Deconstructing the posterior medial episodic network

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Abstract

Our ability to remember or imagine specific events involves the construction of complex mental representations, a process that engages cortical and hippocampal regions in a core posterior medial (PM) brain network. Existing theoretical approaches have described the overarching contributions of the PM network, but less is known about how episodic content is represented and transformed throughout this system. Here, we review evidence of key functional interactions among PM regions and their relation to the core cognitive operations and representations supporting episodic construction. Recent demonstrations of intra-network functional diversity are integrated with existing accounts to inform a network-based model of episodic construction, in which PM regions flexibly share and manipulate event information to support the variable phenomenology of episodic memory and simulation.

Elements of episodic representation

As we remember or imagine an event, we build a dynamic mental representation of its specific details integrated into a single episode. For past events, this constructive process is often accompanied by a sense of vivid re-experiencing and mental time travel [1]. A great deal of research has linked **episodic construction** (see Glossary) to activity in a core cortico-hippocampal brain network, referred to here as the **posterior medial (PM) network** [2,3]. Although the significance of such a network for episodic processes is widely accepted, the functional diversity of its component parts — its regions and connections — is only just starting to be understood. Identifying the intra-network dynamics of the PM network may prove essential for explaining the complex phenomenology of episodic representations.

When considering the functions of the PM network, it is useful to consider the **cognitive operations** and **representations** [4] that constitute episodic thought. At the core of episodic thought is the set of features defining a unique event — for example, a birthday party. These include the people, objects, places, and other contextual details, such as thoughts and emotions associated with the event (e.g., friends, the local park, a feeling of nostalgia). These event features must be able to be accessed and represented with varying degrees of **specificity**, including their gist (e.g., there was cake) and specific details (e.g., the color of its frosting). They must be embedded within a coherent relational framework that represents the associations among features (e.g., friends standing around a picnic table), producing a unified experience. They can be related to one's self, such that the event takes on a first-person perspective and/or includes details about one's internal state during the original experience. Event features and their relations are informed by existing **schema**, that is, knowledge of how they tend to go together based on past experience [5] (e.g., a birthday cake typically has candles on it). Finally, episodic representations are accompanied by a degree of imageability or reliving, reflecting the clarity or detail with which an event can be imagined.

The multi-faceted nature of event representations can pose a challenge for disentangling the neural processes supporting them. In this Review, we deconstruct the PM network, identifying region- and network-level contributions to episodic construction. First, we review existing evidence of the functional properties of the PM network, including patterns of activity during episodic tasks as well as patterns of **functional connectivity**. Second, we outline existing models of the overarching role of the PM network and highlight key lines of evidence suggesting intra-network diversity of function. Finally, we synthesize these findings within an integrated, network-based framework for understanding how episodic information is represented and transformed throughout the PM system.

PM network involvement in episodic representations

Much episodic memory research has focused on the important and necessary functions of the medial temporal lobe (MTL), including the role of the hippocampus in integrating episodic features [6–11]. Beyond the MTL, there is a large-scale neocortical network of brain regions that is consistently coactivated with the hippocampus during the **recollection** of past events [12–15]. This network comprises a set of posterior medial temporal and parietal regions including parahippocampal cortex (PHC), retrosplenial cortex (RSC), precuneus, angular gyrus (AG), posterior cingulate (PCC), and medial prefrontal cortex (MPFC). We refer to this network as the PM network, a term initially coined to emphasize anatomical differences between cortical networks connected to the MTL [2,3]. Here we have adopted this term to retain anatomical specificity but constrain our focus to highlight the specific role of this network in episodic processes.

Robust evidence that PM regions are commonly sensitive to episodic retrieval has come from a wide range of experimental paradigms (Figure 1A), including recall of the personal past events [14,16,17], memory for source or contextual information [18,19], and subjective indications of recollection [20,21]. Reflecting continuous variability in memory quality, activity of PM regions parametrically scales with ratings of vividness and the amount and **precision** of information remembered [22–25]. Moreover, the PM network contains information about specific memory contents. Reactivation of contextual information, as defined by similarity in patterns of activity across voxels, increases with activity of PM regions [26], and multivariate representations of unique episodic memories can be decoded throughout the PM network [21,27–29]. The specificity of neural event representations in the PM network relates to the amount of detail recollected [30] and memory vividness [31], suggesting that both mean activity and patterns of activity within this network have implications for episodic memory phenomenology. Although the PM network is often studied in relation to episodic memory, its activity is consistently related to simulation of future events [13,14] as well, and PM regions represent specific features of those generated events, such as semantic and particularly spatial details [32,33]. Thus, in line with prior accounts [34–39], a central, common role of the PM network seems to be the construction and representation of episodic information, whether it is in the service of memory or otherwise.

