

Parietal lobe contributions to episodic memory retrieval

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Although the parietal lobe is not traditionally thought to support declarative memory, recent event-related fMRI studies of episodic retrieval have consistently revealed a range of memory-related influences on activation in lateral posterior parietal cortex (PPC) and precuneus extending into posterior cingulate and retrosplenial cortex. This article surveys the fMRI literature on PPC activation during remembering, a literature that complements earlier electroencephalography data. We consider these recent memory-related fMRI responses within the context of classical ideas about parietal function that emphasize space-based attention and motor intention. We conclude by proposing three hypotheses concerning how parietal cortex might contribute to memory.

Introduction

Episodic memory – conscious memory for everyday events [1] – has long been known to depend on the medial temporal lobe (MTL) memory system [2,3] and on prefrontal contributions to encoding and retrieval [4,5]. Although theoretical and experimental emphasis remains on specifying how MTL and prefrontal structures mediate the acquisition, consolidation and retrieval of episodic memories, an emerging body of functional imaging evidence suggests that a full understanding of episodic memory might also require specification of parietal contributions to retrieval [6,7]. Here we review this surprising new literature and develop hypotheses regarding how parietal cortex might support remembering.

The basic phenomenon that has sparked interest in parietal contributions to episodic retrieval is that differential parietal responses are observed when individuals correctly recognize previously encountered *old* items (hits) as compared with correctly identifying *new* unstudied items (correct rejections; CRs). The earliest observations of such ‘old/new’ effects (alternatively labeled ‘retrieval success’ effects; [8]) were obtained with electroencephalography, wherein the magnitude of event-related potentials (ERP) differed at left and medial parietal scalp electrode sites during hits and CRs (for review, see [9]). More recently, event-related functional MRI (fMRI) studies

have documented greater activation during hits than during CRs in posterior parietal cortex (PPC), including inferior and superior parietal lobules, as well as medial structures that extend from precuneus into posterior cingulate and retrosplenial cortices.

Beyond simply identifying neural regions that demonstrate old/new effects (Box 1), fMRI studies have suggested a range of distinct memory-related influences on parietal activation. For example, activation in PPC modulates based on the perception that information is old (or familiar) even when that perception is in error [10,11]. PPC activation also increases when recognition is accompanied by the recollection of event details [12–15], and, in forced-choice recognition designs, regions in PPC are engaged when retrieval is oriented towards recollecting episodic details as compared with detecting item familiarity [13,16,17]. This article surveys these recent fMRI findings of PPC activation during episodic retrieval. In the course of doing so, we consider how these findings from the memory literature relate to classical attention and intention accounts of parietal function. We conclude

Box 1. Early PET and fMRI observations

Early PET and fMRI studies that compared extended epochs (blocks) of episodic retrieval with non-memory control conditions consistently revealed activation in PPC, including during recognition of words, sentences, and pictures (e.g. [28,64–66]) and during cued-recall for words and pictures (e.g. [67–70]). Initial studies emphasized retrieval-related activations in the precuneus – although activations often extended to lateral PPC – with one hypothesis being that precuneus participates as part of the ‘mind’s eye’ to reinstate visual content during retrieval [71]. Modest debate emerged as retrieval correlates in multiple parietal regions were observed to generalize across content domains (e.g. [70]).

Other early block-design studies attempted to isolate correlates of successful retrieval, either by manipulating the percentage of old and new items in retrieval blocks (for review, see [72]) or by varying encoding conditions to elicit differential levels of subsequent retrieval success (e.g. depth-of-processing manipulations; [28,73,74]). Whereas some studies failed to observe modulations in parietal activation as a function of retrieval success (e.g. [28]), others revealed increased activation during conditions fostering greater retrieval. For example, Tulving *et al.* [64] observed greater parietal activation when performing recognition on blocks of predominantly old versus blocks of predominantly new stimuli. Habib and Lepage [75] performed a meta-analysis that combined these data with four other independent PET studies. Anticipating the results of many later studies, their meta-analysis revealed greater activation in left lateral PPC and in precuneus when many old items occurred within a recognition block as compared with few items.

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Available online 28 July 2005

by proposing a set of hypotheses about how parietal cortices might contribute to remembering.

The old/new effect – a multi-study analysis

Event-related fMRI studies of retrieval have revealed greater PPC activation during hits as compared with CRs. Across experiments, such old/new effects generalize across verbal and visual-object targets (e.g. words and faces, [8,18–20]) and across yes/no recognition, remember/know, recognition confidence, and source recollection paradigms [11,12,14,15,21,22], demonstrating that certain PPC regions are sensitive to, or signal some aspect of, successful retrieval [8,10,12,23]. Although PPC old/new effects are frequently obtained, it is also the case that activation in certain PPC regions does not exclusively track retrieval success, as indexed by old/new effects. For example, although Herron *et al.* [24] observed old/new effects in portions of left PPC irrespective of the percentage of old items within a recognition test (which varied from 25% to 75%), old/new effects in one region of left superior parietal cortex were probability dependent, only being observed during the 25% old condition. Thus, there may be heterogeneity across parietal cortex in relation to memory.

