

The contribution of the human posterior parietal cortex to episodic memory

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Abstract

The posterior parietal cortex (PPC) is traditionally associated with attention, perceptual decision making, and sensorimotor transformations but more recent human neuroimaging studies support an additional role in episodic memory retrieval. In this Opinion article, we present a functional–anatomical model of the involvement of the PPC in memory retrieval. Parietal regions involved in perceptual attention and episodic memory are largely segregated and often show a push–pull relationship potentially mediated by prefrontal regions. Moreover, different PPC regions carry out specific functions during retrieval— for example, representing retrieved information, recoding this information based on task demands, or accumulating evidence for memory decisions.

Introduction

The posterior parietal cortex (PPC) is traditionally associated with visuo-spatial and sensorimotor functions on the basis of neurophysiological studies in monkeys ^{1,2}, and neuroimaging ^{3,4} and lesion studies ^{5,6} in humans. The PPC represents the egocentric positions of objects in multiple coordinate systems, contains multisensory maps in which stimuli are represented according to their behavioral priority, and holds multiple representations of motor effectors ⁷⁻⁹. Thus, the PPC is perfectly suited for the orienting and reorienting of attention to particular sensory stimuli, guided by either internal goals or intrinsic adaptive value ⁴, and for integrating sensory signals toward a decision appropriate for guiding movement ¹⁰.

However, the contribution of the PPC to human behavior is not limited to these functions. In the past decade, several hypotheses have been proposed to explain the surprisingly consistent response of the PPC during the retrieval of episodic memories (reviewed in ¹¹⁻¹⁵). Activity is usually stronger in the left hemisphere ¹⁶ and generalizes over cue modality ¹⁷, stimulus material ¹⁸ and reward contingencies ¹⁹. At the same time, the parietal response is sensitive to key memory manipulations, such as those involving the strength ²⁰ and depth ¹⁷ of encoding and the distinction between recollection (retrieval of contextual details) and familiarity (mere sense of oldness) ^{13,21}. PPC activity during episodic retrieval is particularly intriguing since patients with PPC lesions do not show clear amnesic symptoms (reviewed in ^{22,23}). This paradox may reflect the insensitivity of standard tests of memory performance to subtle memory deficits (see ²⁴) or the correlative nature of neuroimaging data, since ancillary processes might recruit the PPC during memory retrieval.

The simplest episodic memory task — for example, deciding whether a picture or word is new or seen before — requires the interplay of several cognitive processes, such as perceptual analysis of the probe stimulus, guided retrieval of relevant memory representations, and accumulation of evidence for a decision that may feed into a motor plan. Most hypotheses about the role of the PPC in memory retrieval have proposed a role in one or two processes, including attention ^{12,25}, event representation ^{13,26}, decision making ²⁷ or subjective experience ²⁴. However, later studies ¹⁵,

^{28, 29} have shown that several parietal subregions are characterized by distinctive functional properties during memory retrieval, indicating the implausibility of ‘single process’ accounts.

In this Opinion article we provide a novel functional–anatomical model of memory-related activity in the human PPC (Box 1) that builds on functional neuroimaging studies focusing on the topography and the temporal profile of retrieval-related activity. These studies highlight the incidence of multiple processes that dynamically interact during memory tasks and are localized to different parietal subregions. We believe that this signal-based approach considerably advances our understanding of the involvement of the PPC in episodic memory retrieval.

Perceptual attention and episodic retrieval

Topographic segregation

Because the PPC has long been associated with visuo-spatial and sensorimotor functions, a fundamental question surrounding its role during memory tasks concerns the degree of overlap between activity related to memory retrieval and perceptual attention. Since the only comparison to date involved a meta-analysis of the memory retrieval and perceptual attention literatures ³⁰, several years ago we performed a direct contrast in the same group of participants ³¹.

Classical item-recognition paradigms tend to squeeze perceptual, mnemonic, decision and motor processes within a short time period that is below the temporal resolution of fMRI. As a result, activity related to one process, such as attending to the probe stimulus, cannot be temporally distinguished from activity related to another process, such as memory retrieval. Therefore, we designed tasks in which memory or perceptual search extended over a sustained period and these processes could be more easily separated. We found that parietal regions showing positive responses to perceptual and memory search were adjacent but non-overlapping (Fig. 1a). Memory search-related activity was observed on the lateral aspect of PPC, including the angular gyrus (AG), the lateral bank of the intraparietal sulcus (latIPS) and the post-central sulcus (PoCS), and medially along the precuneus (PreCu), the posterior cingulate cortex (PCC) and the retrosplenial cortex (RSPL). Many of these regions overlap with the default mode network (DMN) ^{32, 33}. **[G ‘default mode network’]** Perceptual search-related activations were observed along the medial bank of posterior IPS (pIPS), the ventral IPS (vIPS), and in regions of the superior parietal lobule (SPL), which together form part of the dorsal attention network (DAN) ^{4, 34}. **[G ‘dorsal attention network’]** This anatomical segregation was evident in both hemispheres and in individual subjects.

Causal support for a segregation of parietal regions involved in memory (albeit semantic) retrieval and perceptual attention comes for a recent study ³⁵ that combined electroencephalography (EEG) with the inhibitory effect of repetitive transcranial magnetic stimulation (see ^{36, 37}). **[G ‘repetitive transcranial magnetic stimulation’]** during task anticipation. We found that both performance and anticipatory alpha desynchronization were affected by stimulation of the pIPS only during the perceptual attention task, and of the AG only during the semantic retrieval task, demonstrating a double dissociation between PPC regions and task demands.

Another study ³⁸ reported a greater overlap between a memory and a perceptual search task, especially in the IPS. According to the authors, the overlap reflects the involvement of the same area in orienting attention to memory and perceptual stimuli, as suggested by the Attention to Memory (AtoM) model ^{12, 39}. This model proposes that dorsal PPC regions maintain retrieval goals whereas ventral PPC regions monitor retrieval output, paralleling a model of attentional orienting that links dorsal parietal regions to top-down attention and ventral parietal regions to bottom-up

attention⁴. However, a greater overlap compared to our study³¹ might also reflect the constant presence of visual stimulation in both of the search tasks developed by Cabeza and colleagues, and thus shared perceptual attention to the target (probe) stimulus. Free recall paradigms could help resolve this issue, as they offer a way to study memory-orienting activity in the absence of perceptual stimulation. A recent study by Kragel and colleagues indicates the absence of sustained activity in dorsal PPC during long periods of free-recall⁴⁰, but more studies on this issue are needed.