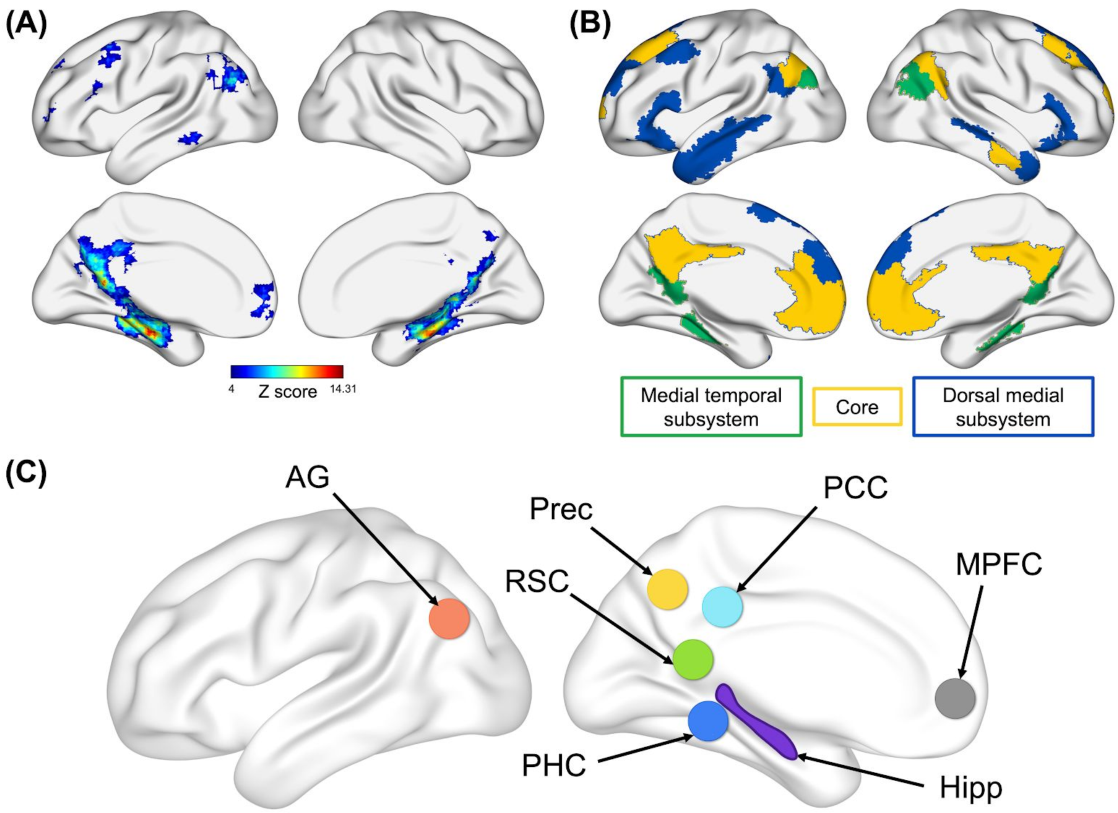

Fig.1. Functional specification of the PM network. A) A Neurosynth (https://www.neurosynth.org/) meta-analysis of 488 studies using the term "episodic", showing a positive association between activity at a particular coordinate and the term. For visualization: the minimum cluster size is 100 voxels and minimum z = 4. B) The default network subsystems. Network parcellation is plotted from a 400-region whole brain cortical atlas [132], named and visualized in accordance with default subsystems identified by Andrews-Hanna et al. [45]. C) Nodes of the PM network, including the hippocampus (HIPP), parahippocampal cortex (PHC), retrosplenial cortex (RSC), precuneus (PREC), angular gyrus (AG), posterior cingulate cortex (PCC), and medial prefrontal cortex (MPFC). These nodes reflect 'core' and 'medial temporal subsystem' regions of the default network that coactivate during episodic tasks.

Functional communication of the PM network

Not only do PM regions coactivate during episodic recollection and simulation tasks, they are strongly structurally (Box 1) and functionally connected with one another, thus supporting the idea that they form an integrated network (Box 2). PM regions have been predominantly grouped into the same broader functional brain system — the **default network** — defined by strong intra-network coherence during rest and collectively enhanced activity during internally-directed cognition [40,41]. In line with an episodic role of PM regions, the overarching function of the default network is thought to be to create **mental models** of situations or perspectives [42]. In addition to PM regions, the default network includes lateral temporal cortex, dorsal MPFC, and lateral orbitofrontal cortex. However, the default network is not a homogenous system, but is best characterized by functionally-dissociable subsystems

[43–45]. A distinct frontal and lateral temporal subsystem appears to support conceptual knowledge and thinking about mental states, whereas an extended medial temporal subsystem, characterized by strong connectivity to PHC [44], appears specialized for episodic representations, with the subsystems converging in PCC and MPFC to facilitate self-projection [40,45,46] (for a detailed review, see [41]) (Figure 1B). Therefore, the PM network can be specified as medial temporal subsystem and core regions of the default system that are engaged during episodic tasks (Figure 1C), thus accounting for both patterns of connectivity and task-related activity.

Coherence with PM regions during rest is a more prominent characteristic of posterior MTL, including PHC, compared to anterior MTL regions [47–50]. Posterior hippocampus is functionally connected to PHC, parietal cortex, and ventral MPFC, whereas anterior hippocampus is connected to the amygdala, orbitofrontal cortex, and anterior temporal lobe [47,51]. Moreover, the strength of intra-PM network connectivity predicts similarity in memory-related functional activity among constituent regions [48] as well as instances of episodic remembering [52,53]. Despite the coherence of the PM network, emerging evidence suggests intra-network variation in functional connectivity that may indicate the flow of information through this system. AG and PCC/precuneus tend to be particularly strongly correlated during rest [54], and some evidence suggests that RSC acts as a mediating hub between these more dorsal PM regions and PHC/hippocampus [55]. Other research points to PCC as a critical hub integrating MPFC with posterior cortical regions [45], with partial correlation analyses highlighting a number of ‘direct’ connections between PCC and other PM areas [56]. In contrast to neighboring PCC, precuneus (particularly dorsal precuneus) exhibits a more flexible alliance with the default network, also connecting to a frontoparietal control network depending on the task demands [57,58]. Further research into PM network functional connectivity is necessary to refine a model of the direct functional connections within this episodic system (Box 2).

