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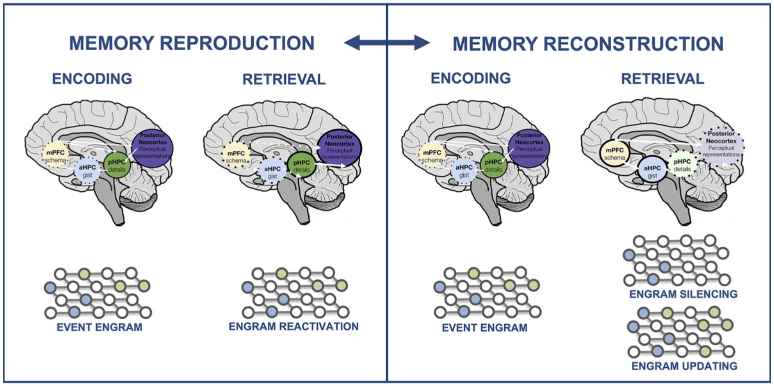
REVIEW ARTICLE

ADAPTIVE EPISODIC MEMORY: HOW MULTIPLE MEMORY REPRESENTATIONS DRIVE BEHAVIOR IN HUMANS AND NONHUMANS

Memory reproduction and reconstruction: Multiple representations adaptively guide memory across species



Multiple memory representations are reproductive and reconstructive as needed, shifting with prior knowledge, time, task demands, and individual differences

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KEY WORDS

cross-species comparison; episodic memory; hippocampus; medial prefrontal cortex; schemas

CLINICAL HIGHLIGHTS

- Memories for events are supported by multiple, coexisting representations, ranging from highly detailed and vivid recollections to schematic or skeletal knowledge structures.
- The relative weighting of these representations determines how information is experienced in memory and used in everyday life.
- Experiential details are associated with functioning of the hippocampus, whereas schematic memory and relation to general knowledge are associated with the medial prefrontal cortex.
- Representations are affected by connection to prior knowledge, sleep, remoteness, and preexisting individual differences in information processing capacities, among other factors.
- Memories transform with time, predominantly through increased schematic representation, although hippocampally supported vivid memories can persist.
- Anatomical distinctions across representations are evident in studies of patients with memory impairment, where hippocampal damage selectively affects detailed recollection and medial prefrontal damage affects schematic memory.
- Mental health conditions involving memory can be characterized by their relative emphasis on distinct memory representations. Posttraumatic stress disorder (PTSD) can overengage episodic memory. Such intrusive recollections of traumatic events dominate consciousness even when the actual threat is long past. On the other hand, psychopathology can be supported by overactive dysfunctional schemas, such as low self-efficacy in depression and social anxiety.
- Memory impairment can also influence nonmemory functions and abilities, such as decision-making, problem-solving, social interaction, language, and perception.
- Clinical translation from nonhuman samples could be enhanced by adopting an adaptive memory framework such as the one proposed here.

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REVIEW ARTICLE

ADAPTIVE EPISODIC MEMORY: HOW MULTIPLE MEMORY REPRESENTATIONS DRIVE BEHAVIOR IN HUMANS AND NONHUMANS

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Abstract

Episodic memory is a declarative long-term memory of a specific past experience. As such, it is multifaceted, encompassing both the objective and subjective components of that experience. These components can be flexibly represented at different levels of granularity, from precise, context-specific details to generalized, gistlike representations. In this review, we suggest that *1*) multiple representations of an episodic memory at different levels of granularity are simultaneously encoded into a memory trace and *2*) the relative weighting of these representations determines the extent to which a memory is reconstructed or reproduced at retrieval. We propose that this representational flexibility drives adaptive behavior by prioritizing reconstruction or reproduction depending on the age of the memory, its relationship to prior knowledge, current attentional goals or task demands, and individual differences. Drawing on research in humans and nonhuman animals, we show a close correspondence between psychological and neural representations of a memory across encoding, consolidation, and retrieval. Specifically, we discuss how hippocampal activity in humans and engram formation and activation in rodents support the reproduction of detailed memory representations, whereas schema formation across species, mediated by the medial prefrontal cortex, facilitates reconstruction and generalization to guide behavior. Finally, we consider how species- and individual-level differences shape episodic memory representations. By integrating findings across species, we illustrate how the correspondence between neural and psychological representations enables multiple memory representations to balance stability and flexibility, ultimately driving adaptive behavior.

cross-species comparison; episodic memory; hippocampus; medial prefrontal cortex; schemas

