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Review

The Neural Representations Underlying Human Episodic Memory

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A fundamental question of human episodic memory concerns the cognitive and neural representations and processes that give rise to the neural signals of memory. By integrating behavioral tests, formal computational models, and neural measures of brain activity patterns, recent studies suggest that memory signals not only depend on the neural processes and representations during encoding and retrieval, but also on the interaction between encoding and retrieval (e.g., transfer-appropriate processing), as well as on the interaction between the tested events and all other events in the episodic memory space (e.g., global matching). In addition, memory signals are also influenced by the compatibility of the event with the existing long-term knowledge (e.g., schema matching). These studies highlight the interactive nature of human episodic memory.

What Gives Rise to the Neural Signals of Episodic Memory?

Episodic memory is the ability to recall and recognize previously encountered objects, people, and events, and to discriminate them from those that were not experienced. A fundamental question of human episodic memory concerns the cognitive and neural representations and processes that give rise to the neural signals of episodic memory. Theoretical and computational models have long characterized memory as a multidimensional collection of features which serve to discriminate one memory from another and to act as retrieval mechanisms for a target memory [1–4]. However, owing to methodological limitations, early neuroimaging studies primarily relied on **univariate brain activation** (see Glossary) as neural measures of memory signals. Although these studies have significantly advanced our understanding of the role of different brain regions in various mnemonic processes, they were not enough to capture the aspects of memory content/ representation and their interactions that contribute to mnemonic behaviors.

By integrating feature models of memory with **multiple voxel pattern analysis** (MVPA) of neuroimaging data, recent studies have started to examine in richer detail the 'mental representation' of individual events. This has led to a major shift in research – from a focus on the functional localization of memory processes to a focus on understanding the nature of representations at different memory stages and their interactions (an early comprehensive treatment of this topic is given in [5]). The field has progressed rapidly over the past 5 years, and many exciting new findings have been reported. Thus, the current review aims to summarize recent advances in this field.

In particular, the author examines what aspects of representations during encoding and retrieval contribute to episodic memory and **mnemonic decisions**. The author then focuses on the emerging evidence showing the interactions between representations, including the interaction between the representation of an event during encoding and that during retrieval, between the representation of a given event and that of other events in **episodic memory**

Highlights

Recent studies combining neural activation patterns and computational models enable a more mechanistic understanding of the neural representations and processes that give rise to human episodic memory.

The neural pattern similarity during encoding, which reflects the fidelity of neural representations and study-phase pattern reinstatement, is predictive of later subsequent memory.

Episodic memory performance is linked to neural pattern reinstatement during retrieval, which is related to hippocampal activation and is affected by the extent of cue overlap between encoding and retrieval.

Episodic memory is also affected by the interaction between the representations of all studied items in memory space, as well as with the representations of pre-existing knowledge.

A better understanding of the nature and dynamic changes of memory representations will lead to deeper insights regarding how memory is formed and transformed with experience.

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space, and between the representation of an event and pre-existing long-term knowledge (Figure 1). This framework highlights the interactive nature of human episodic memory.

Predicting Memory from Encoding: The Fidelity of Representation

Memory formation involves the transformation of a given experience into a long-lasting trace. Memory is therefore partially determined by the encoding processes. To explore how encoding might influence memory, early studies used functional imaging techniques and the **subsequent memory (SM) paradigm** [6,7] to compare the neural activity of items that were either subsequently remembered or forgotten (minutes to days after learning). The SM effect was linked to greater activation in material-specific regions, frontoparietal attention regions, and medial temporal lobe (MTL) binding and storage regions, and greater deactivation in the other areas of the **default mode network** [8].

Although these studies provided a straightforward account regarding how processing strength/depth and neural activation level are associated with memory strength, they did not specify how these processes affect the quality of the memory representations and memory duration. Therefore, more recent studies have used MVPA and the SM paradigm to directly examine neural representations that underlie subsequent memory formation. They have revealed that the neural pattern similarity across repeated presentations of the same stimulus (i.e., item-level similarity) in several brain regions is positively associated with later recognition or recall of that stimulus [9–15] (Figure 2). These regions included the frontoparietal cortex, sensory cortex, and posterior cingulate cortex (PCC).
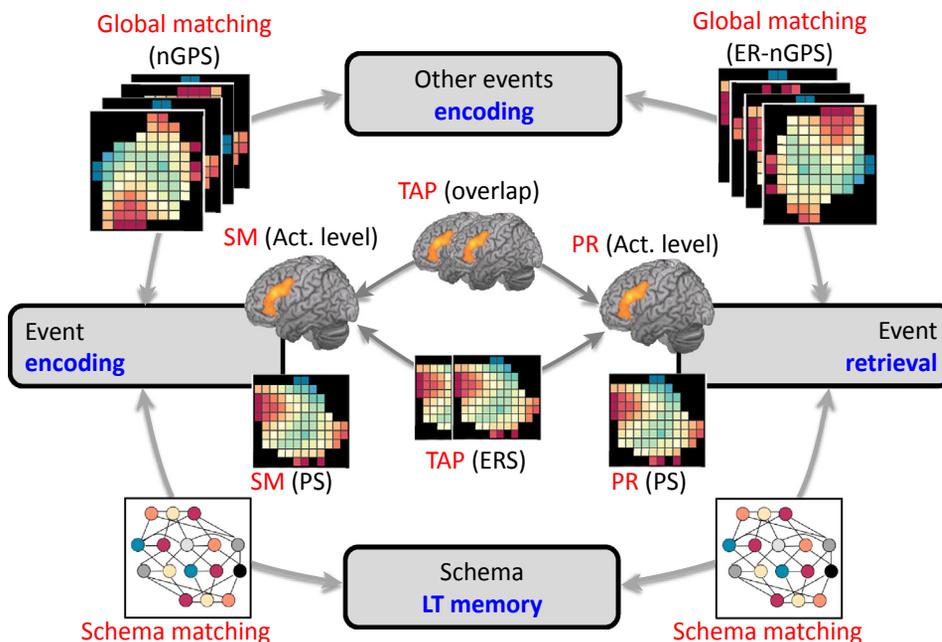
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Figure 1. Schematic Depiction of the Interactive Nature of Human Episodic Memory. Episodic memory not only depends on the activity (Act.) and representation during encoding and retrieval but also on the interplay between encoding and retrieval (transfer-appropriate processing), the interaction between a given item with all other items in episodic memory space (global matching), as well as with pre-existing long-term knowledge (schema matching). Abbreviations: ER-nGPS, encoding–retrieval neural global pattern similarity; ERS, encoding-retrieval similarity; GPS, global pattern similarity; LT, long-term; PR, pattern reinstatement; PS, pattern similarity; SM, subsequent memory; TAP, transfer-appropriate processing.

Glossary

A–B/A–C learning paradigm: an experimental paradigm in which cue (A) is first paired with association B (old association) and then with association C (new association). This paradigm is widely used to study memory updating, interference, integration, inference, and so on.

Complementary learning systems: theoretical and computational models that posit two learning systems, namely a fast learning system supported by the hippocampus, and a slow learning system supported by the neocortex.

Context maintenance and retrieval (CMR): a more generalized version of the temporal context model to account for semantic, source, and temporal organization during memory search in free recall.