Importantly, overlap between perceptual attention and episodic memory tasks is expected whenever the contrast between two memory conditions reflects a difference in the amount/duration of perceptual attention to the probe stimulus, or when information retrieved from memory is used to complete a perceptual or motor task, as in a study by Summerfield and colleagues⁴¹ (see also⁴² for similar results). In this study, memory-based orienting [**G 'memory-based orienting'**] evoked activity in both dorsal (pIPS) and ventral (AG) PPC regions. Therefore, when retrieved memory information is used to perform a perceptual task, visuospatial responses in the dorsal PPC co-occur with retrieval-related responses in the ventral PPC.

Attention to memories.

The results of our study³¹ and the aforementioned meta-analysis³⁰ argue against a strict anatomical and functional correspondence between attention to episodic memory and perceptual attention. The available literature also suggests a similar dissociation for re-orienting responses in the two domains^(30, but see 38), although this issue is still debated^{43,44}. Importantly, these results do not preclude the functional distinctions drawn by Cabeza and colleagues¹² and their mapping to relatively more dorsal and ventral parietal regions. The AtoM explains several findings in the memory literature by associating difficult retrieval conditions, characterized by weak memories and low-confidence responses, with the need for top-down attention, and vivid, strong, detailed retrieval conditions with bottom-up attentional capture by memory contents^{12,39}. Nonetheless, we emphasize the difficulty of isolating signals related to the orienting of attention to memories in traditional item recognition paradigms, as researchers also inevitably measure other intervening processes, including perceptual attention to the probe stimulus. Furthermore, some of the memory effects reported in the SPL, including the preference for old vs. new items and for low vs. high confidence judgments, can be explained by alternative factors^{13,15}, such as general task relevance¹³ or time-on-task effects⁴⁵, as opposed to the orienting of attention to memories.

In addition, there are several open questions about the analogy between mechanisms for orienting and re-orienting attention to memory and the environment. In dorsal parietal cortex, multi-voxel patterns distinguish between attention to different perceptual features (e.g. red vs green⁴⁶) or dimensions (e.g. location vs. color^{47,48}), indicating that parietal signals depend on the specific aspect of a stimulus that is attended. Moreover, dorsal parietal signals exert a causal influence over the activity of the visual cortex^{49,50}. However, it is unknown if multi-voxel patterns in dorsal parietal cortex also depend on the detailed content of what is being retrieved from memory, as well as whether those signals causally influence medial temporal regions. Similarly, dorsal and ventral attention systems work in concert during re-orienting of perceptual attention, with co-activation of both systems³⁴, but it is unclear if dorsal and ventral parietal regions also work together to re-orient retrieval from episodic memory⁴. Co-activation was not observed in a study that specifically investigated the re-orienting response to memories⁵¹, although the available literature on this issue is limited (see also^{25,52}).

Dynamic competition

The segregation of mechanisms for perceptual and episodic memory search is further supported by analyses of the BOLD-activity time series in the two search tasks³¹. Regions activated during one task were deactivated during the other task, and the amplitude of this negative covariation was proportional to search duration and related to behavioural performance in both tasks. Although this pattern of ‘push–pull’ (see also^{53,54}) was observed using an atypical retrieval paradigm, it nonetheless suggests a dynamic competition between perceptual and memory systems, which might serve to suppress task-irrelevant regions and reduce crosstalk between potentially competing representations. Alternatively, BOLD signal deactivation might indicate more selective, task-relevant responses (‘filter’), although this hypothesis is less parsimonious since the regions should reverse their functional role according to task demands.

Other lines of evidence support a competitive interaction between perceptual and memory systems. Sustained deactivation in the DAN, coupled with sustained activity in ventral regions of the DMN, were observed during long (75 s) periods of free recall from a study list⁴⁰. Further support is provided by an item-recognition study in which participants were presented with multiple pictures and had to identify the previously studied one⁵⁵. Trials that required more perceptual attention, in order to suppress false recognition, evoked greater activation in dorsal PPC, but lower activation in ventral regions that distinguished between true and false memories. Also, behavioural studies have shown that the division of attention between memory retrieval and a concurrent visual continuous reaction-time task produces a memory deficit, especially in free recall⁵⁶. Finally, we have shown that transitory inhibition of the AG through rTMS significantly decreased item-recognition accuracy compared with SPL stimulation, with sham stimulation producing an intermediate level of performance⁵⁷. One interpretation of this pattern of results is that a subtle negative effect of AG stimulation was enhanced by contrasting it with a subtle positive effect of SPL stimulation, in line with a competitive interaction between these regions.

In summary, human PPC regions that are involved in perceptual attention and episodic memory are not only anatomically segregated, but also appear to be organized in a dynamic competition.

Prefrontal control of PPC competition

A mechanism of direct inhibition between different PPC regions might also co-exist with the presence of a higher-order system that modulates PPC activity. For example, top-down interactions between associative regions and occipital cortex can enhance or suppress the processing of sensory information^{4,58-60}. By analogy, we asked whether the push-pull pattern in PPC subregions might depend on top-down signals from other cortical regions⁶¹.

Because this top-down function could only be performed by regions active during both perceptual and memory search, we first identified ‘domain-general’ regions (Fig. 1b, top) showing a sustained response during both tasks of our previous study³¹. The most consistent overlap across subjects coincided with the so-called ‘cingulo-opercular network’ (CON), a set of regions that have been associated with maintenance of a task set⁶². These regions also flexibly changed their interaction with perceptual and memory PPC regions, as indexed by functional connectivity [**G ‘functional connectivity’**] (FC), depending on task demands (Fig. 1b, bottom). This result is consistent with a role mediating the push-pull in PPC (see also⁶³). Although some authors have proposed the CON to be part of a larger fronto-parietal network involved in cognitive control (FPCN) [**G ‘fronto-parietal control network’**]^{64,65}, we observed a functional distinction, both at rest and during task

execution, between the CON and putative nodes of the FPCN⁶¹. This result fits with the hypothesis that the two networks are involved in different aspects of cognitive control⁶⁶.

These results are consistent with the hypothesis that the CON partly mediates a push–pull relationship in PPC, but they are only suggestive. FC measures are bidirectional and do not imply causation, which is better supported by measure of effective connectivity (see⁶⁷). Furthermore, our results are compatible with an alternative hypothesis, according to which activity in the CON reflects the general availability of cognitive resources^{68,69}.

