48 Parietal Lobe Mechanisms Subserving Episodic Memory Retrieval

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ABSTRACT Episodic memory enables conscious remembrance of events past and the recognition of previously encountered stimuli. Functional neuroimaging investigations of episodic retrieval indicate that retrieval-related activity extends well beyond the medial temporal lobe and prefrontal cortex, and consistently includes multiple, functionally distinct retrieval effects in lateral posterior parietal cortex (PPC). Here we review what is known about PPC activity at retrieval and how this activity relates to the broad range of cognitive operations subserved by PPC (e.g., attention, multifeatural binding, decision making, and action intention). We conclude by introducing a working model of PPC contributions to episodic remembering.

Episodic memory enables humans to discriminate novel from previously encountered stimuli and to retrieve details of past events. Given its importance for everyday functioning and its disruption in disease, extensive neuroimaging research has sought to delineate the neural mechanisms that subserve episodic remembering in healthy humans. Extant functional MRI (fMRI) data implicate several large-scale brain regions and their network interactions in episodic retrieval, including the medial temporal lobe (MTL), prefrontal cortex (PFC), and posterior parietal cortex (PPC; figure 48.1). While rich neuropsychological literatures demonstrate that MTL and PFC damage can lead to noticeable memory impairments (Shimamura, 1995; Squire, 1992), lateral PPC damage is associated with subtle memory changes (Berryhill, 2012). This puzzling result has sparked debate about the function of lateral PPC (hereafter PPC) during retrieval.

Interest in PPC contributions to episodic retrieval emerged from event-related functional MRI (fMRI) observations of "old/new" or "retrieval success" effects, wherein PPC activity (predominantly left-lateralized) is greater during recognition of previously encountered stimuli as "old" (hits) relative to classification of novel stimuli as "new" (correct rejections). Initial studies suggested a dorsal/ventral axis of PPC functional organization (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In general, fMRI blood oxygen level–dependent (BOLD) activity in dorsal PPC (dPPC)

tracks differences in item-memory strength or *familiarity*—that is, the sense of prior encounter that is unaccompanied by remembrance of contextual detail. By contrast, ventral PPC (vPPC) is engaged during *recollection*—that is, the retrieval of contextual details of a prior event. While this coarse dorsal/ventral distinction in PPC old/new effects has prompted multiple hypotheses and motivated novel experimentation, recent meta-analyses and empirical studies indicate a more fine-grained parcellation of PPC retrieval-related effects (figure 48.2; e.g., Hutchinson, Uncapher, & Wagner, 2009; Hutchinson et al., 2014; Sestieri, Shulman, & Corbetta, 2010), calling into question whether two-process (dorsal/ventral) models are sufficient to account for PPC computations during retrieval.

This chapter summarizes fMRI research on PPC function during episodic retrieval, and considers how multiple PPC mechanisms may influence memory-guided action. We first introduce prominent hypotheses regarding PPC contributions to retrieval and briefly review the current state of the field. Critically, we argue that any model of PPC contributions to retrieval must take into account the fine-grained functional heterogeneity in PPC. We then offer a working model of PPC function that incorporates seemingly conflicting hypotheses. Broadly, we suggest that multiple PPC functions—including mechanisms of attention, multifeatural binding, decision making, and action intention—may each explain a particular subset of PPC retrieval effects and interact to support retrieval-guided behavior.