Default mode network: a large network of highly connected brain regions that show elevated activation when a person is not involved in a task.

Encoding–retrieval similarity (ERS): a measure of similarity between neural activation patterns during encoding and during retrieval.

Episodic memory space: the set of episodic representations within which memory search and comparison are performed in a memory decision task.

Familiarity-based recognition: the situation where one has only a sense of experiencing a prior event without remembering the details.

Global matching: the hypothesized matching process between the representation of one item with those of all other items in episodic memory space; the resulting product of this process (i.e., global similarity) is used for mnemonic decisions and categorization.

Mnemonic decisions: decision tasks in which one uses the retrieved memory evidence to judge the order, context, and veridicality of memories.

Multiple voxel pattern analysis (MVPA): analytic methods that link the distributed patterns of neural activities with the underlying processes or representations. Typical methods include multivariate decoding/classification and representational similarity analysis.

Pattern reinstatement: the replay or re-enactment of neural processes/

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This similarity may reflect the fidelity of item-level encoding and/or the reinstatement of previously encoded representation. The reinstatement account is based on earlier behavioral studies on study-phase retrieval (i.e., the reactivation of prior representations when restudying the item again), which serves as a crucial mechanism for the memory practice effect [16,17]. Since the same materials are repeated multiple times, using fMRI techniques it was difficult to disentangle the neural representations associated with the re-encoding of the same stimulus from those associated with the reactivation of prior learning. However, with electroencephalography (EEG) and magnetoencephalography (MEG) techniques that yield high temporal resolution, this question can be addressed by examining the time-window in which the pattern similarity supports subsequent memory. This technique relies on the assumption that an early time-window reflects bottom-up sensory processing, whereas a late window reflects study-phase retrieval of prior representations. A recent EEG study using this strategy found that the pattern similarity that predicted subsequent memory occurred approximately 500 ms after stimulus onset, consistent with the reinstatement hypothesis [14]. The study-phase retrieval can be further addressed using the **A–B/A–C learning paradigm**. In this paradigm, item A is initially paired with item B, and later paired with item C (B and C are usually from different stimulus categories to aid interpretation), and either the old memory (i.e., A–B association) or newer memory (i.e., A–C association) is probed in a later test. These studies found clear evidence of B reactivation during later A–C learning, and this reactivation could help to resist the forgetting of old memory [18,19] and also interfere with the acquisition of newer memory [20].

According to the fidelity account, greater similarity reflects more faithful and less noisy representations of encoded materials, thus items with greater representational fidelity should show greater similarity to items belonging to the same category than to different categories. Supporting the fidelity account, it was found that, during learning, items subsequently judged as remembered show greater category-level similarity (across items from the same vs different category) than items subsequently forgotten [13]. Older adults show both reduced item-level and category-level pattern similarity in the visual cortex, which underlies memory decline during normal aging [21]. These studies converge to suggest that greater fidelity of item- or category-level representations during learning are associated with better memory.

Further supporting the fidelity hypothesis, pattern similarity in the ventral visual cortex reportedly correlates with both activation level [15] and pattern similarity [13] in the frontal and parietal lobes, consistent with their role in enhancing the fidelity of cortical representation [22]. The correlation with frontal activity was higher in old adults than in young adults, perhaps reflecting a top-down compensatory process related to impaired visual representations in older adults [21]. Focused attention could also stabilize the representation in the hippocampus and improve later memory [23]. In support of a causal role of the frontal cortex in enhancing cortical pattern similarity, anodal stimulation of the prefrontal cortex was found to enhance the spatiotemporal pattern similarity (STPS) and improve memory [14].

It should be noted that, although future studies will be necessary to disentangle the contribution of the study-phase retrieve and item-specific encoding to the observed pattern similarity, they could work together to increase the distinctiveness of memory representation. According to the differentiation model of memory [24], when an early memory trace is retrieved, additional encoding leads to the storage of additional information (such as the new context) in a single episodic memory trace representing the same event. As the memory trace is updated, its similarity to other, similar items decreases. This then results in more unique and faithful input to the hippocampus and aids hippocampal pattern separation and context binding.

representations that occurred at the encoding stage when the memory is retrieved.
Recollection-based recognition: the situation where one can vividly remember the details of an event.
Schema: a pre-existing knowledge structure that could be depicted as an organized network of overlapping representations.
Subsequent memory (SM) paradigm: an experimental paradigm that uses the cognitive and neural processes and representations during encoding to predict later memory performance.
Temporal context model (TCM): a formal computational model of free recall, which was designed to explain the phenomena of temporal organization in memory search.
Transfer-appropriate processing (TAP): the interactive nature of encoding and retrieval, where the effectiveness of encoding activity is modulated by the cue type and goals during retrieval.
Univariate brain activation: reflects the activity level of individual voxels in a given experimental condition as revealed by voxel-wise analysis.
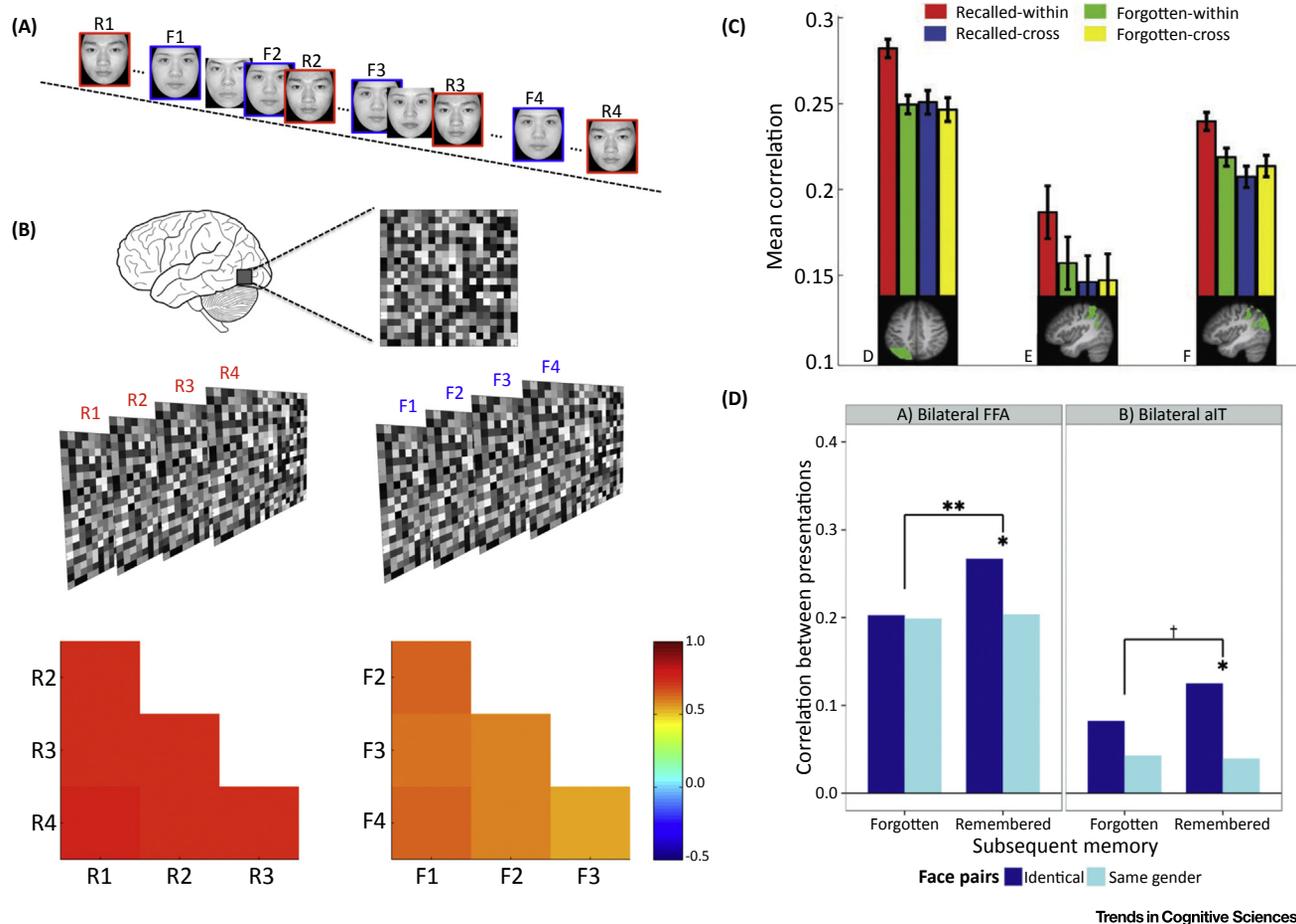
Figure 2. The Fidelity of Cortical Representation during Encoding Predicts Subsequent Memory. (A) The subsequent memory paradigm where each item was repeatedly studied (e.g., 2–4 times) in a study session. (B) Schematic depiction of the analytic strategy to compare the neural pattern similarity between subsequently remembered and forgotten items. (C) Subsequently remembered words showed greater item-level pattern similarity than forgotten words [12]. This pattern similarity reflects item-specific representation, as the within-item similarity was greater than between-item similarity (within, within-item pattern similarity; cross, pattern similarity between items belonging to the same mnemonic status). (D) Only subsequently remembered faces were associated with individual-specific face representations in bilateral fusiform face area (FFA; left) and anterior inferior temporal lobe (aIT; right) [9]. Panels A–C are adapted, with permission, from [12]; panel D is reproduced, with permission, from [9].

