

# 49 Memory as Decision Making

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**ABSTRACT** Memory researchers investigating the brain regions involved in successfully retrieving a past event have revealed a robust and ubiquitous pattern of activity across lateral regions of the left prefrontal and parietal cortex. While some of these regions may play a direct causal role in episodic memory retrieval, such as the accumulation of mnemonic evidence or the buffering of retrieved representations, we present evidence that much of the activity can be accounted for by decision and control processes and not memory retrieval per se. Two general lines of research demonstrate that brain activity greater for hits than correct rejections can reflect decision biases and/or reorientation. We present a biasing and orienting model of parietal contribution that converges with studies of patients with parietal lobe damage and syntheses with research on visual attention and valuation.

Episodic or event memory pervades our everyday lives, but its study is challenging because inferences about memory functioning are fairly indirect. These inferences rely on establishing the links between the original events that yield the potential for subsequent memory expression and a retrieval demand that may take place minutes, days, or years following the events. The researcher cannot directly manipulate raw memory signals in the same manner he or she might manipulate frequency in, say, an audition experiment. Instead, the properties of memory representations must be inferred through far more indirect methods. Hence, the advent of functional brain imaging using positron emission tomography (PET) and then functional magnetic resonance imaging (fMRI) provided the opportunity to more directly observe the process of episodic memory retrieval (a.k.a. *ecphory*) that guides our behavior in a wide variety of contexts. The overarching message of this chapter is that while these techniques have greatly informed our understanding of episodic recognition memory, in doing so, they suggest that much of the observed brain activation reflects various decision and control processes and not memory-retrieval processes per se. Thus the “simple” act of recognition appears to tap a host of complex control processes geared toward tuning and biasing memory judgments.

In everyday life, episodic memories are retrieved in various ways, including spontaneous encounters with cues that trigger the retrieval of a memory, as well as through purposeful searches of past events. We also make decisions throughout the course of the day that

depend on episodic memory evidence; for example, did I park the car in this lot? have I read that book before? did my wife tell me to pick up the kids? Strategic decision processes are involved in each of these mnemonically guided decisions, although sometimes in subtle ways. For example, judging whether one read a particular book (a recognition task) may be influenced by factors other than the memory “signal” itself, such as an assessment of one’s general familiarity with the author, knowledge of the release date of the book, or other factors, which may bias one toward a positive or negative final conclusion (Johnson, Hashtroudi, & Lindsay, 1993; Mandler, 1980; Schacter, 1996; Tulving, 1983). Recognition tests have been used to probe the contents of memory as early as 1913, when Hollingworth stated in his report in *The American Journal of Psychology* that “the value of a single presentation is greater in recognition than in recall, and the difference between the values of repetitions becomes still greater the more meaning the material possesses” (Hollingworth, 1913, p. 543). As George Mandler put it, to “recognize is the act of perceiving something as previously known ... the recognition of the prior occurrence of an event” (1980, p. 252). He postulated that recognition consists of two separate and additive processes: (1) the *recognition of familiarity* which is a continuous value retrieved quickly and automatically based largely on the perceptual characteristics of the previous exposure, and (2) the *identification as a result of a retrieval process* that is thought to be initiated once the familiarity judgment fails to provide an unequivocal decision. These two processes are now commonly known as familiarity and recollection (Jacoby, 1991; Yonelinas, 1997), although current models generally assume that recollection is sought during every recognition trial in standard recognition tests, and not merely those trials that yield ambiguous sensations of familiarity, and it is thought that familiarity is often based on conceptual characteristics of the previous exposure.

Mandler’s well-known analogy of these two separable forms of memory content invites you to imagine walking onto a bus and seeing a man whose unexpected familiarity convinces you that you have seen him before, but you cannot immediately recall where or when. Following a deliberate search of memory where various

candidate possibilities are considered, you realize that the man is a baker in your neighborhood. In order to understand the neural representations of these various forms of memory content, cognitive neuroscientists typically contrast the recognition of a previously encountered item (hit) with the correct judgment that a memory probe is newly encountered (correct rejection). The natural inclination is to assume that regions demonstrating greater activation for the former than the latter are directly involved in the retrieval or representation of memory evidence. However, further inspection reveals that many original candidate regions support processes aside from episodic retrieval itself. It is important to emphasize that functional imaging researchers, like animal researchers, have relied heavily on recognition tasks for the study of episodic memory for the simple reason that they are amenable to available methodologies. Not only are recognition tasks relatively easy to train nonhuman animals on, but they also enable controlled timing and trial intermixing that is essential for event-related fMRI approaches. Thus, we know considerably less about other types of memory demands, such as free recall and the recall of other types of complex materials (cf. Long, Öztekin, & Badre, 2010).

### *The elusive “successful retrieval” map*

One of the goals of the early neuroimaging work on memory was to distinguish between regions signaling successful episodic retrieval from those supporting the ability to deliberately engage in a retrieval attempt (Buckner, Koutstaal, Schacter, Dale et al., 1998; Kapur et al., 1995; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Schacter, Alpert, Savage, Rauch, & Albert, 1996; Tulving et al., 1994). Brain activity associated with new items on a recognition test would necessarily contain little to no information regarding the study session, and therefore the attempt to retrieve episodic content from new items would contain more information about the attempt itself than the product of that attempt. On the other hand, brain activity associated with old items would contain information both about the retrieval attempt as well as the product of that retrieval attempt. These early neuroimaging studies necessarily relied on contrasts between blocks of trials. Therefore, the typical design included blocks of mostly old items compared with blocks of mostly new items, often “hidden” within the context of periods in which old and new items were equally frequent so as to avoid triggering nonmemorial response strategies. Comparison of mostly old and mostly new blocks revealed a pattern of activity that was commonly referred to as the “old/new” effect or the

“successful retrieval” effect. While many of these early studies produced differential activity within the prefrontal cortex (Buckner, Koutstaal, Schacter, Dale et al., 1998; Rugg et al., 1996; Schacter, Alpert et al., 1996), Kapur and colleagues (1995) did find greater activity for mostly “old” blocks versus mostly “new” blocks in parietal regions, including the medial precuneus and the left lateral parietal cortex. Since both conditions were thought to include equal amounts of retrieval effort, the extra activity associated with mostly “old” blocks was interpreted as activity associated with *ecphory*, that is, the successful retrieval of episodic information in response to the recognition memory probe.