Representing retrieved information

Episodic retrieval often occurs in the service of a particular behavioral goal. For example, we may need to retrieve an episode in which we put away our computer in order to determine which desk drawer to open. Our model proposes a distinction between retrieving and representing the episode, and selecting specific information from that representation relevant to the task at hand. We suggest this distinction corresponds anatomically to two different regions in PPC: AG and lat-IPS.

An influential set of hypotheses maintains that PPC regions represent retrieved information¹¹, either by holding an actual representation¹³ or by linking distributed memory traces²⁶. According to Vilberg and Rugg¹³, this function implies the generation and maintenance of an integrated representation of information retrieved from episodic memory, meaning the PPC may act as an episodic buffer [**G ‘episodic buffer’**]⁷⁰. According to the CoBRA (cortical binding of relational activity) hypothesis²⁶, with the passage of time from the event, the parietal lobe substitutes for hippocampal functions during retrieval by binding episodic features that are stored in different cortical regions into a coherent representation.

There is substantial support for the view that activity in the AG reflects retrieved information, including processes associated with this information. The AG is activated when memory retrieval involves recollection of specific details of an event¹³, and AG responses are stronger as more episodic information is retrieved⁷¹. Perhaps the strongest evidence that the AG represents what is being remembered comes from a recent study that used multi-voxel pattern classification to decode the content of retrieved information from the BOLD signal during recall of word-picture associations⁷². In this study, activity in a region of the AG that was associated with subjective vivid remembering could be used to distinguish not only the reactivated category (face versus scene) but also the individual event (associated face versus non-associated face) cued by words. Interestingly, the vividness of recollection is reported to decrease in patients with parietal lesions^{73,74}.

The representational role of the AG may generalize to other forms of memory. Recent meta-analyses have demonstrated that the AG is the region most reliably activated by general semantic memory tasks⁷⁵ and shows considerable overlap with the region showing recollection-specific effects⁷⁶. On the basis of the pattern of activity across several semantic tasks, Binder and Desai⁷⁷ have proposed that the AG plays a unique role in the representation of event concepts, implying a stronger (neurobiological) link between episodic and semantic memory than previously assumed on the basis of theoretical distinctions⁷⁸. The AG might also have a similar representational role in the imagination of hypothetical/future events⁷⁹.

Angular Gyrus vs. Lateral IPS

The above results for the AG are consistent with either the binding (CoBRA) or buffer hypothesis. However, the way in which the timecourse of AG activity depends on the memory task may reveal more clues. One study⁸⁰ tracked the timecourse of activity as participants maintained the retrieved information in working memory for a variable interval, as they waited to answer one of three possible questions. A region of the AG showed sustained activity over the entire delay period, whereas the response in the medial temporal lobe (MTL) was transient, being associated with picture presentation but not with delay activity.

However, when retrieved information is continuously recoded in accord with task demands, rather than simply maintained, the activity in the AG, as well as the MTL, is only transient. We showed this by exploiting the large variability in decision times in our memory search paradigm²⁹ to track how parietal activity unfolded over time (Fig. 2). Activity in both the AG and the Medial Temporal Lobe (MTL, particularly the posterior parahippocampus) scaled in amplitude with retrieval duration, yet remained transient, peaking approximately at the same time across trials, even in trials with long decision times (>8 s). This result is consistent with a role for the AG in the initial representation of retrieved information. In contrast, activity in the lateral IPS (latIPS), as well as the post-central sulcus (PoCS), exhibited a sustained activation until a final decision was made, followed by transient activity in the motor cortex. The timecourse of the BOLD response in latIPS is expected for regions involved in manipulating retrieved information according to task dictates.

The functional dissociation between AG and latIPS is supported by results from other lines of research. Wheeler and colleagues²¹ were probably the first to point to a functional distinction between AG and latIPS on the basis of their profile of BOLD activity during familiarity vs. recollection judgments. In addition, the two regions cluster with different resting state networks. The AG along with the PCC and the MTL, clusters with the DMN (²⁹, see also Vincent, 2006 #17}). A general link between the DMN and episodic memory can be traced back to the work of Andreasen and colleagues (⁸¹ see also ⁸²), but a more recent study emphasized the key role of a sub-network including the AG and the MTL⁸³. In contrast, more dorsal and anterior regions of the latIPS and PoCS cluster with the FPCN^{64, 84}.

Supporting evidence for a dissociation between AG and latIPS comes also from primate research, although interspecies comparisons are complicated by both the considerable expansion of the inferior parietal lobule (IPL) in humans⁸⁵ and the difficulty of designing comparable retrieval tasks across species⁸⁶. Anatomical studies have shown that the MTL is selectively connected with the IPL in both monkeys (e.g. ^{87, 88}) and humans⁸⁹. The MTL may thus have a key mediating role in providing access to stored information (see ^{90, 91}) in both species. In addition, a recent fMRI study on awake monkeys demonstrated a similar functional dissociation between regions PG/PGOp in IPL and PEa/DIP in IPS, based on the pattern of evoked activity during a serial probe recognition task and the pattern of anatomical and functional connectivity⁹². In particular, region PG/PGOp might correspond to the human AG, given its anatomical position, the presence of a primacy effect (thought to reflect long-term memory retrieval) and the pattern of connectivity with the MTL. In contrast, the more dorsal region PEa/DIP, which showed a recency effect (associated with working memory functions) and strong connectivity with prefrontal regions, might be homologous to human latIPS.

In summary, the current evidence supports a division of labour between the MTL, which is involved early in the retrieval processes, the AG, which represents details of retrieved information,

and the latIPS/PoCS, which participates in transforming and manipulating the retrieved information in accord with the task at hand.

Decision-making and motor intention

Accumulating memory-decision evidence

The sustained response of the latIPS and PoCS regions in our memory search experiment²⁹ is also compatible with decisional aspects of the retrieval task. Wagner and colleagues first proposed that parietal regions might serve as a ‘mnemonic accumulator’ of evidence for memory decisions¹¹ (see also²⁷), based on the well-known association between parietal activity and perceptual decisions established in electrophysiological studies⁹³. Specifically, the ramp-like activity observed in the lateral intraparietal area (LIP; a sensorimotor area) in monkeys during simple perceptual decisions¹⁰ matches the accumulation-to-bound mechanism proposed by mathematical models of decision making, such as the drift diffusion model⁹⁴. Interestingly, an early formulation of the drift diffusion model described retrieval as a process of evidence accumulation about the relatedness between probes and items in the memory set⁹⁵.