1. INTRODUCTION

Episodic memory is the explicit, long-term memory for an experience that occurred at a particular time and place, encompassing both objective and subjective components of the event. A fundamental goal in memory research is to relate neural representations of episodic memories to their behavioral expression. In pursuit of this goal, Semon (1, 2) introduced the term "engram" to describe the physical, neural substrate of a memory. Recent advances have provided compelling evidence for the existence of engrams, identifying cell assemblies that encode neural representations of specific past events (for reviews see Refs. 3, 4). These engrams remain latent or "silent" until they are reactivated by environmental cues or artificial stimulation, a process Semon termed "ecphory," leading to behavioral expressions of memory at retrieval. In this way, memory, the behavioral expression of an engram, necessarily depends on the relationship between neural representations and behavior (5). However, rather than a veridical reinstatement of past events, it has been long appreciated that memory is also influenced by schemas, prior knowledge, and expectations, leading to flexibility, alterations, and distortions in memory representations (6). How do neural and psychological representations support both the stability and flexibility of memory?

Building on these foundational ideas, significant advances in human and rodent research have shed light on the correspondence between neural and

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psychological representations of memory. However, the extent to which memories manifest as stable reproductions of past events or as flexible reconstructions remains debated. On one hand, influential theories propose that memory retrieval is inherently reconstructive, with multiple memory sources guiding episodic recall and leading to schema-based alterations (6–8). According to this perspective, memories are not stored as veridical records of past events but rather as fuzzy, dynamic reconstructions (9). On the other hand, recent findings suggest that the recalled contents of episodic memories tend to be highly accurate (10–13). Accordingly, findings demonstrating a correspondence between neural representations at encoding and retrieval (14–18) suggest that precise reproduction of neural activity patterns at least partially governs retrieval processes (14), analogous to findings of putative engram activation in rodents (19).

Whether a memory is retrieved as a faithful reproduction or as a reconstruction may depend, in part, on the nature of its underlying representational content, ranging from detailed, perceptually rich information to more abstract, generalized knowledge such as gist or schemas. Detailed episodic memories are rich in perceptual and contextual information that is unique to a specific event, for example, recalling what everyone at a birthday party wore, how the cake looked and tasted, the configuration of the room, and where people were located. Some episodic memories, however, retain only the gist of the event, effectively a summary of its central elements without the peripheral, incidental, or perceptual details (9). One useful way to conceptualize the distinction between detailed and gistlike memories is as a continuum of representational granularity, ranging from fine- to coarse-grained descriptions of the same event. Supporting this view, detailed and gistlike memories have been proposed to rely more strongly on posterior and anterior hippocampal regions, respectively (see below, Refs. 20–26). Whereas gist memories retain some contextual specificity (e.g., a particular birthday party), schemas are more abstract, referring to generalized knowledge distilled across many similar experiences (e.g., what typically happens at a birthday party, including common elements such as cake, balloons, family, and friends). Schemas often include scripts or action sequences that support generalized behavior across situations (e.g., knowing that only the birthday celebrant blows out the candles). The medial prefrontal cortex (mPFC) has been implicated in the representation and use of schemas (27–31). In contrast, semantics refers to conceptual knowledge divorced from specific events, for instance, understanding that a "birthday party" is a celebration of a person's date of birth, without any episodic or script-based content. Semantic memory is thought to rely primarily on the anterior and lateral temporal cortex as well as the inferior lateral frontal cortex (32–35).

Trace transformation theory (TTT) (22, 23, 26, 36, 37) posits that multiple representations of an event, ranging from precise, episode-specific details to gistlike and schematic representations, are simultaneously formed at encoding (**FIGURE 1**) and dynamically interact during retrieval (**FIGURE 2**) (see Refs. 38, 39 for similar ideas). Events closely aligned with prior knowledge are more likely to be retrieved as generalized, schematic representations, both immediately and increasingly so over time (6, 40, 41). When there is limited prior knowledge available to scaffold new learning, memory traces tend to shift in relative strength over time, with gist and schematic representations becoming more dominant at remote time points, even as some episodic details are retained.

The concept of neural-psychological correspondence (26, 42) provides a useful heuristic for understanding how memory representations dynamically evolve and interact. Psychological representations depend on their underlying neural substrates (26, 43). A more dominant detailed neural representation of an event is likely to support detailed memory expression, whereas a dominant schematic representation leads to schema-driven memory retrieval, regardless of the passage of time.