Attention

ATTENTION TO MEMORY From one perspective, PPC old/new effects reflect the differential engagement of attention depending on retrieval outcomes. A particularly influential attention-based hypothesis—termed *attention to memory* (AtoM; Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008)—builds on a model of perceptual attention (Corbetta, Patel & Shulman) in which dPPC supports goal-directed ("top-down") orienting of attention, while vPPC supports stimulus-driven
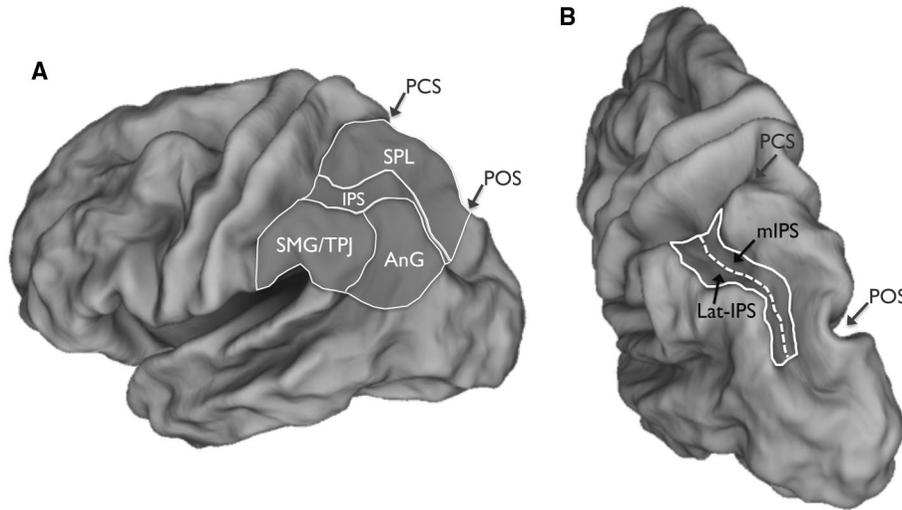
FIGURE 48.1 PPC anatomy. (A) Lateral view, with macroanatomical regions labeled: SPL, superior parietal lobule; IPS, intraparietal sulcus; SMG, supramarginal gyrus; TPJ, temporoparietal junction; AnG, angular gyrus; PCS, postcentral sulcus; POS, parietal-occipital sulcus. (B) Dorsal view, with medial IPS (mIPS) and lateral IPS (lat-IPS) labeled (dotted line; fundus of the IPS).
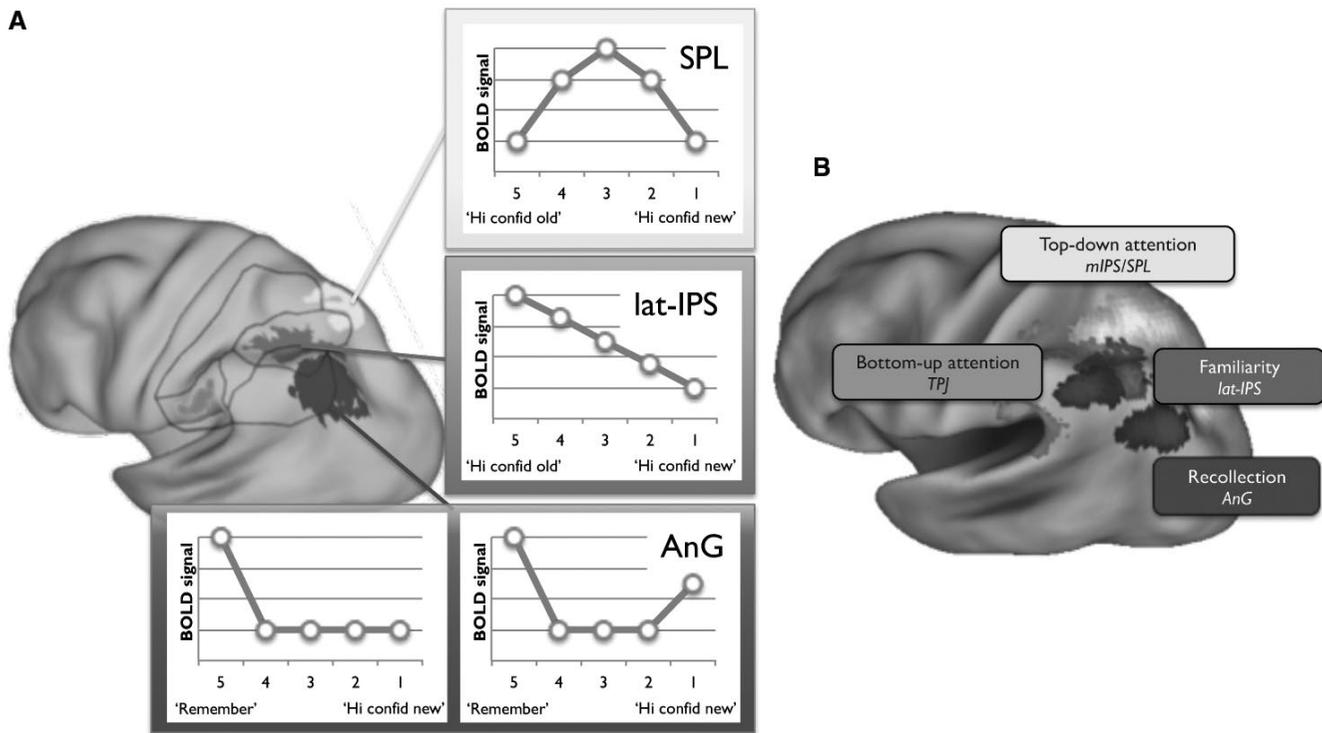

FIGURE 48.2 PPC functional dissociations. (A) Hutchinson et al. (2014) revealed a quadruple dissociation of activity patterns during retrieval: lat-IPS (red) activity showed a monotonic relationship with item-memory strength; AnG (blue) activity tracked recollection of event details; mIPS/SPL (yellow) demonstrated a decision uncertainty effect, with TPJ (green) qualitatively showing the reverse. Black lines indicate parcellation identified by Nelson et al. (2010) using graph-theoretic analyses of resting-state and task fMRI data. Line graphs depict schematics of representative activity patterns. Note: AnG activity tracks recollection (left graph) and sometimes also shows a novelty effect (right graph). "Remember," Remember responses; "hi confide," high confidence. (B) Meta-analyses of top-down and bottom-up attention effects, and recollection and familiarity-based retrieval effects reveal largely nonoverlapping parietal regions supporting attention and memory (adapted from Hutchinson et al., 2014). (See color plate 39.)