The involvement of parietal regions in the accumulation of mnemonic evidence is consistent with studies showing that regions near or at the IPS track perceived ‘oldness’, the feeling that an item is old regardless of whether the response is correct or incorrect^{20,96}. Moreover, as evidence for a decision accumulates over time, a region involved in decision-making is expected to show sustained activity until a response is made, as observed for latIPS and PoCS regions in our memory-search study²⁹.

We recently⁹⁷ investigated the relationship between parietal activity and the putative mnemonic accumulator by manipulating the amount of evidence for old and new responses and inserting a temporal delay before response execution (Box 2). Notably, the BOLD signal in latIPS increased in a graded manner with the amount of evidence for an old decision but not for a new decision, consistent with an asymmetric accumulator, i.e. an accumulator only for old responses. Thus, the latIPS may be involved in a relatively late stage of the retrieval process in which decisions about oldness are made.

A definitive test of the mnemonic accumulation hypothesis will require techniques that can track evidence accumulation with higher temporal resolution than fMRI. Several studies conducted with electroencephalography (EEG) in the nineties have identified a parietal effect that starts around 400-500ms post-stimulus and is strongly associated with recollection (reviewed in⁹⁸). However, the spatial resolution of the EEG does not allow one to distinguish the contribution of different PPC regions and techniques with better spatial resolution, such as magnetoencephalography, have not yet provided a robust functional parcellation of the PPC (reviewed in⁹⁹, see also¹⁰⁰). Very recently, an electrocorticography study¹⁰¹ reported greater sustained high-frequency gamma power, a proxy signal for multi-unit activity, for old versus new correct decisions in the IPS, which decayed only 200 ms before the motor response, consistent with an accumulator hypothesis.

Memory decisions and motor intentions

Neurophysiological studies in monkeys have demonstrated a close relationship between signals related to evidence accumulation in the LIP and motor planning, leading to the view that decisions are inseparable from the actions that are used to report them (‘intentional framework’⁹³). Human studies have also shown that perceptual decision-related signals can be observed in parietal effector-specific regions when the task involves specific sensorimotor associations¹⁰²⁻¹⁰⁴. For

example, during difficult face–place discriminations¹⁰², activity in saccade-^{105, 106} and pointing-^{107, 108} preferring regions of the PPC was modulated by the amount of evidence (that is, noise in the test stimulus) pointing toward their preferred effector (Fig. 3a). Thus, parietal activity during memory retrieval might partially reflect the preparation of manual responses¹⁵. This issue was first explored in a study that required participants to manually respond only to old or new items in different sessions¹⁷ and reported no dependence of activity in PPC on response contingency (but see comments in¹⁵).

This account also makes the key prediction that memory-related activity should be localized in effector-specific PPC regions that code for the particular effector used to report the decision. We recently tested this prediction by examining whether signals in sensorimotor regions reflected the accumulation of evidence during memory decisions as observers reported old judgments through eye movements and new judgments through hand movements, and vice versa⁹⁷. Importantly, decision-related activity in effector-preferring regions of the PPC was independent of the amount of evidence associated with a particular action (Fig. 3b), and therefore did not reflect the strength of action–intention processes. Moreover, the graded preference for older items in latIPS was consistently observed regardless of whether old decisions were associated with eye or hand movement responses, supporting the independence between evidence accumulation and motor intention.

We conclude that it is unlikely that retrieval effects in the PPC reflect action intention, and that a large difference exists in the extent to which key variables for memory and perceptual decisions are encoded in sensorimotor areas.

Memory versus perceptual decisions

Several features of the signals observed in the human PPC during memory decisions do not fit a simple analogy with the pattern of firing rate observed in the monkey LIP during perceptual decisions. First, unlike perceptual decision, no link was found between decisions and motor intentions in effector-specific regions. This might reflect the relevance of the decision in guiding actions. Because hand and eye movements are routinely made to objects based on their perceptual characteristics, it is plausible that evidence signals from different perceptual systems feed continuously into intentional mechanisms. Conversely, it is less clear whether different kinds of memory-based decisions are routinely coupled to effectors. While some information we retrieve from memory is highly relevant to motor planning (such as whether an object is a source of nutrients), much of the information we retrieve (for example, ‘what movie did I see last night?’) is not.

Second, whereas perceptual accumulation signals in LIP are thought to generalize across different perceptual discriminations (albeit most evidence comes from variants of a random dot motion paradigm [**G ‘random dot motion paradigm’**]), it is unclear which types of memory-based decisions involve a parietal accumulator. Accounts of decision-related parietal activations during episodic retrieval have largely focused on old–new judgments¹¹. However, naturalistic uses of episodic memory often involve additional retrieval of the information associated with an object or event. The invariant preference of the latIPS for old items across different paradigms suggests that the proposed accumulator might just reflect evidence for oldness. A lack of flexibility might explain why parietal regions, including right latIPS, have been shown to track the overall memory strength of a pair of old stimuli (that is, the frequency of repetition at encoding of both stimuli) but not the evidence supporting the actual memory decision (judging which of the two stimuli was presented

more frequently)¹⁰⁹. The absence of generalization does not fit the traditional view of a general decision mechanism.

In summary, activity in latIPS is compatible with an asymmetric accumulator of evidence for old decisions, but, unlike perceptual decisions, the accumulation mechanism is uncoupled from motor intentions and its generalization to other memory judgments appears to be limited.

Conclusions

In this Opinion article, we have discussed experimental findings on the relationship between memory retrieval and other processes associated with the human PPC, with particular emphasis on neuroimaging studies that followed the temporal evolution of activity during a memory task. The resulting parcellation scheme is consistent with other schemes based on resting state functional connectivity^{84, 110} and task-evoked activity^(15, 28, 45). All these schemes agree on the presence of at least three sets of PPC regions: dorsal regions of the DAN (pIPS, SPL) that are related to visuospatial attention and eye movements; regions of the FPCN (latIPS) that track the sense of familiarity or perceived memory strength; regions of the DMN (AG) that show recollection-specific effects. These schemes can be helpful to optimize both the targeting during TMS experiments and the neuropsychological analysis of deficits caused by neurosurgical ablations and strokes that affects the human PPC.