An obvious limitation of the block design is that the signal must be averaged across trial types other than the trial type of interest. For example, a mostly “old” block must include some new items in order to keep the subject honest, and it must also include incorrect responses to old items (i.e., misses). Another less obvious problem is that the design may force unintended psychological effects. For example, blocking trials according to the probability of a target may affect the subjects’ strategies (Buckner, Koutstaal, Schacter, Wagner et al., 1998) or the saliency of the targets (Herron, Henson, & Rugg, 2004) depending on the block. The advent of event-related designs in fMRI allowed for a more precise comparison of old and new items by removing unsuccessful trials from the successful retrieval effect. Trials could now be selected based on the response of the subject, allowing a direct comparison of hits (correctly recognizing an old item) to correct rejections (correctly rejecting a new item). No longer did errors need to muddy the interpretations. The consequence of this advancement was that studies produced a more robust pattern of activation associated with successful retrieval (Buckner Koutstaal, Schacter, Wagner et al., 1998; Herron et al., 2004; Konishi, Wheeler, Donaldson, & Buckner, 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000; Nolde, Johnson, & D’Esposito, 1998). Recent meta-analyses reveal that the typical pattern of activations for this effect includes regions of the anterior prefrontal cortex (PFC), anterior insula, thalamus, anterior cingulate, dorsolateral prefrontal cortex, medial prefrontal cortex, medial parietal cortex, and lateral posterior parietal cortex (e.g., Spaniol et al., 2009; see figure 49.1).

This widespread activation pattern associated with successful retrieval was quite surprising, because many of the regions that were found to exhibit successful retrieval activity were not thought to play a role in simple recognition judgment. For example, neuropsychological studies had shown that although the PFC was

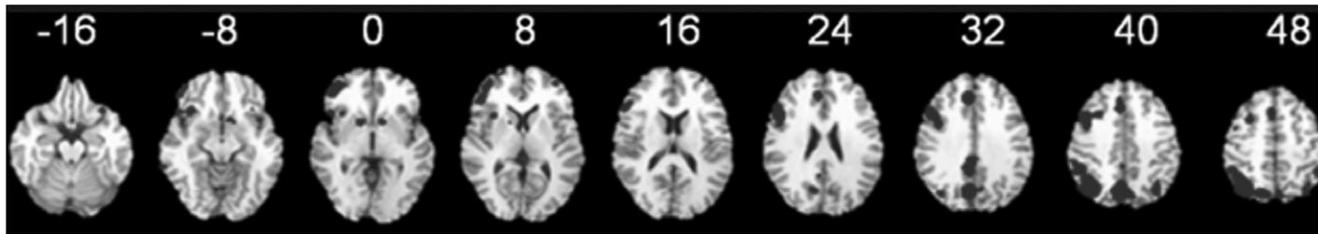


FIGURE 49.1 Activation likelihood map of “retrieval success” effect during recognition. (Taken from Spaniol et al. 2009.)

important for source-memory attribution and other complex recall tasks, patients with fairly extensive PFC damage were thought to be quite normal on simple verbal recognition tasks (Janowsky, Shimamura, & Squire, 1989; Milner, Corsi, & Leonard, 1991; Shimamura, Janowsky, & Squire, 1990; though see Wheeler, Stuss, & Tulving, 1997). These neuropsychological studies suggested that memory tasks that made demands on executive functioning or inhibitory control, such as free recall, source memory, and temporal ordering, were impaired by PFC damage because these secondary processes were damaged; however, basic recognition ability remained intact (Shimamura, 1995). The prefrontal cortex has reciprocal connections throughout the cortex, and it appears to filter and control much of the flow of information between sensory inputs and motor outputs (Miller & Cohen, 2001). However, these connections vary greatly across PFC regions, indicating considerable functional heterogeneity in this large region.

#### *Functional specialization in prefrontal cortex during retrieval attempts*

Although considerable uncertainty remains, a better understanding of the functional contribution of some of the PFC regions to memory is beginning to develop. Here we briefly consider two regions and outline putative functions supported by functional imaging findings.

**LEFT VENTROLATERAL PREFRONTAL CORTEX (~BA 47)**  
This region, located along the inferior frontal gyrus, is not only revealed by the retrieval success contrast, but it is also implicated in studies examining source memory and semantic memory. In source-memory studies, subjects encode information that originated from a particular context within the study session. Then, at test, on some trials subjects are asked to determine the particular context through which the item was encoded, whereas on other trials, they are asked to make an item memory judgment and are not required to recall the context. Brain activity associated with source-memory

judgments is then compared to activity associated with item memory judgments alone. Even when stimulus materials are completely matched across source and item memory conditions, source judgments are associated with greater activity in left ventrolateral PFC (Dobbins, Foley, Schacter, & Wagner, 2002). However, the level of activation is quite similar regardless of whether or not the source attribution is correct (Dobbins, Rice, Wagner, & Schacter, 2003). In addition, the magnitude of activity in this region during the source task appears to be linked to the degree that the probe’s semantic as opposed to perceptual characteristics are potentially relevant for the source judgment (Dobbins & Wagner, 2005). Consistent with this finding, damage to this region (Thompson-Schill et al., 1998) and disruption via transcranial magnetic stimulation (Gough, Nobre, & Devlin, 2005) have impaired semantic processing. Collectively, these findings suggest that the left ventrolateral PFC region supports the controlled or strategic semantic processing of probes during source-memory attempts and presumably during memory attributions in general. This process, known as semantic elaboration, can improve retrieval outcomes to the extent that the semantic features evident during the initial encounter match the features attended to at test (Roediger & Geraci, 1990; Tulving & Thomson, 1973).