To begin our consideration of parietal retrieval effects, we sought to localize regions consistently showing old/new effects. To this end, we constructed a multi-study convergence map detailing regions showing old/new effects across seven independent retrieval contrasts [8,11,15,25]. The experiments included auditory and visual items, verbal and non-verbal stimuli, and required different responses. For each independent contrast, a whole-brain activation map was constructed identifying voxels showing an increased hemodynamic response for hit relative to CR trials (thresholded at $p < 0.001$). Convergence across these maps was assessed by plotting the number of studies demonstrating an old/new effect, with this convergence projected onto the cortical surface using a novel atlas approach developed by Van Essen and colleagues [26] (using Caret software [27]). Strikingly, prominent old/new effects were obtained in precuneus extending into posterior cingulate and retrosplenial cortices, as well as in left lateral parietal cortex in 100% (7 of 7) of the included contrasts (Figure 1). Identified lateral parietal regions included an expanse of inferior parietal cortex, notably in intraparietal sulcus (IPS) and laterally in inferior parietal lobule (IPL), and a more focal region in superior parietal cortex.

Factors that modulate parietal responses at retrieval

PPC regions show old/new effects that generalize across different item modalities, variable response conditions, and multiple data samples across laboratories (Figure 1), suggesting that these regions consistently track processes correlated with the successful retrieval of episodic information. However, comparisons between hits and CRs do not specify the particular mnemonic attributes that give rise to the observed activation differences, because the processing of hits and CRs can differ along several dimensions (e.g. old/new differences could reflect recollection, item familiarity, repetition priming, or

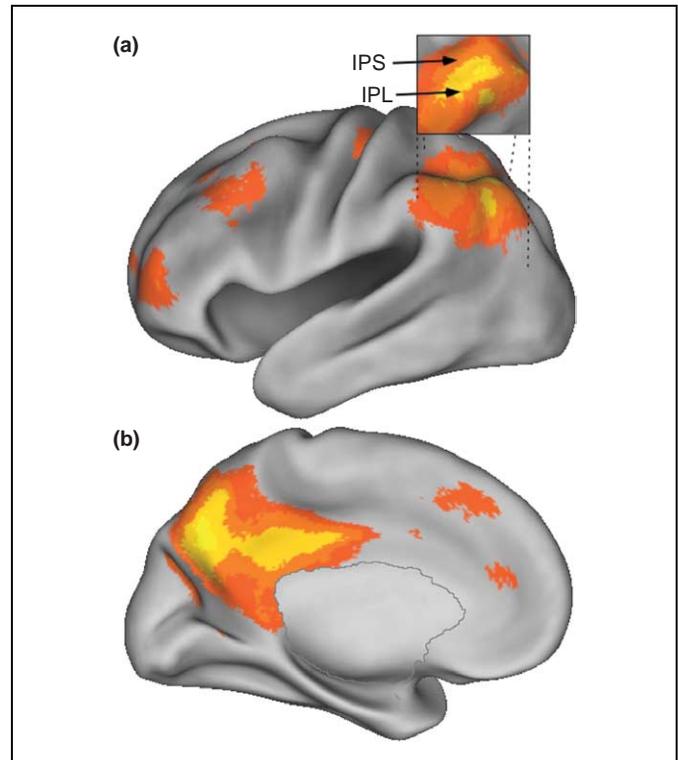


Figure 1. Convergence analysis of the old/new effect. Consistent old/new effects are plotted on the (a) lateral and (b) medial cortical surface of the brain, based on their reproducibility across studies using the PALS approach [26]. The left hemisphere is illustrated. The inset shows the inferior parietal lobule (IPL) and the intraparietal sulcus (IPS). Old/new effects were identified at a threshold of $p < 0.001$ in seven separate event-related fMRI contrasts (data included from [8,11,15,25]). All contain direct comparisons of hits and correct rejections (CR) during recognition tasks. Voxels independently significant in 4 or more of the 7 contrasts are shown (yellow=7 of 7). Clear convergence is observed in lateral parietal cortex (inferior parietal and a small focus in superior parietal), as well as along the medial surface extending from precuneus into posterior cingulate and retrosplenial cortex. The midline region within the outlined area is not part of the cortical surface and is therefore masked.

memory-gated orienting effects). Recent fMRI data indicate that PPC activation can be modulated by (a) the subjective perception that items are old, (b) recollective- as compared with familiarity-based recognition, and (c) retrieval oriented towards the recollection of episodic details versus detecting differential stimulus familiarity.

The subjective perception that information is old

Figure 1 highlights regions showing greater responses when subjects correctly identify old information as old (hits) and new information as new (CRs). What about memory errors? People often fail to recognize previously encountered items (misses), and sometimes mistakenly claim to recognize new items (false alarms). Examining memory errors can provide evidence regarding whether parietal old/new effects are associated with the conscious perception that an item was previously encountered or, alternatively, with the item's history irrespective of its perceived memory status.

Two recent fMRI studies addressed this important issue, measuring parietal activation not only during accurate responses but also during memory errors [10,11]. Inclusion of misses and false alarms allowed determination of whether activation tracked item history (i.e. misses > false alarms, which would support a

repetition priming account of old/new effects) or perceived recognition (i.e. false alarms > CRs). Wheeler and Buckner [10] and Kahn *et al.* [11] both observed strong activation in left inferior parietal cortex to false alarms consistent with a perceived recognition account (Figure 2). Intriguingly, Kahn *et al.* further observed that this region, although modulated by perceived oldness, was not modulated by the recollection of episodic details, raising the question of how left PPC activation relates to recollection and familiarity (Box 2).