However, several outstanding issues should be considered in future research. The nature of the push–pull mechanism between ventral and dorsal PPC regions is still unclear and more research is needed to unravel its underlying physiological mechanisms and its relevance for behaviour in a variety of perceptual and memory-retrieval tasks. A related issue concerns the putative role of the CON in orchestrating the push–pull dynamics in PPC, which should be assessed with analyses of causation. Also the apparent difference between the brain mechanisms for memory and perceptual decisions deserves further investigation. However, different neuroimaging techniques and decision paradigms should be employed in the memory domain to fill the gap with the current understanding of perceptual decisions. Finally, a consideration of memory-related activity in medial PPC regions, and the relationship between parietal and other cortical regions involved in memory retrieval (including the MTL¹¹¹, prefrontal cortex¹¹² and basal ganglia¹¹³) will lead to a more comprehensive model of PPC involvement in the retrieval of information from long-term memory.

Box 1 | A model of parietal involvement in episodic memory retrieval.

The figure presents a parcellation scheme of the left PPC (left, adapted with permission from REF⁹⁷) and a functional–anatomical model (right) of the relationship between PPC regions involved in memory retrieval and other cortical regions associated with memory formation/consolidation, movement execution, perceptual attention and task-level control. The functional role of each region is indicated in *italics* in the corresponding color. Arrows indicate the direction of information processing between areas. The label TD-biases and BU-biases refer to top-down and bottom-up modulatory signals. A similar scheme might also apply to the right hemisphere.

In this model, PPC regions associated with perceptual attention (green) and episodic memory retrieval (pink, red), are largely segregated³¹, although they can co-activate when retrieved information is used for a perceptual task⁴¹. Regions involved in perceptual attention (posterior intraparietal sulcus, pIPS, and superior parietal lobule, SPL), part of the dorsal attention network (DAN), provide top-down modulation to sensory regions. Regions involved in memory retrieval (angular gyrus, AG, lateral intraparietal sulcus, latIPS, and postcentral sulcus, PoCS), part of the default mode network (DMN, pink) and frontoparietal control network (FPCN, red), co-activate with MTL regions involved in memory formation and consolidation. PPC regions for perceptual attention and memory retrieval further show a push-pull relationship³¹, due to either mutual suppression (double arrows between DAN/DMN regions) or modulation by a Cingulo-Opercular Network (CON)⁶¹, which includes anterior cingulate cortex/presupplementary motor area (dACC–preSMA) and anterior insula/frontal operculum (aINS-fO). The influence of the CON on PPC may reflect either task control or sustained attention/arousal.

Within the memory component of PPC, the AG (purple) and the latIPS (red) serve different functions²⁹. The AG shows strong connectivity with the DMN, including the MTL, and is involved in the representation of retrieved events. Regions in latIPS and PoCS show connectivity with the FPCN and participates in transforming and manipulating the retrieved information in accord with the task at hand. Further evidence suggests that the lat-IPS (delimited by black borders) works as an accumulator of mnemonic information⁹⁷, receiving signals from the AG, and possibly directly from the MTL, for familiarity judgments or for recoding retrieved information to answer questions about past events. Differently from perceptual accumulators, the putative mnemonic accumulator is not coupled to motor intention, thus requiring an additional step before action preparation, and only tracks evidence towards old responses, rather than serving as a general purpose mechanism for memory-based decisions.

Box 2 | Evidence accumulation during memory-based decisions.

An open question about the mnemonic accumulator hypothesis concerns the way BOLD activity tracks the manipulation of decision evidence¹⁵. A neural accumulator predicts a steeper accumulation process when more evidence is available (easier decisions)¹¹⁴. However, the BOLD response does not reflect the instantaneous neural activity, but rather the integral of the neuronal activity over time. Thus, if subjects respond as soon as a decision is reached (reaction time paradigm), more evidence is typically associated with lower BOLD activity^{115, 116}, as easier decisions are also faster. In this context, it is difficult to isolate accumulator regions, as their predicted pattern is similar to that of regions showing mere time-on-task effects. Instead, if subjects hold responses until a 'go-signal' (delay paradigm), the relationship between amount of decision evidence and BOLD activity is reversed. Specifically, under the assumption that accumulator regions maintain the level of activity reached during the decision process until the response, easier decisions are now associated with higher BOLD activity, as the accumulation process reaches the bound more rapidly and the integral of neural activity is larger.

Secondly, it is not clear whether the hypothetical accumulator tracks the amount of evidence favoring both 'old' and 'new' responses (symmetric) or just show a preference for older items (asymmetric). Whereas symmetric accumulation is common in perceptual decision-making^{10, 93, 102}, the original diffusion model of episodic retrieval⁹⁵ proposed that new responses are driven by the absence of a memory signal, rather than the presence of a novelty signal. In this model, old responses are produced when enough evidence toward relatedness (that is, the number of matching features between probes and items in the memory set) is accumulated, whereas new responses are returned when these comparisons terminate in non-matches. Therefore, old-new decisions might be supported by an asymmetric accumulator that tracks perceived memory strength (older > newer).

We recently manipulated the amount of evidence for old and new decisions in a picture recognition paradigm with delayed responses⁹⁷. Evidence toward old and new responses was varied through the frequency of image presentation at encoding and the similarity between new and old images at retrieval, respectively. Participants had to delay their memory judgments, which were indicated by either an eye or hand movement. Consistent with a mechanism for the asymmetric accumulation of evidence toward old decisions, the peak of decision-related activity in the left latIPS scaled parametrically with the amount of perceived memory strength. Adapted with permission from REF⁹⁷.

Figures captions.

Figure 1 | Perceptual attention and episodic memory retrieval in PPC: segregation and competition.

a | Top: Conjunction map of BOLD activity for searching in episodic memory to judge the veridity of statements about a previously watched TV show (memory search, red) and searching for specific visual targets in movie clips (perceptual search, green). A minimal overlap (yellow) is observed in PPC. Bottom: The timecourses of BOLD activity from the angular gyrus (AG, left) and the superior parietal lobule (SPL, right) indicate a push-pull mechanism between sustained activation for the preferred task and sustained deactivation for the un-preferred task that scaled with search duration (early, late). Similar results were observed in the right hemisphere. Adapted with permission from REF ³¹. **b** | Top: conjunction map of sustained activity during the memory (red; search) and perceptual tasks (green; average of search and audiovisual stimulation). The cingulo-opercular network (CON ⁶², black circles), which includes bilateral anterior insula and frontal operculum (aINS/fo) and dorsal anterior cingulated cortex and presupplementary motor area (dACC/preSMA), showed task-independent activity (yellow). Bottom: the coupling of CON regions (Left aINS/fo in the figure) with perceptual (bilateral pIPS and Frontal Eye Fields) or memory regions (bilateral AG and PCC/PreCu) was higher during the preferred task. Error bars represent SEM. This flexible pattern of connectivity is consistent with the idea that the CON mediates the dynamic competition between PPC regions. Adapted with permission from REF ⁶¹.