The distinctiveness of the event representation can be further enhanced by hippocampal pattern-separation processes by which similar representations are stored in a distinct and orthogonalized fashion. This pattern separation is supported by the dentate gyrus (DG), whose granule cells are able to orthogonalize overlapping/distributed representations from the entorhinal cortex (ERC). This signal could then drive pattern separation in the CA3 subfield of the hippocampus [25,26]. Supporting this view, several studies using MVPA found that the hippocampus could disambiguate overlapping spatial and temporal contexts during successful learning in navigation [27,28]. Furthermore, better subsequent memory was associated with weaker within-category pattern similarity in the hippocampus (CA1, CA2/3/DG, and subiculum) [29], suggesting that hippocampal pattern separation supports better memory.

To summarize, cumulative evidence using MVPA has suggested that the fidelity of representation during encoding could support enduring memory traces. Greater fidelity of representation, as indicated by greater category-level and item-level similarity, can improve the

distinctiveness of cortical input to MTL. Several mechanisms, including top-down attentional control, study-phase **pattern reinstatement** and integration, and hippocampal pattern separation, may contribute to the distinctiveness of memory encoding. Future studies should apply MVPA to further examine study-phase retrieval and the differentiation model, which would help to answer the fundamental question regarding how repeated studies enhance memory.

Memory Signal during Retrieval: Pattern Reinstatement

Computational models have long suggested that retrieval involves the active re-enacting of encoding operations [30]. At the neural level, this echoes the pattern reinstatement process included in several neurally inspired models of episodic memory [31–33]. For example, the Norman and O'Reilly model posits that encoding establishes a sparse and non-overlapping representation in the hippocampus, particularly CA3 and DG [26]. Retrieval cues reactivate this representation, which in turn leads to reinstatement of the cortical activation pattern during encoding [32]. It has been further argued that the pattern-completion process, by which partial representations are filled-in based on previously stored representations, is specific for cued recall and **recollection-based recognition**, whereas **familiarity-based recognition** depends on pattern matching between retrieval cues and stored representations [32,34].

Evidence for Item-Specific and Transformed Pattern Reinstatement

The reactivation perspective of memory retrieval suggests that retrieval should involve the reinstatement of representations in the sensory cortex where the events were initially encoded, and that memory strength should scale with the fidelity of the reinstated neural activation pattern. Supporting this hypothesis, early univariate studies found that successful retrieval was accompanied by reactivation of sensory/motor cortices involved in encoding [35,36]. However, this overlapping activation could not specify the nature (e.g., item-specificity and fidelity) of pattern reinstatement. Using MVPA classification, it has been shown that successful memory retrieval is accompanied by the reinstatement of the categorical activation patterns that had occurred during encoding [37–40]. More recently, using representational similarity analysis, studies have revealed event-specific reinstatement, as indicated by greater within- than between-event **encoding–retrieval similarity** (ERS) [41–45], providing strong evidence that pattern reinstatement is associated with successful retrieval of specific events. Finally, the fidelity of cortical reinstatement is predictive of retrieval decision times and decision accuracy [46].