Recollection versus familiarity

Several event-related fMRI studies have explored whether parietal activation varies according to whether recognition is accompanied by recollection or familiarity. Initial data indicate that, when sorting retrieval trials by remember/know, source recollection, and study-depth status, recollection-sensitive activation is observed in certain medial and lateral parietal regions [12–15,22]. A convergence analysis across studies from our laboratories identified recollection-sensitive parietal foci in precuneus, extending into posterior cingulate and retrosplenial cortex, and in left-lateralized PPC (excluding the IPS) (Figure 3).

Although Figure 3 points to some convergence, evidence from studies examining the consequences of depth of

Box 2. Dual-process models of recognition

Dual-process theories of recognition suggest that two types of mnemonic information can support recognition decisions. As one basis for recognition, the test probe can be used to retrieve contextual details regarding the previous encounter with the stimulus, yielding **recollection** of the past event (the essence of episodic memory; [1]). Alternately, a test probe might be recognized because it yields a perception of a recent encounter, or item **familiarity**, despite the fact that no contextual details are recollected [63,76,77]. Recollection and familiarity are often measured using 'remember/know' and source-memory tasks. The remember/know procedure is posited to reveal differential reliance on recollection and familiarity, such that subjects respond 'remember' to items recognized based on conscious recollection of contextual details and 'know' when there is a sense that the item was previously encountered but an absence of recollection (e.g. [78,79]; but see, [59]). In source paradigms, subjects discriminate between previously studied and new items, and try to recollect a particular (source) detail about each studied item's past encounter; recollection is essential to accurate source memory [55]. Accordingly, neural correlates of recollection are operationalized as the contrast between hits accompanied by remember versus know responses or the contrast between Source-Hit and Source-Miss trials. Anticipating findings in fMRI studies, the ERP literature has revealed parietal-situated old/new effects (400–800 ms post-stimulus onset) that track the presence or absence of recollection in remember/know and source memory paradigms (for review, see [80]).

