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Review article

From remembering to reconstruction: The transformative neural representation of episodic memory

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ABSTRACT

Although memory has long been recognized as a generative process, neural research of memory in recent decades has been predominantly influenced by Tulving's "mental time traveling" perspective and focused on the reactivation and consolidation of encoded memory representations. With the development of multiple powerful analytical approaches to characterize the contents and formats of neural representations, recent studies are able to provide detailed examinations of the representations at various processing stages and have provided exciting new insights into the transformative nature of episodic memory. These studies have revealed the rapid, substantial, and continuous transformation of memory representation during the encoding, maintenance, consolidation, and retrieval of both single and multiple events, as well as event sequences. These transformations are characterized by the abstraction, integration, differentiation, and reorganization of memory representations, enabling the long-term retention and generalization of memory. These studies mark a significant shift in perspective from remembering to reconstruction, which might better reveal the nature of memory and its roles in supporting more effective learning, adaptive decision-making, and creative problem solving.

1. Introduction

Memory, by definition, is the mental faculty that encodes, stores and retrieves information. The scientific research of memory has shifted in drastically divergent directions since its inception. Ebbinghaus, who deliberately used novel nonsense syllables to avoid the influence of existing long-term knowledge, documented our incredible ability to form precise memories in our brain and the law of forgetting (Ebbinghaus, 2013). Later, Tulving emphasized that *"[episodic memory] makes possible mental time travel through subjective time, from the present to the past, thus allowing one to re-experience, through autonoetic awareness, one's own previous experiences"* (Tulving, 2002). Other psychologists, however, took a different perspective to emphasize the imprecise, unreliable, malleable, and constructive nature of human memory. As Bartlett noted, *"Remembering is not the re-excitation of innumerable fixed, lifeless and fragmentary traces, but rather an imaginative reconstruction or construction"* (Bartlett, 1932). Subsequent studies by Schacter (Schacter, 1999) and Loftus (Loftus, 2005) revealed that our long-term memories are not faithfully reproduced but instead are distorted, leading to false memory.

The theoretical development of memory transformation is significantly advanced in reevaluating memory consolidation theory. Several alternative theories have been developed to address the limitations of standard consolidation theory (SCT) by emphasizing the never-ending and transformative nature of memory traces (Dudai et al., 2015; Moscovitch and Gilboa, 2021). More recently, researchers have expressed increasing enthusiasm to examine the neural representations underlying episodic memory (Xue, 2018). Using more sophisticated analytical approaches, recent studies have made significant strides in characterizing the representational formats in different brain regions, including low-level sensory, high-level conceptual and semantic, schematic, and contextual representations, as well as at various memory stages, including encoding, short-term memory maintenance, consolidation, and retrieval. When carefully comparing the representational contents and formats in different brain regions and memory stages, memory representations are clearly transformed within and across memory stages (Favila et al., 2020, 2018; Linde-Domingo et al., 2019; Wimmer et al., 2020; Xiao et al., 2017; Xue, 2018).

These advances prompt a shift in our current perspective of episodic memory from "reinstatement" to "reconstruction", which is characterized by the transformation of neural representations at various memory stages. Here, the term transformation specifically refers to the changes in representational formats and contents but not the overall change in

strengths, such as strengthening, weakening or forgetting.

The present paper will review recent progress in this area. I will first provide a brief historical review of the development of memory consolidation theories, which shifted significantly from the strengthening to transformation of memories. Building upon these models, the current review will focus on human studies that have directly examined the neural representations of memory and the representational transformation at different memory stages, including encoding, maintenance, consolidation and retrieval. I will start by describing recent methodological developments and the novel findings that characterize the multifaceted and distributed nature of memory representations. In the next three sections, I will focus on studies that characterize (1) the nature of memory representations and their transformation across various memory stages for a single event, (2) the representational transformation when multiple events are simultaneously activated, including memory updating, integration and differentiation, and (3) the transformation for the memory of sequential events, such as compressed, reversed and reorganized replay. I will conclude by discussing future directions under the transformative framework of episodic memory.

2. The transformation of memory consolidation theories

Formal theoretical models addressing memory transformation have primarily focused on memory consolidation. The term consolidation was coined to describe the observation that associative memories become resistant to interference after a certain period of learning (Müller and Pilzecker, 1900). Meanwhile, studies of patients with brain damage revealed more memory impairments for recent events than for remote events (Burnham, 1903; Korsakoff, 1889; Ribot, 1882). In the 1950 s, a series of studies showed that damage to the medial temporal lobes, particularly the hippocampus, caused severe and lasting anterograde amnesia but preserved more remote memories.

The classical standard consolidation theory (SCT) accounts for these findings by positing that the hippocampus plays an initial role in binding the content and context of an event into memory. During consolidation guided by the hippocampus, direct links among the memory components stored in the neocortex are strengthened, and links between the hippocampus and the neocortex are weakened (Squire and Zola-Morgan, 1991). As a result, consolidation involves a shift in the underlying neural substrates from the hippocampus to the neocortex, although researchers have not specified whether the nature of memory remains unchanged due to consolidation.

The differences between the hippocampal and cortical memories were emphasized by the model of complementary learning systems (McClelland et al., 1995). It posits that the hippocampus and the neocortices constitute a rapid and a slow learning system, respectively. The hippocampal system permits rapid learning of new items via synaptic changes. In contrast, the neocortex learns slowly to discover the structure in ensembles of experiences and gradually accommodates or assimilates the hippocampal memories into structured knowledge. To explain the findings of rapid cortical consolidation (Tse et al., 2007), a recent simulation based on this model has found that when high resonance exists between the new memory and existing knowledge, neocortical learning is activated and information is rapidly integrated into existing cortical knowledge networks (McClelland, 2013).

Meanwhile, although the SCT adequately accounts for the anterograde amnesia resulting from hippocampal damage, it is not compatible with the findings that the hippocampus is reliably involved in retrieving remote episodic memory (Nadel and Moscovitch, 1997). The multiple trace theory (MTT) addresses this limitation and proposes that the hippocampus forms a separate memory trace each time an old memory is retrieved (Nadel et al., 2000). As a result, the hippocampus is always involved in the retention and retrieval of episodic memories, regardless of the age of the memory. Meanwhile, older memories will have more nonoverlapping memory traces stored in the hippocampus than recent memories and thus are more robust to hippocampal damage. The context binding model (CBT) proposes an alternative account of anterograde amnesia in patients with hippocampal damage. Namely, the hippocampus is involved in binding items and context into episodic memory, and forgetting occurs due to contextual interference (Yonelinas et al., 2019). As recent memories share a greater overlapping context with new learning, they are more prone to interference and forgetting. Both models suggest that the hippocampus is involved in context-rich episodic memory, which is different than cortical memory.

Recent developments highlight the transformation of memory traces during consolidation. For example, the competitive trace theory (CTT) proposes that many partially overlapping memory traces will be present as memories age. The hippocampus can reconstruct memory using overlapping traces during memory retrieval to avoid competition or confusion. The resulting memory will be decontextualized and become more semantic. Therefore, the consolidation of events involves the transformation from episodic memory to semantic memory, which is accompanied by shifts in neural correlates from the hippocampus to the neocortex (Yassa and Reagh, 2013).

This idea that consolidation involves memory transformation is more systematically articulated in the recent trace transform theory (TTT). The TTT consists of several core principles. First, memory representations are multifaceted, including gist, semantics, schema, and episodes, each of which is supported by distinct neural substrates (Robin and Moscovitch, 2017; Sekeres et al., 2018). Second, following the principle of neural-psychological representation correspondence (NPRC)(Gilboa and Moscovitch, 2021), the TTT asserts that the shift in the neural substrates is also accompanied by the transformation of the psychological characteristics of memory. Consequently, memories will continue to depend on the hippocampus for retention and retrieval as long as they remain detailed and context-specific, but those relying less on the hippocampus as a result of consolidation would necessitate a transformation in memory representation, e.g., from episodic to semantic and schematic representations (Moscovitch and Gilboa, 2021).

In summary, the theoretical accounts of memory consolidation have been significantly transformed over the years. These developments emphasize that consolidation is dynamic, generative, and transformative, resulting in the modification and reconstruction of experience-dependent internal representations. In addition to the transformation of memory representations, other researchers suggest memory consolidation is a never-ending process; the once fixed memory will become labile again when it is reactivated and thus is subject to subsequent changes (Dudai, 2012).