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("bottom-up") reorienting of attention. Extending this attention model from perception to memory, AtoM posits that dPPC mechanisms are recruited to allocate attention to the goal of memory retrieval (e.g., when effortful pre- and/or post-retrieval processing is required to make a memory decision), and that relevant memory cues or recollected memories result in vPPC bottom-up attentional capture.

The dorsal component of AtoM garners support from studies in which demands on top-down attention at retrieval are thought to differ across conditions. First, relative to high-confidence decisions, low-confidence decisions, which should require greater top-down attention, elicit greater dPPC activity (Cabeza et al., 2008; Vilberg & Rugg, 2008). Second, recognition decisions accompanied by familiarity may be associated with greater dPPC activity relative to recollective decisions largely because, in the framework of many studies, familiarity-based decisions are more effortful and thus more demanding of top-down attention (Cabeza et al., 2008). When a recollective task was designed to be more effortful than an item-memory task, greater dPPC activity was observed in the recollection condition (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010). Third, attentional orienting during a visual search task was shown to engage dPPC regions that are similar to those engaged during a memory search task (Cabeza et al., 2011).

The ventral component of AtoM also garners support from multiple lines of evidence. First, the detection of recollected or high-strength mnemonic information is proposed to be analogous to the detection of target information in perception (Ciaramelli et al., 2008), such retrieval events are thought to be salient and thus should elicit bottom-up attentional capture (putatively associated with vPPC activity). Consistent with this account, greater vPPC activity is observed (1) when recognition is accompanied by the subjective report of "*remembering*" the past event—putatively indicating retrieval of some detail(s) of the original study episode—relative to when recognition is accompanied by the subjective sense of familiarity ("*know*" and high-confidence "*familiar*"/"*old*" responses), and (2) when participants objectively recollect details associated with a test probe's past encounter, including retrieval of a specific contextual (source) detail, retrieval of an associate of a cue, and retrieval of more rather than fewer event details (Cabeza et al., 2008; Rugg, Johnson, & Uncapher, in press; Vilberg & Rugg, 2008; Wagner et al., 2005). Second, consistent with bottom-up attention being engaged when expectations are violated (e.g., oddball effects and invalid vs. valid trials during attention cueing; Corbetta, Patel, & Shulman, 2008), *memory-based*

expectation violations elicit activity that overlaps old/ new effects in vPPC (O'Connor, Han, & Dobbins, 2010). Similarly, old/new effects overlap with effects posited to be a proxy for bottom-up attention (Ciaramelli et al., 2010): greater vPPC activity was observed when participants were presented with recombined word pairs that may elicit a memory-based expectation violation relative to intact word pairs (which presumably confirm memory-based expectations). Third, in a study that investigated (bottom-up) target detection in a memory task and a perceptual task, activity during mnemonic and perceptual target detection overlapped in vPPC (Cabeza et al., 2011). While none of these studies directly relate PPC activity during recollection or high-confidence memory decisions to that during conditions known to demand bottom-up attention, they can be interpreted as suggesting that vPPC-mediated attentional processes are engaged under various retrieval conditions.

BEYOND DUAL-ATTENTION ACCOUNTS While the preceding findings (and others) lend support to AtoM, a growing literature demonstrates that the PPC regions engaged during attention tasks are not the same as those typically showing old/new effects. First, Sestieri and colleagues (2010) demonstrated that top-down perceptual and mnemonic search tasks elicit activity in adjacent but nonoverlapping regions of dPPC, with the perceptual task recruiting medial intraparietal sulcus (IPS) and the memory task recruiting lateral IPS. Second, Hutchinson and colleagues (2014) reported complementary findings (figure 48.2A): while BOLD activity in angular gyrus (AnG) tracked recollection and activity in lateral IPS tracked item-memory strength, medial IPS/superior parietal lobule (SPL) activity tracked (1) top-down visuospatial attention (as evidenced by overlap with "attendotopic maps"— that is, topographic maps indicating where in visual space top-down attention is allocated) and (2) retrieval decision uncertainty (i.e., low-confidence > high-confidence recognition decisions). Moreover, activity in a fourth region—temporoparietal junction (TPJ)— demonstrated a pattern that qualitatively resembled the inverse of that in medial IPS/SPL. In a third line of evidence, Uncapher and colleagues (Uncapher, DuBrow, Hutchinson, & Wagner, 2011) manipulated when attention and memory operations were likely to occur during a retrieval task, and demonstrated parallel dissociations as reported in Hutchinson et al. (2014): AnG activity tracked recollection success, SPL activity tracked top-down attentional orienting, and TPJ activity exhibited bottom-up attentional reorienting effects.