If communication throughout the PM network facilitates the construction of episodic representations, then connectivity strength of the system should increase during tasks placing high demand on episodic processes, and changes in connectivity strength should be related to the quality and/or content of episodic memory. Recent research has supported both of these predictions. Much of this work has focused on the hippocampus as an integrative hub during episodic construction compared to other types of cognitive tasks. Specifically, consistent evidence has emerged for task-dependent increases in hippocampal-cortical connectivity, particularly with PM regions, during memory reactivation or simulation of events compared to rest [59], semantic memory [60], reasoning and perception [61], and episodic encoding [25,62]. Moreover, functional connections between the hippocampus and other PM regions are particularly strong during retrieval of spatial context compared to retrieving temporal order [63]. Functional connectivity increases among PM regions as event sequences become familiar, perhaps reflecting the emergence of a contextual framework [64]. Critically, the strength of PM network connections also tracks the level of detail within an episodic representation. Hippocampal-cortical functional connectivity increases with successful compared to unsuccessful memory retrieval [63,65,66], as well as with subjective ratings of episodic reliving, vividness, and coherence [62,67], particularly during elaboration of memory details [68]. Moreover, in a recent study, we found that connectivity among PM network nodes increases with the overall amount and precision of recollected episodic information [25]. Therefore, enhanced communication throughout the PM network likely supports the richness of a reconstructed event.

Existing cognitive models of the PM network

Recollection and construction-based accounts

Process-level accounts explaining co-activation of the hippocampus and cortical PM regions (as well as other default network regions) have focused on their roles in recollection-based memory, leading to their description as a “core recollection network” [12], as well as other constructive processes. Early observations of overlapping activation during recollection and future-thinking were attributed to their shared reliance on constructive episodic simulation, a process that involves accessing episodic details and recombining them to construct a remembered or hypothetical event [13,36,69]. Extending from this research, the “core network” was proposed to specifically support the projection of one’s self into a constructed situation, explaining network involvement in episodic memory and future-thinking as well as theory of mind and spatial navigation [37,40]. Other accounts have emphasized the role of spatial information in organizing event constructions, arguing that these regions-- especially the hippocampus-- serve to bind together event details into a spatially coherent scene [34,35]. Most recently, it has been argued that the constructive function of cortical default network regions in episodic tasks is dependent on the reactivation of conceptual processing [70]. All of these accounts have been concerned primarily with describing the overarching process that spans the cognitive functions served by the network, but there have been few predictions regarding specific operations and representations supported by different components of the network (c.f.,[4]). Among those, constructive episodic simulation depends on relational processing in the hippocampus [69], and scene construction may involve spatial transformations mediated by the RSC and monitoring processes supported by ventro-medial PFC [34].

Content-based accounts

Content-based accounts of the PM network extend from models explaining the functional heterogeneity of MTL subregions. Such models have emphasized the differential connections of the perirhinal cortex and PHC to the ventral and dorsal visual streams, which support perirhinal specialization for object information and PHC specialization for spatial information [8–10], with these features integrated by the hippocampus. Such differences, however, extend to connections outside of the visual streams [2,71,72]. Whereas the PHC is connected with the rest of the PM network, the perirhinal cortex is preferentially connected with anterior portions of lateral temporal cortex, amygdala, and lateral orbitofrontal cortex. These observations led to the proposal that there are two cortico-hippocampal networks involved in episodic memory: an anterior temporal (AT) network supporting item representations and their relation to conceptual knowledge, and a PM network supporting context representations and their relation to event schema [2]. Thus, in this PMAT framework, functional distinctions are primarily aligned with representational content (i.e., items and contexts), with network composition informed by anatomical and functional connections. Within the PM network, the PHC and RSC were proposed to process specific contextual features as they are experienced in the environment, whereas other default network regions store mental models of event structure, that is, a gist-like representation of the relationships among items and contextual features of an event as well as schematic information [73]. According to this view, contexts are not necessarily spatial in nature, whereas other accounts have argued that spatial information is primary in the PM network [33,74], involving the transformation from **allocentric** to **egocentric** spatial frameworks between the MTL and parietal cortex [75].

Specificity-based accounts

Another approach to explaining the role of the PM network in episodic construction has focused on its representational granularity rather than content per se, proposing an anterior-posterior shift from coarse, gist-like representations to precise, detailed representations [76]. Like the PMAT framework, this account was largely derived from functional dissociations within the medial temporal lobe. Changes in representational granularity occur along the hippocampal long-axis, with increasing precision of representations in posterior relative to anterior hippocampal subregions [77–79]. Therefore, according to a specificity-based account, the gist of an event is represented by anterior hippocampus in communication with ventral MPFC [38,76], which integrates new information with prior knowledge to build and update schemas [5], whereas posterior regions (including regions in the PM network, as well as areas along the ventral visual stream) work with posterior hippocampus to construct the specific details of events [76,80]. The shifting granularity of representations along the hippocampus has been projected to the PM network in part due to evidence of strong functional connections between posterior hippocampus and PM regions [47–49,81], in addition to the network's sensitivity to unique event representations [29,30,33]. In fact, sensitivity to high-resolution information in the posterior hippocampus has been proposed to be a consequence of its communication with PHC and posterior cortical regions, which may provide specific perceptual details [76,77]. Thus, specificity-based accounts suggest that the role of the PM network (and other posterior regions) is to support detail-rich episodic information regardless of content per se.