Despite these theoretical developments, most supporting evidence for the TTT model is derived from the observed changes in expressed behaviors (such as the vividness, specificity, and generalization) and the shift in active brain regions (Moscovitch and Gilboa, 2021). Without directly examining the formats and contents of neural representations, the transformation of neural representation is largely inferred rather than observed. As will be discussed in detail below, several limitations to this inference have been noted. First, the definitions of the representations are primarily psychological and conceptual, which must be refined using neural data. Second, the map between the neural representations and behavioral performances might be complex and is modulated by many factors. Third, direct characterization of the neural representations and their changes in different brain regions might provide additional insights into the mechanisms of memory transformation. The last few years have witnessed the significant development of novel analytical methods to characterize memory representations and address these issues. In the next section, I will describe how these methods are used to advance our understanding of the nature of memory representations in distributed brain regions.

3. The multifaceted and distributed neural representations of memory

One primary goal and a major challenge in memory research is to

define and characterize memory representations. Psychological definitions of memory representations draw distinctions in terms of the content, precision, and subjective feelings. For example, researchers have distinguished between familiarity and recollection (Mandler, 1980), implicit and explicit memory (Jacoby, 1991), and verbatim and gist memory (Reyna and Brainerd, 1995). The implicit vs. explicit and familiarity vs. recollection distinctions refer to subjective feelings and the level of consciousness. In contrast, the gist/verbatim representation refers to the content and precision of memories. In particular, verbatim memory refers to memory of exact perceptual details, whereas gist memory refers to imprecise, "skeletal" or "generic" and essentially semantic representations. The TTT model makes a further distinction between gist, schema, and semantics. In particular, the gist of the event is a summary of its central elements without the peripheral details, schemas refer to the shared features across a series of similar events, and semantics refer to the conceptual aspect of an event (Moscovitch and Gilboa, 2021).

Building upon these conceptual developments, recent studies have tried to provide more direct characterizations of memory representations in different brain regions. This analysis is facilitated by several recently developed methods to examine the content and formats of memory representation in distributed brain regions. One potent

approach is to use various psychological and computational models to decompose the stimuli into specific features, such as different levels of perceptual representations, abstract and concrete semantic features, as well as time, place, and other episodic features (Fig. 1A). Meanwhile, we can characterize the neural representations using various features from neural data, such as single neuron spikes, multiunit response patterns, local field potentials, power and phase of the oscillations, regional activation patterns, and distributed connectivity patterns (Fig. 1B). Critically, using the representational similarity analysis framework (Kriegeskorte et al., 2008), we can link the neural representations with these model representations and infer the representational formats embodied in the brain activation pattern. Additionally, various decoding models (Fig. 1C) and inverted encoding models (IEM) (Fig. 1D) have been used to "read out" the specific information encoded in the brain. Using these novel approaches, we now have a deeper understanding of the nature of representations in different brain regions.

3.1. Different levels of perceptual representations in the sensory cortex

The majority of research on sensory representations is conducted in the visual domain. Based on accumulating evidence, the visual stimulus consists of a large number of visual features spanning many levels of
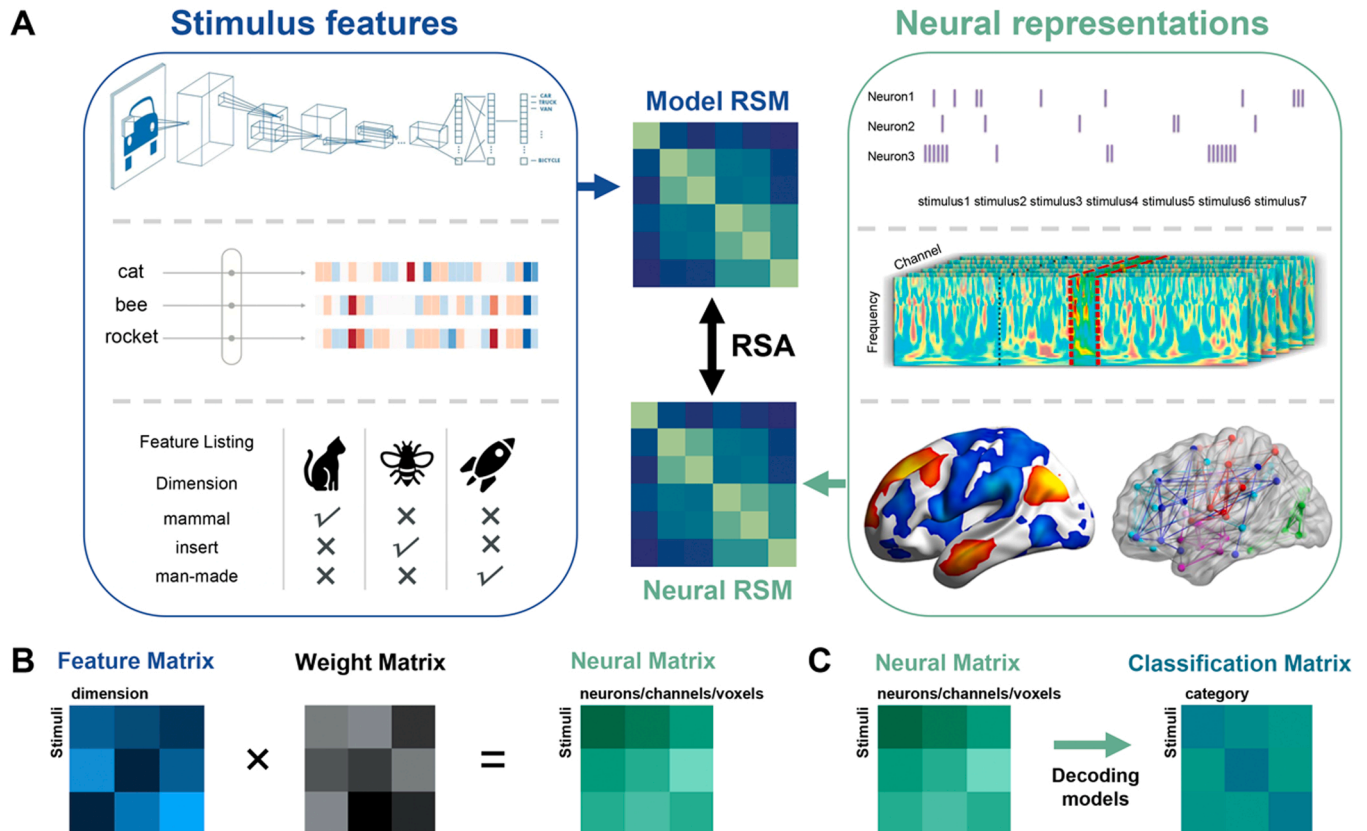

Fig. 1. Characterization of the contents and formats of memory representations. A. Linking the neural representations with different models using representational similarity analysis (RSA). Left panel: This schematic illustrates stimulus features generated by deep neural networks (DNN) for visual images (top panel) and words (middle panel) and by psychological models of objects that involve human ratings (bottom panel). The DNN models convert stimuli into high-dimensional features that usually do not have interpretable meanings, whereas the features in psychological models are usually more directly interpretable. Right panel: This schematic illustrates the neural representations measured across different levels of brain organization, including single neuron spikes, multiunit responses, regional activation patterns, and global connectivity patterns. Middle panel: The RSA framework. The similarity matrix for the stimulus set (i.e., representational similarity matrix, RSM) is constructed separately for features generated by computational and psychological models and features of neuronal responses using various algorithms to characterize the pairwise distances. The correspondence of the model and neural RSMs is then examined to infer the contents and formats of neural representations. B. Inverted encoding models used to read out the content of neural representations. In these models, the first step is to establish the mapping (weight matrix) between stimulus features and neural responses. Then, the content of unknown stimuli is reconstructed using its neural response pattern and the weight matrix. C. Decoding models used to read out the content of neural representations. Decoding models (i.e., classifiers) are first trained based on the neural responses and labels (e.g., visual category, semantic, and other features) of the training dataset, and this model is then used to determine the neural response to new stimuli and determine the probability of belonging to particular labels.

abstraction, from lower-level colors and orientations to middle-level shapes and textures and to high-level objects and actions (LeCun et al., 2015; Russ and Leopold, 2015; Zeiler and Fergus, 2014). Using the decoding approach on fMRI or EEG/MEG data, many studies have shown that information is reliably decoded in different regions along the ventral visual stream at different time points. However, knowing when and where discriminative information about visual objects occurs does not directly inform on the nature of these representations, such as whether they primarily reflect (low-level) visual features or (high-level) conceptual aspects of the objects (Clarke and Tyler, 2014). Other studies using inverted encoding models have successfully reconstructed the orientations (Ester et al., 2015) and faces (Cowen et al., 2014) from the activation patterns. However, these studies emphasize the similarity of the presented and reconstructed stimuli but did not examine their qualitative differences.