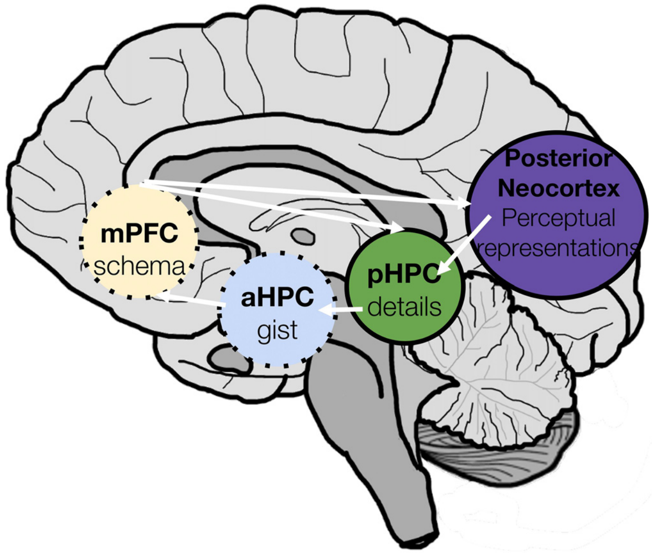


FIGURE 1. Multiple memory representations at encoding. At encoding, sensory input is processed in posterior neocortex and is sent to the hippocampus, where multiple elements of an episode at different levels of granularity are bound into a memory trace. These elements are represented hierarchically, with posterior hippocampus (pHPC) representing details, anterior hippocampus (aHPC) representing gist, and medial prefrontal cortex (mPFC) representing schemas. We hypothesize that these representations are simultaneously formed at encoding. Schemas also have top-down influences on hippocampus and posterior neocortex representations at encoding, biasing perception and memory and highlighting that memory encoding is a constructive process and influenced by prior knowledge from the outset.

From this perspective, memory reproduction and reconstruction may coexist, with the relative contribution of each depending on factors such as prior knowledge, time, and task demands (26, 43).

In this review, we draw on evidence from both humans and nonhuman animals to illustrate the relationship between neural and psychological representations of memory, emphasizing how these multiple representations interact to support both stability and flexibility in behavior. We first review evidence from human studies demonstrating that the extent to which a memory is reproduced or reconstructed at retrieval is closely linked to its underlying neural representation and shaped by prior knowledge, the passage of time, and task demands. Next, we explore how reproduction and reconstruction are modulated by individual differences in mnemonic processing styles. We then examine research in nonhuman animals, focusing on stability and flexibility in memory engrams and their transformation over time, highlighting a remarkably similar correspondence between neural representations and behavior. We argue that the balance between detailed and schematic representations in memory drives adaptive behavior across species. We conclude by identifying key directions for future research, with an emphasis on further elucidating the relationship between neural and psychological representations of memories at multiple levels of granularity.

2. NEURAL AND PSYCHOLOGICAL FOUNDATIONS OF MEMORY REPRESENTATIONS

Despite Semon's (1, 2) early theorizing of an engram, it was not until later that the neural foundations of memory began to be elucidated (4). After the landmark case of H.M., it became clear that the hippocampus and the surrounding medial temporal lobe (MTL) were necessary structures for episodic memory (44). Today, the consensus view is that the hippocampus binds the cortical and subcortical neurons that are coactivated during an event into a coherent memory trace (45, 46), forming a sparse code that integrates both the objective content of an experience and its subjective awareness. During retrieval, a partial cue can reactivate the memory trace through pattern completion, triggered by recurrent excitatory connections within the hippocampus (Ref. 47, but see Ref. 48). This process reinstates memory for both the observable content and subjective aspects of the original experience across distributed cortical networks (49).

Indeed, the recovery of perceptual details and the engagement of associated multimodal brain networks (50) give rise to a feeling of subjective reexperiencing, or mental time travel. James (51) described this reexperiencing as a "warmth and intimacy associated with the sense that the memory belongs to oneself." He contrasted such recollection with familiarity, which is the recognition of having encountered an item before without the accompanying sense of reexperiencing the event. Tulving (52–54) later expanded on the traditional what-where-when criteria of episodic memory, incorporating this "autonoetic" consciousness as a signature aspect of episodic memory.

Importantly, psychological states are inherently subjective and can only be coarsely approximated through objective measures. Although quantifying subjective experiences, such as pain or mood, has profound implications for health and well-being, it is equally crucial for psychological theory and the study of brain-behavior relationships. It is, therefore, a major challenge in human memory research to understand how both easily verifiable objective components and more elusive subjective components are represented in memory and the brain. This challenge is even greater in assessing memory in nonhuman animals, a topic we address below.