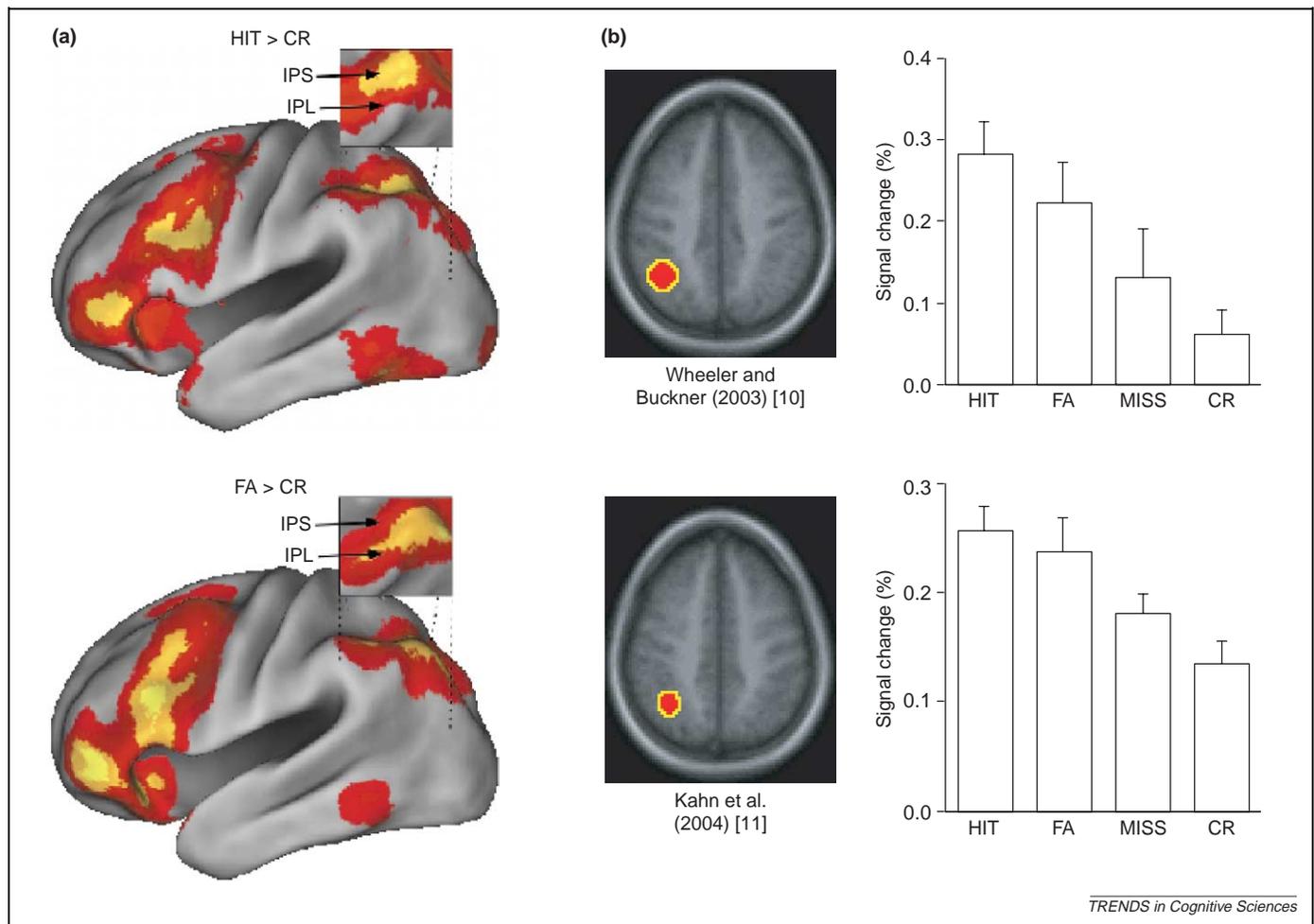


Figure 2. Parietal activation tracks the *perception* that an item is old. (a) Statistical parametric maps from Kahn *et al.* [11] show increased activation during hits vs. CR and during false alarm (FA) vs. CR responses. (b) Activity associated with correct and incorrect responses are plotted from two recognition experiments [10,11]. The mean signal magnitude (bar graphs) across response types is plotted from a targeted left inferior parietal region showing old/new effects (axial plane). Crucially, in both experiments, incorrect responses (MISS, old items endorsed as new; FA, new items endorsed as old) were accompanied by activity magnitudes that fell between those elicited by correct responses (HIT and CR).

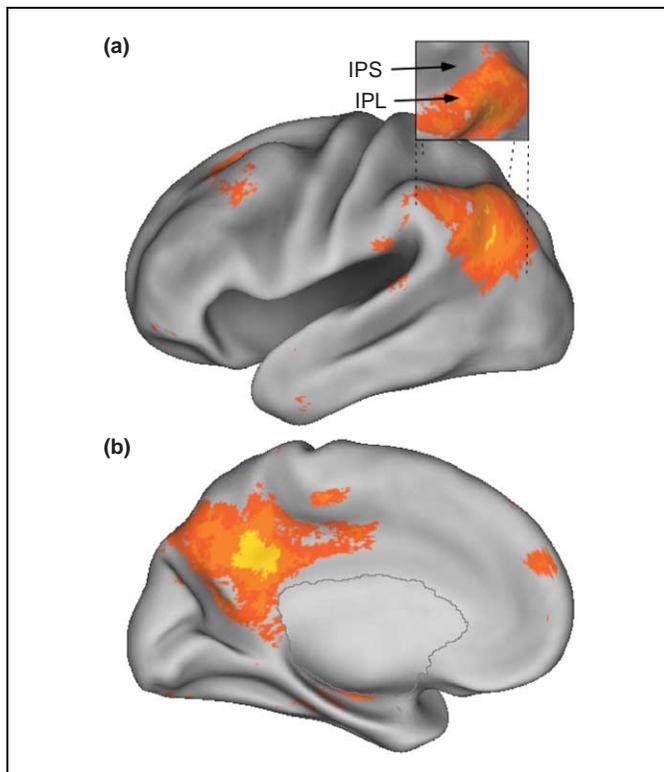


Figure 3. Convergence analysis of successful recollection. Activity is shown on (a) lateral and (b) medial cortical surfaces, as in Figure 1, reflecting convergence across event-related fMRI conditions that contrast remember vs. know recognition trials [15], Source-Hit vs. Source-Miss recognition trials [11,13], and recognition following Deep vs. Shallow encoding [25]. All contain direct comparisons of hits accompanied by high levels of recollection as compared with hits based preferentially on familiarity. Voxels independently significant in 2 or more of the 4 contrasts are shown (yellow=4 of 4).

processing during encoding for subsequent recognition-related parietal activation is mixed. For example, Shannon and Buckner [25] observed greater parietal activation during recognition following deep encoding than following shallow encoding. By contrast, Kahn *et al.* [11] observed comparable activation following deep and shallow encoding (see also, [28]), with activation tracking whether subjects recollected having performed the shallow task. It is unclear whether these divergent findings partly reflect a difference in the size of the study depth effect (0.38 in Shannon and Buckner compared with 0.17 in Kahn *et al.*), the encoding tasks (abstract/concrete and uppercase/lowercase vs. meaning-based imagery and orthographic-to-phonological transformation), or type of recognition test (yes/no vs. source recognition).

The sensitivity of some parietal regions to recollection is also, on first glance, difficult to reconcile with other observations of old/new effects that are almost surely correlated with familiarity-based decisions. For example, parietal old/new effects can occur (i) following repetitive shallow encoding designed to maximize familiarity-based responding [29], (ii) for both fast and slow recognition responses [23], and (iii) when comparing know responses with CRs (e.g. [12,15,30]). Possible resolution of this apparent inconsistency is suggested by recent evidence that functionally distinct PPC subregions are differentially sensitive to recollection success and perceived familiarity [15,31].