To date, deep learning provides the most comprehensive computational models to encode and extract hierarchically organized features from natural pictures or videos (LeCun et al., 2015). Specifically, the superficial layers are associated with lower-level visual features, such as contrasts and blobs, and intermediate layers reflect the processing of surfaces, textures, and object parts. In contrast, deeper layers are associated with increasingly complex features, such as objects and categories. By combining representational similarity analysis and deep neural network models, the different layers of DNN have been shown to be hierarchically correlated with neural activity along the visual stream (Cichy et al., 2016; Güçlü and Gerven, 2015; Kriegeskorte, 2015).

These methods are now increasingly used to examine the content and format of sensory/perceptual representations during working memory maintenance and retrieval. Emerging findings show the distributed nature of neural representations during working memory (Christophel et al., 2017; Dotson et al., 2018; Lee and Baker, 2016). For long-term memory, successful memory retrieval is accompanied by the reinstatement of encoded representation in the sensory cortex (Ritchey et al., 2013; Staresina et al., 2012; Tompary et al., 2016; Yaffe et al., 2014; Zhang et al., 2015).

Despite similar representations during encoding, maintenance, and retrieval, very few studies have directly compared representations at different memory stages, which will inform us on whether representations are transformed. Even less studies have been performed to specify the nature of representations during maintenance and retrieval, which can be achieved using the same DNN models. I will return to this issue in the next section.

3.2. The embodied and symbolic forms of semantic representation

In addition to perceptual representation, another important form of representation is conceptual/semantic representations. A clear distinction between perceptual and conceptual/semantic representations is complicated. By definition, conceptual representations refer to features of an item that reflect its functions or value rather than its physical appearance (Noppeney and Price, 2004). For example, conceptual features of an orange might be "a great source of vitamin C" and "grows in sunny places", whereas "round shape" and "sweet taste" refer to sensory features.

Binder and colleagues proposed 65 experiential features to represent semantics covering sensory, motor, spatial, temporal, causal, social, emotion, drive, and attention (Binder et al., 2016). These features, however, have not been systematically used to characterize semantic representations in episodic memory or to draw distinctions between semantic and perceptual representations. In practice, perceptual and semantic aspects are inferred based on whether one could recall the exact item and its perceptual details compared with its name or meaning. Perceptual and semantic memories are also loosely inferred based on the involved brain regions. For example, the posterior sensory regions are involved in perceptual memory, whereas the anterior regions are involved in semantic memory.

Recently, several corpus-based models derived from natural language processing (NLP) have been used to examine semantic representations. These models are based on the hypothesis that lexemes with similar linguistic contexts have similar meanings (Harris, 1954). The semantic representations are then achieved by counting the co-occurrences, e.g., latent semantic analysis (Landauer and Dumais, 1997), or building prediction models, e.g., word2vec (Mikolov et al., 2013), from a large corpus. Recent models, such as BERT (bidirectional encoder representations from transformers) (Devlin et al., 2018) and GPT-3 (generative pretrained transformer 3) (Brown et al., 2020), better characterize the word meaning in a particular context.

Several issues should be noted when using corpus-based models to characterize semantic representations. First, unlike the feature models (Binder et al., 2016),

these corpus-based models only examine the overall semantic similarity but do not specify the semantic features. Second, using representational similarity analysis to associate neural representations and semantic representations, the corpus-based model contributes mainly to the decoding of sentences containing linguistically oriented "abstract" words. In contrast, the model based on experiential features improves the decoding of more concrete sentences (Anderson et al., 2019). Third, the corpus-based model nevertheless identifies some perceptual information of the corresponding objects, as the semantic representation of words generated based on the word2vec model is strongly correlated with the visual similarity of the corresponding pictures based on Alexnet (Liu et al., 2020). These results are consistent with the dual form model of semantic representation based on sensory-deprived subjects (e.g., congenitally blind) (Striem-Amit et al., 2018; Wang et al., 2020), which proposes that semantics contains both sensory/motor experience and a non-sensory, language-derived representation (Bi, 2021).

Together, existing studies have refined the definition of semantic representations and have provided useful models that might be readily used to examine semantic representations during episodic memory.

3.3. Spatial and temporal context representation in the hippocampal-entorhinal system

An emerging consensus in the memory field is that the hippocampus does not represent object information per se but is involved in binding events into the spatiotemporal context (Yonelinas et al., 2019). Any internally and/or externally generated and temporally adjacent events, as well as spatial, temporal, or other details, might be defined as context. In practice, the context mainly refers to the spatial and temporal information surrounding the events. According to the temporal context or temporal drift model (Howard et al., 2005), the context refers to the randomly and slowly changing neuronal background activity present at the time of encoding and to which an episodic element is 'tagged.' In addition to the one-shot, slowly and randomly drifting temporal context, a well-trained, highly predictable sequential context also exists. One example of the latter type of context is the CA1 "time cells", which showed context-specific activities at unique time points of an experience when animals traveled along with well-trained spatiotemporal sequences (MacDonald et al., 2013).

The hippocampal-entorhinal system carries representations of both types of spatiotemporal context. For example, a human fMRI study found that the spatial and temporal aspects of autobiographical experiences are coded within the hippocampus across various scales of magnitude (Nielson et al., 2015). In addition, the hippocampal representation can differentiate items with different temporal distances and is sensitive to event boundaries (Ezzyat and Davachi, 2014). Meanwhile, the hippocampus also carries sequential information about objects and differentiates the same object that appears in different sequential contexts (Hsieh et al., 2014).

A recent study provided substantial evidence to support the role of the hippocampus in these aspects of context representations. In this study, participants were trained to use the method of loci (MOL) to

memorize word orders. The study yielded several relevant results. First, it showed temporal context reinstatement during retrieval in the hippocampal CA1 area, with greater pattern similarity for item pairs studied at closer versus more distant temporal intervals. Second, the hippocampal representation was modulated by sequence boundaries, showing lower cross-boundary similarity than within-boundary similarity. Third, the hippocampal representations were modulated by the sequential distance and spatial location of the loci (C. Liu et al., 2021; J. Liu et al., 2021; Y. Liu et al., 2021).

3.4. Schema representation in the VMPFC and hippocampus

The concept of schemas, developed by the British psychologist Frederic Bartlett, refers to the preexisting 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 other parameters (Gilboa and Marlatte, 2017; Preston and Eichenbaum, 2013).

Several lines of evidence suggest that the VMPFC and hippocampus are involved in the acquisition and representation of schemas (Gilboa and Marlatte, 2017; Moscovitch and Gilboa, 2021; Preston and Eichenbaum, 2013; Xue, 2018). The VMPFC may support the detection of 'resonance' (Van Kesteren et al., 2012) or the 'goodness of fit' between incoming information and this activated schema (Gilboa and Moscovitch, 2017; Hebscher and Gilboa, 2016; Moscovitch and Winocur, 2002) and then biases the engagement of neocortical and hippocampal learning. In particular, although schema-inconsistent memory is encoded in the hippocampus, schema-consistent memory is encoded via VMPFC-hippocampal interactions (Brod et al., 2016; Tse et al., 2007; van Kesteren et al., 2010). Sensitivity to schema consistency was reduced in patients with VMPFC damage (Spalding et al., 2015). The authors of one human study trained subjects with paired associations over several months and reported a shift in the brain substrate from the hippocampus to the VMPFC. The encoding of novel information into the acquired knowledge was also supported by the VMPFC (Sommer, 2017).

Given the complex nature of schemas, few studies have directly mapped the neural representation of schemas. Recently, Baldassano and colleagues presented subjects with stories conforming to two familiar but different scripts, i.e., eating at restaurants and going through the airport. They found that the VMPFC, together with the posterior medial cortex (PMC) and superior frontal gyrus (SFG), exhibited sequences of activity patterns that were specific to each of the two scripts but generalized across stories, modalities, and subjects. In addition, presenting events in a scrambled order disrupted schematic effects on the MPFC (Baldassano et al., 2018). The strength of the schematic representations during encoding potentially predicts subsequent recall (Masís-Obando et al., 2022). In another study, researchers designed three virtual cities that shared a common spatial layout with partially shared stores and found that the VMPFC represented an abstract spatial layout that was generalized across cities (Zheng et al., 2021).

3.5. Cognitive map in the entorhinal cortex and medial prefrontal cortex

Similar to schema, the cognitive map (Tolman, 1948) is also a systematic organization of knowledge that might facilitate new learning. Unlike schema, the cognitive map is characterized by its role in enabling the flexible generalization of knowledge to solve novel problems. For example, after becoming familiar with the environment, rats may form a cognitive map that allows them to take shortcuts to reach rewards (Tolman and Honzik, 1930) or find new routes when old ones are blocked (Tolman et al., 1946). Although the study of the cognitive map has traditionally focused on spatial navigation in rodents, emerging studies have been conducted in humans across various cognitive domains.