Several recent MVPA studies further examined item-specific reinstatement after removing the perceptual similarity between encoding and retrieval (e.g., caused by using the same cue). One study calculated the ERS between the activation pattern during the recall test (where only the word cue was presented) and that during the recognition test (where only the associated picture was presented) [47]. In another study, pattern reinstatement was measured during free recall of movie scenes where no explicit cues were presented [48]. In a more recent study, each picture was paired with two different cue words, allowing the researchers to examine ERS using encoding–retrieval pairs that did not share the same cue word [49]. All these studies found item-specific pattern reinstatement in the frontoparietal cortex (PFC), but not in the ventral visual cortex (Figure 3). As the representation in the inferior parietal lobule (IPL) is identity- but not view-specific [50], and reflects the progressive abstraction of conceptual knowledge from perceptual experience [51], these studies suggest that the retrieved representation is abstracted and the sensory details might not be faithfully reinstated. More importantly, within-subject ERS was smaller than within-subject pattern similarity during both encoding and retrieval [49], and cross-participant ERS was also smaller than cross-participant similarity during retrieval [48], suggesting that the encoded representations had been transformed during
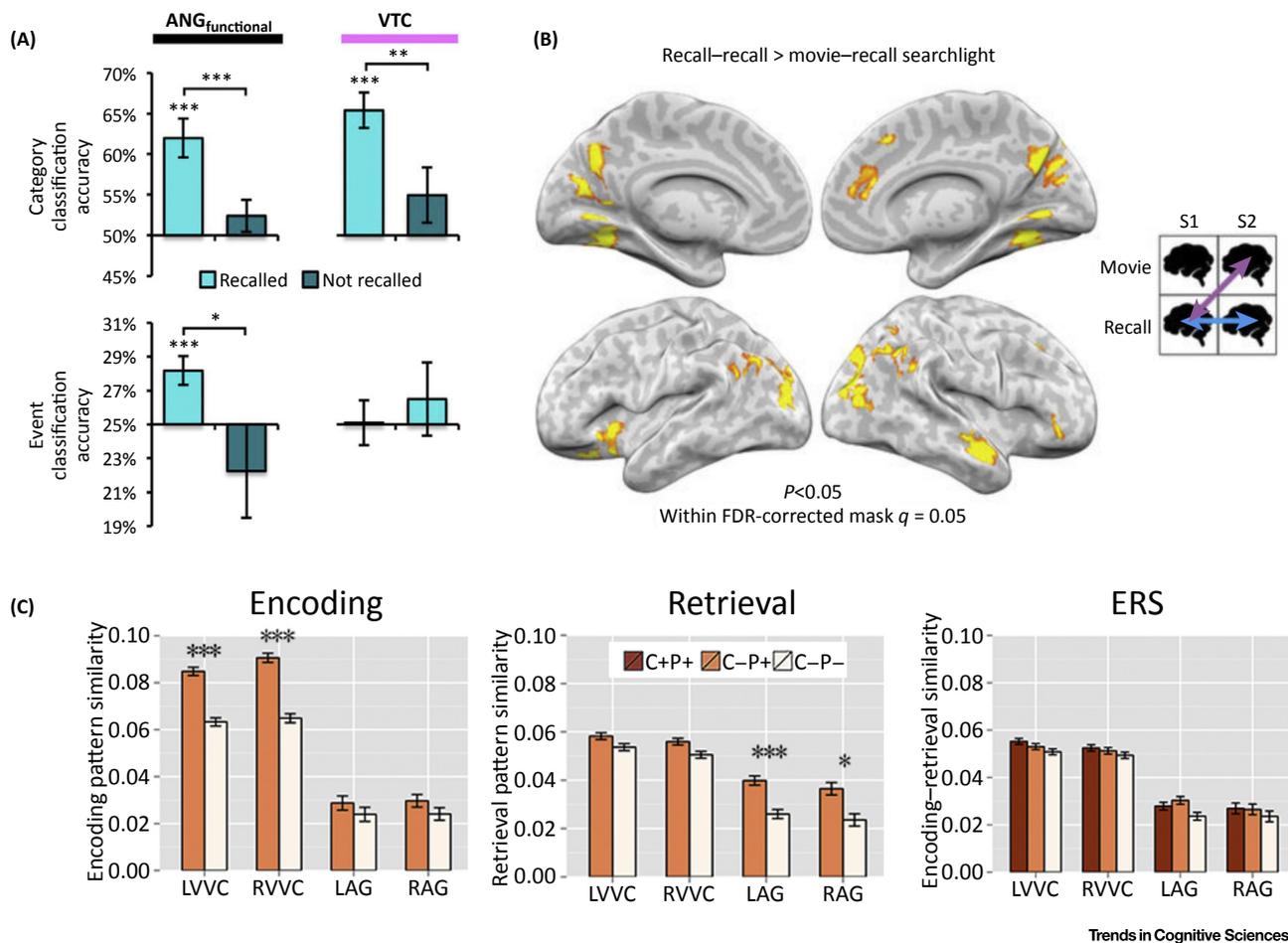
Figure 3. Item-Specific and Transformed Pattern Reinstatement during Retrieval. (A) In the word–picture pairs learning and recall/recognition study [47], category-level reactivation during recall test was measured by training a classifier (scene vs face) using data from study phase and applied to recall phase (50% chance). Event-level reactivation was measured by calculating the similarity between pairs of recall–recognition trials corresponding to the same event, and test if the similarity was higher than pairs corresponding to different events from the same block and category (25% chance). Both angular gyrus (ANG) and ventral temporal cortex (VTC) showed reinstatement of category-level information (top panel), but only the ANG showed reinstatement of item-level information (bottom panel). (B) In a movie-watching and free recall study [48], the between-participant recall–recall similarity was greater than between-participants movie–recall similarity in the posterior medial cortex (PMC), higher visual cortex, and anterior cingulate cortex (ACC), suggesting that the recalled representations had been transformed from that during movie watching. FDR, false discovery rate. (C) In a more recent study [49], each picture was associated with two different word cues, allowing the examination of item-level pattern similarity during encoding, retrieval, and encoding–retrieval similarity (ERS). The ventral visual cortex (VVC) and angular gyrus (AG) showed item-specific representation during encoding and retrieval, respectively. Importantly, the degree of item-specific ERS (within-item minus between-item similarity) in the VVC was smaller the item-specific similarity during encoding, and the ERS in the AG was smaller than item-specific similarity during retrieval, which further suggests that pattern reinstatement during retrieval was transformed. Abbreviations: C+P+, same cue same picture; C−P+, different cue same picture; C−P−, different cue different picture; L, left; R, right. Panel A is reproduced, with permission, from [47]; panel B is reproduced, with permission, from [48]; panel C is adapted, with permission, from [49].

retrieval in a systematic way (Figure 3B,C). A recent study further suggests that the transformation of memory representations during retrieval depends on memory consolidation, and that there is a trade-off between reinstatement of event-specific representation and integration with related memories [52].

Although pattern reinstatement is considered to be a specific neural marker of recollection, cortical reinstatement has been demonstrated during both recollection- and familiarity-based

judgments [37], suggesting that the categorical reinstatement of sensory information alone is not sufficient to differentiate recollection and familiarity. Further analysis revealed that the left lateral temporal cortex, superior frontal gyrus, and inferior frontal gyrus showed common pattern reinstatement for recollection and familiarity, but the posterior medial cortex showed recollection-specific pattern reinstatement. Since recollection and familiarity in this study were based on subjective reports that depend on criterion-based decision-making processes, it is possible that participants might experience some recollection of those familiarity trials. Future studies should examine this possibility with objective measure of familiarity and recollection. In addition, the causal contribution of pattern reinstatement in different brain regions to recollection and familiarity warrants further investigations.

The Role of Posterior Parietal Cortex (PPC) in Memory Retrieval

One interesting finding in memory retrieval research is the consistent involvement of the PPC (see [53–55] for reviews), although it has not been traditionally considered to be a memory region. Human single-neuron recordings have also revealed that PPC neurons encode familiar or novel stimuli, with the response being scaled with memory strength measured by confidence [56]. Mechanistic accounts of the role of the PPC in memory have emphasized either general processes such as attention for internal mnemonic representations [54] and accumulation of mnemonic evidence [53], or specific processes such as representations of retrieved content in an 'output buffer' [57] and binding information from other cortical inputs [58].

Recent MVPA studies suggest there might be finer functional dissociations in this region. In particular, the posterior portion, namely the angular gyrus (AG), represents details of retrieved information and shows content-specific episodic representation during retrieval [15,47,49,59]. By contrast, the anterior portion, namely the lateral intraparietal sulcus (IPS), may act as an accumulator of mnemonic evidence by transforming and manipulating the retrieved information according to the current task requirement [55,60]. Consistently, a recent iEEG study found that the IPS (i.e., the dorsal supramarginal gyrus, SMG; and the ventral superior parietal lobule, SPL) shows greater sustained high-frequency gamma power for old versus new items, which decays only 200 ms before the motor response [61]. During long memory search, the AG shows transient activities whereas the SMG exhibits sustained activation until a final decision is made [60].