**LEFT DORSOLATERAL PREFRONTAL CORTEX (~BA 6/8)**  
This region is often activated in close conjunction with dorsolateral parietal cortex, with which it is directly anatomically connected. In controlled judgment domains outside of memory, these two regions are often described as members of a frontoparietal control network (Dosenbach et al., 2007). The left DLPFC also demonstrates greater activation during source- versus item-memory decisions for matched verbal probes; however, unlike the left ventrolateral region, it appears to be engaged even prior to the arrival of the probes and thus demonstrates a greater activation when the retrieval question dictates a source requirement instead of an item requirement (Dobbins & Han, 2006). The region then increases activation during both types of

tasks when the probes are presented. As with left ventrolateral PFC, activation is not modulated by the success of the source-memory judgment (Dobbins et al., 2003). This pattern is consistent with the longstanding role of the region during verbal working-memory demands (Nystrom et al., 2000; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999) and led to the hypothesis that the region supports the online maintenance of descriptions of sought-after source information along with the maintenance of candidate probes if more than one is available during verbal episodic memory demands. In the cognitive literature, “retrieval descriptions” are quite important and are hypothesized to bias retrieval by foregrounding the general characteristics that the observer believes should be present in to-be-recovered content (Norman & Bobrow, 1979). These characteristics can be gleaned from the retrieval query, but may also be informed by experience with the task and other preexperimental beliefs. Computationally, this may be thought of as a coarse way of incorporating statistical priors into the judgment of recovered memory content. Additionally, recent work using transcranial magnetic stimulation more directly demonstrated that this general area plays a role in the foregrounding or biasing of representations in posterior cortex (Feredoes et al., 2011), a conclusion also suggested by reversible cooling studies in nonhuman primates (Chafee & Goldman-Rakic, 2000).

#### *Functional specialization in parietal cortex during retrieval attempts*

Given the neuropsychological link between the PFC and source- and working-memory processes, it was not surprising that PFC activations were observed with the retrieval success contrast. However, this is not the case with the prominent parietal lobe activations that were also observed with this contrast. This region has never been associated with episodic memory in the longstanding neuropsychological literature, since extensive damage to the region leaves basic recognition abilities intact. Given the robust successful retrieval activation in parietal cortex (perhaps the most reliable of any regions exhibiting this effect), the race to functionally explain the role of the parietal lobe has become something of a quest in the last 10 years (Wagner, Shannon, Kahn, & Buckner, 2005). Wagner and colleagues conducted an influential meta-analysis in 2005 that noted that posterior parietal activity (PPC) was typically modulated by: (1) the subjective perception that an item was old—activity for false alarms was greater than for misses; (2) the retrieval orientation of the subject—the goals of the task-modulated PPC activity regardless of

mnemonic history; and (3) recollection-based versus familiarity-based recognition. These general observations led to the development of three prominent hypotheses that are still currently under debate (see Uncapher, Gordon, & Wagner, this volume). These hypotheses include the attention to internal representations hypothesis, which states that PPC could be involved in shifting attention away from external stimuli to internal representations of memory that were presumably arising from other regions, such as the medial temporal lobe. This hypothesis would certainly be supported by the neuroimaging work showing that the PPC is sensitive to changes in the retrieval goals and orientation (Dobbins et al., 2003; Dobbins & Wagner, 2005). For instance, in a study that separated activations to retrieval cue type (source or item memory) from activation to the actual memory probes, the left lateral parietal response (unlike the lateral premotor PFC) was insensitive to differences in the cues, but then demonstrated a prominent response to probes during source- but not item-memory judgments (Dobbins & Han, 2006). One putative interpretation of this pattern of results is that the response signaled the shift of attention toward recovered recollective mnemonic content that is critical for making source-memory attributions, but less important for endorsing items merely based on familiarity.

Similar ideas were later incorporated into a parietal memory framework termed the attention to memory (AtoM) model, which builds on the visual attention work of Corbetta and Shulman (2002) and posits both top-down and bottom-up attention mechanisms supporting memory in parietal cortex (Cabeza, Ciaramelli, & Moscovitch, 2012). Top-down mechanisms are held to take place in the superior parietal lobule (SPL) and reflect directed attention toward weak memory signals under difficult retrieval circumstances. In contrast, bottom-up processes, held to take place in supramarginal gyrus regions, are thought to reflect the capture of attention by recollective content arising from memory systems, presumably in the medial temporal lobes.