Lateral parietal cortex and contextual integration

The cortical PM region that has received the most attention concerning its role in episodic memory is lateral parietal cortex, specifically left AG. Due to its strong connectivity with PM nodes and accessibility for cortical stimulation, AG has been treated as a gateway to the PM network (e.g. [82]). Although there has been much debate about the function of AG, proposals often emphasize its role in the active accumulation and representation of detailed information during episodic construction [83–85]. Recent theoretical accounts have focused particularly on the idea of AG as a cortical convergence zone [84–88]. The Contextual Integration Model [84] proposes that AG maintains an integrated sensory representation of contextual details, such as colors and emotions, that, when integrated with foundational what-when-where details reactivated by hippocampus, can enhance a sense of vivid recollection. In support, research has demonstrated involvement of AG in more qualitative aspects of memory beyond hippocampal relational binding, including confidence and vividness of remembering [89–91], forming an egocentric perspective during recollection [92], recall of multi-modal associations [27,93,94], and the precision of episodic recall [22,25,95]. Although these ideas focus specifically on AG, what is observed in AG is often reflected in the other cortical regions of the PM network [85]. Thus, the specificity of contextual integration to AG versus the other cortical network nodes remains ambiguous.

Deconstructing the PM network

Key lines of evidence

As described above, there have been many accounts put forth to explain the overwhelming evidence that PM regions are jointly engaged in episodic construction. There have been fewer attempts, however, to identify specific interactions within the PM network supporting different components of the construction process. To understand these interactions, it will be key to characterize the qualities and content of episodic representations in the context of complex, multi-featural events. Here we summarize recent lines of evidence taking this approach, relating PM network activity and connectivity to specific attributes of episodic representation. We focus especially on studies that have attempted to discriminate among PM regions, or sub-groups of regions, as these studies are able to inform a refined view of PM network function.

Studies of episodic memory and simulation have begun to incorporate non-binary measures of episodic quality, including the number of event details, their precision, and subjective vividness [22,23,25,91,96,97]. Although these measures are often correlated with one another and with activity in PM regions, direct comparisons have revealed some dissociations. In one study, participants rated the vividness of their memories for composite scenes and reconstructed its object features, allowing for separate estimates of memory success and precision [22]. Whereas retrieval activity in the hippocampus was associated with memory success, AG activity correlated with its precision, and precuneus tracked subjective vividness (Figure 2A). This dissociation may suggest differential roles in memory access, specificity, and imageability, respectively. In a separate study, AG and precuneus/PCC activity were specifically related to the total number of event details generated during episodic simulation, with the hippocampus related to simulation vividness [96,97] (Figure 2B). While supporting a role of AG in episodic specificity, these findings suggest that multiple PM regions may predict the composite vividness of episodic construction depending on the task demands or comparisons. Temporal dynamics of activity throughout the PM network also reveal regional dissociations, with AG, precuneus, and MPFC signals maintained over the course of event elaboration, and relatively transient signals of hippocampus, RSC, and ventral MPFC possibly serving to access and reactivate core event information during both episodic memory and simulation [14,96,98–100].

Beyond activity, new research has also started to reveal the pattern of PM network interactions that predicts different qualities of episodic memory. Stimulation of the PM network through facilitatory TMS over AG has been shown to result in enhancements in memory precision [95], with a corresponding increase in functional connectivity of the PM network predicting episodic memory, especially among medial temporal and medial parietal regions [101]. However, distinct connections may support different aspects of episodic quality. In a recent study [25], we asked participants to encode objects associated with item-specific and spatial context details, that varied continuously around a color spectrum and panoramic environments, respectively. Both the AG and precuneus exhibited content-specific connections related to memory precision, suggesting that these regions play a flexible role in representing and integrating different kinds of episodic detail. In contrast, connections with RSC and PHC supported the precision of reactivated spatial information specifically, suggesting a preference for the representation of fine-grained spatial context (Figure 2C).