Not all memories involve such a vivid reexperiencing of the original event. Memory representations are multifaceted, with distinct psychological and neural

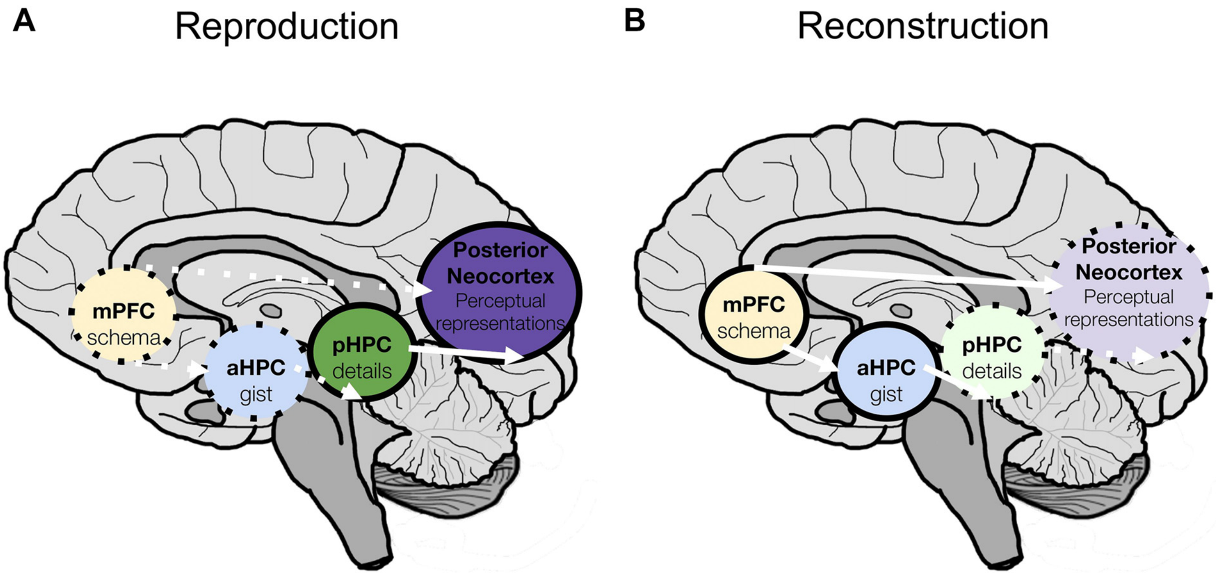


FIGURE 2. Relative strength of multiple memory representations differentially shapes retrieval. *A*: reproduction leads to the retrieval of detailed memory representations, supported by representations in the posterior hippocampus (pHPC). Posterior hippocampal activity mediates reinstatement of activity patterns from encoding in posterior neocortex, including parietal and occipital cortex, which represent subjective and perceptual features of memory. This reinstatement is associated with accurate memory retrieval in behavior. Gist and schematic representations are present but relatively weaker than detailed ones and are not expressed unless necessary. Reproduction tends to dominate retrieval at recent time points or when reminders or task demands prioritize detail, even at remote time points. Regardless of time since encoding, when episodic details are retrieved they will continue to engage the hippocampus. *B*: reconstruction leads to retrieval dominated by medial prefrontal cortex (mPFC)-mediated schematic representations or anterior hippocampus (aHPC)-mediated gist representations, potentially aided by connectivity from mPFC to hippocampus or posterior neocortex. Reconstruction tends to dominate when memories are strongly linked to prior knowledge or when episodic details are unavailable or forgotten, such as at remote time points. Darker circles indicate stronger representations. Solid lines indicate which representation is dominant and more likely to be expressed.

underpinnings. Following James and Tulving, researchers differentiate between familiarity and recollection (51, 54, 55). These psychological distinctions are mediated by distinct neural mechanisms: familiarity relies on the perirhinal cortex, whereas recollection depends on the hippocampus, which is necessary for retrieving detailed episodic memories (Refs. 56–58, but see Refs. 59, 60). As described above, memory representations can also range from detailed, perceptual representations to gistlike ones, capturing the skeletal structure of an event (9). These representations are thought to be hierarchically organized across the hippocampal long axis, with the posterior hippocampus supporting detailed memory representations and the anterior hippocampus supporting more generalized, gistlike representations (Refs. 20, 21, 25, 61, 62, but see Refs. 63, 64).

Evidence for this long-axis specialization is supported by the hippocampus's functional connectivity with the neocortex. The posterior hippocampus is functionally connected to posterior neocortical regions, including the parahippocampal cortex and parietal areas (such as retrosplenial cortex and angular gyrus) (22), which represent both the perceptual content of an experience and some subjective aspects of memory, such as vividness (65–69). These connections enable the reactivation of precise details from encoding. In contrast, the anterior hippocampus is connected to the anterior and lateral temporal cortex, regions implicated in semantic memory (22), as well as the medial prefrontal cortex (mPFC), which plays a key role in representing schemas, integrated representations of commonalities and regularities extracted across multiple events (27–30, 70, 71). Thus, the anterior hippocampus is well suited for representing the gist of a memory and the mPFC for representing schemas (**FIGURE 1**).