An alternative to the assumption that inferior lateral parietal responses reflect the capture of attention during memory is the idea that these responses reflect the accumulation of recovered memory evidence toward a decision bound. This hypothesis draws its inspiration from studies using single-cell recordings of monkeys in monkey area LIP while making a simple choice that is based on the integration of sensory signals until a decision is reached (Shadlen & Newsome, 2001), and behavioral research supports the idea that recognition evidence accumulates during the course of trials as

well (e.g., van Zandt & Maldonado-Molina, 2004). Support for the accumulation hypothesis of parietal activation has been gained by demonstrating that activation tracks the number of original contextual details that are recovered by the participant (Vilberg & Rugg, 2009a). However, a recent fMRI study on frequency judgments found that parietal activity tracked with the absolute amount of information even when that information was not the basis of the decision (Guerin & Miller, 2011). Finally, a related hypothesis suggests that parietal responses reflect the operation of an episodic-memory output buffer, in which the recovered contents of episodic memory are temporarily stored in a buffer that makes them rapidly accessible to decision making. Such a buffer had been proposed by Baddeley (2000) as the missing component to his working memory model, and it would work similarly to visual and verbal working memory buffers.

#### *Criteria for fashioning a parietal lobe functional model*

Despite a host of candidates, there remains little consensus on the functional roles of the parietal lobe during recognition memory. Building on the discussion of Wagner, Shannon, Kahn, and Buckner (2005), we propose a series of criteria that a successful model must achieve.

1. The characterization must be compatible with extant neuropsychological findings and be able to account for the historical absence of any link between parietal damage and recognition-memory impairment.

2. The characterization must clearly distinguish between causal and noncausal functional models with respect to memory-retrieval ability. A causal interpretation reflects a characterization that would be essential for successful retrieval behavior to occur. For example, the episodic buffer account is causal because damage or removal of the buffer would yield behavioral amnesia, since the contents of episodic memory would be unavailable. In contrast, a model that assumed the response reflected the implementation of a decision bias would be noncausal, in that damage would yield an inability to flexibly bias memory decisions but would not prevent basic memory functioning.

3. The characterization should incorporate both condition-level blood oxygen level-dependent, or BOLD, effects (e.g., hits greater than correct rejection) and it should anticipate individual differences. For example, the episodic buffer model would predict that individual differences in accuracy should track with increases in blood oxygen level-dependent activity.

#### *A biasing and orienting model of parietal contributions*

We propose a model that arises out of two general lines of research: one in which observers are required to shift memory decision biases adaptively during blocks of trials, and one in which they are required to incorporate biases into their recognition judgments on a trial-by-trial basis. Both lines of research suggest that parietal regions are important for the implementation and adjustment of decision biases during recognition. Before briefly describing these paradigms and their findings, it is important to note why bias during decision making is critical, particularly in the case of memory decisions.

The phrase “successful retrieval effect” implies that the effect directly supports retrieval processes; however, a more appropriate phrase might be the “recognition judgment effect,” which does not presuppose a direct link between the activations and the availability of memory content. Critically, optimal decision making in recognition (and all discrimination tasks) depends not only upon the current stimulus evidence, but also upon the context in which that evidence is encountered. This is formalized under Bayesian reasoning through the incorporation of prior probabilities with current observed evidence in order to arrive at a posterior probability. Equivalently, under the signal-detection framework, the observer uses a decision bias that can be adjusted in order to maximize outcomes. Thus the use of informative priors in Bayesian reasoning and flexible biases (a.k.a. criteria) in signal-detection theory serve an identical function, namely, to modulate decisions using information other than that which is directly perceived or remembered. For example, even if recognition evidence were quite strong, one would nonetheless want to be highly cautious in judging an individual as recognized in a context in which there was little prior probability that familiar individuals would be encountered (e.g., a foreign airport terminal). In such situations, under the signal-detection framework, ideal observers would use what is termed a “strict” or “conservative” decision bias, requiring extremely high levels of evidence to judge an individual as recognized. In contrast, in more familiar environments they would use a more “lax” or “liberal” bias. The adopted bias can also be informed by the relative benefits and costs of correct and incorrect judgments as well as the prior probabilities (Gold & Shadlen, 2001; Green & Swets, 1966; Macmillan & Creelman, 2005). Thus, unlike the pejorative lay use of the term “decision bias,” ideal responding actually requires biasing one’s judgments; the same

TABLE 49.1

Sample subjects from two studies: Aminoff et al. (2012), using a target probability manipulation, and Kantner, Vettel, and Miller (submitted), using a payoff manipulation. In the initial condition in each study, the subjects have equal discrimination ability ( $d'$ ) and they are both relatively equivalent in criterion ( $c$ ). But in the contrasting condition only one of the two subjects appropriately adapts their criteria, which benefits that subject's proportion correct (PC) relative to the other subject. ( $H$  = hit rate;  $CR$  = correct rejection rate.)

subject	High target probability					Low target probability					When adapting to the conservative condition ...
	H	CR	$d'$	$c$	PC	H	CR	$d'$	$c$	PC	
s#111	.81	.41	.64	-.56	.68	.48	.79	.77	.43	.70	now avoids false alarms.
s#051	.90	.27	.64	-.93	.70	.85	.39	.76	-.65	.53	still avoids misses.
subject	Conservative payoff					Liberal payoff					When adapting to the liberal condition ...
	H	CR	$d'$	$c$	\$	H	CR	$d'$	$c$	\$	
s#161	.43	.71	.39	.37	4.00	.86	.20	.23	-.95	4.40	now avoids misses.
s#59	.34	.77	.34	.57	4.60	.29	.77	.18	.65	-2.60	still avoids false alarms.

recognition evidence should *not* lead to the same response on all occasions.

Recent behavioral work from our labs demonstrates that there are considerable individual differences in observers' ability to appropriately bias their recognition judgments using blockwise manipulations of target probabilities, blockwise manipulations of payoffs, or trialwise manipulations of target probability (Aminoff et al., 2012; Selmecky & Dobbins, 2012). An example of this variability and its consequences is shown in table 49.1.