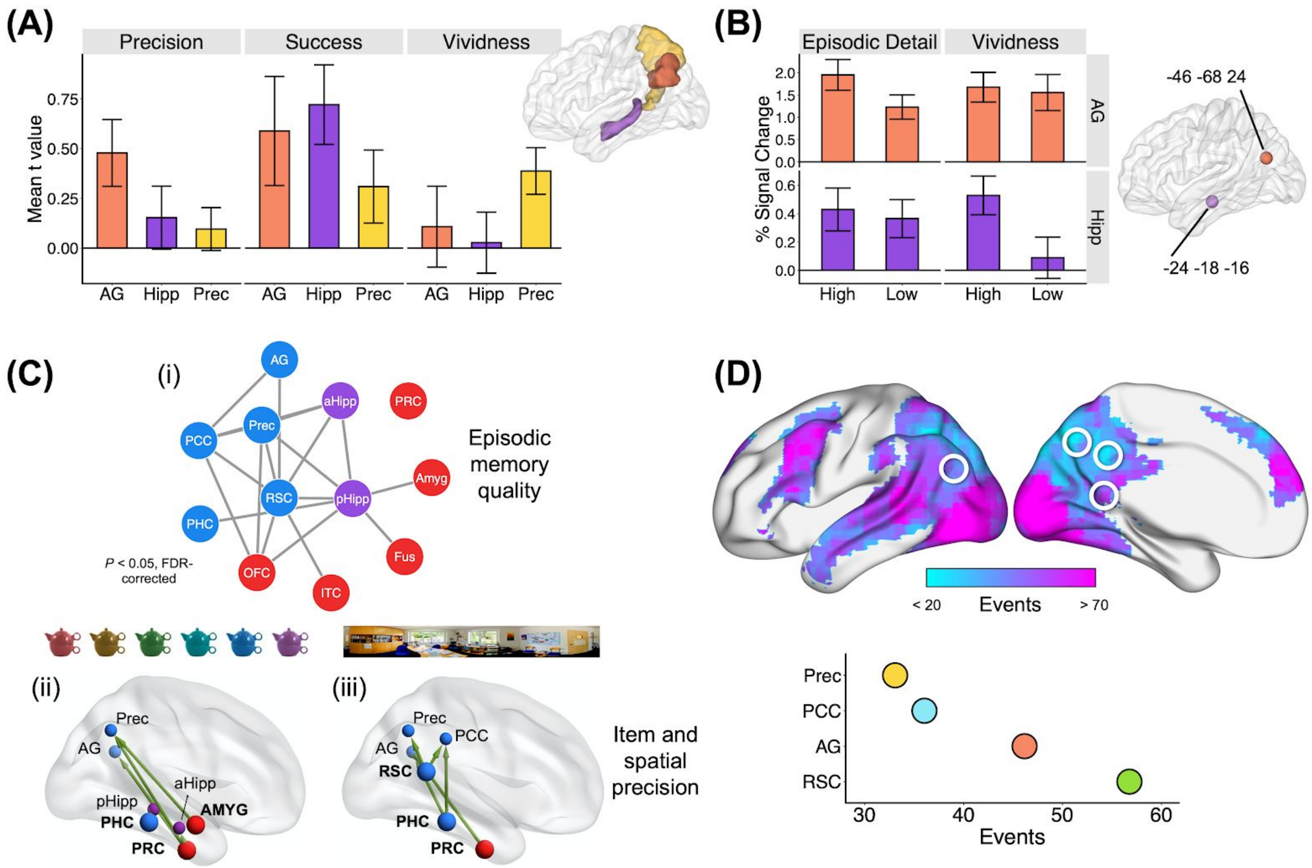

Fig.2. Functional dissociations within the PM network. A) Activity associated with memory precision, success, and vividness within left hemisphere PM regions from the AAL atlas — angular gyrus (AG), hippocampus (Hipp), and precuneus (Prec). Data are from [22]. Participants studied scenes with 3 objects and, in a later memory test, reconstructed the features of each object (orientation, color, and location) in 360-degree space. Success reflects retrieval of at least the gist of an object feature, precision is the inverse absolute error for successfully retrieved features, and vividness is a subjective rating in response to a background scene cue. B) Activity associated with vividness and number of episodic (internal) details for imagined future events, illustrating a dissociation between peak hippocampus and AG signals. Data are from [97]. C) Network connections during episodic retrieval. Top panel: Connectivity among cortical PM, AT, and hippocampal (a = anterior, p = posterior) regions increases with the overall quality (total amount and precision of detail) of episodic retrieval, as measured through a series of independent seed-to-target psychophysiological interaction (PPI) analyses. Bottom panel: Connections (seeds in bold font) that increase in strength with the precision of item-specific color (left) and spatial context (right) in memory. Figure adapted from [25]. D) Patterns of event structure in cortical PM regions during movie watching, illustrating sensitivity to changes in event context (boundaries) at varying levels of specificity. A greater number of events reflects greater sensitivity to context changes. PHC and MPFC voxels did not meet criteria for inclusion in the original analysis and so are not shown. Data are from [106].

Other lines of research have focused on characterizing the role of PM network regions in representing episodic content. Multivariate methods have revealed that regions throughout the PM network carry information related to unique combinations of event features [33]. Furthermore, memory quality has been shown to correlate with event-specific memory reactivation in AG [23], PCC [30], and precuneus [29,102], supporting the influence of these regions' representations on episodic detail and imageability. Although spatio-contextual information appears to be most strongly represented throughout the PM network [33,103], some PM regions, such as AG, represent multiple forms of perceptual details during memory retrieval, including items such as faces and objects [23,104,105]. In AG, PCC, and precuneus, representations generalize across visual and auditory modalities [106], whereas posterior PHC and RSC are especially selective for scenes and are thought to represent a scene's relational layout and convert between allocentric and egocentric spatial perspectives, respectively [75,107]. In support, recent studies have observed a dissociation between memory for locations in PHC and RSC and memory for people in more dorsal PCC and MPFC [108,109]. New work on event segmentation has additionally shown that the temporal specificity of PM representations to changing event features follows a decreasing gradient from visual areas, to RSC, to AG, and finally to PCC and precuneus [106] (Figure 2D). These findings are consistent with a hierarchical organization of multivariate representations in the PM network, integrating information about specific spatio-contextual details with gist-like and schematic representations [2,73,110].

Finally, research on autobiographical memory, or memory for personal life events, has revealed a link between PM network function and the contents and self-relevancy of retrieval. Autobiographical memories are especially well-integrated with existing knowledge about one's self and others, recruiting regions in both the PM network and the dorsomedial PFC subsystem of the default network [46]. In one study, whereas activity in precuneus, PHC, and AG was associated with retrieval of spatio-contextual aspects of memory, PCC activity was associated with retrieval of conceptual details, perhaps through its connections with the dorsomedial subsystem [111]. In addition to interactions with MPFC involved in self-referential processing [112], autobiographical retrieval involves interactions between medial temporal regions classically associated with recollection and regions associated with visual imagery, such as precuneus [17]. Memory-related information represented in the precuneus has been shown to correlate with subjective vividness of autobiographical memories [102], and there is some evidence that precuneus is specifically related to adopting or updating visual perspectives during retrieval [113], perhaps especially those involving an egocentric perspective [16,114,115].