Wheeler and Buckner [15] identified a region along the banks of the IPS that showed similarly increased activity for remember and know responses compared with CRs, thus showing an effect that tracked item familiarity. Earlier remember/know studies also revealed that left IPS is insensitive to recollection [12,30], and source memory studies demonstrated similarly increased activity in left IPS during Source-Hits and Source-Misses compared with CRs [11,22]. In contrast to IPS, Wheeler and Buckner [15] identified two additional left PPC regions, lateral and posterior to the IPS, that responded preferentially to remember decisions (see also, [31]). Again, earlier Remember/Know studies also observed selective increases during remember responses in similar left lateral PPC regions [12,14,15].

Our convergence maps lend further support for this anatomic distinction, revealing consistent old/new effects in left IPS (see Figures 1 and 2) but recollection-sensitive effects in more lateral inferior parietal regions (Figure 3). Although not apparent in Figure 3, source retrieval studies also point to an additional region – near left superior parietal cortex – that is responsive to recollection outcome, as evidenced by increased activation during Source-Hits compared with Source-Misses [11,13,24,32]. Collectively, it appears that multiple distinct foci in PPC can be modulated by recollective experience: lateral and posterior inferior parietal regions (lateral to IPS), medial regions near precuneus, and (to a lesser extent) superior parietal cortex [11–15,25]. Responses in left IPS, by contrast, appear to correlate with item familiarity rather than recollection.

Retrieval orientation

Although parietal responses are influenced by the mnemonic status (or perceived status) of the recognition probe, recent data indicate that PPC activation also modulates based on the type of mnemonic information to which subjects orient during attempts to remember ('retrieval orientation'; e.g. [13,16,32–38]). Important data come from fMRI studies of forced-choice recognition, wherein retrieval orientation was manipulated by varying whether the retrieval task required recollective- (source decisions) or familiarity-based (item novelty and temporal recency decisions) information, holding the mnemonic history of the test probes constant ([13,16,17], see also [39]).

Initial evidence for retrieval orienting effects was obtained by Dobbins *et al.* [13], who compared activation during source recollection decisions with that during temporal recency decisions. Whereas greater MTL activation was observed during source vs. recency judgments, with hippocampal activation tracking source recollection success, increased left PPC activation was present during recollective-orienting independent of recollection success (i.e. activation did not differ between successful vs. unsuccessful source decisions). This pattern suggests that specific parietal mechanisms may be recruited during attempts to selectively retrieve event-specific details, consistent with an 'attention to memory' (or internal representations) hypothesis (see below).

Two subsequent studies explored the generalizability of recollective-orienting effects in left PPC [16,17],

contrasting source recollection to item novelty decisions using three-alternative forced-choice with words or pictures. Dobbins and Wagner [17] included two source recollection conditions – one requiring attempts to recover perceptual episodic details and the other requiring attempts to recover conceptual episodic details. Both studies revealed greater left PPC activation during source recollection as compared with novelty detection attempts [16,17], with a convergence analysis revealing high across-experiment overlap in left IPL and IPS (Figure 4). Thus, recollective-orienting effects in left PPC generalize across word and picture stimuli, and across attempts to recollect conceptual and perceptual episodic details. Moreover, these left PPC recollective-orienting effects converge with other observations of differential left parietal activation when comparing source with item recognition [40,41].

Given the apparent overlap between the IPS and IPL regions sensitive to recollective-orienting (Figure 4) and those showing old/new effects (Figure 1), intriguing questions arise regarding how to understand the functional contributions of left PPC during retrieval. One possibility is that recollective-orienting effects may be superimposed on old/new effects, although presumably familiarity-based old/new effects did not differ across the recollective- and familiarity-orienting conditions in these experiments because the mnemonic history of the test probes was held constant. To the extent that this account has merit, it raises the possibility that some PPC old/new effects may reflect memory-gated engagement of PPC selective attention mechanisms that support strategic orienting to memory. We return to this, and other possibilities, below in the course of proposing hypotheses regarding PPC contributions to retrieval.

Relation to classical accounts of parietal function

Lesions to parietal cortex can result in neglect, an attentional deficit, or apraxia, a deficit in planning motor movements [42,43]. Such observations, together with data from single-unit recording studies in monkeys,

have motivated the space-based attention and motor intention theories of parietal function [44,45]. An important question is whether memory-related parietal responses can be explained in terms of these classical ideas. For example, given that eye movements [46] and response times often vary between old and new items, might old/new effects in IPS and superior parietal lobule reflect attentional or intentional processes differentially engaged as a result of perceived familiarity?

This possibility was recently tested by Shannon and Buckner [25], who demonstrated that old/new effects in left and medial parietal regions persist across manipulations designed to affect visuospatial attention and motor planning (Figure 5). For example, PPC old/new effects were observed when test materials were natural sounds (e.g. a dog barking) as well as visual pictures. Assuming that old and new sounds are unlikely to elicit differential attention to specific spatial locations, these findings suggest that a spatial attention account cannot fully handle memory-related PPC effects (for related recollective-orienting results, see [17]). In a second study, Shannon and Buckner manipulated response contingencies. In one condition, standard old/new recognition decisions were made, whereas in two other conditions, subjects either responded only to the old items or only to the new items. All three conditions yielded PPC old/new effects, including increased activation to old items even when responses were made only to new items. These data suggest that PPC old/new effects are unlikely to predominantly reflect memory modulation of motor intention mechanisms.