The Processes and Representations in the Hippocampus

One crucial question concerns the contribution of hippocampus and the adjacent MTL cortical structures (e.g., the perirhinal cortex, PRC; and parahippocampal cortex, PHC) to memory retrieval. According to one model, the PRC supports familiarity-based recognition, while the hippocampus supports successful recollection [62]. Alternatively, it is posited that the hippocampus supports recollection and familiarity-based recognition with high confidence [63]. Meanwhile, other models focusing on the representational characteristics of the MTL posit the respective roles for the PRC, PHC, and hippocampus in the representation of information about items, contexts, and their binding [64,65].

Two lines of MVPA research might contribute to these debates. The first line concerns the role of the hippocampus in cortical pattern reinstatement. Consistent with its role in memory retrieval and pattern completion, several studies have found that the magnitude of hippocampal activation during retrieval covaries with the fidelity/strength of pattern reinstatement. This was true both in studies examining the reactivation of task and source information [18,46] and in studies examining item-level encoding-retrieval similarity [40–42]. This representation-informed activation analysis thus confirms the role of hippocampus in pattern completion. As very few

studies have compared cortical reinstatement between recollection and familiarity, it remains unknown whether the hippocampus contributes to pattern reinstatements specifically associated with recollection, or also with familiarity, if such reinstatement exists.

The second line of research focuses on the information representations in the hippocampus and MTL. Using MVPA, cumulative evidence suggests the PRC is sensitive to faces, objects [29,66], and semantic distance [67], whereas the PHC is sensitive to scenes [29,66,68]. Similar to research with animals [69], human studies have found grid-cell like representation in the entorhinal cortex (ERC) [70–72]. During retrieval, the PRC and ERC activation patterns distinguish familiar from novel faces [73] and objects [74], whereas the pattern in right PHC differentiates buildings [73] and scenes [41,74].

By contrast, existing evidence suggests that the hippocampus does not represent object information *per se*, but rather object–context binding, including maintaining temporal information [75], constructing internal scene 'models' [76], and the integration of space and time [77]. The hippocampus shows no content-sensitivity to faces, scenes, or objects during encoding [29,49,78], but carries temporal information about objects, and hence can differentiate the same object that appears in different sequential contexts [79]. Another study found that hippocampal pattern similarity was higher for stimulus pairs subsequently judged as temporally close than those judged as far [80]. Using 7 Tesla high-field fMRI, only the activation pattern in the subiculum subfield could discriminate scenes, but not faces or objects [81]. During retrieval, although there is no evidence of familiarity signals for any object category in the hippocampus [73,74], it carries recollection signals for all three types of stimuli [74]. Item-specific representations have also been found in CA1 and CA3/DG during cued retrieval when episodic details are emphasized [49]. Finally, during navigation, strong spatiotemporal representation has been consistently found in the hippocampus. For example, place-responsive cell activity was reinstated during episodic memory retrieval [82]. Hippocampal activation patterns were found to support prospective representation of future navigational goals [83].

Although fMRI studies have failed to reveal object coding in the hippocampus, single-neuron recordings have found object/face-selective neurons in the hippocampus [84]. One possible reason is that the hippocampal code features the representation of continuous dimensions of experience, integrating elements of space, time, and object. This rich contextual representation is proposed to be realized through neuronal ensembles, which can be captured with fMRI [77]. By contrast, hippocampal object representation is very sparse [84,85], making it hard to probe with fMRI owing to the limited spatial resolution. Consistent with this view, iEEG studies have found that hippocampal high-frequency activity (HFA) during retrieval contains item-specific representations [44,86]. Using this approach, one study found that the hippocampal HFA was modulated by the strength of both recollection and familiarity [87]. Since the strength of recollection and familiarity was estimated by reaction time rather than by subjective confidence or more objective measures, and no attempt was made to connect HFA patterns with memory content, it is thus unclear whether the HFA encodes memory representations or decision-related signals. Applying representational accounts to high-resolution fMRI and iEEG, future studies will help to elucidate the hippocampal contribution to subjective experience of familiarity and recollection.

Overall, supporting the computational models, existing studies find that the neural activation patterns during retrieval reflect the reinstatement of encoding processes/representations, which is supported by the hippocampal pattern-completion function. Recent evidence further suggests that item-specific reinstatement during retrieval is more robust in higher-level cortical

regions representing abstract information than in lower-level regions representing sensory information. More importantly, emerging evidence suggests that, instead of a faithful replay of the encoded trace, retrieval-induced pattern reinstatement might reflect a more constructive process. Future studies should examine the coding scheme of the hippocampus, and examine how its activities and representations contribute to pattern reinstatement during recollection and perhaps familiarity.

Memory by Encoding–Retrieval Interaction: Transfer-Appropriate Processing

Memory performance is not only determined by the depth of processing but also by the relationship between encoding and retrieval. From this perspective, whether or not a particular encoding activity is effective depends on the goals and testing situations. Similarly, whether the retrieval cue is effective or not depends on the processes engaged during encoding. The **transfer-appropriate processing** (TAP) [88] and encoding specificity [3] hypotheses argue that, to have successful memory, the encoding and retrieval processes should be substantially similar. The TAP hypothesis gains support from a vast body of behavioral research [89]. In particular, it has been suggested that better memory can be achieved when the context/environment of study and test were matched [90]. This matching of modality not only increased true memory but also reduced false memory [91].

The TAP predicts that stronger cue/context overlap should result in a greater overlap in neural activation patterns between encoding and retrieval (see [92] for an early review). Early fMRI studies that directly compared encoding and retrieval processes revealed substantial overlaps (albeit also differences) in neural activation [93]. The subsequent memory effect for visually presented words was modulated by the use of spoken words versus pictures as retrieval cues during test [94]. Congruent cues were associated with better memory performance and greater overlap with the neural activation during encoding [95].

To date, very few studies have used MVPA to test the TAP hypothesis. One study used fMRI to scan the encoding and recognition of visual scenes, and MVPA was applied to evaluate the neural similarity between individual scenes at encoding and retrieval. They found that the item-level encoding–retrieval similarity is higher for subsequently remembered than forgotten items [42]. Since ERS could reflect the cue/context overlap and/or the reactivation of encoded representation, it is thus somehow difficult to disentangle them when the same stimulus is presented at encoding and retrieval. Meanwhile, it is unclear whether ERS is the driving force or the outcome of the TAP.

The retrieval cues not only come from environmental input but also can be generated internally by retrieval of prior contextual states, which depends on the way the contexts were encoded. This feature nicely demonstrates the intimate interactions between encoding and retrieval. According to the **context maintenance and retrieval** (CMR) model of memory search [96], which was developed from the early **temporal context model** (TCM) [97], the semantic, temporal, and source contexts are encoded together with the items, and the retrieval of a given item reinstates the associated context and drives contextual drift. This model has wide implications for our understanding of the organizational prosperities in free recall. The association principle and reactivation principle (termed 'first principles') have been recently incorporated into a neurally constrained model to account for free recall performance [98].

Supporting the context model, many studies have provided evidence for context coding, in particular in the hippocampus [41,79,80], as well as in the prefrontal cortex [99], which was reactivated during memory retrieval [82,100]. Using iEEG and scalp EEG and pattern analysis,

one study examined the neural representations that supported the categorical organization during free recall [101]. They found that category-specific patterns increased strength as multiple same-category items were studied sequentially (i.e., category-specific neural integration). Interestingly, participants were more likely to rely on categorical organization in later recall if they showed greater category-specific context integration during encoding. This study provides very clear evidence to support the interplay between encoding and retrieval.