An integrated network-based model of episodic construction

Based on heterogeneity within the PM network, as well as past work characterizing the overarching function of this system, episodic construction may be best described as a dynamic network process, with sub-groups of PM network regions working together through **core alliances** to construct and elaborate episodic representations. Below, we integrate recent evidence with prior accounts into a single framework, highlighting the dimensions along which PM regions appear to vary and the core alliances that might support different aspects of episodic thought.

As described above, during episodic construction, event features must be accessed, represented with varying degrees of specificity, embedded within a relational framework, related to one's self and to existing schema, and evoke a sense of imageability. Although these elements are often correlated with one another, the available evidence allows for some conjectures about how these components may be differentially related to specific regions and connections within the PM network. Importantly, there appears to be variability among PM regions in their involvement in cognitive operations and representations important for episodic thought, and these dimensions are also separable from one another (Figure 3). Thus, models of PM network function must incorporate multiple dimensions, as no single dimension will lead to predictions that generalize across the entire network. Synthesizing the experimental evidence reviewed above, we identify the following themes: First, PHC, RSC, and, to some extent, hippocampus and precuneus seem to be preferentially involved in representing spatio-contextual features, whereas other areas of the PM network, including AG, PCC, and MPFC, may be more likely to include non-spatial, conceptual information in their representations. Second, representations in RSC and precuneus appear to contain egocentric information, suggesting sensitivity to self-relevancy as also observed in MPFC. Third, among PM regions, AG appears most sensitive to the scalar precision of feature representations, with other parts of the PM system organized hierarchically from precise representations in posterior hippocampus and PHC to gist-like and schematic representations in anterior hippocampus, PCC, and MPFC. Fourth, whereas the hippocampus, AG, and MPFC appear to actively guide integration of event features, other PM and sensory representational regions may be responsible for providing specific content to these areas. Finally, PM regions appear to operate at complementary timescales, with hippocampus, RSC, PHC, and ventral MPFC guiding early episodic construction, and AG, precuneus, and MPFC mediating the sustained elaboration of episodic detail.

PM Region	Access vs elaboration	Integration	Relative specificity	Spatial preference	Self preference
Hippocampus ●	A	✓	↓↑	↑	↓
Parahippocampal Cortex (PHC) ●	A	-	↑	↑	↓
Retrosplenial Cortex (RSC) ●	A	-	↑	↑	↑
Precuneus ●	E	-	↓	↑	↑
Angular Gyrus (AG) ●	E	✓	↓↑	↓	↓
Posterior Cingulate (PCC) ●	E	-	↓	↓	↓
Medial Prefrontal Cortex (MPFC) ●	A + E	✓	↓	↓	↑

Fig.3. Dimensions of episodic thought in PM regions. Regions of the PM network and their hypothesized position along key dimensions reflecting episodic operations and representations, including timescale of activation (access versus elaboration), integrative processing, representational specificity, and relative preference for spatial and self-related content. Regional differences along each of the dimensions are indicated by a grayscale, highlighting variability across regions and dimensions. Bidirectional arrows for representational specificity indicate an anterior-posterior gradient in the hippocampus and sensitivity to scalar precision in AG.

Despite the heterogeneity of representations, operations, and timescales throughout the PM network, it is clear that none of these individual regions has attributes that are entirely independent from the rest of the network [11]. Rather, each PM region may form part of a sub-network core alliance (Figure 4), and it is the interactions within and between these small, overlapping groups of regions that provide the diverse content and qualities of episodic thought [38]. Taking this view, existing evidence and key insights from accounts of PM network function can be integrated into the following framework. At the core of the PM network, the hippocampus interacts with the PHC and RSC to activate the contextual framework that organizes event features, which are themselves maintained in sensory representation areas and in the AT network [2,3,73]. Together, these regions code for specific contextual details of the event, with the hippocampus performing the binding operation [8,9,11,109]. Hence, functional communication within this core alliance should be required for accessing episodic context. RSC additionally interacts with precuneus to orient context with respect to one's own perspective [75]. Information about specific event features is then projected to AG, which maintains an integrated, multi-modal event representation [84,85] through feature-specific connections that we predict are weighted by precision. Together, communication between AG and precuneus is hypothesized to support the imageability and elaboration of the integrated event representation, which may be further guided by precuneus interactions with frontoparietal control regions [58]. Individual events are not constructed de novo, of course, but must be informed by conceptual knowledge about the self and other schemas, which is mediated by the core nodes of the default network, PCC and MPFC [5,30,46], and their interactions with the rest of the PM network. Notably, another prediction that emerges from this view is that no single region or alliance ought to be related uniquely to the self-reported vividness of episodic memory, as this is likely influenced by multiple aspects of the representation.

By integrating existing theories with recent evidence, this framework accounts for observed differences in function and connectivity among PM regions. Thus, we view it as a useful tool for combining and testing ideas about PM network interactions and their relation to episodic construction. A benefit of the integrated framework is its emphasis on the multidimensional nature of episodic thought along operational and representational dimensions, which motivates specific predictions regarding the functional significance of core alliances within the network. Understanding these core alliances, and particularly the temporal dynamics of PM network communication, will be crucial to advancing a network-based model of episodic construction (see Outstanding Questions).