Collectively, these findings (and others) point to a quadruple dissociation in PPC (figure 48.2A). In dPPC, medial IPS/SPL regions appear to support top-down attention and are engaged during uncertain retrieval decisions, whereas lateral IPS supports a mechanism (or mechanisms) that positively varies with item-memory strength. In vPPC, TPJ appears to track bottom-up attention, which may be disengaged or suppressed during uncertain retrieval decisions, whereas AnG supports a mechanism (or mechanisms) that varies with event recollection. The partitioning of PPC into four functional regions is further supported by meta-analyses of the attention and retrieval literatures (figure 48.2B). Specifically, Hutchinson and colleagues (2009, 2014) observed a quadruple dissociation within these broader literatures, with the four retrieval-identified PPC foci (figure 48.2A) anatomically overlapping the four regions observed in the meta-analyses (figure 48.2B). As such, there is now considerable evidence for at least four functionally separable PPC regions in which activity varies during episodic retrieval, with lateral IPS and AnG demonstrating old/new effects distinct from medial IPS/SPL and TPJ regions demonstrating attention effects.

Posterior Parietal Cortex Anatomical and Functional Heterogeneity   A broader literature demonstrates that PPC is comprised of multiple subregions, each with unique receptor composition and structural connectivity (Nelson et al., 2013). For instance, cytoarchitectonic parcellation of PPC reveals at least 11 distinct subregions: seven in vPPC (Caspers et al., 2006), and at least four in dPPC (Scheperjans et al., 2008). Such structural partitioning relates to functional partitioning, as regions exhibiting similar receptor architectonics have been shown to belong to the same functional network (e.g., Zilles & Amunts, 2009). Diffusion tensor imaging (DTI) studies also reveal fine-grained parcellation of PPC, with multiple subregions of vPPC showing macroscopically distinct structural connectivity profiles (Caspers et al., 2011; Uddin et al., 2010).

Heterogeneity within PPC is also reflected in functional profiles. First, at least seven dPPC regions (IPS0–IPS5 and SPL1) contain "attendotopic maps" (Silver & Kastner, 2009); these regions appear separable from the lateral IPS region showing item-memory strength effects, and partially overlap with the medial IPS/SPL region demonstrating a retrieval decision uncertainty effect (Hutchinson et al., 2014). Second, "resting-state functional connectivity" analyses indicate that distinct aspects of PPC functionally connect with distinct large-scale networks (Nelson et al., 2013). For example, four to eight large-scale networks include PPC nodes (Yeo

et al., 2011). Within vPPC, (1) SMG and AnG show differing, if not opposite, connectivity with the MTL, and only AnG appears to belong to a functional network that includes parahippocampal gyrus and hippocampus; (2) boundary detection and graph theoretic analyses reveal an abrupt transition between SMG and AnG in their global functional connectivity profiles; and (3) these boundaries are functionally meaningful, with AnG—but not SMG—seeds being sensitive to retrieval outcomes (for visualization of boundaries in relation to the retrieval effects discussed above, see figure 48.2A). As such, extensive evidence indicates that considerable structural and functional heterogeneity exists in PPC, making it unlikely that a coarse dorsal/ventral account can explain the full pattern of PPC activity during retrieval.