Spatial navigation is primarily supported by "Place" cells in the hippocampus (O'keefe and Nadel, 1978) and "Grid" cells in the medial entorhinal cortex (Hafting et al., 2005). Human studies have shown that this grid modulation during navigation occurs in both the LEC and the VMPFC (Chen et al., 2021; Doeller et al., 2010; Jacobs et al., 2013; Kunz et al., 2015). Neurobiologically inspired computational models suggest that the grid representations in the EC might reflect basal functions for statistical transitions in two-dimensional (2D) topologies that can, in principle, enable animals and artificial agents to compose new routes and find shortcuts to reach goals in spatial environments (Banino et al., 2018; Behrens et al., 2018; Whittington et al., 2020).

The transfer of learning has also been examined in reward learning. When rodents are trained to discriminate a rewarding stimulus from an unrewarding stimulus, they exhibit increasingly better abilities to learn new discriminations (Harlow, 1949). This transfer requires an abstract representation of the structure of the task, abstract representations of the relationship between stimuli, contingency of the reward, and other processes, which is termed a cognitive map of the task space (Wilson et al., 2014). Human neuroimaging studies have found that the VMPFC/OFC represents a cognitive map of task space during reinforcement learning (Schuck et al., 2016), which is associated with task performance.

In addition to spatial navigation and reward learning, the cognitive map has also been examined in other cognitive domains. For example, the grid-like hexagonally neural code has been observed in nonspatial stimulus dimensions, including the sound frequency (Aronov et al., 2017), odor concentration (Bao et al., 2019), and artificial conceptual spaces (Constantinescu et al., 2016). According to a recent study, humans use a grid-like code in the entorhinal cortex and medial prefrontal cortex to infer direct trajectories between entities and guide discrete decisions (Park et al., 2021).

In summary, significant progress has been achieved in understanding multifaceted and distributed memory representations in the brain, including hierarchical sensory representations, embodied and abstract semantic representations, spatiotemporal contextual representations, and structured knowledge representations (i.e., schema and cognitive maps) in various domains. These findings allow researchers to describe the content and format of memory representation in great detail, which have also operationalized (e.g., context and schema), enriched (verbatim), and clarified (e.g., semantic) some definitions of memory representations and call for a more precise definition of other terms (e. g., gist).

4. Rapid and continuous transformation of memory representations

Building upon these deep insights into the nature of neural representations, an increasing number of studies have examined representations during different memory stages and in different brain regions, which helps elucidate the dynamic and transformative nature of memory representations. This section will review new findings on the representational transformation during encoding, short-term maintenance, and retrieval by focusing on a single event (Fig. 2).

4.1. Representational transformation during encoding

As described above, perception includes a series of feedforward processing steps along a hierarchically organized neural pathway, during which different forms of neural representations are formed in corresponding regions. Through feedback processing (Kietzmann et al., 2019), the representations also change dynamically within single areas (Ghuman and Martin, 2019). For example, a nonhuman primate study showed that V1 neurons respond to visual orientation bars during early encoding but exhibit effects of contour integration 50–100 ms later that likely reflect feedback from V4 (Liang et al., 2017). Similar evidence has been obtained from an iEEG study showing that FFA first identifies face-specific information at ~50–75 ms after the onset of face images
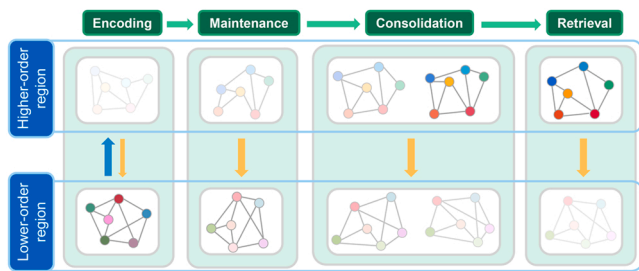
Fig. 2. Transformation of representations across memory stages. The incoming information flows through lower- to higher-order brain regions during encoding, with more abstract information represented in the higher-order areas. Meanwhile, the higher-order regions interact with the lower-level regions to reshape the representations according to task requirements or assimilate them into preexisting knowledge representations. During maintenance, the representations have been transformed in both representational formats and brain regions: from lower- to higher-level visual features in the first second of the post-encoding maintenance period, as reflected by the decay of the representational strength of lower-level features and an increase in the representational strength of higher-level features. After maintenance, the representational patterns continue to transform during a consolidation stage that may occur during rest or sleep. During retrieval, the representations of stimuli become predominantly semantic, and the representations of lower-level features become much weaker. (The intensity of the color and the changing patterns of the circles indicate representational strengths and transformations, respectively.).

and then forms invariant face identities at 200–500 ms, which might result from recurrent top-down and bottom-up interactions (Ghuman et al., 2014).

Several studies have shown that this dynamic encoding processing varies systematically across subjects (Chadwick et al., 2016; Xiao et al., 2020) and materials (C. Liu et al., 2021; J. Liu et al., 2021; Y. Liu et al., 2021), which affects subsequent memory performance. For example, one human study revealed that the semantic representation in the temporal pole, the so-called semantic hub, correlated with the likelihood of false memory in an independent memory test (Chadwick et al., 2016). The within-subject neural-behavioral correlation was significantly more substantial than the between-subject correlation, suggesting that each subject had a partially unique semantic representation that influenced memory. According to a recent study, greater representational transformations during encoding, which are characterized by the fast and prominent emergence of abstract semantic representations, are associated with better subsequent long-term memory performance (C. Liu et al., 2021; J. Liu et al., 2021; Y. Liu et al., 2021).

These results provide neural representation evidence to support the hypothesis that effective memory encoding entails interactions between external inputs and preexisting knowledge (Gilboa and Marlatte, 2017; Moscovitch et al., 2016; Xue, 2018). This representational transformation during encoding further suggests that existing knowledge facilitates memory encoding by assimilating the neural representations of incoming information. Consistently, schema-consistent pairs have been shown to involve additional semantic and associative-binding processes (Liu et al., 2016). Furthermore, existing knowledge might shape the neural representations of perceived features over time (Bein et al., 2020; Hasson et al., 2015). Interestingly, the items showing greater transformation from perceptual to semantic representation were also associated with greater item-specific representations, which mediated the effect of representational transformation and subsequent memory (C. Liu et al., 2021; J. Liu et al., 2021; Y. Liu et al., 2021). Based on these results, the transformed neural representations might be more readily integrated into existing long-term knowledge and be stabilized via a fast, cortical consolidation mechanism. This hypothesis could be tested by examining the microstructural plasticity in the cortical regions using diffusion-weighted magnetic resonance imaging and functional tests of brain activity (Brodt et al., 2018).

4.2. Transformation during short-term memory maintenance

According to the sensory recruitment hypothesis of visual short-term memory (VSTM), the same brain regions engaged in sensory processing are also active during WM maintenance (Scimeca et al., 2018). Consistently, many studies have shown that simple visual features are decoded or reconstructed during working memory maintenance (Oh et al., 2019; Yu and Shim, 2017). Recent studies, however, have revealed significant transformations during short-term maintenance in both brain regions and representational formats, which challenge the strict sensory recruitment hypothesis.

Regarding brain regions, recent studies emphasize the contributions of parietal and prefrontal cortices to VSTM storage (Bettencourt and Xu, 2016; Xu, 2017). These regions carry distinct neural representations, and their involvement depends on various factors, including the complexity of the stimulus, task requirements, and interference. For example, using a computational model to separate the guessing rate and precision of simple visual information maintained in working memory, several studies suggest that precision depends on the early visual cortex (Jia et al., 2021; Rademaker et al., 2019; Zhao et al., 2020). However, the sensory representation during working memory is abolished (Bettencourt and Xu, 2016) or shows reduced fidelity (Lorenc et al., 2018; Rademaker et al., 2019) in the presence of a distractor. In contrast, the intraparietal sulcus (IPS) shows robust representations when predictable distractors are present (Bettencourt and Xu, 2016; Rademaker et al., 2019). Although the IPS also showed a transient shift toward the orientation of the distractor after distraction presentation, the orientation was shifted back to the target orientation before the response (Hallenbeck et al., 2021; Lorenc et al., 2018). Perceptual training also enhances the parietal representation of the working memory content (Jia et al., 2021). Together, these results suggest that the parietal representation might provide a robust representation to support short-term memory in the presence of distractions.

Several studies have subsequently revealed differences in representational formats between encoding and maintenance. Using a visual DNN, a recent study showed that higher-order complex visual formats rather than early visual formats were shared between perception and visual imaginary (Xie et al., 2020). Similarly, using pictures rather than simple colors, orientations, or contrasts as stimuli, an iEEG study found that only high-level perceptual and abstract semantic information (i.e., after regressing out the visual representations from the semantic representation) was maintained during working memory (Liu et al., 2020). Furthermore, target memory representations are protected in the parietal cortex by storage in a different format from that used to represent sensory information in the presence of a distractor (Rademaker et al., 2019). Corroborating these results, classifiers trained on perceptual data better classify perceptual than imagery data (Zeithamova et al., 2012), and an "imagery" classifier outperforms a "perceptual" classifier in classifying imagery data (Albers et al., 2013).