Figure 2 | Different roles for AG and lat-IPS during episodic memory retrieval.

Left: Conjunction map showing the superimposition of memory search-related activity (red) and the Default Mode Network (blue surrounded by white border), independently defined through resting state functional connectivity analysis. Regions of overlap (pink) include the AG but not the lat-IPS or the PoCS. Right: when retrieved information is continuously recoded as part of the decision process during long memory search trials (> 8s), intra-DMN regions of the MTL (blue) and the AG (pink) show more transient activity than do extra-DMN regions of the lat-IPS (light red) and PoCS (dark red). A transient BOLD response is last observed in motor cortex (black). Adapted with permission from REF ²⁹.

Figure 3 | Distinction between perceptual and memory-based decision-making.

a | Coupling between evidence accumulation and motor intention in perceptual decisions. Top: Between-subject overlap of the individual (anterior) parietal reach region (aPRR) and posterior intraparietal sulcus (pIPS) that exhibit a preference for pointing and saccadic movements, respectively, in a localizer experiment. Both an anterior and a posterior PRR were identified, although the two regions showed a very similar response profile. Only the left hemisphere is displayed. Bottom: Decision-related activity in these regions (aPRR in the example) was modulated by the amount of evidence toward the preferred effector. Adapted with permission from REF ¹⁰². **b** | Independence between evidence accumulation and motor intention in memory-based decisions. Left: Between-subject overlap of the individual PRR and pIPS from the localizer experiment. The decision-related activity in these regions (PPR in the example) was not modulated by the amount of evidence for memory-based decisions associated with their preferred effector (eye, hand). Right: activity compatible with a putative mnemonic accumulator in left latIPS is not modulated by the amount of evidence for a particular action. Specifically, a constant preference for older items was observed regardless of whether old responses were associated with eye or hand movements, supporting the independence between signals coding for memory strength and motor intentions. Adapted with permission from REF ⁹⁷.

Glossary definitions

Default mode network (DMN):

A set of brain regions that show highly correlated activity at rest and consistent deactivation during externally-oriented, perceptual tasks

Dorsal attention network (DAN):

A set of brain regions putatively involved in the orienting and reorienting of attention based on internal goals or expectations

Kernel:

The shape of the function that is used to take the average of the neighbouring points

Memory-based orienting:

The ability to use long-term memory to orient visuo-spatial attention and optimize detection of objects

Repetitive transcranial magnetic stimulation:

A non-invasive method of brain stimulation that can be used to transiently modulate the activity of specific cortical regions

Functional connectivity:

The temporal correlation of the fMRI signal between distinct regions of the brain measured at rest or during task execution

Episodic buffer:

Putative limited-capacity temporary storage system that maintains an integrated representation of retrieved information

Fronto-parietal control network:

A set of brain regions. anatomically interposed between DAN and DMN, putatively involved in the flexible, adaptive control of behavior

Random dot motion paradigm:

A perceptual decision task that requires to indicate the apparent direction of motion of a cloud of dots

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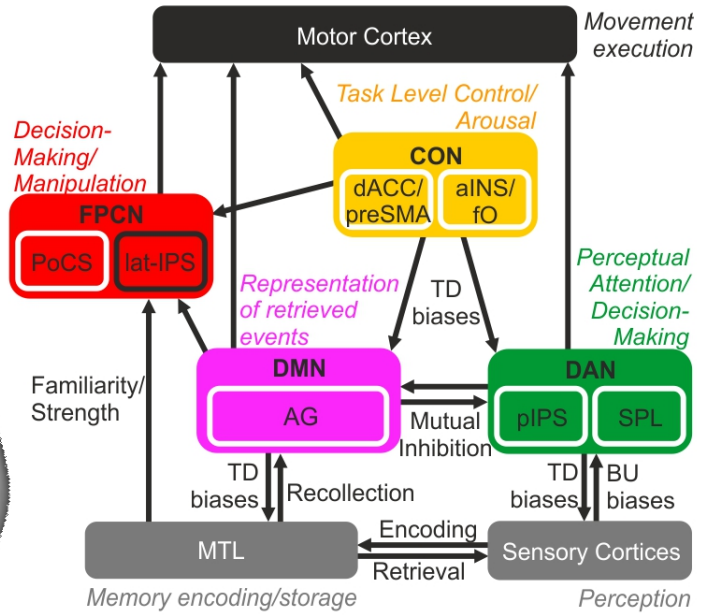
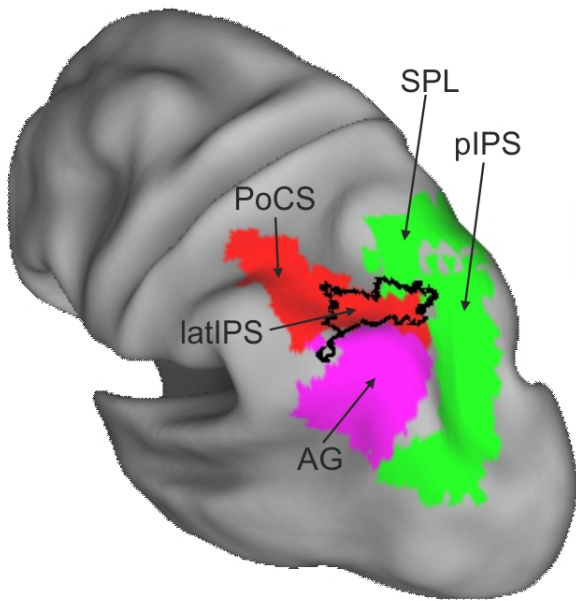
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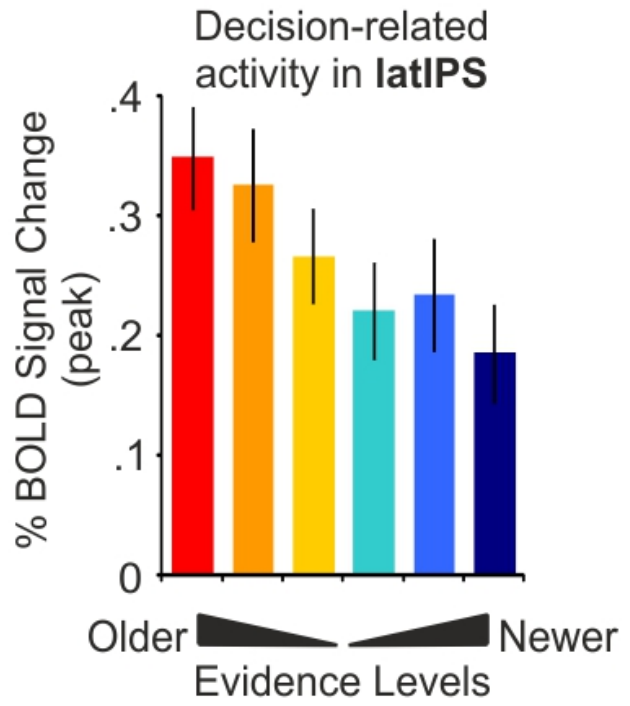
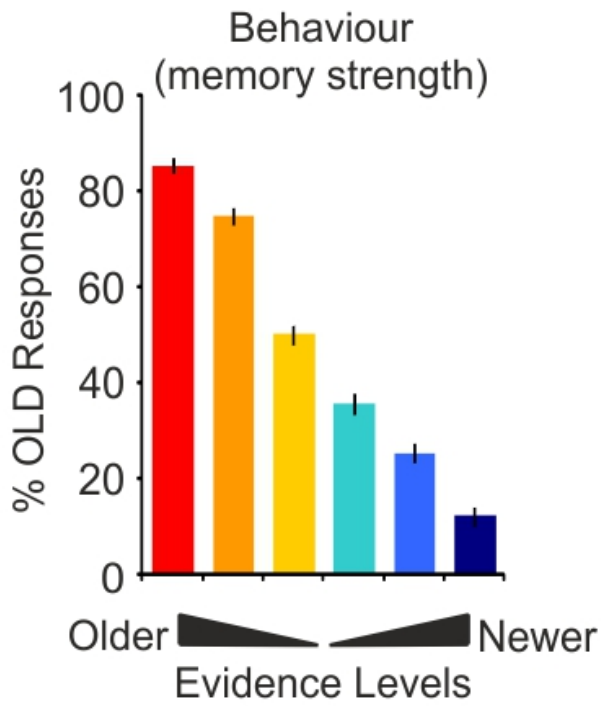
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Box Figure 1