Building on this connectivity-based distinction, neural memory representations vary in their level of detail, supported by distinct regions in hippocampal-prefrontal networks. The posterior hippocampus tends to maintain low overlap between activity patterns for related experiences, supporting detailed, event-specific representations that preserve perceptual detail (Refs. 72–74, but see Refs. 63, 64). In contrast, the anterior hippocampus and medial prefrontal cortex (mPFC) show greater overlap in activity patterns across related events, consistent with the formation of integrated representations (61, 63, 72, 75–79). These generalized codes may support gistlike or schematic memory, enabling flexible inference and generalization but at the cost of fine-grained detail (80–82). Note that such differences in representational overlap also vary by hippocampal subfield (see Ref. 82 for a review).

Recent work further suggests that memory representations vary along a continuous spectrum of granularity. The hippocampus exhibits systematic anatomical and functional variation along its long axis (20, 21). Furthermore, spatial and temporal signals are similarly organized along this gradient, with increasing temporal autocorrelation and larger receptive fields in progressively anterior regions, properties that may enable integration over broader windows of space and time, facilitating the abstraction of gistlike representations (25, 62, 83, 84). Similar anterior-posterior gradients have been observed in the mPFC (83), as well as in parahippocampal and retrosplenial cortex (85), suggesting a broader organizing principle across memory-related networks. This hierarchical structure is evident not only within regions but also across them: progressively more anterior brain areas represent increasingly longer timescales (86–88). Taken together, these findings imply that memory-related brain regions may be organized along a shared gradient of representational scale rather than by discrete functional boundaries. Distinctions between detailed, gist, and schematic memories may reflect continuous representations that vary with anatomical position, enabling memory systems to flexibly capture both the fine details and broader structure of experience.

In line with these representational correspondences, vivid episodic memory is linked to the engagement of posterior hippocampal circuits (89), followed by late-emerging connectivity between the hippocampus and the neocortex, particularly sensory (visual) regions and heteromodal association areas (23, 65, 90, 91). Through this hippocampal outflow, memory traces can be modified or reencoded (92). Interactions with prior knowledge and the influences of various factors on memory transformation (such as time- or sleep-dependent forgetting) introduce significant variation in the subjective experience of memory, which can be quantified and related to both behavioral measures and brain imaging data. Notably, mnemonic responses that appear indistinguishable at the behavioral level can be reliably dissociated with clever experimental paradigms (e.g., process dissociation procedure) (93, 94) or by incorporating ancillary behavioral (e.g., eye tracking) (95) and neuroimaging (14, 96) data.

As described above, TTT explains how brain regions interact to represent events at different levels of granularity and how the balance of these representations shifts over time (22, 23, 36, 37). Unlike standard systems consolidation theories, which suggest that episodic memories become hippocampus independent as they come to rely on the neocortex over time (97), TTT suggests that memory representations in these regions are formed simultaneously and coexist. Initially, behavioral expressions of detailed memories tend to dominate, supported by representations in the posterior hippocampus. Over time, as details fade, anterior hippocampus and medial prefrontal cortex (mPFC) representations become more dominant, leading to the expression of generalized, schematic memories. However, even at remote time points, episodic details may still be retrieved and continue to engage the posterior hippocampus (98), whereas schematic representations can dominate even at recent time points, particularly when the memory aligns with a preexisting schema or when task demands prioritize schematic information (40, 99). Moreover, shifts in memory representations can be bidirectional or reversed by cues that restore memory for details that were previously inaccessible (100–102). These observations on the dynamic nature of memory led Gilboa and Moscovitch (26, 43) to propose replacing the term "systems consolidation," which implies a unidirectional process culminating in a stable, immutable memory trace (97), with "memory reorganization" to better describe the dynamic representational transformation of memories.

Consistent with our prior work, we propose that detailed, gistlike, and schematic representations are formed simultaneously at encoding (**FIGURE 1**), supported by the posterior hippocampus, anterior hippocampus, and mPFC, respectively. At retrieval, the dominant representation is more strongly expressed, with detailed representations supporting the reproduction of past experiences and gistlike or schematic representations driving reconstruction (**FIGURE 2**). Which representation is expressed depends on factors such as its relationship to prior knowledge, the passage of time, and task demands, with some representations remaining latent until needed (19, 99). At the core of this framework is the fundamental correspondence between the neural and psychological representations of memory (26, 42). Of note, we mainly focus on neurotypical adults in the present article, as recent advances in detection of precise neural representations have primarily been applied to these populations. We have recently discussed multiple memory representations in lesion patients elsewhere (26, 43, 103). Below, we review convergent evidence across species demonstrating how multiple memory representations shape reproduction and reconstruction in behavior.