**THE LINK BETWEEN PARIETAL CORTEX AND THE BIASING OF DECISIONS** In the visual attention literature, the link between biasing judgments and parietal cortex is well established. When observers use predictive cues that reliably anticipate the spatial location of subsequent perceptual probes, activation is increased in the PPC, specifically in the intraparietal sulcus (IPS), compared to situations in which environmental transients occur at the same location as an upcoming target (e.g., Kincaide, Abrams, Astafiev, Shulman, & Corbetta, 2005). The former is typically referred to as an endogenous shift of spatial attention; however, it is equally appropriate to refer to it as a spatial judgment bias. In contrast, when probes are encountered at unexpected locations, compared to validly endogenously cued locations, there is increased activation in ventral parietal regions surrounding the temporoparietal junction. As noted by Hutchinson, Uncapher, and Wagner (2009) and Nelson, McDermott, and Petersen (2012), these regions do not coincide with those implicated during recognition memory. However, as suggested by Cabeza et al. (2012), they may serve similar roles at the algorithmic level.

An early fMRI study suggested a role for recognition decision bias in the parietal cortex (Miller, Handy, Cutler, Inati, & Wolford, 2001). Using a block design, Miller and colleagues crossed manipulations of criteria

with manipulations of sensitivity. A group-level analysis revealed that more activation occurred in dorsolateral prefrontal and dorsolateral parietal cortex during blocks in which the decision criterion shifted on a trial-by-trial basis compared to blocks in which the decision criterion remained stable. However, a similar analysis with blocks of high  $d'$  (sensitivity) compared to blocks of low  $d'$  revealed only medial activations, with no activations in parietal cortex whatsoever. A more recent event-related fMRI study of 95 subjects found that similar regions were activated for trials in which the criterion shifted compared to trials in which the criterion remained the same (Aminoff et al., submitted; see figure 49.2). Further, Aminoff and colleagues found that the regions sensitive to criterion shifting significantly overlapped with regions that exhibited greater activity for hits compared to correct rejections. Even the regions of successful retrieval activity that did not overlap with regions of criterion-shift activity using the strict thresholds were significantly correlated with individual differences in the conservativeness of the criterion (see below).

In a recent fMRI study, Vilberg and Rugg (2009b) manipulated the test-wide prevalence of targets (25% or 75%) during a combined source- and item-recognition judgment task. At test, subjects indicated that they recognized the items and remembered one of two source contexts, merely recognized the items but couldn't recollect the source context, or believed the items to be new. Critically, they found that regions in the lateral post-central gyrus and dorsal superior parietal lobule that demonstrated "retrieval success" effects were modulated by the target base rates. However, they also found that more lateral and inferior parietal regions, along with the middle portion of the IPS, demonstrated a "retrieval success" effect that was insensitive to the listwide target probabilities, with the authors suggesting this pattern was directly reflective of retrieval.

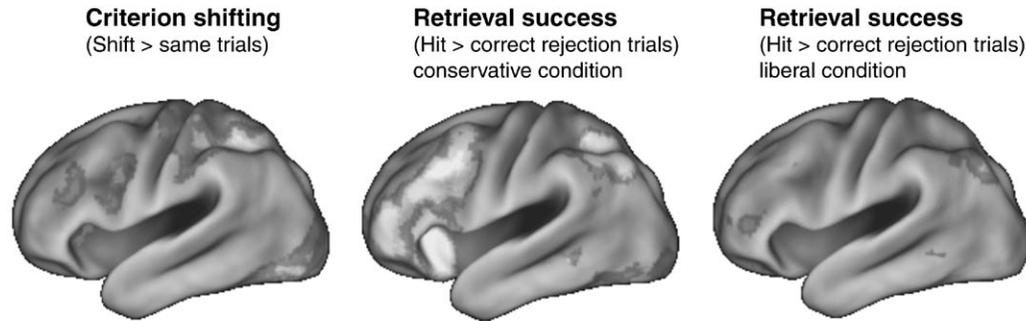


FIGURE 49.2 A comparison of activation maps ( $n = 95$  subjects;  $p > .05$ , false-discovery rate corrected) for the shifting criterion contrast and the “retrieval success” contrast in the conservative and liberal conditions (see Aminoff et al., submitted).

But this interpretation was hampered by the fact that the subjects were explicitly instructed to ignore any changes in the base rate of the targets, and the changes in the target probabilities were not cued in any way. Several behavioral studies have demonstrated that criterion shifts only occur if the subject is aware of the change in the conditions (Estes & Maddox, 1995; Rhodes & Jacoby, 2007; Wixted & Stretch, 2000). Indeed, the listwise density manipulation in the Vilberg and Rugg (2009b) study failed to induce any behavioral decision biases. As we discuss below, in paradigms yielding clear behavioral evidence of biases, whether due to the shifting or the conservativeness of the bias, much of the lateral parietal response is affected.

For example, Aminoff et al. (submitted) used a blockwise biasing paradigm in which target probability (70% or 30%) was indicated by a color cue for small blocks of six to nine trials for both face and word stimuli that were tested in separate runs. Participants were informed of this contingency and displayed prominent behavioral biases induced by these cues. In terms of the behavioral results, Aminoff and colleagues (2012) recently reported clear individual differences in the degree that biases were induced across participants. These were stable domain-general differences that were observed across materials. As for the brain activation, there were three critical effects that emerged from the study (Aminoff et al., submitted). First, as noted above, when observers were required to shift the bias, there was a transient response at the beginning of the block in the SPL that extended along the IPS, regardless of the direction of shift or the accuracy of the response. Second, although an apparent “retrieval success” effect was observed in dorsolateral parietal cortex during blocks inducing a conservative bias (i.e., strong expectation of new materials), the effect was virtually eliminated under blocks that induced a liberal bias (i.e., strong expectation of old materials; see figure 49.2). Finally, activity associated with “retrieval success”

in both the conservative and liberal conditions was significantly related to individual differences in criterion but not to individual differences in accuracy. Overall, these data suggest that the parietal retrieval response must take into account the adopted decision biases.