Given these differences between encoded and maintained neural representations, a follow-up question is when does the transformation occur? Several studies have shown that working memory is a dynamic process that involves a substantial and continuous transformation (Fan et al., 2021; Stokes, 2015; Stokes et al., 2013). However, this dynamic processing might either reflect the encoding of information along the ventral visual stream (Cichy et al., 2014), the transformation of perceived stimuli into internal representations (Stokes et al., 2013), or the mapping of VSTM representations onto appropriate motor plans (Spiegel et al., 2013). A recent iEEG study used an extended maintenance period (7 s) to separate these processes and revealed relatively stable neural representations in the maintenance period (Liu et al., 2020), consistent with previous animal findings that after initial dynamic coding processes, task-relevant neural representations in VSTM may be retained in a relatively stable format (Stokes, 2015). Importantly, by carefully examining the changes in the representation across encoding and short-term memory maintenance, researchers found

substantial transforms in the first second of the maintenance period (Liu et al., 2020), suggesting a rapid transformation of the representations after stimulus offset.

4.3. Transformation during post-encoding reactivation and retrieval

For long-term memory, successful memory retrieval is accompanied by the reinstatement of neural representations during encoding (Estefan et al., 2019; Jafarpour et al., 2014; Polyn et al., 2005; Ritchey et al., 2013; Staresina et al., 2012; Staudigl et al., 2015). Challenging the pattern reinstatement hypothesis of memory retrieval, recent studies have also provided strong evidence for the transformation of representations from encoding to retrieval.

Convergent evidence has shown that late, abstract, and semantic representational formats support long-term memory. First, scalp-EEG studies suggest that the stability of representations across repetitions in late time windows (500 ms after stimulus onset) supports subsequent memory (Feng et al., 2019; Lu et al., 2015). Second, similar to short-term memory periods in which representations from a late encoding time window are maintained (Liu et al., 2020), representations from a late encoding phase (approximately 1000–2000 ms after stimulus onset) are reinstated during successful memory retrieval (Yaffe et al., 2014; Zhang et al., 2018), whereas greater encoding-retrieval similarity with stimulus-specific representations from an early processing period is observed for forgotten items (Zhang et al., 2018). Third, item-specific representations were detected in the visual cortex during encoding but in frontoparietal cortices during retrieval (Favila et al., 2018; Xiao et al., 2017). Using a visual DNN model and a semantic model to examine the perceptual and semantic formats during retrieval, a recent iEEG study showed that memory retrieval involves strong abstract semantic representations but lacks perceptual representations (C. Liu et al., 2021; J. Liu et al., 2021; Y. Liu et al., 2021).

The transformation of neural representations from encoding to retrieval was further observed by directly comparing the nature of representations in the two memory stages. One fMRI study systematically examined pattern similarity during encoding, retrieval, and between encoding and retrieval (ERS) (Xiao et al., 2017). The authors proposed that if item-specific ERS is smaller than that during both encoding and retrieval, then the retrieved representations must be transformed rather than being weakened. Supporting this hypothesis, the authors observed significant item-specific representations during encoding in the visual cortex and item-specific representations during retrieval in the parietal lobe but no item-specific ERS in either region. This result was replicated in a later study (Favila et al., 2018). A recent iEEG study compared representations during encoding, maintenance, and retrieval and revealed significant item-specific encoding-maintenance similarity and maintenance-retrieval similarity, but not item-specific ERS (J. Liu et al., 2021; Y. Liu et al., 2021; C. Liu et al., 2021). Using a cross-subject representational analysis, the patterns observed in many higher-order cortical regions during recall are more similar between participants than between encoding and retrieval of the same participant, suggesting that the encoded memories are transformed into shared representations (Chen et al., 2017). A subsequent study suggested that this transformation might be achieved by a stage-specific representational strength and cross-region reinstatement from encoding to retrieval (Xiao et al., 2020). These results together suggest a continuous transformation from encoding to maintenance to retrieval, resulting in different representations between encoding and retrieval.

Transformations of perceptual to semantic representational formats might occur during the post-encoding consolidation (Dudai et al., 2015; Moscovitch et al., 2016). Reactivation during the postlearning rest (Tambini and Davachi, 2019) and sleep (Diekelmann and Born, 2010) periods has been systematically reviewed, focusing on how reactivation might strengthen memory traces. Interestingly, weaker memories are replayed more frequently during the subsequent rest period, and more replay predicted better subsequent memory for these items (Schapiro et al., 2018). One recent study documented that stimulus-specific activity from a late encoding stage was reactivated during offline periods and sleep (Zhang et al., 2018). Notably, memory reactivation during wakefulness and sleep might result in different changes. While memory reactivation during sleep may lead to strengthening, reactivation during awake rest could exert a destabilizing effect (Diekelmann et al., 2011). More studies are needed to examine the representational formats during the post-encoding awake and sleep periods and how reactivation in these periods further transforms memory representations.

Recent studies further suggest that retrieval is a constructive process that transforms memory representations. For example, the temporal order of these multifaceted representational formats was reversed from encoding to retrieval in several studies (Griffiths et al., 2019; Linde-Domingo et al., 2019; Mirjalili et al., 2021). Compared to repeated learning, repeated retrieval practice not only strengthens the target memory (Karpicke and Roediger, 2008) but also transforms memory representations, resulting in greater reliance on the frontoparietal region than on the visual cortex (Ye et al., 2020). As a result, the brain might rely less on sensory information for mnemonic decisions with retrieval practice. Another study found that retrieval practice increased both hit and false alarm (FA) rates to similar lures, which was predicted by the item-level and category-level reactivation during retrieval practice, respectively (Lee et al., 2019). A recent study reported a similar behavioral effect of retrieval practice on increasing both true and false memory, and these behavioral changes were associated with representational changes in the posterior parietal cortex and medial temporal lobe (Zhuang et al., 2022). These results provide neural accounts of the behavioral findings that retrieval practice does not improve the quality of sensory memory (Sutterer and Awh, 2016) and may even promote gist-based false memory (McDermott, 2006).

Several possibilities might account for the discrepancies between item-specific encoding-retrieval similarities reported in earlier studies (Ritchey et al., 2013; Staresina et al., 2012) and the substantial transformations observed in the studies described above. First, several previous studies either examined neural pattern reinstatement at the category level (Jafarpour et al., 2014; Polyn et al., 2005; Staresina et al., 2012) or did not test item-specific representational reinstatement (Staudigl et al., 2015). These findings may thus reflect reinstatement at a relatively coarse categorical level rather than at a fine-grained item level. Second, several studies have tested long-term memory using recognition memory tests, in which item-specific pattern similarity may be introduced by shared perceptual inputs (Estefan et al., 2019; Ritchey et al., 2013). Finally, one study used a cued-recall task and found item-specific encoding-retrieval similarity (Yaffe et al., 2014). However, words were used as materials in this study, and neural reinstatement was observed in higher-order brain regions (e.g., hippocampus and anterior temporal lobe) where visually invariant semantic representations are encoded. Thus, reinstatement in this study may be based on semantic rather than stimulus-specific perceptual information.

Taken together, accumulating evidence suggests rapid and substantial memory transformations at various memory stages when the rich representations of a single event are examined and compared. This transformation from encoding to maintenance and retrieval is characterized by a shift of neural regions from the early sensory cortex to higher-order sensory and semantic areas. The neural representations were substantially transformed within the same brain regions, likely due to an interaction between incoming novel information and existing long-term knowledge. Across encoding, maintenance, spontaneous reactivation, and memory retrieval, the effect of long-term knowledge becomes increasingly stronger (Fig. 2). These interactions might facilitate the assimilation of novel information into existing knowledge and thus support the long-term retention and generation of memory.

5. Transformation during the study and reactivation of multiple events

Learning usually involves the presentation of several events and the reactivation of partially overlapping events. Due to the interactive nature of memory representations (Xue, 2018), the simultaneous activation of multiple memory representations will lead to representational and behavioral changes, such as integration and differentiation. With repeated exposure to partially overlapping events, the contextual information becomes less salient, semantic content can be extracted, and schemas can be formed (Fig. 3).

5.1. Memory transformation via goal-directed updating

Adaptive behaviors require the updating of memory in the changing environment, such that old memories are replaced with new memories (Fig. 3A). Existing studies in the reconsolidation literature suggest that reactivated memory might be updated by behavioral methods, including retrieval-extinction (Schiller et al., 2010), counterconditioning (Goltseker et al., 2017), and interference approaches (James et al., 2015). When subjects were asked to replace the old A-B memories with the new A-C memories, neural representational analyses revealed increased reactivation of new C memories and reduced reactivation of old B memories after memory updating (Kluen et al., 2019; Ye et al., 2020).