In summary, although the TAP hypothesis has been well supported by behavioral data, recent neural pattern studies have offered a more detailed and mechanistic examination of this important feature of human episodic memory. In particular, they find that the exact contexts by which studied materials are organized determine the performance (in terms of accuracy, speed, and order) in memory retrieval, which is mediated by the neural context coding and reactivation. Future imaging studies should manipulate the cue/context overlap, and the compatibility of context organization during encoding and retrieval, which should advance our understanding of the neural implementations of context association, context reactivation, and their interactions, and help to develop neurally realistic models.

Memory Signals Arise from Global Matching

The majority of studies have emphasized how memory for a given item is determined by its encoding and/or retrieval processes, but they have not been able to address two related questions – why is memory affected by the learning of other items, and why does false memory occur? In the early memory strength model, generalization occurs by assuming that unstudied items gain a strength that is proportional to the similarity to the presented items [102]. However, the similarity among all non-identical stimuli is assumed to be constant and factors that determine similarity are not specified. To address this issue, **global matching** models posit that the memory strength of a given item derives from the matching (measured as similarity) between its representation and the representations of all other studied items [103,104]. The match value or memory strength is then subjected to a decision-making process (e.g., signal detection model) to determine a response when performing a memory retrieval task. As is clear here, the global matching models assume a single familiarity-based recognition mechanism for retrieval [103].

The global matching models provide an algorithmic explanation for why recognition memory is affected by the similarity of an item to other studied items. Using representational similarity analysis (RSA) to calculate the neural global pattern similarity (Figure 4A), recent studies examined and supported the hypothesis that higher neural global similarity during encoding resulted in better recognition memory [29,105,106] (Figure 4C). Using EEG and RSA on spatiotemporal features, a study also found that higher global spatiotemporal pattern similarity was associated with better recognition memory of novel symbols [14]. Furthermore, words describing living things showed higher neural global pattern similarity in the MTL than those describing non-living things, and that this mediated the animacy effect of memory [107].

The global matching models also provide an account for false memory. According to the global matching models, false memory occurs when there is a high level of similarity between the unstudied item and stored memories because of overlap in item and/or context information. In particular, the sum of many partial matches to memory traces could provide a strong overall match, leading to the global similarity effect [103,104]. Recently, we tested the hypothesis that the strengths of both true and false memories arise from the global similarity between neural activation pattern of an item during retrieval and those of all studied items during encoding (i.e., the encoding–retrieval neural global pattern similarity, ER-nGPS) [59] (Figure 4A). Using the
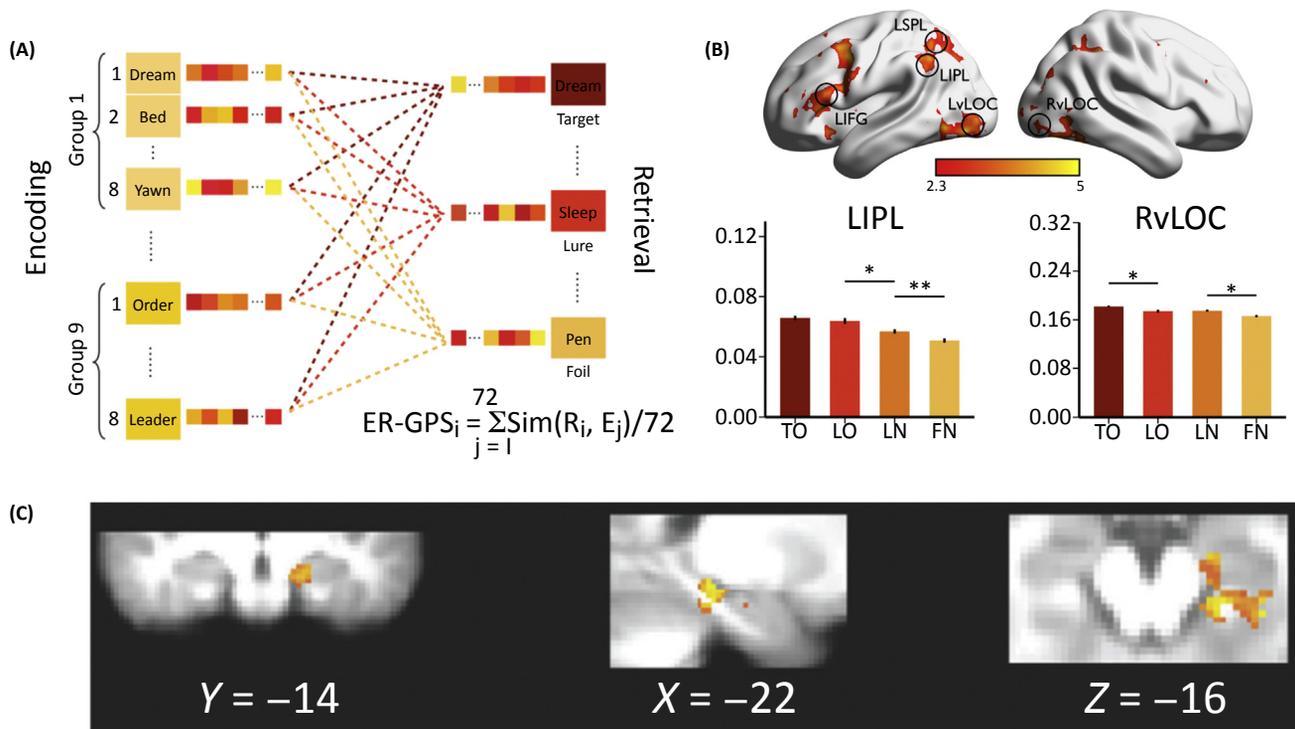
Figure 4. Global Matching and Memory Strength. (A) A depiction of the neural global pattern similarity between encoding and retrieval [59]. The Deese–Roediger–McDermott (DRM) paradigm was used, where participants were asked to study nine lists of eight words that were semantically related. The global pattern similarity between encoding and retrieval (encoding–retrieval neural global pattern similarity, ER-nGPS) was calculated by averaging the neural activation pattern similarity (Fisher's *z* scores) of each test item (including studied items, i.e., the target; not studied but semantically related items, i.e., the lure; and not studied and semantically unrelated items, i.e., the foil) with all studied items. (B) Regions showing greater ER-nGPS for targets judged as old (target old, TO) than for foils judged as new (foil new, FN). Notably, there were multiple ER-nGPS signals that carried distinct information and contributed differentially to true and false memories: Whereas the ER-nGPS in the parietal regions was scaled with the recognition strengths of both true and false memories, ER-nGPS in visual cortex contributed solely to true memory. Abbreviations: IFG, inferior frontal gyrus; L, left; R, right; SPL, superior parietal lobule; vLOC, ventral lateral occipital complex. (C) The neural pattern similarity for a given studied item with all other studies item (i.e., the neural global pattern similarity, nGPS) in the medial temporal lobe (MTL) predicted subsequent memory performance. Panels A,B are reproduced, with permission, from [59]; panel C is reproduced, with permission, from [105].