In order to examine the interaction between expectations and memory evidence, O’Connor, Han, and Dobbins (2010) used a trial-wise cuing paradigm in which each recognition memory probe was preceded by a verbal cue (Likely Old or Likely New) that indicated its probable memory status. During critical runs, these cues were valid on 80% of trials. Consistent with Aminoff et al. (submitted), these cues yielded prominent decision biases. With respect to brain activity, the critical comparison of invalidly versus validly cued trials (figure 49.3) resulted in prominent prefrontal and parietal activations. The results also demonstrated that invalid cuing activations occurred in supramarginal and angular gyrus regions for both old and new materials that were correctly identified. This invalid cued response partially overlaps with the response demonstrated when observers must shift the criterion applied to memory judgments (figure 49.2); however, it appears to extend more laterally. Because correctly identified new materials are unlikely to have any episodic content, these researchers concluded that the functional role of these regions cannot reflect episodic retrieval or the accumulation or buffering of episodic content. Furthermore, in an independent fMRI data set of basic uncued recognition, activation in these parietal regions was shown to correlate with individual differences in adopted decision bias, and not retrieval accuracy. Specifically, this analysis demonstrated that for individuals who were increasingly conservative, there was an increase in the hits>correct rejections signal difference. This corresponds to an increase during identification of the memory class least expected by the participant, and the lateral parietal region was held to signal disconfirmations of decision biases that were either cue-induced or

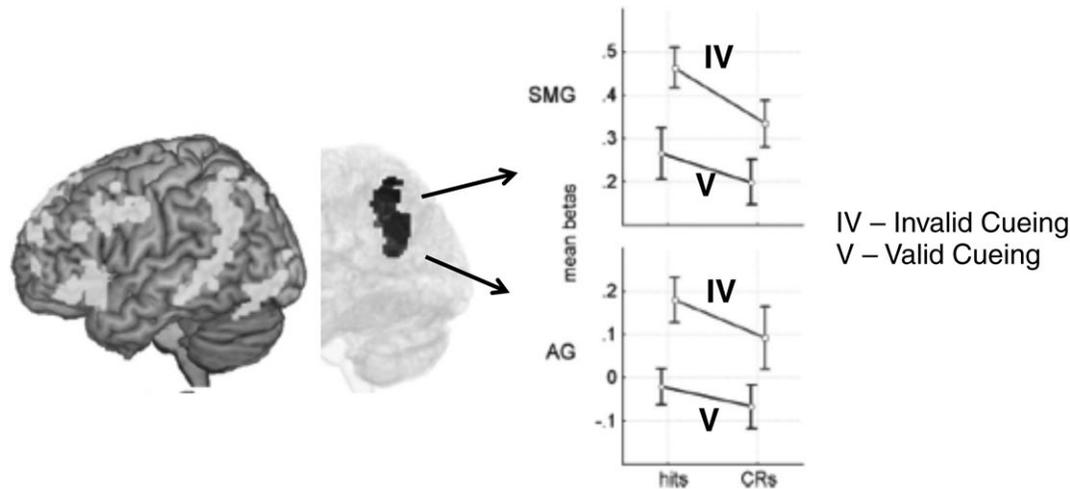


FIGURE 49.3 The violation of cued recognition memory expectations. Left panel shows activations that result when recognition memoranda violate expectations cued on a trial-wise basis (invalid > validly cued recognition memory probes; voxelwise threshold  $p < .001$  with greater than 5 continuous

voxel extent). This invalid memory cuing effect occurs in both supramarginal and angular gyri (middle panel) and results in an increased response for both correctly identified old materials (hits) and new materials (correct rejections). Right panel: taken from O'Connor et al. (2010).

general characteristics of the participants (see also Herron & Rugg, 2003).

A final recent fMRI study looking at trialwise decision biases afforded sufficient power to separately examine the two types of violations possible, namely unexpected familiarity following the Likely New cue and unexpected novelty following the Likely Old cue (Jaeger, Konkel, & Dobbins, 2013). Figure 49.4 shows three regions demonstrating three different patterns, including sensitivity to unexpected familiarity; sensitivity to unexpected novelty; and sensitivity to both unexpected familiarity and unexpected novelty. Postcentral gyrus and medial SPL areas demonstrated greater activation for new than old materials following the Likely Old cue, consistent with orienting toward unexpectedly novelty. This interpretation is further supported by the failure to detect any discernible signal difference in these regions when observers instead expected new materials following the Likely New cue. The opposite pattern of results occurred in anterior angular gyrus. Here differential activation occurred following the Likely New cues, in which there was a stronger response for old versus new materials, which is consistent with orienting toward unexpected familiarity. There was no signal difference between the materials when the observers instead expected familiarity following the Likely Old cues. Finally, the intraparietal sulcus demonstrated increased activation for whichever class of memoranda was unexpected. This pattern of activation led to the conclusion that this region supported the orienting of attention toward unexpected memory content, and hence may be critical for overriding adopted decision

biases. From this overall perspective, the saliency of memory signals is governed by the bias induced by the cues. This notion is further supported by the results of an individual differences analysis of the anterior angular gyrus response. Within this region, the unexpected familiarity response (hits vs. correct rejections following the Likely New cue) was strongly associated with individual differences in accuracy. This might have been mistakenly construed as evidence that the region supports retrieval in a causal manner. However, the activations under the Likely Old and uncued conditions bore no relationship to individual differences in accuracy within those conditions. This is precisely the marker of saliency anticipated under an orienting model, in that those individuals who discriminate well showed the most marked differential response to unexpectedly familiar stimuli that conflicted with the Likely New bias versus expected novel stimuli that confirmed the Likely New bias.