Proponents of AtoM argue that extensive PPC functional heterogeneity is more apparent than real, particularly in vPPC, since they interpret the literature as revealing "largely overlapping [effects] with some differences around the edges" (Cabeza, Ciaramelli, & Moscovitch, 2012). This position seems difficult to reconcile with the considerable evidence detailed above, including the retrieval-related dissociations between AnG and TPJ (figure 48.2). Moreover, Nelson, McDermott, and Petersen (2012) point to the sharp connectivity boundary between AnG and TPJ/SMG as strong evidence against such a view of vPPC functional organization. Following criteria for defining a distinct cortical area—a region possessing unique function, architectonics, connections, and topography (Felleman & Van Essen, 1991)—the findings reviewed above suggest that PPC contains at least four, but more likely six or more, major subdivisions. Given extant data, the AtoM hypothesis may explain retrieval-related effects in medial IPS/SPL (top-down attention to retrieval cues and/or mnemonic evidence) and TPJ (bottom-up attention that is suppressed during top-down attention allocation required for retrieval; figure 48.3). However, AtoM leaves unspecified the functional significance of the old/new effects in AnG and lateral IPS (which appear sensitive to recollection and item-memory strength, respectively). Indeed, while proponents of AtoM posit that the anatomical separability of memory and visual attention effects in dPPC and in vPPC do not pose a challenge to AtoM, as they may reflect common attentional computations oriented either to external inputs (medial IPS/SPL and TPJ) or internal representations (lateral IPS and AnG; Cabeza et al., 2012), it is unclear how this can account for the dissociable activity profiles that are observed during retrieval (figure 48.2A)—specifically, the monotonic function in lateral IPS together with the nonmonotonic function in medial IPS/SPL;
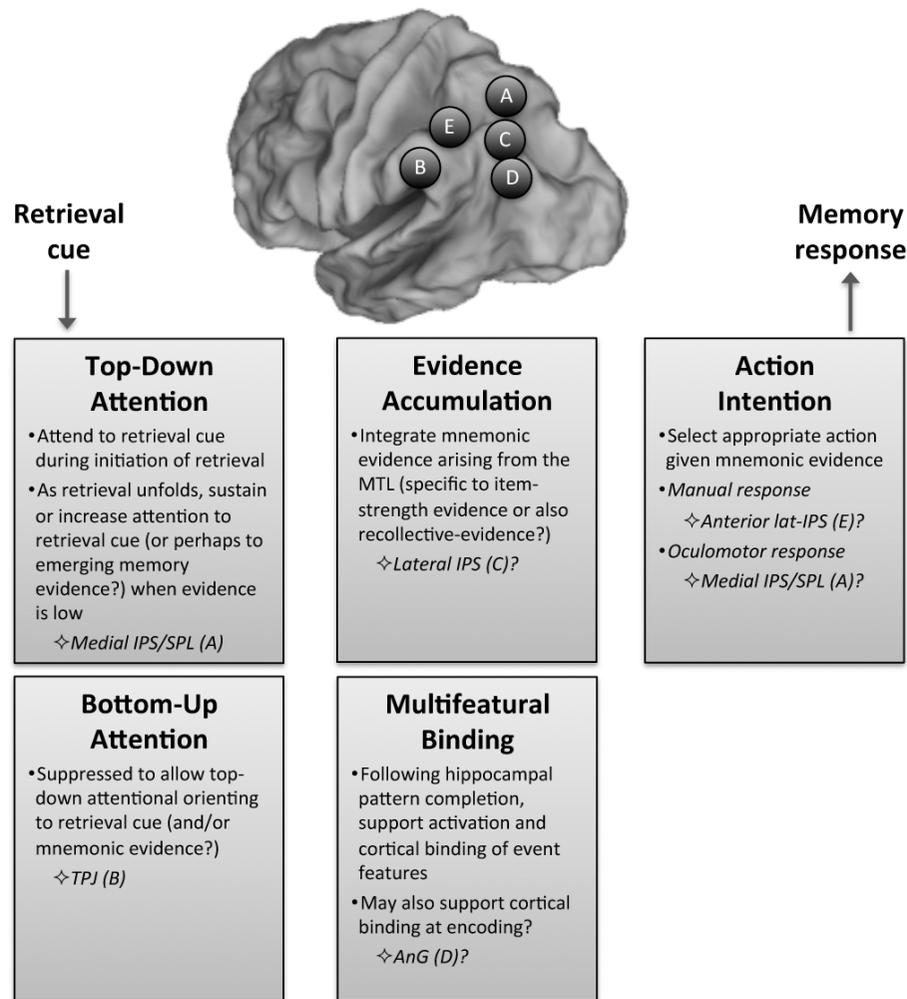
FIGURE 48.3   Working model of PPC operations during episodic retrieval (see text for details).

the same holds for the distinct functional profiles in TPJ and AnG. We next discuss other hypotheses advanced to understand retrieval effects in AnG and lateral IPS.

Buffer/binding accounts of angular gyrus function

As reviewed above, extensive evidence indicates that AnG activity tracks recollection at retrieval. Two closely related hypotheses—the *episodic buffer* (Vilberg & Rugg, 2008) and *cortical binding of relational activity* (CoBRA; Shimamura, 2011) accounts—posit that AnG operates on the products of hippocampally mediated pattern completion (see Davachi & Preston and Leutgeb & Leutgeb, this volume). AnG is thought to be well positioned to represent and operate over the multifeatural information reinstated by the MTL, given that AnG (1) receives strong disynaptic input from the hippocampus by way of parahippocampal gyrus and retrosplenial cortex, and (2) functionally couples with these MTL structures at rest and during tasks.