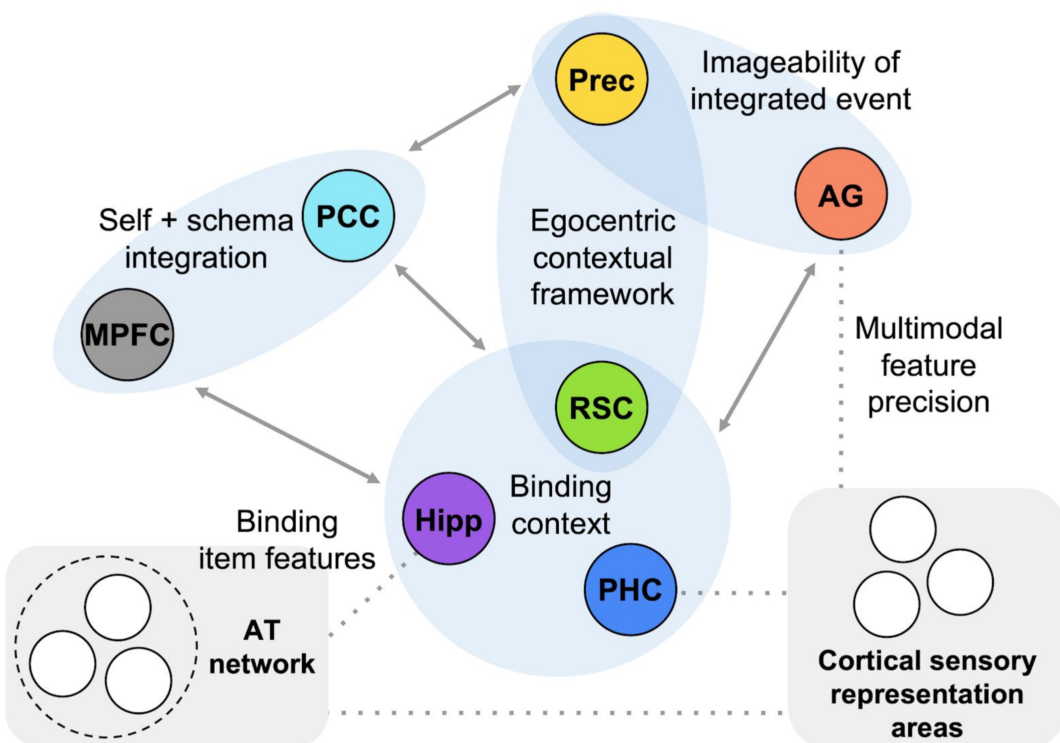

Fig.4. An integrated model of the episodic PM network. Core alliances within the PM network are depicted as region groupings highlighted in light blue. It is assumed that functional interactions of these alliances are particularly important for the

annotated functions. Arrows depict proposed interactions between alliances in the PM network. Dotted lines indicate connections between PM nodes and regions or networks outside of this system (gray boxes) that are important for the episodic representations constructed by the PM network-- for example, the input of item features from the anterior temporal (AT) network to the hippocampus to integrate with context information.

Concluding Remarks and Future Directions

Episodic construction provides us with a window to our past as well as the ability to imagine fictitious or possible future events -- in essence, allowing us to mentally jump through space and time. This dynamic process relies on coordinated interactions of the hippocampus with large-scale cortical networks, the complexity of which must match the diversity of episodic thought. Here, we have synthesized recent evidence of functional connectivity and task-related dissociations within the PM network to extract what seem to be the most likely components of prior accounts, integrating them within a network-based model of episodic construction. In particular, we propose that PM regions are best considered along multiple dimensions of episodic thought, and we highlight the core alliances that may perform complementary operations within the network. It will be important for future research to determine how functions within the PM network additively and interactively construct the variable content of episodic representations [11]. To this end, we highlight several questions to guide such work, which will likely benefit from an integration of network analysis methods (Box 2) and multidimensional memory measures (see Outstanding Questions).

One important future direction is greater refinement of functional connectivity networks and their relation to memory functions across individuals and populations. This will likely be facilitated by delineating the PM network and its interactions on an individual level (cf. [44]), accounting for variations in network structure that may have meaningful implications for episodic processes. A second important future avenue is to characterize how information is shared and overlapping between an episodic PM system and default network systems required for other forms of mental construction, including emotions [116] and semantic representations [70], whose interactions shape the way we weave together past, present, and future. Through the integrated framework outlined here, we aim to characterize how the operations and representations of episodic construction are linked through dynamic interactions among the PM network, accounting for differences in the quality of episodic memory and simulation.

Glossary

Allocentric framework: The spatial relationships between objects defined in relation to one another, independent of a specific viewpoint.

Cognitive operation: A computation, performed by the brain, that transforms inputs (e.g. separate items A and B) into an output (e.g. associated pair A-B).

Cognitive representation: A unique pattern of neural activity that codes for a specific attribute of our environment (e.g. a location or a person).

Core alliance: A subgroup of interacting brain regions within a stable large-scale network that contribute a specific operation and/or representation to the network-level cognitive process.

Default network: A collection of brain regions that show reduced activity during externally-guided attention, increased activity during internally-directed cognition, and strong functional connectivity with each other compared to the rest of the brain.

Egocentric framework: The spatial relationships between an observer and objects in their environment, dependent on their specific viewpoint.

Episodic construction: Generating a complex mental representation of a specific event by combining known details and inferred details so that the experience appears coherent.

Functional connectivity: The statistical association, over time, between activity in one brain region and activity in another. It is inferred that a stronger association reflects meaningful communication or perhaps the sharing of information between two regions.

Posterior medial network: A group of structurally and functionally connected brain regions that tend to be co-activated during episodic tasks. Here, the posterior medial network is assumed to comprise the medial temporal subsystem and core nodes of the default network.

Precision: A measurement of the objective resolution or specificity of a mental representation.

Mental model: A mental representation or framework describing how entities in our environment are related to one another.

Recollection: The process of explicitly remembering a specific prior experience in response to an internal or external cue, often accompanied by a subjective sense of vividness.