Understanding parietal contributions to retrieval

Clues about parietal contributions to memory come from anatomy. Lateral parietal, retrosplenial, and posterior cingulate cortices are connected directly or indirectly to the MTL [47–49]. Monkey IPL has direct reciprocal projections to parahippocampal cortex [48,50] and direct projections to hippocampus [51]. Along the midline, afferent connections to retrosplenial cortex are dominated

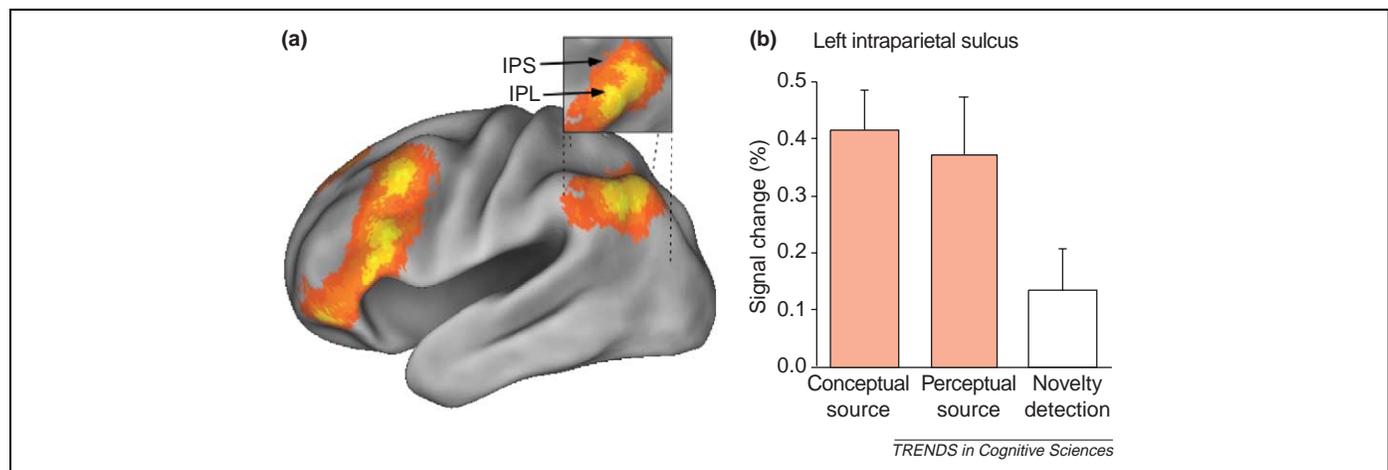


Figure 4. Convergence analysis of recollection orienting. (a) Using a format similar to Figure 1, the convergence across three forced-choice recognition experiments contrasting conceptual source recollection vs. item recency decisions [13], conceptual source recollection vs. novelty detection [16], and both perceptual and conceptual source recollection vs. novelty detection [17] is shown. Across all three contrasts, the items are held constant with the retrieval instructions differentially orienting the subjects to recollection. Voxels independently significant in 1 or more of the 3 contrasts are shown (yellow=3 of 3). Consistent effects were observed in IPS and laterally in IPL. (b) The peak signal magnitudes in left IPS are plotted for the conceptual source recollection, perceptual source recollection, and novelty detection conditions of Dobbins and Wagner [17]. Above baseline percentage signal change was comparable during both recollection conditions, whereas orienting to novelty did not markedly deviate from baseline.

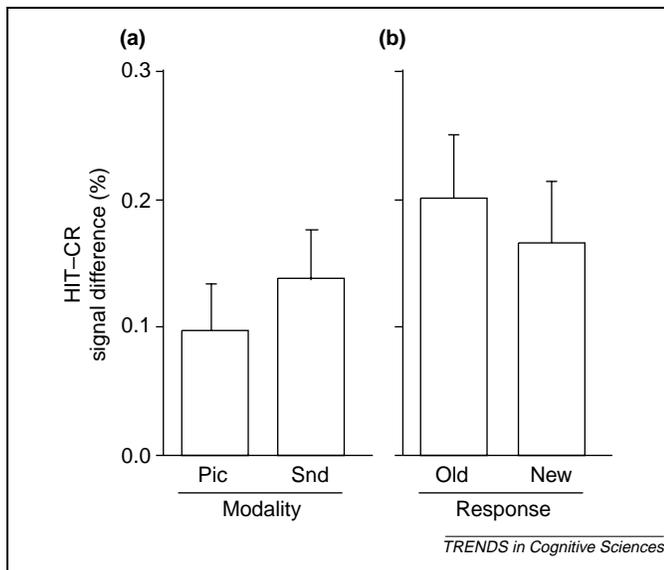


Figure 5. Parietal regions showing mnemonic effects do so across manipulations of visuospatial attention and motor intention. Regions selective for old/new effects are plotted across manipulations of (a) modality of retrieval cue and (b) response target during old/new recognition paradigms. Data are from Shannon and Buckner [25]. The mean signal magnitudes represent the difference between HITs and CRs in each of the four conditions. In (a) the modality of the test cues is manipulated between pictures (Pic) and sounds (Snd). In (b) the response is manipulated between responding only to Old item targets or only to New item targets. In all conditions, HITs show greater activity than CRs suggesting a contribution to mnemonic processes that cannot be explained by differences in visuospatial attention and motor planning.

by MTL projections. Kobayashi and Amaral [49] speculate, based on this anatomy, that retrosplenial cortex acts as an interface zone between the working memory (executive) functions enabled by prefrontal cortex and the declarative memory functions subserved by the MTL (see also, [52]). Although homologies between human and macaque anatomy must be considered cautiously, there are likely to be anatomical projections that provide a route for MTL to interact with parietal cortex in the service of declarative memory. PPC and retrosplenial cortex might reflect major pathways through which the MTL influences cortical information processing.