The episodic buffer hypothesis proposes that AnG acts as an interface between episodic memory operations and executive processes engaged in service of memory-guided decisions. By this account, AnG mechanisms serve to *maintain* recollected memory content, so that the retrieved mnemonic information can be interrogated in service of retrieval goals (Vilberg & Rugg, 2008). Consistent with this account, AnG demonstrates a "recollection load effect" (Hutchinson et al., 2014; Rugg et al., in press; Vilberg & Rugg, 2008)—that is, activity is greater when more versus less information (or more specific vs. more general information) is recollected, and thus presumably when more information must be maintained. Moreover, Vilberg and Rugg (2012) demonstrated that, whereas hippocampus is only transiently engaged during recollection, AnG activity persists for variable durations depending on how

long recollected information must be held to meet task demands, consistent with the notion of a "buffer" that maintains retrieved representations.

CoBRA draws from the connectivity of AnG, wherein AnG serves as a cortical convergence zone of multimodal information, and thus may be engaged during retrieval to facilitate reactivation of the disparate details of a recollected event (Shimamura, 2011). As such, CoBRA is closely related to the episodic buffer account in that AnG mechanisms are proposed to operate on the output of hippocampal pattern completion operations, in this case to support cortical reactivation of event features. It has been argued that CoBRA differs from the episodic buffer account in that AnG processes operate on cortically stored representations, rather than acting as a separate store of these representations. In this manner, it can be considered an activation model of the episodic buffer hypothesis (Shimamura, 2011). While both accounts predict a recollection load effect, given the putative role of AnG in multimodal or multifeatural integration, the binding account may explain why AnG activity is sometimes greater for high-confidence relative to low-confidence correct rejections (perhaps reflecting the encoding/binding of novel associations during retrieval; figure 48.2A).

Mnemonic accumulator accounts of lateral intraparietal sulcus and angular gyrus

Many acts of memory retrieval can be construed as a decision process, in which retrieved mnemonic evidence is computed in relation to decision criteria (Ratcliff, 1988). The mechanisms governing memory-based decisions, which depend on internally generated evidence, may parallel those supporting perceptual decisions, which depend on external inputs. Theoretical models, which posit that evidence is accumulated toward one or more bounds over the course of a decision (Ratcliff, 1988; Usher & McClelland, 2001), can successfully account for a range of behavioral phenomena from mnemonic and perceptual decision tasks, including speed-accuracy tradeoffs, the positive skew in reaction time (RT) distributions, and slower RTs for incorrect versus correct decisions.

In two-choice perceptual decision tasks, neurons in lateral intraparietal cortex (LIP, the putative nonhuman primate homolog to human IPS; e.g., Van Essen et al., 2001) gradually increase their firing rates until a decision is made (Shadlen & Newsome, 2001), with greater perceptual evidence eliciting steeper slopes in LIP firing rates. These data suggest that LIP neurons, along with neurons in the frontal eye fields (FEF) and principal sulcus of PFC, code for a cumulative decision variable during perceptual decisions. In humans, BOLD activity in IPS and FEF is greater (e.g., Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Kayser, Buchsbaum, Erickson, & D'Esposito, 2010) and more temporally extended (Ho, Brown, & Serences, 2009; see also Ploran et al., 2007) during low- versus high-evidence perceptual decisions, suggesting a role for these regions in an accumulative decision process.

As reviewed above, BOLD activity in lateral IPS tracks item-memory strength during recognition decisions (figure 48.2A), with activity typically being greater for high- than low-confidence hits, which in turn is greater relative to misses and correct rejections. Moreover, lateral IPS activity tracks *perceived* memory strength rather than veridical experience, being greater for false alarms than misses or correct rejections (Wagner et al., 2005). One hypothesis is that lateral IPS contributes to the accumulation of mnemonic evidence toward a decision bound. By this account, greater memory strength leads to greater accumulative activity, perhaps reflecting a steeper response slope on stronger memory strength trials.