Deese–Roediger–McDermott (DRM) paradigm [108], we revealed two ER-nGPS signals that carried distinct information and contributed differentially to true and false memories: whereas ER-nGPS in parietal regions reflected semantic similarity, and was scaled with the recognition strengths of both true and false memories, ER-nGPS in visual cortex contributed solely to true memory (Figure 4B). Interestingly, the discrepancy between the two global matching signals triggered a conflict-resolution mechanism implemented by the lateral prefrontal cortex.

How the global matching computation is implemented to generate the neural global similarity signal remains unclear. During encoding, the temporal, source, and semantic contexts are integrated. This episodic representation shares great similarity with the test items, resulting in strong representation matching and familiarity for both true and false memory. Manipulation of list length, list strength, word frequency, and stimuli grouping would affect global matching and familiarity. During retrieval, this strong representation overlap may trigger pattern completion, which further increases neural global pattern similarity. Notably, pattern completion might also be involved in false memory as previous studies have found erroneous pattern completion [109] and false neural pattern reinstatement [46,110]. This recall-like pattern-completion mechanism

(A)

Item
Pine
Oak
Rose
Daisy
Robin
Canary
Sunfish
Salmon

Relation
ISA
IS
CAN
HAS

Representation

Hidden

Attribute
Living thing
Plant
Animal
Tree
Flower
Bird
Flower
Pine
Oak
Rose
Daisy
Robin
Canary
Sunfish
Salmon

Pretty
Tall
Living
Green
Red
Yellow

Grow
Move
Swim
Fly
Sing

Bark
Petals
Wings
Feathers
Scales
Gills
Roots
Skin

(B)

Canonical false memory likelihood vs Temporal pole neural overlap
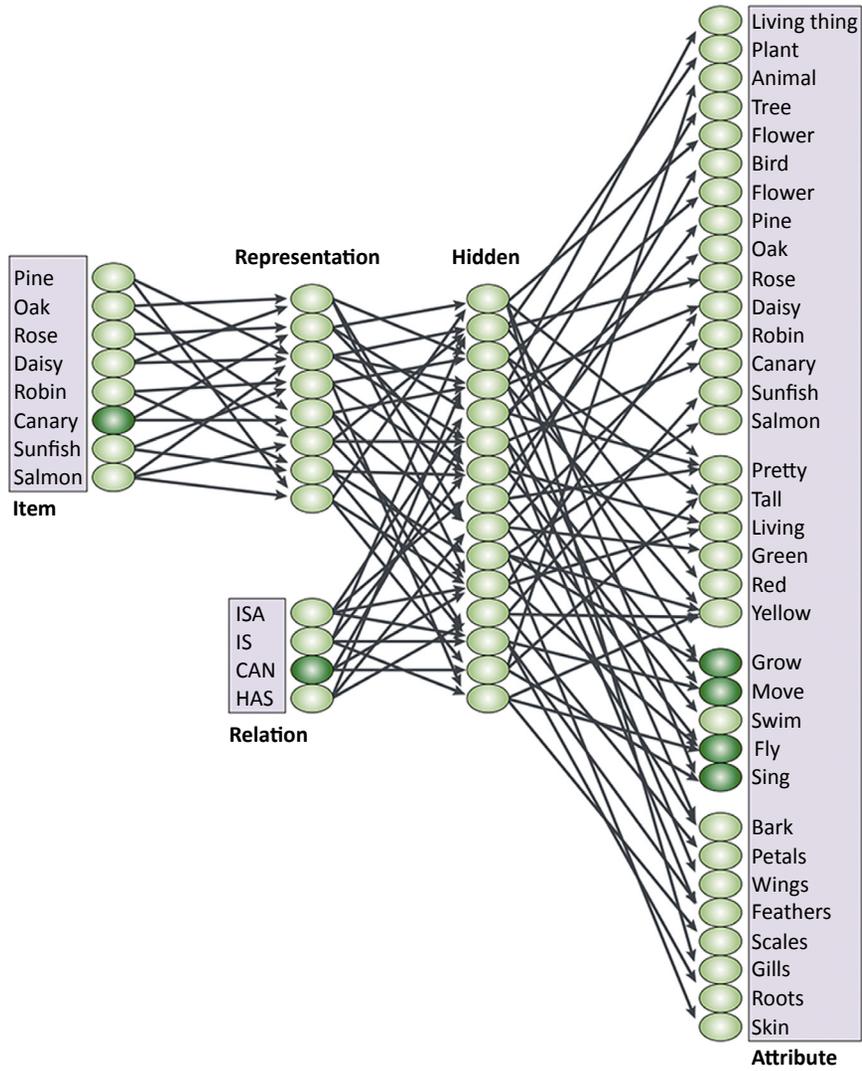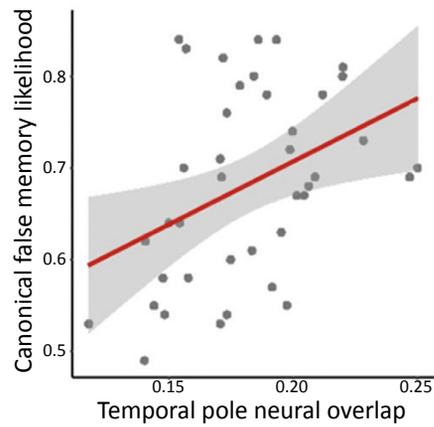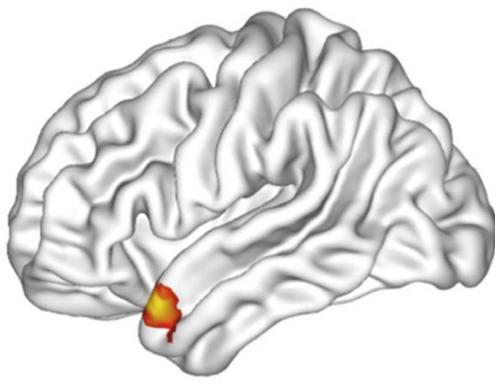
(See figure legend on the bottom of the next page.)

has been suggested to be necessary in the global matching models, as the single familiarity-based recognition mechanism could not account for the dissociated effect of the above manipulations on item recognition and associative recognition performance [103]. Future studies examining the involvement of global matching and hippocampal pattern completion in both true and false recognition memory would help to address this important issue.

Clearly, the global matching models inspire a novel way to link neural activity with memory strength. Unlike existing fMRI studies that consider the activation for each studied item as mainly reflecting the 'strength' gained for that item, the global matching models posit that a test item could gain a degree of 'strength' from each of the studied items, which is determined by the similarity between the tested item and other studied items. Unlike the single global matching signal in the current models, the imaging evidence suggest that temporal, perceptual, categorical, and semantic similarity may give rise to separate global matching signals, and contribute differentially to mnemonic decisions depending on current goals. Finally, global similarity might trigger both global matching (i.e., familiarity) and perhaps (erroneous) pattern completion (i.e., recollection), and this needs to be examined further.

Pre-Existing Knowledge (Schemas) and Memory Signals

Whereas the TAP and global matching models emphasize the similarity between retrieval cue and the content in the episodic memory space, many studies have also suggested that current episodes may interact with long-term knowledge to determine memory strength. In his classic 1932 monograph on remembering [111], British psychologist Frederic Bartlett developed the concept of **schemas** to refer to the pre-existing knowledge structures into which newly acquired information can be incorporated. In practice, a schema is broadly defined as an organized network of overlapping representations, including gist, concepts, categories, statistical regularities, semantics, and so on [112,113].

