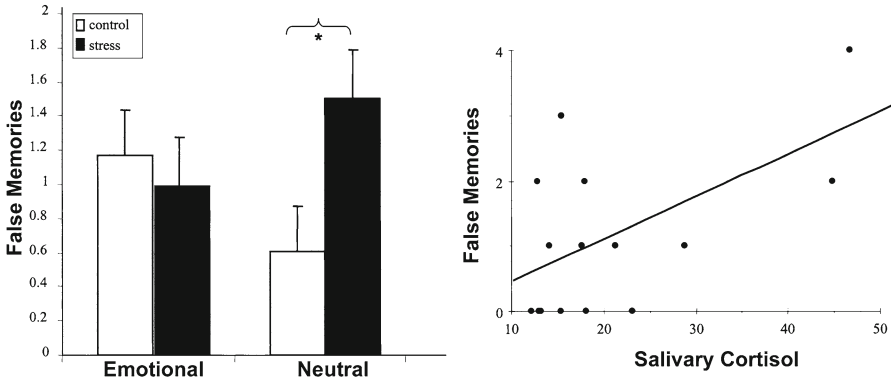


Fig. 8 Inducing stress increased false memories only for a neutral story (*left*); salivary cortisol levels and false memories were positively correlated (*right*) (Adapted with permission of author and copyright holder from Payne et al., 2007, copyright © 2007 Cold Spring Harbor Laboratory Press)

Stegeren). In one study (Grossman et al., 2006), PTSD and control participants were given hydrocortisone or a placebo before various cognitive tasks. Hydrocortisone did not affect the performance of either group on digit span forward and digit span backward tasks but the PTSD patients showed greater disruption than controls on working memory and long-term memory tasks that required more executive control. This pattern could suggest that individuals with PTSD show glucocorticoid-mediated impairments in memory (especially for more reflectively demanding tasks) at lower glucocorticoid levels than controls. Alternatively, additional cortisol may be added to an already elevated cortisol level, raising it to levels that impair performance.

Such individual differences in responsiveness to emotional stimuli are potentially important for understanding the etiology and/or maintenance of depression, anxiety, or other clinically significant symptoms (Etkin et al., 2004; Manuck, Brown, Forbes, & Hariri, 2007) associated with memory deficits (Hertel, 2000; Williams et al., 2007). In addition, recent studies suggest that some individual differences may be related to genetic variants (Canli & Lesch, 2007; Canli, 2004; Hariri et al., 2002; de Quervain et al., 2007; Rasch et al., 2009; see commentary by Todd & Anderson, 2009).

Administration of propranolol (a beta-adrenergic blocker) reduces the amygdala response to emotional expressions (Hurlmann et al., 2010), and reduces the startle response to items previously paired with a loud noise, without disrupting explicit memory for the item-noise contingency (Kindt, Soeter, & Vervliet, 2009; see also Kroes, Strange, & Dolan, 2010). Such findings have raised the possibility that dysfunctional emotional responses might be modified by drugs (e.g., in PTSD populations). However, the effects of propranolol may depend both on how arousing the emotional stimuli are (van Stegeren et al., 2005), and the current level of cortisol (van Stegeren, Wolf, Everaerd, & Rombouts, 2008). A new bioethics controversy has arisen from the possibility that drugs could be used to “change” memories by reducing the emotional response to an experienced event or by later reducing the emotional

response associated with the memory of an emotional event (e.g., see Henry, Fishman, & Youngner, 2007, and associated commentaries). This possibility may create new “memory wars” arising again from the fact that memories are not fixed, but reflect a dynamic origami of past, present, and future (Johnson & Sherman, 1990).