3. HOW IS MEMORY EVALUATED IN HUMANS?

The questions we ask about memory and the theories we hold influence our choice of stimuli and memory testing methods. The clearest examples date to the dawn of the experimental study of memory. In an attempt to study memory in its pure state without the confounds of other cognitive factors such as meaning, Ebbinghaus (104) tested his own memory for nonsense syllables, a method oriented toward a reproductive view of memory. Bartlett (6), on the other hand, assessed free recall of naturalistic narratives, manipulating schema congruence by including narratives from non-Western cultures unfamiliar to participants. This method corresponded to Bartlett's view that real-life memory is adaptive and influenced by prior knowledge such as meaning and schemas one has formed of the world and of oneself.

Contemporary memory research typically uses stimuli between these extremes, from single meaningful stimuli, such as words and pictures as proxies for more complex events, to verbal or pictorial narratives and autobiographical experiences. Episodic memory is often assessed via cued or free recall. In recognition as compared to recall, memory cues provide control over the nature of recognition judgments upon various elements of the memoranda (e.g., identity, location, featural characteristics, source, temporal order). Moreover, retrieval demands can be manipulated with probes requiring fine discrimination between elements of the encoded stimuli and lures (e.g., Ref. 14). Although lacking experimental control, free recall is both more naturalistic and, in some cases, more sensitive to reconstructive processes, particularly forgetting that is mitigated by the use of cues (105). Indeed, it was the freely recalled errors and distortions that led Bartlett to conclude that memory is reconstructive.

The autonoetic element of episodic memory is considered more challenging to assess as it involves reports on the conscious experience of the rememberer, as in Tulving's (54) procedure whereby "remember" responses are assigned to recognized items accompanied by a sense of conscious reexperiencing of the encoding episode, whereas "know" responses are not. These responses can be incorporated into algorithms that separate recollection from familiarity (94). Taking these subjective elements into consideration is important when using such assessments and can enhance prediction and correspondence to supporting brain mechanisms (106).

As reviewed in detail below, assessment of memory transformation and reconstruction often requires testing beyond the timescales (i.e., minutes) typical of laboratory studies. Not surprisingly, the more complex and multifaceted the event, and the longer the delay, the more likely that the test draws on reconstructive processes at retrieval. In some instances, memory for laboratory-encoded stimuli is assessed after days, weeks, or longer. In other instances, researchers turn to content from across the lifespan, with memory for temporally and spatially specific events considered to reflect episodic autobiographical memory (91). Assessment of these events inspired the earliest investigations into memory transformation in amnesic patients (107).

Autobiographical event recall is a cognitively complex task, with retrieved contents composed of both episodic and nonepisodic components. The Autobiographical Interview (108) segments autobiographical narratives into "internal" and "external" details, with internal details corresponding to temporo-spatially specific contents unique to the event (e.g., perceptual detail, discrete events) versus semantic or other narrative content (e.g., metacognitive statements or generalities). The designation of a detail as "internal" was meant to characterize its relationship to the cued event. The extent to which internal details reflect episodic memory is a matter of interpretation, as evidenced by amnesic patients' recall of episodic-like details from rehearsed events in the absence of episodic memory (109). Interpretation can be aided by cuing relatively unrehearsed autobiographical events, or staged events (see below and Refs. 91, 110 for discussion).

Recent research has increasingly used other naturalistic stimuli to study memory for complex experiences in a controlled setting. Naturalistic stimuli, such as movies (111, 112), stories (113, 114), sports events (115), and immersive virtual reality (85), require individuals to process rich sensory input, track multiple pieces of information over time, draw on prior knowledge, and integrate these elements into a memory trace. These naturalistic paradigms enable researchers to examine how memory for complex, dynamic, and temporally extended events unfolds by measuring neural and psychological representations at both encoding and retrieval. For example, individuals may watch a movie and later recall its contents in functional (f)MRI, allowing researchers to examine the relationship between neural representations at encoding and retrieval for naturalistic yet controlled experiences. These advances have been driven by the advent of computational tools for analyzing brain and behavioral data, such as representational similarity analysis (116), hidden Markov modeling (87), and natural language processing (113, 117). Such tools have made it possible to track brain and behavioral dynamics during memory encoding and retrieval of complex, naturalistic events and to link them to high-level stimulus properties, providing a window into how memories are represented in real-world contexts.

4. RECONSTRUCTION AND REPRODUCTION OF EPISODIC MEMORIES IN HUMANS

How do multiple representations of an event in memory influence behavior in humans? As described in sect. 1, influential theories propose that memory retrieval is a reconstructive process, driven by the influence of multiple sources of information, including prior knowledge (6, 7, 118). However, recent brain imaging work suggests that memories can also be faithful reproductions of past events, at least as determined by neural recapitulation representations present at encoding (14–18). In this section, we argue that multiple representations of an event in memory underlie both the reconstruction and reproduction of episodic memories in humans, and that this flexibility is an adaptive hallmark of episodic memory. We first briefly describe how memories are constructed from multiple sources of information during encoding. Next, we review past work in humans showing that retrieved memories are readily altered reconstructions but can also be faithful reproductions of experienced events. Prior knowledge, time-dependent memory transformations, and task demands may influence the degree of reconstruction. Finally, we describe both similarities and differences between memory representations at encoding and retrieval. We interpret these concurrent similarities and differences through a multiple memory representation framework and posit that they can help us elucidate the dynamic interaction between memory representations and the quality of their behavioral expression.