Critically, the findings in Jaeger et al. (2013) point to considerable functional heterogeneity in parietal cortex during recognition judgment. Neither the unexpected familiarity nor unexpected novelty responses have been previously isolated, but their close proximity to the more general mid-IPS response may mean that these various responses may have been collapsed in prior designs and discussions. Furthermore, the three patterns of response in figure 49.4 corresponded well with recent parcellations of parietal cortex suggested by the analysis of resting connectivity data via graph theory (Nelson et al., 2010). Moving forward, then, it may be important to distinguish between general control

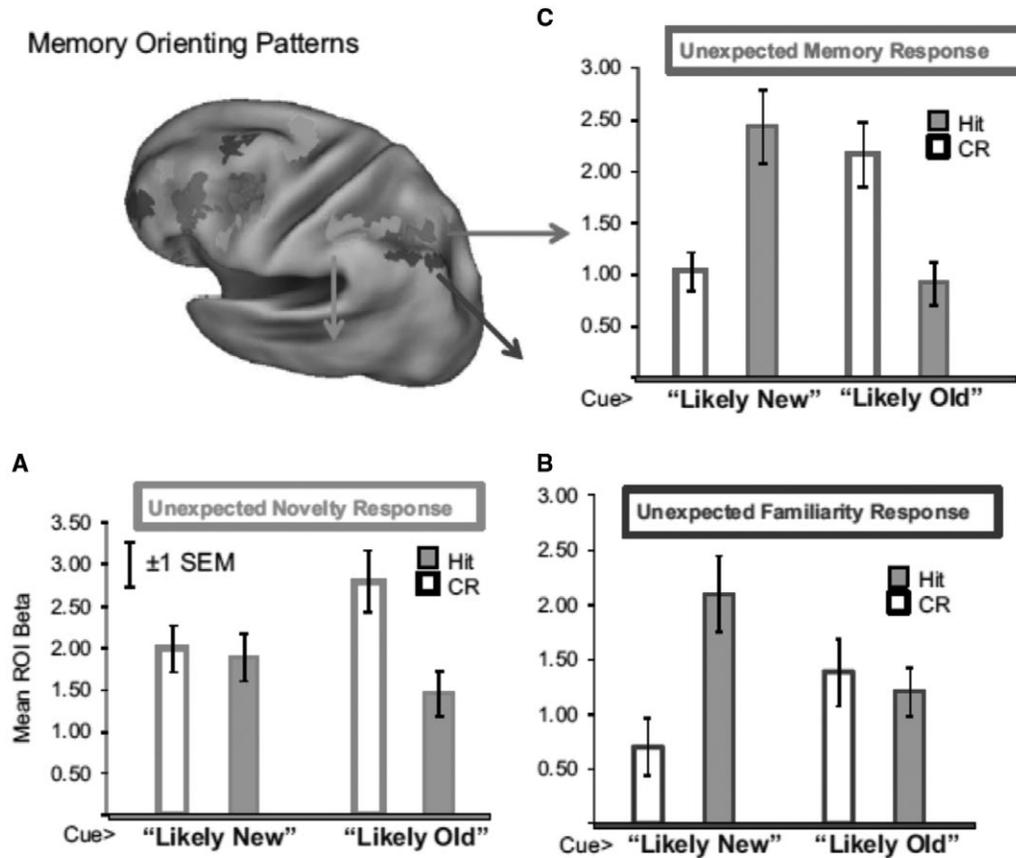


FIGURE 49.4 Selective responses to particular types of violations of memory expectations. Targeted contrasts and masking procedures isolated three different patterns of response in left lateral parietal cortex. The left anterior IPS/PoCG region in green illustrated an unexpected novelty response pattern, with bar plot (A) illustrating the pattern across cue conditions and item types. The posterior anterior angular gyrus region

in blue demonstrated an unexpected familiarity response, with bar plot (B), illustrating the pattern of response across cue conditions and item types. The mid-IPS region in red demonstrated a general unexpected memory effect, with bar plot (C) illustrating the pattern of response across cue conditions and item types. (Taken from Jaeger et al., 2013.) (See color plate 40.)

mechanisms that underlie criterion shifts and violations of adopted criteria (that presumably engender shifts) from material specific effects, such as unexpected novelty, and unexpected familiarity responses that may be linked to mobilization of different investigatory responses depending on the nature of the violation. For example, figure 49.2 illustrates that the most prominent response to facing a requirement to shift the recognition criterion occurs along the IPS (figure 49.2, left panel), regardless of the direction of shift. Somewhat analogously, the mid-IPS response in figure 49.4 occurred whenever a memorandum violated the expectation held under the current bias/criterion. Additionally, both contrasts also implicated similar lateral PFC regions, and so both may capture a process or processes that are important when an observer must update or reevaluate the adequacy of the current decision criterion, regardless of whether it is liberal or conservative.