While the accumulator framework may provide a way to link activity in LIP neurons with BOLD data in human IPS, there are several challenges for this account. First, it is unclear how accumulative activity in LIP neurons translates to BOLD activity. Some have argued that *lower* evidence should be accompanied by greater BOLD responses in regions where decision signals are accumulated (Ho et al., 2009; Kayser et al., 2010), assuming (1) the neural response slope is shallower and thus takes longer to reach the bound, and (2) accumulative processes terminate once the bound is reached. The BOLD pattern predicted by this view would appear to better fit that seen in medial IPS/SPL, which demonstrates greater activity for lower-confidence memory decisions (a decision uncertainty effect). Alternatively, it is possible that decision evidence may continue to accumulate even after the decision bound is reached, which would give rise to greater activity in situations of greater mnemonic evidence, and is the pattern seen in lateral IPS. Second, retrieval-related activity in multiple PPC regions varies with decision bias, including when bias is shifted (see chapter 49, this volume); it is presently unknown how shifts in decision bounds impact BOLD activity reflecting accumulative processes. Third, from one perspective, activity in a mnemonic accumulator region might be expected to track greater strength of evidence, regardless of whether the evidence favors an "old" or a "new" response. That is, a test probe may elicit stronger evidence that it is old (high- vs. low-confidence hits) or that it is novel (high- vs. low-confidence correct rejections). If evidence for novelty

is accumulated (rather than correct rejections being based on the absence of strong evidence that the probe is old), then a U-shaped activity function might be predicted (rather than a monotonic item-memory strength function). Such a pattern is sometimes observed in AnG, rather than lateral IPS, during recognition decisions (figure 48.2B).

Others have directly posited that AnG implements an accumulative integration-to-bound mechanism during retrieval (Criss, Wheeler, & McClelland, 2013). Criss and colleagues observed that AnG BOLD activity peaked more quickly when participants rejected foils in a block that contained strongly encoded old items relative to a block that contained weakly encoded old items, which offers tentative support for the view that the level of evidence (as indexed by perceived novelty) influences the rise rate of AnG activity (N.B., this result is also consistent with binding/buffer accounts). Other data potentially challenge an accumulator account of AnG function. Guerin and Miller (2011) had participants encode faces that occurred with low (once or twice) or high frequency (five or six times), and then make a frequency discrimination between pairs of faces ("which face appeared more often?"). Test pairs consisted of easy versus difficult discriminations (low-high pairs vs. low-low or high-high pairs). Importantly, AnG activity was greater when frequency discriminations involved high-frequency faces (i.e., high-high > low-high > low-low), rather than when discriminations were easy versus difficult, suggesting that AnG activity may scale with the amount of retrieved information independent of decision certainty. This pattern appears to favor binding/buffer accounts of AnG function during retrieval.

Action intention

PPC computations support the planning of movements, as evidenced by extensive data on the role of PPC in eye, arm, and hand movements (Andersen & Cui, 2009). The vast majority of retrieval studies required participants to indicate their memory decisions by manual button press, raising the possibility that aspects of PPC activity during retrieval reflect action-intention processes (which may interact with processes of attention, binding, and evidence accumulation). From this perspective, some PPC old/new effects may reflect the preparation of memory-guided actions, with the strength of memory evidence serving to modulate the strength or duration of action-intention processes. This hypothesis predicts that (1) extant PPC old/new effects will localize to regions that exhibit preference for hand movements, and (2) the localization of old/new effects will shift depending on the memory-guided action to

be performed (e.g., manual vs. oculomotor responses). To date, no study has directly tested either prediction. Here, we review evidence from the action-intention literature that suggests a pattern of effector-specificity compatible with this hypothesis.

In nonhuman primates, effector-specificity is observed in PPC during preparation of eye, arm, and hand movements (Andersen & Cui, 2009). Neurons in the "parietal reach region" of LIP exhibit preferential activity during preparation of arm movements and anterior intraparietal cortical neurons show preference for grasping movements, whereas a "parietal eye field" in LIP shows strong preference for eye movements. Although monkey-human homologies are underspecified, it is thought the human homolog of the parietal eye field is medial IPS, anterior intraparietal area is thought to be homologous to anterior IPS, and the parietal reach region may dissociate into two regions in humans, medial IPS and superior parietal-occipital sulcus (Vesia & Crawford, 2012).

There is growing fMRI evidence for effector-specificity in human PPC (Vesia & Crawford, 2012), with a saccade bias in more posterior/medial areas and a hand/arm bias in more anterior/lateral areas. For instance, Beurze, de Lange, Toni, and Medendorp (2009) demonstrated that anterior IPS exhibits hand-specific activity, the superior parietal-occipital sulcus exhibits eye-specific activity, and medial IPS is sensitive to both effectors. Interestingly, recent data suggests that this posterior-anterior gradient may not reflect effector-specificity *per se*, but instead may relate to the different functional goals that different effectors enact (i.e., saccade goals operate on eye-centered reference frames, whereas limb goals interact with both eye- and body-reference frames; Vesia & Crawford, 2012).