4.1. What Are Multiple Memory Representations for?

From our perspective, differences in episodic memory representations, including fidelity to the encoded event, are tied to their underlying neural representations, which reflect multiple, coexisting representations of the same event in memory. The dominant representation at retrieval is more likely to be expressed (26). Building on this, reconstruction and reproduction are not simply two sides of the same coin. Instead, they arise from dynamic interactions between these coexisting memory representations, which each serve distinct adaptive purposes, allowing memory to balance both stability and flexibility.

Past theoretical work has emphasized that memories can be flexibly used in the service of adaptive behavior (for reviews see Refs. 8, 119, 120). Although errors in veridical memory representations are often viewed as failures or distortions arising from memory reconstruction (40, 121, 122), they can instead be understood as a reflection of this adaptive nature of memory (120). From this perspective, “errors” may not reflect simply forgetting but an active pruning process, retaining meaningful information while discarding irrelevant details to optimize behavior (123). Indeed, past work has shown that influences on episodic memory arising from prior knowledge serve to increase overall accuracy across multiple experiences (124). Aligning episodic memories with prior knowledge and schemas allows us to build structured knowledge about the world to guide a range of adaptive behaviors (for a review see Ref. 125). In this sense, the utility of a memory is prioritized at the cost of its precision.

Although past research has tended to emphasize how generalized, schematic representations are adaptive (120, 123, 125), it is also the case that precise and detail-rich memories can be adaptive for guiding behavior. For example, we can draw on detailed memories to recall the specific location of where an item was in a crowded space (126, 127) or on specific associative memories to make optimal decisions that maximize rewards (128–130). One recent study demonstrated that the hippocampus represents context-specific temporal structure memories to guide predictions about upcoming events (85). These specific representations may be especially advantageous when the context of the originally encoded event remains somewhat stable. As time passes, the likelihood of encountering an identical situation is reduced and memory for specific episodic details is more likely to fade, whereas generalized patterns will be more useful in guiding behavior in novel yet analogous contexts (70). Although this shift from detailed to gistlike memory representations is well documented (23), some events are remembered with vivid detail despite the passage of time (13, 101, 102, 131), with recent theories proposing that the persistence of detail may depend on factors such as task demands and goals from encoding (26, 132) and the balance of neurotransmitters in the brain, such as norepinephrine (131, 133). The balance between reproductive and reconstructed memories in adaptive, memory-guided behavior, such as decision-making, problem-solving, attention allocation, and future prediction, remains an active area of investigation. Future research should explore how coexisting detailed and schematic memory representations flexibly interact to complete tasks, build structured knowledge of the world, and apply such knowledge within and across contexts over short and long timescales.

Ultimately, the shift between detailed and gistlike representations may reflect how memory representations interact with respect to immediate and long-term demands on the memory system. From this perspective, the balance between reconstruction and reproduction of past events is predicated on the adaptive nature of simultaneous multiple memory representations and their relative strength to one another. With this viewpoint in mind, we review how memory representations are constructed at encoding and how they shift in dominance with prior knowledge, the passage of time, and task demands to drive reconstruction and reproduction at retrieval.

4.2. Preencoding Factors Set the Stage for Adaptive Memory

For episodic memory to be adaptive, it should serve an individual's current and future goals, which are often in place before an event occurs. In this way, the likelihood of encoding a memory depends not just on the information to encode but on the state of the individual before encoding. Such preencoding states, occurring seconds to minutes before an event, can predict subsequent memory performance (for review, see Ref. 134). These states may be shaped by attentional processes, internal state, and external context, all of which influence how incoming stimuli are perceived, potentially strengthening or even distorting memory representations (135, 136).

Supporting the hypothesis that preencoding states influence memory representations, rodent studies have shown that the most excitable neurons before learning are preferentially allocated to the engram for that event (see Ref. 137 for review). In humans, the similarity of multivoxel brain activity patterns between preencoding and encoding representations in the hippocampus, as well as neocortical regions functionally connected to the hippocampus, is related to memory for the encoded event (138). These findings suggest that preencoding activity influences how a memory is subsequently represented. We do not know, however, whether the neuronal activity underlying preencoding representations reflects a random fluctuation in the excitability of neurons, as one might surmise from the rodent work, whether they are related to attention, or both.