Summary

Together, behavioral and neuroscience findings provide a perspective on issues of central relevance to the recovered/false memory debate. Like visual illusions help clarify the mechanisms of perception, the fact that memory distortions occur and that we can manipulate them in the laboratory helps us understand the mechanisms of memory. The fact that memory generally functions as well as it does and that it is not a hopeless quagmire in which all information is “equal” (or all source information is lost) points to the operation of critical reality/source monitoring mechanisms that differentiate experiences. The empirical findings discussed here, as well as many others, highlight that these mechanisms give rise to both true and false memories. Although our understanding is far from complete, various aspects of a cognitive model such as the SMF can be associated with different brain regions or networks.

Information (whether derived from perception or reflection) is encoded in various representational areas (such as faces in the fusiform gyrus), and different features are bound together as a consequence of MTL activity, especially in the hippocampus. Hippocampal activity is also modulated (e.g., disrupted or sustained, depending on the situation) by signals from the amygdala and PFC. For example, amygdala activity drives attention (e.g., orienting to and lingering on a stimulus), and PFC activity underlies the kind of strategic, organizational activity that creates associations crucial for voluntary recall. Emotion has both positive and negative effects on memory, depending on whether it sustains or disrupts processing relevant to later memory contexts. During both reflectively guided (voluntary) and spontaneous (involuntary) remembering, cues activate representational areas; activated information from different representational areas converges in the parietal cortex, potentially yielding an integrated, complex mental experience. The more cumulative and cohesive (i.e., differentiated) the resulting mental experience, the more it seems like a coherent and specific episode.

As in encoding, the prefrontal cortex is also involved in a number of aspects of remembering—setting and holding the agenda for what one is looking for, generating cues for retrieval, and evaluating activated information with respect to agendas and criteria. Emotion is a feature, much like any other, that is taken as evidence about the source of a mental experience. At the same time, emotion can facilitate or disrupt the PFC-mediated executive processes necessary for effective revival and evaluation of information. Although there can be top-down modulation at many levels of representation, it appears that remembering typically involves PFC-mediated evaluation processes targeted at parietal representations.

Hence, in fMRI studies of both encoding and remembering, activations of frontal, parietal, and MTL regions are frequently observed. Consistent with this picture, brain damage in any of these areas disrupts remembering. The most profound disruptions occur from MTL damage, especially hippocampal damage, because feature binding is crucial for any episodic memory experience. PFC damage disrupts strategically driven feature binding, and monitoring (retrieval and evaluation) processes. Parietal damage disrupts the subjective confidence in memories that is otherwise associated with cohesive and integrated representations (perhaps by disrupting the ability to shift to different features of mental experiences). An experience of familiarity can, of course, occur in response to features that may be fragments of actual events (or fragments of past imaginations). Such mental experiences can arise involuntarily, via cues of which a person may be unaware, and may arise from any level of representation in the cognitive system (including levels that may ordinarily be difficult to access deliberately). Whether these fragments are judged to be memories depends on the same kinds of factors relevant to more complex mental experiences. Hence, a very vivid, highly emotional, or apparently meaningful mental experience, even if quite incomplete, can seem real.

There are individual differences in the kinds of mental experiences individuals typically have, which may be related to differences in resolution of representational systems (e.g., FFA, PPA, LOC, etc.), or that may be related to differences in the levels of representation accessed or attended to during remembering. There are individual differences in the functioning of structures that support feature binding and executive function. And there are individual differences in the kinds and levels of emotion that energize or disrupt encoding and retrieval. In short, individuals differ in how vivid (perceptually, emotionally, semantically, etc.) their mental experiences are, which cues they weight most heavily in making memory attributions, how often they attempt to explicitly access the past, how often they deflect or attempt to inhibit memories, the availability of cues to past events in their environment, how much particular experiences are reflectively integrated with other autobiographical events, their likelihood of having engaged in similar events (real or imagined) that may be confused with a target event, the evidence they need to attribute a mental experience to memory, and their response to doubt about the origins of mental experiences. These myriad factors make memory a sometimes comforting and sometimes disturbing individual experience, but an always fascinating scientific pursuit.

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