This updating has been achieved by selectively strengthening (Jonker et al., 2018) or weakening (Wimber et al., 2015) coactivated memories, and the lateral prefrontal cortex (LPFC) may regulate reactivated memories to support these goal-directed memory changes (Kluen et al., 2019; Kuhl et al., 2012). For example, intentional suppression of memory retrieval reduces hippocampal activity (Hulbert et al., 2016) and memory representations in the sensory cortex (Fellner et al., 2020; Meyer and Benoit, 2022) via control mechanisms mediated by the LPFC. For target memory, LPFC activation is positively correlated with cross-repetition representational similarity and subsequent memory performance (Xue et al., 2013; Zheng et al., 2018). Anodal stimulation of the LPFC enhances representational similarity and improves memory (Lu et al., 2015).

In addition to selectively strengthening and weakening memory components, a recent study found that motivated forgetting also transforms memory representations. Using intracranial EEG recordings from the lateral prefrontal cortex and temporal cortex, researchers found that memory traces of successfully remembered items show stronger encoding-retrieval similarity (ERS) in gamma frequency patterns. In contrast, the ERS of item-specific memory traces of actively forgotten items depends on the activity at alpha/beta frequencies. Interestingly, intentional forgetting relies more on top-down inhibitory connections than intentional remembering. This connectivity pattern and top-down information flow are also integrated into the memory traces of intentionally forgotten items (Ten Oever et al., 2021). This study nicely shows how goal-directed processes potentially transform memory representations to support adaptive memory updating.

5.2. Representational differentiation to reduce interference

Beyond memory updating, a growing literature suggests that the brain may differentiate coactivated memories and hence increase memory flexibility in different contexts (Fig. 3B). In particular, the brain may transform its representations during short-term memory maintenance to render the distractor less similar to the target. For example, a behavioral study showed that when the second interference served as a to-be-ignored distractor, the first target grating was shifted toward the distractor orientation (Rademaker et al., 2015). Using IEMs, Yu et al. (2020) found that the orientation and location representation of the distractor was rotated relative to the target in the visual cortex and IPS, respectively (Yu et al., 2020). In the 2-back memory task where the same item served as a distractor and target in different trials, the representational format of the orientation was remapped into a rotated representation when it was unprioritized and then mapped back into its initial format when subsequently prioritized (Wan et al., 2020). These studies indicate flexible remapping based on priority, which increases the distance between prioritized and unprioritized items to protect the target representation.

The conflict may be greater when the coactivated representations partially overlap. Existing studies have shown that the hippocampal DG area contains pattern separation mechanisms to orthogonalize similar inputs (Yassa and Stark, 2011). In addition to this widely accepted pattern separation mechanism revealed by MVPA (Lohnas et al., 2018), learning might also reduce the similarity of overlapping events. For example, one study directly compared the change in pattern similarity of related memories before and after learning, showing that reduced pattern similarity of related memories within the hippocampus as a result of interleaved retrieval and restudy correlated with
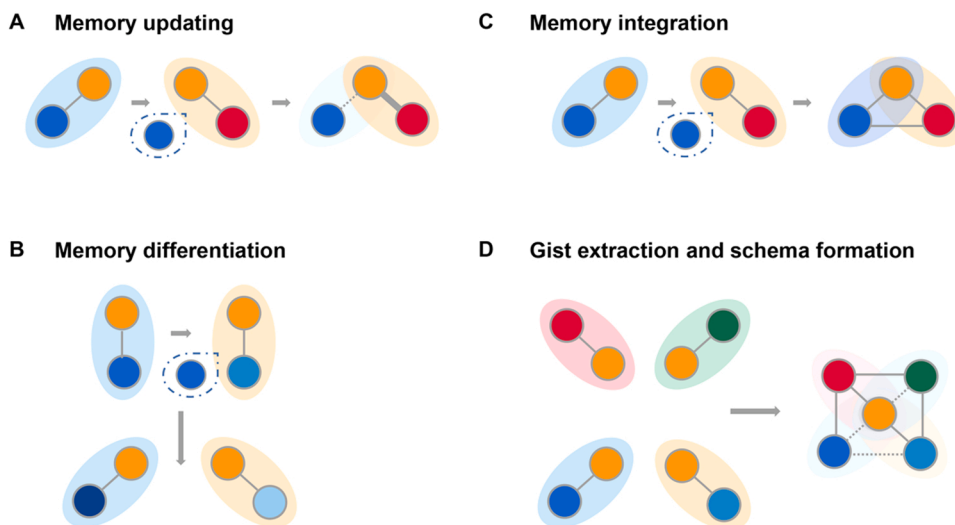

A Memory updating

B Memory differentiation

C Memory integration

D Gist extraction and schema formation

Fig. 3. Memory updating, differentiation, integration, and schema formation. Circles represent either episode elements or schema units, and lines connecting the circles represent their associations. The thickness of the lines indicates the association strength. A. Memory updating. When old memories are reactivated and enter into a labile state, a new experience may change or update the reactivated memories, create associations with old memories, and disrupt old associations. B. Memory differentiation. Overlapping events may be differentiated to reduce interference via pattern separation and "repulsion", resulting in nonoverlapping memory representations. C. Memory integration. The overlapping element (the yellow circle) triggers the reactivation of memories of prior experiences (the blue circle). Old and new memories are then integrated to form an association among the three elements. D. Gist extraction and schema formation. When multiple events sharing similar elements are learned, the overlapping elements may be extracted as gist, and structured knowledge (i.

e., a schema) is formed according to the relationships among the elements in memory space.

retrieval-induced facilitation of competing memories (Hulbert and Norman, 2015).

Learning also triggers an additional "repulsion" among hippocampal representations, i.e., the similarity among overlapping events is *lower* than the similarity among nonoverlapping events. For example, these hippocampal representations of overlapping routes (Chanales et al., 2017), overlapping item pairs (Favila et al., 2016), overlapping object sequences (Hsieh et al., 2014), or overlapping episodic contexts (Dimsdale-Zucker et al., 2018) become more distinct than nonoverlapping pairs. Several studies reported a lower pattern similarity for spatially near than far items (Kunz et al., 2019; Kyle et al., 2015), and the CA2/3 and DG regions showed lower pattern similarity when both spatial and temporal information was correctly retrieved than when only spatial or temporal information was retrieved (Copara et al., 2014). Using a "method of loci" strategy to encode multiple items in the same loci, a recent study obtained clear evidence of representational "repulsion" for both spatial and sequential information. In particular, lower pattern similarity for items encoded in the exact location than in different locations was observed in the CA1 region during retrieval, and representations of more adjacent pairs were more distinct than representations of more distant pairs in the CA2/3 and DG regions (J. Liu et al., 2021; Y. Liu et al., 2021; C. Liu et al., 2021). According to a recent study, the decorrelation of similar memory representations was temporally coupled with the behavioral expression of interference resolution (Wanjia et al., 2021), providing direct evidence that neural repulsion contributes to the resolution of episodic memory interference in humans. In summary, these results suggest that hippocampal representations may be flexibly configured to reduce interference and improve the precision of episodic memory.

5.3. Memory transformation as a result of reactivation-based integration

Other studies have shown that old reactivated memories are integrated into a new memory and context (Fig. 3C). An early behavioral study showed that when participants had been reminded of List 1 (studied on Day 1) before studying List 2 (on Day 2), they showed more intrusions from List 2 items when recalling items from List 1 (Hupbach et al., 2007). This effect is time dependent, such that the cross-list intrusion does not occur immediately but only on Day 3. Notably, although these results are viewed as evidence for memory reconsolidation, alternative accounts, such as reactivation-induced memory integration, have also been suggested (Gisquet-Verrier and Riccio, 2018). This integration account is also supported by the simulation based on the temporal context model (Sederberg et al., 2011). Integration might also occur when the new memories are semantically related to the old memories (Antony et al., 2022; C. Liu and G. Xue, 2022).

Using representational similarity analysis, a series of studies using the AB-AC paradigm showed that old B memory is reactivated during later AC learning, which is directly related to behavioral performance that reflects memory integration (Schlichting et al., 2015). Another study using the AB-AC paradigm found that the MPFC represents integrated memories, but only one week after AC learning (Tompary and Davachi, 2017). In a cleverly designed study, Collin and colleagues asked subjects to first study three seemingly unrelated events A, B, and C from a narrative. They then sequentially presented subjects with two linking events that allowed subjects to directly link A-B and B-C events. They found that the hippocampus represented the integrated narratives at different scales: the posterior hippocampus represented the most recently directly associated events, the middle hippocampus concurrently represented multiple directly associated events, and the anterior hippocampus represented the whole narrative, including the linked A-B and B-C events and the inferred A-C events (Collin et al., 2015).