Given the central role of dPPC regions in action intention, a largely unexplored hypothesis is that PPC activity during retrieval—particularly in IPS—reflects the transformation of mnemonic evidence to action intention. As noted, during manually signaled memory decisions, medial IPS/SPL demonstrates a decision uncertainty effect, whereas lateral IPS (often spanning mid- to anterior IPS) monotonically tracks perceived item-memory strength, raising an intriguing possibility that retrieval-related dissociations may partially reflect the role of action computations during recognition decisions. In the only study (to our knowledge) to investigate action intention during retrieval (Shannon & Buckner, 2004), participants made button presses either to old items or to new items, withholding responses to the other class of items (manipulated between experiments). While PPC old/new effects did not vary according to response contingency, which seems to argue

against an action-intention account of retrieval-related PPC activity, it remains possible that participants prepared (although did not execute) a response on every trial. Given the apparent co-localization of some dPPC retrieval-related effects with dPPC regions implicated in action intention, further studies are needed to directly investigate the degree to which retrieval-related activity varies with the specific effector used to make memory-guided actions.

Working model

Retrieval-guided behavior emerges from multiple neurocognitive processes—including processes mediated by PPC—that are triggered by retrieval cues and end in action. PPC subregions influence retrieval through their participation in large-scale functional networks (Nelson et al., 2010), and retrieval-guided behavior likely depends on dynamic interactions between these networks. Here, we briefly introduce a working model that posits putative roles for specific PPC regions during retrieval, and we highlight fundamental open questions.

Retrieval is initiated by cues that are encountered in the external environment or are internally generated (figure 48.3). Top-down attention is likely engaged during retrieval initiation, supporting the allocation of attention to cues; subsequently, top-down attentional allocation likely unfolds dynamically over the course of the retrieval act, depending on the nature of the emerging memory signals. In particular, top-down attention to retrieval cues, and perhaps also to the products of retrieval, is likely to be maintained or even increase over the course of uncertain or difficult retrieval trials (giving rise to the decision uncertainty effect). Extant evidence suggests that medial IPS/SPL supports top-down attention, and that engagement of these regions is accompanied by suppression of TPJ-mediated bottom-up attention during retrieval attempts; however, more evidence is needed to fully assess both hypotheses.

Attended retrieval cues can elicit two types of mnemonic signals (see chapter 45, this volume): (1) MTL cortex-dependent item-memory strength evidence that supports familiarity-based retrieval decisions, and (2) hippocampal-dependent pattern completion that drives reinstatement of event features and supports recollection-based retrieval decisions. Extant data suggest that pattern completion gives rise to MTL interactions with AnG, which may contribute to the reactivation and maintenance of multifeatural event details in cortex. A role for AnG in multifeatural binding may also be present during the encoding of novel events. At present,

it is unclear whether pattern-completed evidence is combined with item-memory evidence during memory-based decisions, or whether recollective and item-memory signals are independently accumulated.

The role of parietal cortex in memory decisions is also complicated by questions related to the transfer function that maps neuronal firing rate to BOLD activity, and to the anatomical overlap between parietal regions that support perceptual and mnemonic decisions. Specifically, it is unclear how accumulative decision processes observed at the neuronal level should manifest in BOLD data. It also remains to be seen whether the posterior IPS region implicated in the accumulation of perceptual evidence is dissociable from the lateral IPS region that has been shown to track item-memory strength.

Another important question concerns the extent to which mnemonic evidence accumulation and action-intention processes are separable. During manual actions, which may be supported by anterior IPS in humans, it is possible that processes that select such actions are at least partially distinct from the item-memory strength patterns seen in lateral IPS (which likely only partially overlap with anterior IPS). Although no data are presently available, we hypothesize that memory-guided oculomotor actions will result in medial IPS/SPL activity that will be distinct from the observed lateral IPS item-memory strength effects, establishing the partial functional independence of putative evidence accumulation and action-selection processes.

Conclusion

The present review and working model may serve as a starting point for considering how the fine-grained functional heterogeneity of PPC influences memory-guided behavior. Continued progress in understanding PPC contributions to retrieval is fundamental to building cognitive neuroscience models of memory, and will have implications for understanding parietal contributions to attention, decision making, and action. Further progress likely will come through a next wave of experimentation that leverages methods with higher spatial and temporal specificity. First, marked across-participant anatomical and functional variability in PPC may necessitate a shift toward more subject-level analyses, employing within-subject comparisons of regions supporting perceptual decision making, manual versus oculomotor action selection, and top-down and bottom-up attention. Second, many of the hypothesized roles of PPC in retrieval entail dynamically unfolding computations that play out with distinct temporal profiles, and could thus be further characterized using

methods with greater temporal resolution. For example, a better understanding of PPC mnemonic accumulative processes could be obtained with measurements of the slope of neural responses during retrieval. We are optimistic that such investigations will continue to reveal the unexpected, multifaceted nature of PPC contributions to memory.

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