Schemas not only help the acquisition of new memories [114–116] but also facilitate consolidation [117,118] and retrieval [119,120] (see [112,121] for review). The main characteristic of schema-consistent learning is captured by new simulations [122] using a parallel distributed processing approach to knowledge learning and representation [123] (Figure 5A). According to the **complementary learning systems** theory (CLST) [33], cortical learning is slow to avoid catastrophic interference of new knowledge that is inconsistent with prior knowledge. This is complemented by a fast hippocampal learning system that can store arbitrary new knowledge. Memory acquired through the hippocampus can be reactivated to guide behavior and to support interleaved training of the neocortex, allowing new knowledge to be integrated gradually into neocortical knowledge networks. The new simulation has found that the speed of cortical learning can be either slow or fast depending on whether a given item is schema-consistent [122].

Recent evidence suggests that the hippocampus and prefrontal cortex (in particular the ventromedial prefrontal cortex, VMPFC) support the assimilation of new episodic memory into existing schemas [113]. In particular, whereas schema-inconsistent memory is encoded via the

Figure 5. Schema Matching and Episodic Memory. (A) The artificial neural network model introduced by Rumelhart [132], which was designed to simulate the learning of structured knowledge about living things. Each oval represents a neuron-like processing unit. Connections between units are represented with arrows. It should be noted that only a subset of the connections are shown as each unit in a layer connects to all units in the next layer to its right. This general framework can used to simulate the learning of other structured knowledge. IS, ISA, CAN, and HAS are logical relations. (B) Cortical semantic representation predicts false memory. The neural pattern similarity between the Deese–Roediger–McDermott (DRM) concept word and the four DRM list words (40 lists in total) were calculated and used to predict the likelihood of false memory tested several weeks before. Searchlight analysis revealed that only the representational similarity in the temporal pole (TP) could predict false memory (left). The right panel plots the group-averaged neural similarity for each of the 40 DRM lists against canonical false-memory likelihood. Panel A is reproduced, with permission, from [123]; panel B is reproduced, with permission, from [131].

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hippocampus, schema-consistent memory is encoded via VMPFC–hippocampal interactions [114,116,117]. Sensitivity to schema consistency was reduced in VMPFC damaged patients [124] and by pharmacogenetic inhibition of the medial prefrontal cortex in rats [125]. By tracking the neuronal responses during the whole learning periods, rodent research has examined the role of the hippocampus in schema formation and updating [126]. One human study trained subjects with paired associations over several months [119], whereas another study trained subjects simple rules over 2 days [120]. Both studies found a shift of brain substrate from the hippocampus to VMPFC after a 24 h delay. Given the complex nature of schemas, these studies did not characterize the neural representation of schemas. As a result, schema matching was not directly measured at the representation level (i.e., no measures of similarity between the representations of new memory and those of existing long-term memories were employed).

To overcome this challenge, several studies have used MVPA fMRI to examine memory acquisition where a new memory shares overlapping features with old memories. They found that the VMPFC–hippocampal interaction is important for the integration [52] and novel inference [127] of schema-consistent memory. Guided by computational models, recent studies have started to provide a detailed description of neural representations of long-term knowledge such as objects [128], words [129], and semantics [130] in the brain. These studies provide a foundation to examine the interaction between new event and existing knowledge. Using this approach on a smaller set of words, one human study found that the semantic representation in the temporal pole, the so-called semantic hub, determined the likelihood of false memory in an independent memory test administered several weeks before or even on independent samples [131] (Figure 5B). Moreover, the within-subject neural-behavioral correlation was significantly stronger than the between-subject correlation, suggesting that each subject had a partially unique semantic representation that influenced false memory. This innovative study provides a powerful approach to examine how the structure/representation of existing semantic knowledge or schemas affects the formation of new episodic memories.

Both global matching and schema matching are operated on the similarity of representations, but they emphasize different aspects of representations. Whereas global matching emphasizes the impact of episodic context, schema matching is mainly determined by long-term, context-free, and structured knowledge (e.g., semantic). Meanwhile, memory gained from global matching and schema matching likely experiences different post-learning consolidation processes. It would be a fruitful direction for future studies to integrate computational learning models (e.g., CLST) and neural representational analysis to track the dynamic development of schemas, and to examine how schemas affect the acquisition, consolidation, and retrieval of new knowledge.

Concluding Remarks

The representational perspective of episodic memory has helped to achieve a deeper and synergistic integration of behavioral observations, formal computational models, and neuroimaging data. These studies have revealed multiple distinct neural processes and representations that give rise to episodic memory. In particular, memory strength for a given event not only depends on the neural activity associated with the same event during encoding and retrieval but is also affected by the interaction between encoding and retrieval, between the event and other events that co-occurred, and between the new event and pre-existing knowledge. Although these mechanisms (reviewed in separate sections previously) have so far been studied separately, they should act simultaneously and interactively to determine the characteristics of human episodic memory. Future efforts to track the formation of episodic memory and to

Outstanding Questions

How do different neural signals (e.g., categorical vs event-specific) from different brain regions (e.g., sensory cortex vs multimodality region vs hippocampus) converge and compete to support episodic memory decisions? How do their contributions vary according to task requirement and response strategies? Answering these questions requires a detailed characterization of the distributed and multifaceted nature of memory representations and decision-making processes.

Do these neural signals play a causal role in supporting memory experiences, including true versus false memory, recollection versus familiarity? As neuroimaging studies are correlational in nature, experimental manipulations that can introduce the gain and loss of particular memory functions (e.g., lesion; transcranial magnetic stimulation, TMS; transcranial direct-current stimulation, tDCS) would be very valuable.

What neural signals can reliably dissociate recollection and familiarity, as well as true versus false memory? Are there dissociations between objective neural memory signals and subjective memory experiences? Although addressing these questions has been the focus of many existing studies, more reliable neural markers are yet to be discovered.

How do the neural representations and processes underlying episodic memory change as a result of brain development (i.e., maturation and deterioration) and learning (e.g., knowledge accumulation)?

How do memory representations transform with repeated learning, active retrieval, and spontaneous reactivation? What are the neural mechanisms that underlie the coevolution of episodic memory and semantic memory? Addressing these questions will advance our understanding of the dynamic nature of human memory.

What are the neural mechanisms underlying the accommodation and assimilation of schemas, two crucial processes in human–environment interaction throughout development?

examine these complex interactions could help to fundamentally link episodic memory with various processes such as perception, attention, working memory, and the formation of semantic memory.

While still in its early stage, this line of research has clearly manifested the power of examining distributed neural activation patterns, as guided by formal computational models, in episodic memory research. These studies have not only broadened the questions that can be addressed with human neuroimaging studies but also achieved a much more detailed mechanistic understanding of the representations and processes underlying episodic memory. Certainly, there are many intriguing questions that remain to be answered (see Outstanding Questions). In addition to further elucidating the interactive and dynamic nature of human episodic memory, future studies should address the causal role of these neural representations in supporting the sophisticated and subjective experiences of episodic memory, such as recollection versus familiarity, and true versus false memory.

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