In these paradigms, the old memory is spontaneously reactivated during new learning. If we potentiate the reactivation of an old memory, then a more robust representational integration will occur. One study using the same AB-AC learning paradigm compared two types of AC

learning, restudy and retrieval practice, to test this hypothesis. During retrieval practice, subjects must recall the newly learned AC memory instead of repeatedly studying AC memory (e.g., the restudy condition). Compared to repeated learning, retrieval practice resulted in greater reactivation of the old B memory and interestingly more integration (and differentiation) of old and new memories in the MPFC (Ye et al., 2020). These results support the role of the MPFC in integrating and updating reactivated memory traces (Gilboa and Marlatte, 2017; Schlichting and Preston, 2015). Specifically, they are consistent with the hypothesis that retrieval practice will lead to the reactivation of related memory traces. The MPFC might develop integrated neocortical representations of these memory traces resembling the characteristics of rapid system consolidation (Antony et al., 2017).

5.4. Factors that affect the fate of reactivated, overlapping memories

As described above, existing studies have revealed a mixed picture regarding the outcomes of reactivated, partially overlapping memories, including strengthening, weakening/erase, integration, and/or differentiation. In addition to the goal-directed representational changes, these complex results might be attributed to several additional factors, including the strength of the old and new memories and their similarities (Antony et al., 2022; Liu and Ranganath, 2021). For example, strong and consolidated old memories are more likely to be differentiated from and integrated with new memories than to be replaced by new memories (Ye et al., 2020). The hippocampus discriminates events that share either item information (similar items) or context information (same contextual cue) but generalizes across events when they share similar item-context associations (Libby et al., 2019).

In addition, the degree of memory reactivation potentially affects its outcome. According to the nonmonotonic plasticity hypothesis (NMPH), the representational change (memory traces moving apart or together) is a U-shaped function of the coactivation (overlap) of these memories during learning. Low levels of coactivation between two memories lead to no change; high levels of coactivation will strengthen mutual connections and lead to integration, whereas moderate levels of coactivation will weaken mutual connections and lead to differentiation (Ritvo et al., 2019). One study used a novel neural network image synthesis procedure to create pairs of stimuli that varied in similarity in high-level visual regions and found that the representational change in DG was fitted to the NMPH curve (Wammes et al., 2021).

Finally, the inferred cause (i.e., latent cause) of the new event might determine whether the old reactivated memory is replaced by the new event or a new memory is created. According to the latent cause model, memory is used to generate predictions. Consequently, the brain will attempt to infer the latent cause of a new event, and it will create a new memory if it implies a new possible cause for a surprising event (i.e., A-C memory); otherwise, it will update the existing old (A-B) memory (Gershman et al., 2017).

5.5. Gist extraction and schema formation from many overlapping memories

As memories age, many partially overlapping memory traces will be present. The Competitive Trace Theory (CTT) proposed that the hippocampus reconstructs memory using overlapping traces during memory retrieval to avoid competition or confusion (Yassa and Reagh, 2013). The resulting memory will be decontextualized and become more semantic, accompanied by shifts in neural correlates from the hippocampus to the neocortex. This idea is well captured by a formal computational model, SARKAE (i.e., Storing and Retrieving Knowledge and Events), in which knowledge (or semantic memory) is represented as an accumulation of the co-occurrence of features in episodic events (Nelson and Shiffrin, 2013).

In addition to a single word, the co-occurrence of words in different contexts may determine their semantic similarity and the formation of a

semantic network (Harris, 1954) (also see Section 3.2). This process is nicely illustrated in the laboratory using statistical learning paradigms. For example, human subjects are able to learn the statistical regularity of a sequence, and the neural representation in the MTL is more similar for strong pairs (transition probability 1) than weak pairs (transition probability 1/3) and shuffled pairs (Schapiro et al., 2012). In a subsequent study, participants learned the community structure of stimuli based on the transition probability of the sequence and used them to guide the segmentation of the sequence. With learning, the neural representations of stimuli with shared temporal associations became more similar to each other in regions such as the anterior temporal lobe, angular gyrus and inferior frontal gyrus (Schapiro et al., 2013).

Recent studies have used a neural pattern similarity analysis to directly map the formation of schema and cognitive maps (Fig. 3D). For example, one human study asked subjects to learn the spatiotemporal trajectories in a large-scale virtual city. After learning, the neural similarity in the hippocampus scaled with the remembered proximity of events in space and time (Deuker et al., 2016), and representations in the anterior-lateral entorhinal cortex (alEC) specifically reflected the temporal event structure (Bellmund et al., 2019). Another study trained subjects to use the method of loci to remember the temporal order of words and found that the hippocampal CA1 and DG and CA2/3 regions represented the spatial and temporal information of the loci map, respectively (J. Liu et al., 2021; Y. Liu et al., 2021; C. Liu et al., 2021).

Finally, the schemas and cognitive maps might be "inferred" based on discrete and partial experiences, which is analyzed in the lab using a cleverly designed paradigm (Park et al., 2020). On Day 1 and Day 2, subjects were asked to learn the within-group ranks of one of the two groups in each of the two dimensions, i.e., competence and popularity. On Day 3, subjects learned to link two groups based on feedback from between-group comparisons. Critically, this between-group comparison was limited to "hub individuals", which created a sparse path to connect the two groups. Humans constructed a multidimensional cognitive map based on these sparse and discrete experiences. The representation similarity in the hippocampus, entorhinal cortex, and VMPFC is linearly related to the Euclidean distance between the people in the mentally reconstructed social hierarchy map.

In summary, when old and new memories are coactivated, old memories can be replaced by new memories or integrated with or differentiated from new memories. The exact outcomes of the memory transformations depend on both goal-directed control processes and the properties of reactivated representations. These transformations increase the adaptivity and predictivity of memories. Combining these dynamic transformation mechanisms and the unique coding schema in the hippocampal-entorhinal system and the MPFC, schemas could be formed from multiple overlapping memories, facilitating the acquisition and transfer of knowledge.

6. Transformation during the replay of sequential events

Our experiences are continuous and consist of sequences of events (Fig. 4A). Early recording studies in rodents revealed that with repeated learning in a running track, hippocampal place cells would repeat the same sequential pattern of activity during subsequent sleep (Skaggs and McNaughton, 1996; Wilson and McNaughton, 1994). This so-called "replay", which is defined as the sequential reactivation of neuronal activities, is not limited to spatially tuned cells in rodents but also occurs for nonspatial events in humans (Liu et al., 2019; Schuck and Niv, 2019). Similar to the reactivation of nonsequential representations, cumulative studies have revealed several essential characteristics of replay that emphasize its transformative nature (Foster, 2017).

6.1. Compressed and discontinuous replay

A highly reliable observation in rodent is that the replay events (e.g., 50–150 ms) are temporally compressed compared with active running
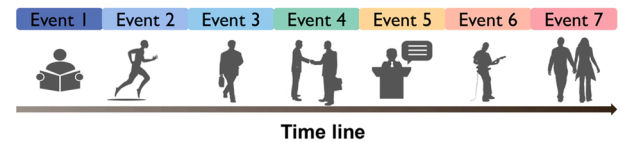
Fig. 4. Compressed, reversed, and reorganized replay of an event sequence. A. This schematic shows one example of a daily life experience. The black arrow represents the timeline. While the experience itself is continuous, it is segmented into a sequence of events (as indicated by the underlying icons) marked by different colors. B. Compressed replay. When replay occurs, the experienced events are likely to be replayed faster than the original experience, with a compression factor of up to 60 in some circumstances. C. Discontinuous replay. The replay of an event sequence at some time is discontinuous and flexible, showing varied compression factors for different events and even skipping certain events. D. Reversed replay. The replay may occur in the reverse direction due to reward or task requirements. E. Reorganized replay. The replay is reorganized according to an existing cognitive map to facilitate the speed and generalization of new learning.

events (e.g., several seconds) (Fig. 4B) (Lee and Wilson, 2002; Skaggs and McNaughton, 1996). Human magnetoencephalography studies have also shown that memory replay is characterized by a compressed reinstatement of temporal sequence patterns from encoding (Liu et al., 2019; Wimmer et al., 2020). For example, by decoding individual episode elements, the authors found that successful retrieval was supported by the replay of consecutive episode elements, with a temporal compression factor of > 60 (Wimmer et al., 2020).

In addition to temporal compression, emerging studies have revealed that replay may be discontinuous and flexible (Fig. 4C). In particular, humans can flexibly skip events during the replay of event sequences. For example, within-event transitions are more likely than across-event transitions in free recall (Heusser et al., 2018). In addition, the transition between subevents takes longer than the transition from one event to another (Michelmann et al., 2019). In a temporal order judgment task, the reaction time for cross-event pairs was faster than that for within-event pairs (Zuo et al., 2020).