In summary, recent fMRI findings demonstrate that adopting a liberal decision bias eliminates previously observed successful retrieval activation differences in intraparietal sulcus and supramarginal gyrus regions. Furthermore, the requirement to shift a recognition decision bias yields prominent activations in these regions as well. There also appears to be functional specificity in the parietal cortex when adopted biases are violated versus confirmed by memory materials, both in the case of novelty (in regions not typically associated with “retrieval success” effects) and familiarity (in regions typically associated with “retrieval success” effects). Finally, individual difference analyses using ROIs in or near the anterior angular gyrus do not support a direct role in retrieval. Instead they suggest that activation for old materials is governed by the salience of familiarity or perhaps recollection signals, which is a function of both the cue condition and the

observer's basic discrimination ability. Thus fMRI data are beginning to converge on the idea that orienting or reorienting toward novelty or familiarity may critically rely upon parietal regions, and that this operation may be critically linked to the initial biasing of memory judgments. Conversely, the data do not suggest a strong role for the regions identified in the actual retrieval or buffering of episodic content. Critically, however, one region typically linked to this function, the posterior/ventral angular gyrus, has not been implicated in studies of recognition bias and remains a viable candidate for a more direct role in retrieval itself.

### *Convergence with neuropsychology*

Additional evidence against a direct causal role for PPC and recognition memory retrieval can be seen in recent neuropsychological investigations on patients with parietal lesions. Since previous studies on patients with parietal damage had not focused on memory impairments, several recent studies targeted memory tests similar to the ones used in neuroimaging studies. Yet they have generally found little to no effect on basic recognition memory accuracy (Ally, Simons, McKeever, Peers, & Budson, 2008; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Dobbins, Jaeger, Studer, & Simons, 2012; Simons, Peers, Mazuz, Berryhill, & Olson, 2010). While parietal patients may freely report fewer details on long-term autobiographical memory tests, they appear to perform normally when given specific probes (Berryhill, 2012; Berryhill, Picasso, Arnolds, Drowos, & Olson, 2010). This lack of an effect due to damage to the parietal lobe is difficult to reconcile with parietal models of memory that ascribe a function that depends on this region to accumulate or buffer the contents of episodic retrieval. Furthermore, Dobbins et al. (2012) examined parietal patients using the trial-wise biasing manipulation and found that unlike frontal patients and controls, the one deficit in their behavior appeared to be the inability to use Likely New cues to appropriately bias their recognition decisions, suggesting a deficit in the ability to integrate externally cued biases into the assessment of recognition evidence. Interestingly, it is the Likely New cue condition that led to the unexpected familiarity response in anterior angular gyrus in Jaeger et al. (2013), and this region was likely heavily compromised in the parietal patients of Dobbins et al. (2012).

### *Synthesis with visual attention and valuation research*

As noted above and suggested by Cabeza, Ciaramelli, and colleagues (2008), different regions of parietal

cortex may perform functions that are algorithmically similar, albeit in vastly different domains. In the case of recognition memory, there remains controversy over the degree to which memory-linked activations overlap with those involved in visuospatial attention. In a direct within-subjects comparison of the parietal regions involved in memory and visuospatial attention, Hutchinson and colleagues (2014) used a field-mapping approach to demonstrate that the medial IPS and SPL response was likely common across visual and memory domains, perhaps reflecting the sustained deployment of visual attention to external probes in proportion to reaction times. In contrast, lateral IPS and angular gyrus memory-linked activations were disjoint with spatial attention regions. Although these researchers cast the lateral IPS and angular gyrus responses in terms of familiarity versus recollection-based retrieval products, respectively, as discussed above, these regions are also heavily modulated by the requirement to shift memory decision biases, and by memoranda that conflict with these adopted decision biases. In addition, these regions demonstrate a pattern of brain-behavior correlation at the subject level that tracks tonic observer biases in uncued recognition, not observer accuracy. In conjunction with the failure to observe even minor recognition accuracy deficits following large parietal lesions, and the initial demonstration that such lesions may impair the ability to flexibly adopt cued recognition biases, the data would suggest that these regions may be important for the differential weighting of novelty, familiarity, and perhaps recollective information depending upon contextually cued biases and not memory retrieval per se. Under this interpretation, memory evidence is necessary, but not sufficient, to drive activation. In addition, the map that results during recognition reflects the relative salience of particular types of memory information in light of the adopted processing biases and other factors discussed below.

The concept of memory orienting is not novel in the cognitive literature (e.g., Mandler, 1980) or in the context of functional brain imaging (Herron & Rugg, 2003). However, it is relatively unexplored. Critically, if memory information, like visual information, is multidimensional or multifeatural, then the relative salience of these different features of recovered memory evidence (e.g., familiarity, novelty, and recollection) is governed by a host of factors, including (1) the adopted bias of the observer (i.e., which features are expected given general task emphasis, biasing cues, task experience/practice, and subject traits), (2) individual differences in core retrieval abilities which govern the basic availability of types of memory evidence, (3) encoding manipulations that determine the availability

of episodic content, and (4) the motivational significance of particular features, which is known to drive parietal activation during saccade decisions in nonhuman primates (Leathers & Olson, 2012; e.g., cells driven by the motivational salience of the cue but not the action value). Thinking about parietal activation at retrieval as a function of the relative salience of different types of memory information is a fairly unexplored framework. However, it is clear that externally cued decision biases, which govern expectations about the types of memory signals that should be encountered and also heavily influence behavioral response patterns, concomitantly have very large effects on the distribution of and nature of parietal responses during recognition. Additionally, the salience of expectations will be modulated by the discrimination ability of the subjects. In other words, those who discriminate well should also show greater response to violations because the conflicting signals will be strong (Jaeger, Konkel, & Dobbins, 2013). Nonetheless, a biasing and orienting framework assumes the functional significance of these activations lies not in directly supporting retrieval success, but instead in biasing judgments for more efficient processing when those biases are confirmed and, alternatively, orienting and exploring memory contents more thoroughly when those biases are disconfirmed.

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