Schema: A generalizable, abstract cognitive structure that extracts features common across multiple experiences to inform our expectation and interpretation of new events.

Specificity: The level of detail within a mental representation of either a real or imagined event.

Box 1: Anatomical connections of the PM network

While functional connectivity is useful for quantifying how information flows within a network, functional connections are constrained by the presence of structural connections [117,118]. Much of what we know about the structural connectivity of the PM network comes from anatomical tracer studies in macaques, which have identified direct connections among the hippocampal formation, PHC, RSC (BA 29 and 30), PCC (BA 23), and MPFC [71,119,120]. These connections are largely mediated by the cingulum bundle, which is composed of multiple fiber tracts targeting areas throughout the frontal and temporal lobes and thalamus. The cingulum bundle includes tracts connecting the PCC with the RSC, PHC, and hippocampus, the RSC with PHC and hippocampus, the PCC and RSC with the MPFC, and the posterior inferior parietal lobule with the hippocampus [121]. In general, RSC (especially BA 29) is more strongly connected with the medial temporal lobes compared to the PCC [119,120] or other parietal regions [122]. The PCC is also more strongly connected with medial prefrontal areas (including BA 10 and anterior cingulate areas 24 and 32) than the precuneus is (BA 7m), but both PCC and precuneus have reciprocal connections with the posterior inferior parietal lobule [122]. Furthermore, the cortical and subcortical connections of PM regions are dissociable from those in other memory-related areas, such as the perirhinal cortex, with the hippocampus and MPFC interfacing with both PM and anterior temporal areas, as reviewed previously [2,71,72].

Similar connections are generally assumed to exist in the human brain, with a couple of important caveats: it is unclear how to define the macaque homolog of the human AG (BA 39; [88]), in part due to human expansion of parietal cortex including AG and precuneus [123]. Structural connectivity has been studied in humans with diffusion weighted imaging (DWI) and fiber tractography, identifying probable pathways connecting the posterior AG and hippocampus along the inferior longitudinal fascicle [124,125], and the AG and precuneus along the occipitofrontal fascicle [126]. Dissociable portions of the cingulum bundle connect the MPFC with the PCC [127], precuneus [128], and medial temporal lobes [128], as well as the RSC with the medial temporal lobes [127]. Supporting the functional significance of these structural connections, individual differences in cingulum bundle integrity have been related to memory for event details and spatiotemporal context [53]. In sum, PM regions are strongly and near ubiquitously interconnected, and the functional significance and dissociability of these specific connections should be investigated further in future work.

Box 2: Mapping brain networks to cognitive functions

In cognitive neuroscience, a ‘network’ describes spatially distinct brain regions, or nodes, that are structurally and/or functionally connected through edges. Methods for identifying brain networks vary by spatial scale, temporal scale, and relation to cognition, but most utilize covariation in brain activity across time or experimental trials. For instance, resting-state network analyses relate regions according to correlations of slow fluctuations of activity across several minutes of rest. Resting-state networks are often defined across the entire brain and assumed to be relatively stable. In contrast, task-related networks are based on correlations of brain activity that are dynamically modulated by task variables (e.g., episodic retrieval). These flexible networks can be defined across the brain or they can be limited to a few key regions that interact only when required by a specific process, referred to as a process-specific alliance (PSA; [38,129]). When PSAs are embedded within a relatively stable network, are correlated with task variables, but do not readily disassemble, we refer to this as a core alliance.

In investigating how networks map onto cognition, researchers face two analytical considerations. First, what is the optimal method for characterizing information flow through a network [130]? Second, what is the optimal scale of network analysis for characterizing a cognitive process [129]? Through functional connectivity, we typically aim to make an inference about causal relationships between regions [130]. However, bivariate associations are affected by confounding variables including not just non-neural ‘noise’, but other regions — an association between nodes A and B can arise indirectly because both are connected to C. Partial correlations are useful here and can provide constraints on causal inferences (see [130] for an in-depth discussion) and ‘direct’ associations. Alternatively, effective connectivity methods, such as dynamic causal modeling (DCM; [131]) can be used when the question is one of causation, yet such methods are better suited to smaller networks or alliances. Therefore, we also need to consider the optimal scale of network analysis for a cognitive process of interest.

Networks are often described according to one overarching process, for instance, the as-named salience network or dorsal attention network. At the same time, we assume that constituent regions make distinct contributions to the network process. The challenge, then, is to balance understanding of the whole network with delineation of its component parts, especially when regions within a network are engaged in broadly similar ways across tasks (e.g. [48]). This may be achieved by identifying the sub-network, core alliances that support distinct cognitive functions, requiring the decomposition of network-level cognitive processes into operations and representations [4].

Outstanding Questions

- How do individual differences in PM network connections predict episodic memory performance, and are intra-network core alliances related to individual variability in episodic memory quality?
- What is the causal influence of PM network communication on the composition of episodic representations?
- What are the temporal dynamics of information flow through the PM network during episodic access and elaboration, and how do they support the hierarchical construction of event features?
- How is multi-modal event information represented in angular gyrus? Can patterns of activity in this region be predicted from separate patterns of activity in representational areas?
- What constitutes a “gist” or “precise” representation? How do they relate to the presence of spatio-temporal context information in memory?
- How do different memory attributes, such as the number of details, imageability, precision, contribute to a subjective sense of memory vividness, and what affects the relative weighting of these attributes?
- How does the PM network represent and integrate bodily states, thoughts, and feelings with other visuo-perceptual details of an episode?
- What are the common and distinct elements of constructing episodic representations versus constructing other experiences, such as emotions or other kinds of mental models that are not event-specific?

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