A natural question to ask is why parietal lesions are not generally associated with robust episodic memory deficits. At present, the source of the divergence between imaging correlates of retrieval and lesion consequences for remembering remains unclear. One possibility is that, although PPC regions are modulated by retrieval demands, these regions do not contribute to episodic memory in a manner that is important for memory expression. On this account, the observations reviewed here are epiphenomenal – that is, PPC does not make direct contributions to retrieval. Alternatively, subtle and as yet undetected mnemonic deficits may follow PPC lesions, deficits that might be revealed only under restricted circumstances. Studies of patients with focal lesions of the specific parietal regions identified by fMRI or transient disruption of these regions with transcranial magnetic stimulation are required to determine whether mild but reliable memory deficits follow focal parietal dysfunction.

A few related observations are worth considering. First, lesions to parietal midline structures do produce memory

impairments – a phenomenon termed ‘retrosplenial amnesia’ [52]. Reviewing case studies of retrosplenial lesions, Kobayashi and Amaral note that memory problems can occur even following relatively circumscribed lesions [49]. Second, Alzheimer’s disease, with its hallmark memory impairment early in disease progression, is associated with metabolic disturbances in medial and lateral parietal regions that overlap fMRI old/new effects, and similar parietal metabolic changes have been reported in amnesia following MTL damage (for review, see [53]). Thus, although a gap exists between neuropsychological and imaging data, there are hints that at least some of the parietal regions modulated during memory retrieval may be relevant to clinical impairment, perhaps as functional components interconnected with the MTL.

As a guide for subsequent investigation and debate, we conclude by speculating about possible ways in which PPC could contribute to episodic retrieval, entertaining three hypotheses. We emphasize that these proposals are speculative, as too little is presently known to develop specific models. Additional forms of data, including single-unit recordings in monkeys performing recognition, will be required to refine and test these ideas.

Attention to internal representations hypothesis

PPC regions may be part of a network that supports attention directed at internal, mnemonic representations. In many situations external cues provide the dominant constraints that drive perception and action, and networks including specific PPC regions participate in stimulus-driven attention [54]. Shannon and Buckner [25] provide evidence arguing against the interpretation that mnemonic modulation of activation in all PPC regions is a marker of stimulus-directed visuospatial attention. However, memory tasks typically demand attentional shifts to representations that rely on derived internal information. PPC regions might contribute to shift attention to, or maintain attention on, internally generated mnemonic representations. Given the apparent sensitivity of some PPC responses to episodic retrieval, including recollective-orienting, these regions may be constrained to directing attention to a limited set of internal representations – perhaps those dependent on the MTL [55,56]. Indeed, it would not be surprising if there were attentional networks specialized for directing information processing to emphasize medial-temporal dependent processes, much as attention can serve to enhance processing in ventral and dorsal visual pathways.

Mnemonic accumulator hypothesis

A second possibility anchors on the observed relation between recognition decisions and activation levels in PPC. Activation in some parietal regions correlates with successful memory retrieval and with memory errors [10,11], raising the possibility that the strength of activation contributes to the eventual decision [31]. Such a property is reminiscent of other proposed forms of information accumulation within PPC regions. For example, monkey area LIP plays a role in integrating sensory signals about motion in the service of eye movements. Shadlen and Newsome [57] have proposed

that ‘Sensory data must be *interpreted* to execute, revise, or delay pending action’ ([57], p. 1916). By their view, LIP participates to accumulate, or temporally integrate, opposing sensory signals until a criterion is reached that leads to the decision.

Recognition memory decisions are likely to require a parallel accumulation of evidence about the history of a stimulus. For example, Ratcliff [58] has proposed that memory retrieval is accomplished by a diffusion process during which evidence for or against a memory decision is accumulated. Similarly, an accumulator hypothesis is consistent with models proposing that recognition decisions are based on a signal-detection process that compares a single memory-strength signal with a decision criterion [59] or that compares the integration of two continuous signals – one recollective- and one familiarity-based – with a decision criterion [60].

We view it as an exciting possibility that subsequent research will establish a more direct link between responses in specific PPC regions and the accumulation of mnemonic evidence – perhaps through interactions with the MTL. Within such a view, parietal cortex contains a set of contiguous areas that perform loosely similar integration functions, but differ depending on the input–output structures. Area LIP might gain its properties from connections to extrastriate visual regions and projections to frontal regions involved in eye movement preparation. Other PPC areas might perform similar integrative functions but gain distinct properties via their connections. Relevant to memory, regions in lateral PPC might perform analogous computations on inputs from the MTL, contributing to decision processes that concern an item’s mnemonic status.