Box Figure 2

A Perceptual vs. Memory Search

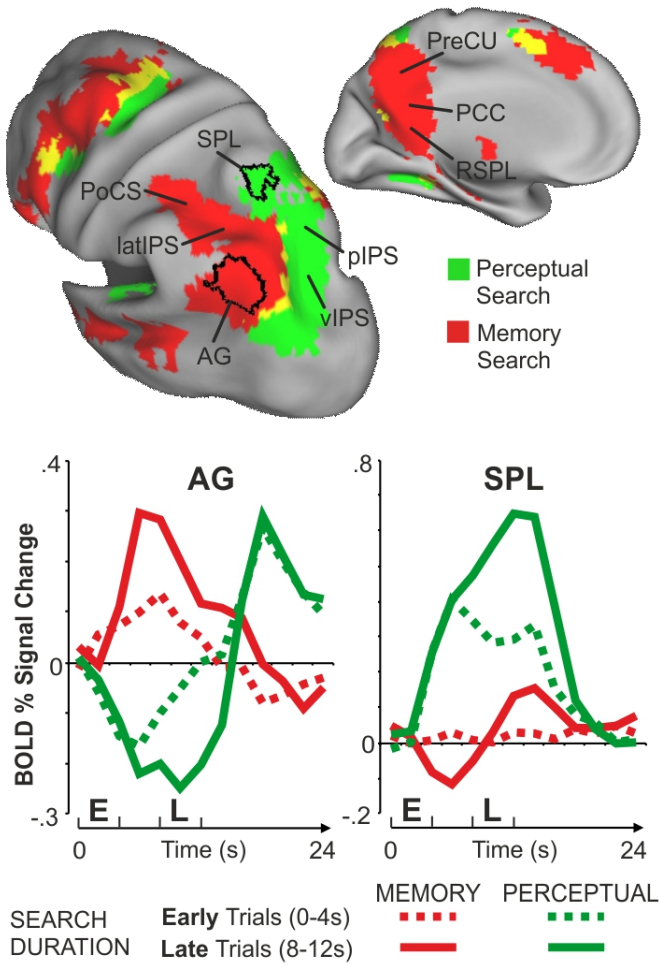


Figure 1

B Potential mediating role of the CON

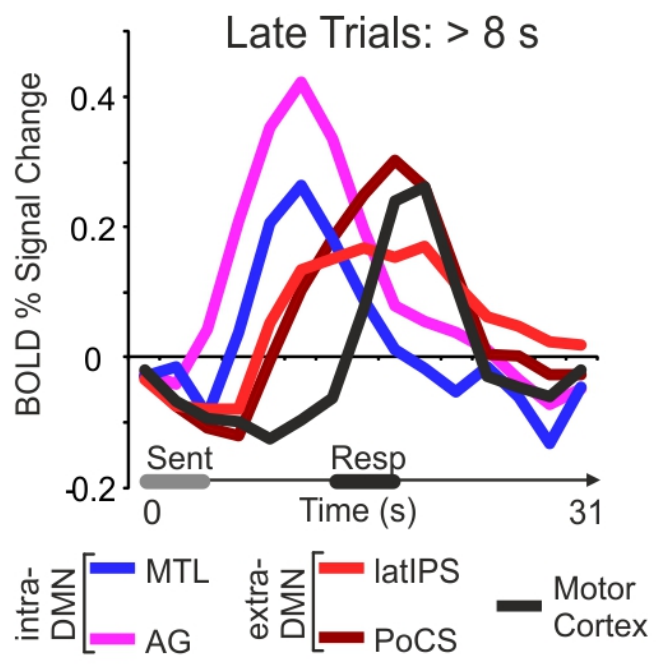