This compressed and discontinuous reactivation might be supported by event segmentation. The continuous experience is segmented at multiple timescales along the cortical processing hierarchy, showing a shift in activation patterns at the event boundary (Baldassano et al., 2017). This segmentation might provide several advantages for memory consolidation and generalization. First, event segmentation theory proposes that ongoing experience clustered in this manner is adaptive, as it promotes efficient online processing, the organization of memory, and the later retrieval of information (Kurby and Zacks, 2008; Shin and DuBrow, 2021). Consequently, event segmentation ability is significantly associated with memory ability (Sargent et al., 2013).

Second, according to the inference-based framework, experiences are grouped according to what is inferred to have generated them (Shin and DuBrow, 2021). In this manner, existing knowledge is employed to organize the events, and the hippocampus is involved when the inference changes and an event boundary is created. Consistently, the hippocampus shows increased activity at higher-order event boundaries (Baldassano et al., 2017; Ben-Yakov and Henson, 2018; Reagh et al., 2020), accompanied by the rapid reinstatement of the just-encoded

events (Silva et al., 2019). The boundary-triggered hippocampal activities predict pattern reinstatement during later free recall (Baldassano et al., 2017) and behavioral performance in the memory test (Reagh et al., 2020).

Third, several studies have shown that replay might serve a planning function (Behrens et al., 2018; Wise et al., 2021). This compressed replay might allow fast simulations of trajectories through the cognitive space (Arnold et al., 2016). Finally, compressed replay allows the cell pairs to co-fire within a time window conducive to inducing synaptic plasticity (Bi and Poo, 1998), leading to strengthened connections between the coactivated neurons (King et al., 1999).

6.2. Reverse replay: the role of task requirement and reward

Although on a similar temporally compressed timescale as in sleep, awake replay often occurs in the reverse order to the order in which the fields are arranged along the track (Foster and Wilson, 2006; Gupta et al., 2010). In humans, reverse replay has also been observed during short-term maintenance (Huang et al., 2018), postlearning rest (Liu et al., 2019), and long-term memory retrieval (Wimmer et al., 2020) (Fig. 4D). Unlike forward replay, reverse replay represents an abstraction from the original experience and a challenge to the original conception of replay as recapitulation.

The direction of replay can be flexibly switched by the current goal, such that forward replay is observed when subjects are asked to retrieve memory components that follow a cued element. In contrast, reverse replay is observed when they are asked to retrieve memory components that precede a cued element (Wimmer et al., 2020).

In addition to goal-directed modulation, researchers have posited that reverse replay might represent a mechanism for associating places with values (Behrens et al., 2018; Foster, 2017). In sequential decision problems such as navigation, planning by a forward search of possible action sequences is prohibitively inefficient due to the substantial combinatorial increase in the number of possible routes. An efficient solution is to start from the goal and move back along incoming trajectories, which is always a single step (Foster, 2017). Supporting the hypothesis that reverse replay is designed to learn values from rewards, increasing or removing reward increases or decreases the rate of reverse replay, respectively, with no effect on the rate of forward replay (Ambrose et al., 2016). One human study also revealed that reward enhanced the reverse replay of event sequences (Liu et al., 2019). In a recent study, the same group provides direct evidence that reverse replay may support nonlocal, model-based learning, enabling inference from indirect experience (J. Liu et al., 2021; Y. Liu et al., 2021; C.Liu et al., 2021).

6.3. Reorganized replay that supports inference and generalization

In addition to compressed and reversed replay, replay might reorganize prior experience (Fig. 4E). Early rodent studies have provided evidence for replaying never-before-experienced sequences (Gupta et al., 2010; Ólafsdóttir et al., 2015). Humans can use a cognitive map of the social hierarchy to infer direct trajectories between entities and guide discrete decisions (Park et al., 2021, 2020). This mechanism might enable generalization and support planning for a route for novel problems (Pfeiffer and Foster, 2013).

In addition, the replay is potentially reorganized based on previously learned rules, allowing the generalization of rules to new sets of stimuli. For example, one study trained participants on a rule that defines the order of objects and then presented participants with a novel set of objects in a scrambled order. Participants were able to replay the novel objects in a new order defined by the rule (Liu et al., 2019). This reorganized replay might involve "factorized" representations of object identities and positions (Fan et al., 2021; Hsieh et al., 2014; J. Liu et al., 2021; Y. Liu et al., 2021; C. Liu et al., 2021). Consistently, the authors found that the replayed information contained both the abstract

sequence position and the object identification (Liu et al., 2019).

In summary, emerging evidence suggests that replay is not simply a recapitulation of prior experience but instead plays an essential role in memory consolidation, schema formation, and generalization. As a result of event segmentation, compressed and discontinuous replay plays a vital role in facilitating the organization and consolidation of memory. In contrast, reverse replay is essential in learning values from rewards, enabling value-based prediction and decision-making. Finally, reorganized replay might facilitate schema formation, supporting the generalization of knowledge to new situations.

7. Conclusions and future directions

Guided by Bartlett's early conceptualization of memory transformation and recent developments of memory consolidation theories, an increasing number of recent studies have carefully examined neural representations in distributed brain regions and at different memory stages. The available evidence emphasizes several vital features of episodic memory representations. First, episodic memory entails multifaceted and distributed representations and involves widespread neural networks. Second, memory is a dynamic and constructive process in almost every memory stage, including encoding, maintenance, retrieval, and consolidation. This process involves substantial representational transformations characterized by a change in representational content and format and sometimes a shift in neural substrates. Third, transformation occurs when memory is in an active state. Old consolidated memories are more likely to be transformed when they are reactivated than when they are not. The fate of the active and reactivated representations depends on the strength and similarity of the reactivated memory, their predictivity, and current goals. Fourth, memory transformation occurs via an interaction with other memory representations, including those from surrounding events and those reactivated from prior experience and long-term knowledge. Finally, these transformations play an adaptive role in facilitating memory acquisition, retention, predictivity, and generalization.

The exciting novel results reviewed here clearly support a transformative perspective of memory representations and will continue to promote a shift in the paradigm in future research. Namely, apart from examining the pattern reinstatement or replay at different memory stages, an examination of the differences in memory representation across stages and the elucidation of the underlying mechanisms are essential. Guided by this transformative perspective of memory, many fascinating questions await to be addressed. For example, future studies should further characterize the multifaceted nature of memory representations and their dynamic changes, which might benefit from imaging tools with high spatial and temporal resolutions and advanced modeling techniques, such as network models and DNNs. From example, recent iEEG studies in humans have revealed novel coding schemes of memories (Liu and Xue, 2022; Rutishauser et al., 2021). One fruitful direction is to extend studies beyond a single event to examine how multiple events and event sequences are represented and transformed in the brain.

Future studies should also further examine the functional roles of these different aspects of memory representations, which might significantly advance the principles of neural-psychological representation correspondence (NPRC). This goal could be achieved by jointly examining the psychological characteristics of memory behaviors (e.g., priming vs. familiarity vs. recollection and true vs. false memory) and the contents and formats of multifaceted neural representations. For example, studies could examine how representations in different brain regions (Zhu et al., 2019) or different representations in the same region (Bone et al., 2020; Lee et al., 2019) contribute to true and false memory, as well as the vividness of memory (Bone et al., 2020). Both experimental manipulations and large-scale individual difference approaches (Sheng et al., 2022) would be very fruitful.

Furthermore, elucidating the driving forces underlying

transformations is essential. On the one hand, researchers should investigate how goal-directed task requirements, attention, different conscious states (awake vs. sleep), and various memory stages (e.g., encoding vs. retrieval) might modulate memory transformations. For example, how do reactivation during rest and sleep differently transform memory representations? On the other hand, future studies should further examine how these transformations are shaped and constrained by the neurophysiological properties, connectivity patterns, and information coding schema in different brain regions. These areas of research might provide a better mechanistic understanding of the roles of different brain regions in memory.

Finally, future studies could place memory into the broader context of brain information processing to understand the evolutionary and computational benefits of memory transformation. For example, these studies may investigate how memory transformation improves prediction, psychosocial well-being, and the chance of survival by contributing to the learning speed, retention rate, and generalization.

Given the unparallel power of representational analysis in informing on the nature of memory, these studies would provide a deep mechanistic understanding of the well-documented dynamic memory behaviors and stronger support to the transformative memory theories. They will also significantly improve our understanding of the nature of memory, its formation and retention, and its relationship to other cognitive functions, such as decision-making and problem-solving. More broadly, progress in these areas will have tremendous potential to reveal the mysteries of the human mind and inspire brain-like artificial intelligence.

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