Output buffer hypothesis

A third possibility is that PPC regions dynamically represent retrieved information in a form accessible to decision-making processes, analogous to Baddeley’s proposed active (working) memory buffers [61]. Indeed, evidence from lesion and functional studies implicate left parietal regions in phonological storage, although the precise relation of these parietal regions to those active during episodic retrieval is unclear. From this perspective, although long-term memories (the ‘engrams’) are not stored in neuronal firing patterns, to influence decision-making, such memories must be expressed in active neuronal response patterns. PPC could act as the buffer into which stored information is transferred. Importantly, such active representations are not likely to be restricted to PPC. The phenomenon of reinstatement (or recapitulation), in which memory retrieval activates modality-specific sensory areas, suggests that at least part of the retrieved information is represented in the corresponding sensory areas [11,62]. Nevertheless, PPC might be centrally involved in the representation process.

Relation to the data

Each of our speculative hypotheses would appear to account for particular portions of the data. For example, the attention to internal representations hypothesis suggests ways to understand the effects of retrieval

orientation, although it less readily explains why attentional resources would be deployed in an uneven manner between successful and failed memory retrieval attempts. In this latter regard, one possibility is that rapidly emerging mnemonic information gates parietal attentional mechanisms, providing a means to control retrieval processing strategies [11]. By contrast, the accumulator hypothesis suggests a form of strength theory that maps parietal processes to memory decisions. To the extent that the left inferior parietal regions that show recollection effects perform such an accumulation process, this finding would appear to diverge from high-threshold models of recollection (e.g. [63]), lending support to signal detection models that operate on continuous measures of recollective information [55,60]. Importantly, the observation of functionally dissociable PPC subregions raises the possibility that these distinct PPC structures contribute differently to episodic retrieval, and therefore are best explained by alternative hypotheses. Moreover, we note that the possibilities are not restricted to the three alternatives advanced here (e.g. it is also possible that PPC could support a mnemonic reference frame). Although we do not know what will emerge from these speculative ideas, the hope is that they will help constrain, or even alter, current models of episodic remembering and parietal function (see also Box 3).

Box 3. Questions for future research

- Data support the view that IPS and IPL are sensitive to retrieval success and recollective-orienting. Are these perspectives mutually exclusive or do orienting effects mark modulatory processes that operate independent of (or interactively with) PPC contributions to retrieval success?
- fMRI data regarding parietal contributions to memory predominantly derive from recognition and source-judgment tasks, and related variations. Will studies using generative memory paradigms – e.g., free recall and cued recall – provide additional important constraints on models of PPC memory function?
- As might be predicted by the accumulator hypothesis, does neural activity in parietal cortex track the timing of recognition decisions? For example, do recognition reaction times correlate with the magnitude of evoked potentials/fields in IPS and IPL? Do the temporal profiles of IPS and IPL responses differ for recollection- and familiarity-based decisions?
- Do lateral and medial parietal cortices make necessary contributions to episodic retrieval, such that focal lesions or TMS-induced transient disruption of these structures result in retrieval deficits that are distinguishable from encoding deficits? To the extent that PPC regions are necessary for intact retrieval performance, does lesion evidence support the fMRI-suggested functional dissociation between IPS and IPL?
- How do PPC regions interact with medial temporal lobe mechanisms that support episodic retrieval? Do PPC regions gate engagement of strategic retrieval processes subserved by the prefrontal cortex and known to be crucial for successful episodic recollection?
- Can we document anatomical connections between PPC and MTL in humans using functional connectivity and white matter track tracing methods? Although studies of monkeys have documented connections between PPC and MTL regions, inferring functional homology between humans and non-human primates is not foolproof. Can we establish across-species functional homologies, perhaps through single-unit recording and fMRI studies of monkeys performing recognition memory tasks comparable with those studied in humans?

Conclusions

As surveyed here, fMRI studies have revealed the surprising (but remarkably consistent) finding that specific parietal regions are active during episodic retrieval tasks. The basic observations can be summarized as follows:

(1) Multiple parietal regions are active during episodic retrieval, including regions within the intraparietal sulcus extending laterally to the inferior parietal lobule, as well as midline structures that extend from the retrosplenial cortex and posterior cingulate to the precuneus.

(2) During episodic retrieval, parietal regions show increased activity to recognized old items (hits) and mistakenly recognized new items (false alarms) as compared with correctly rejected new items and forgotten old items (misses). This observation generalizes across different materials, response conditions, and task formats.

(3) Some lateral and medial parietal regions correlate with the phenomenological experience of remembering – activation increases when the subject reports recollecting the earlier event or recollecting source details surrounding the event, even when memory errors are made.

(4) Some parietal regions are sensitive to whether retrieval is oriented in an attempt to recollect or to detect item novelty/familiarity, even when holding the mnemonic history of the test materials constant.

Taken collectively, these findings encourage consideration of how specific PPC regions contribute to episodic memory, and highlight a potentially rich functional organization in parietal cortex wherein multiple, distinct regions make specific processing contributions to memory.

Acknowledgements

We thank Ian Dobbins for provision of data and for insightful discussions, and David Van Essen for use of Caret software and the PALS approach. Supported by the National Science Foundation, National Institutes of Health, McKnight Endowment Fund for Neuroscience, Ellison Medical Foundation, Alfred P. Sloan Foundation, McDonnell Foundation, and the Howard Hughes Medical Institute.

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