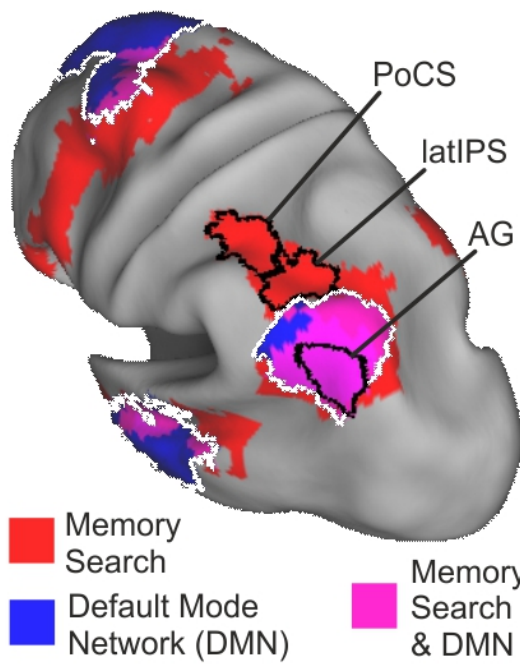
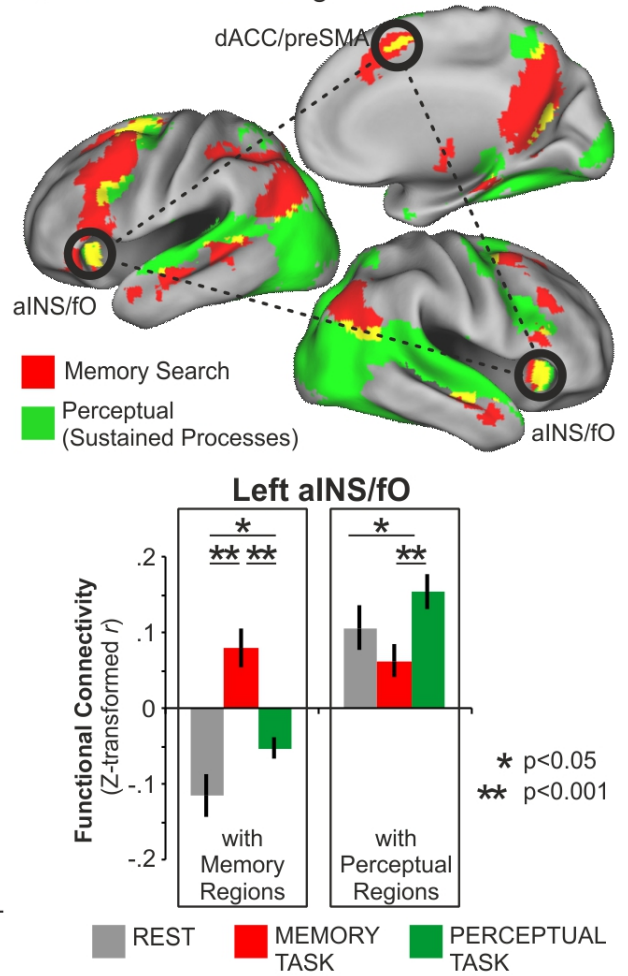


Figure 2

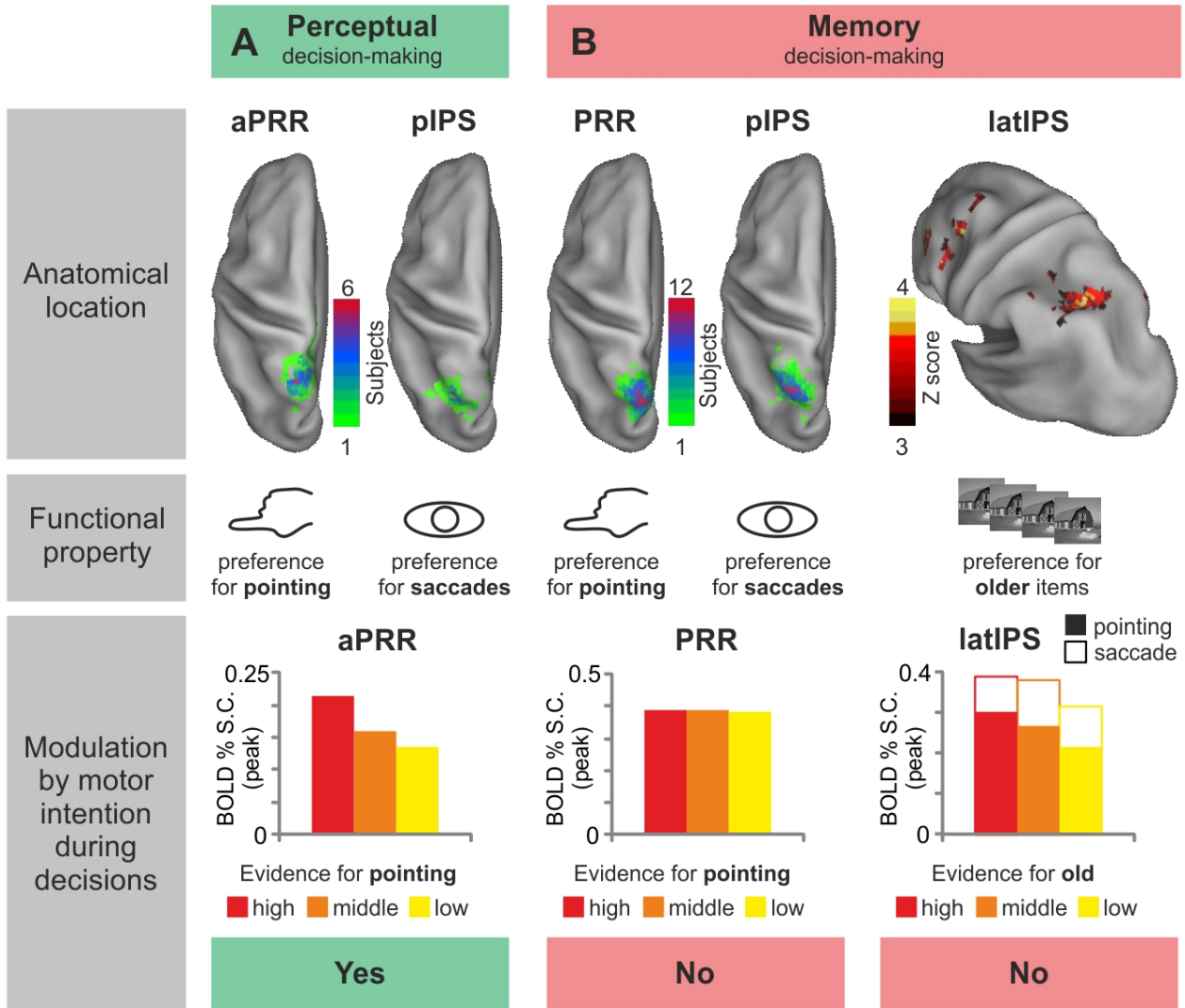


Figure 3