The latter interpretation is supported by studies showing that perception and subsequent memory are related to prestimulus attentional allocation, orientation instructions, and schema reinstatement (139–144). Preencoding attentional states fluctuate dynamically in response to task demands and top-down goals, prioritizing encoding of goal-relevant information (145–151). Representations of such anticipatory attentional goals have been observed in the hippocampus and mPFC (142), which may allow the brain to prepare to encode task-relevant sensory input (152).

One way that attention is prepared before encoding is through orienting instructions that direct participants to focus on specific aspects of an upcoming event or stimulus. Foundational research has shown that directing attention to the semantic meaning of a stimulus, rather than to its perceptual features, enhances memory encoding, in part because of the activation of relevant prior knowledge (139, 153, 154). Indeed, event representations during encoding are influenced by preencoding activation of schemas, which may direct attention to relevant information for the current goal (114, 140). Schema reinstatement in ventromedial prefrontal cortex (vmPFC) before encoding may facilitate classification of incoming stimuli (141, 143), effectively linking new information with existing knowledge structures (28, 155). Such schema activation may bias encoding toward more schematic representations, but the extent to which these preencoding states modulate memory fidelity remains unknown. One possibility is that schema reinstatement before encoding promotes integration of new information into the activated framework, resulting in stronger schematic representations that support memory reconstruction at retrieval. Ongoing studies are actively investigating these possibilities.

In addition to attentional state and schema activation, the brain's neuromodulatory state before encoding also plays a critical role in shaping memory representations. For example, high levels of acetylcholine in the hippocampus before encoding may bias processing toward pattern separation, enhancing the encoding of detailed, distinct representations (147, 156, 157). In contrast, high preencoding dopamine levels may enhance the formation of more integrated, gistlike memories (147, 158). Supporting this distinction, behavioral manipulations linked to increased acetylcholine release in the hippocampus improve memory specificity (150), whereas reward anticipation, which is linked to dopamine release (159), enhances gist memory (160). Motivational states can similarly shape encoding strategy. In states associated with threat or urgency, encoding may favor specific and detailed representations, whereas states that promote exploration may favor gist (161, 162). Together, this evidence suggests that attentional, neuromodulatory, and motivational states before encoding can bias how experiences become represented in memory, shaping whether episodic details are preserved or whether generalized representations dominate. Future research should aim to link preencoding states to both neural and psychological features of memory representations. Such work will be critical for understanding how preencoding states shape the fidelity of memories and influence whether they are later reproduced or reconstructed.

4.3. Memory Encoding as a Constructive Process

Just as preencoding attention prioritizes information relevant to our goals, our perception of ongoing experience is not a passive reflection of the external world but is actively shaped by prior knowledge, expectations, and current goals (141, 143, 163). In this way, encoding is a constructive process from the outset, actively shaped by how we interpret sensory input through the lens of prior knowledge and cognitive state at the time of encoding. This process ultimately determines what we remember and how we remember it. Importantly, the nature of this construction, whether encoding emphasizes specific perceptual details or conceptual features, may influence whether memories are later retrieved as detailed or gistlike. Although many factors influence the construction of experience, here we briefly discuss the roles of scene construction, event segmentation, and attention (for a more comprehensive discussion about these topics, see Refs. 148, 164–167).

Memory encoding is strongly influenced by the context in which it is encoded. In particular, spatial context plays a crucial role in memory formation and retrieval (23). Scene construction theory (164) posits that scenes facilitate the binding of event information—what, when, and where—into a coherent memory (for an extensive review see Refs. 164, 165). This process relies on the hippocampus and associated medial temporal lobe structures (164) and has been theorized to support memory, navigation, and prediction of future events. Because spatial context is a primary organizing principle for our memories (168–170), the manner in which it is encoded will have lasting consequences for our memory representations. For example, during encoding of object locations within a virtual environment, more detailed representations have been associated with activation in the posterior hippocampus, whereas coarse-grained representations activated the anterior hippocampus (171). These findings suggest that the granularity of spatial representations at encoding can shape the nature of the resulting memory from the outset.

Relatedly, our experiences also occur on an ongoing background of temporal context. Our experiences continuously unfold over time, and this flow of experience shapes our perception of the world around us. Event segmentation theory suggests that our experiences are perceived as meaningful units, shaped by changes in this context (166), as well as navigation (172, 173), prior knowledge (71), attention (114), and shifts in goals or the internal state of the individual (174, 175). These event boundaries help update our current, situational model of the world, with consequences for how we perceive events at encoding and later remember those events at retrieval (166, 167). Indeed, event boundaries have been associated with the reactivation of preceding event content, which is thought to reflect encoding of the just-completed event into long-term memory (176, 177). As with spatial context, event boundaries influence the organization of memories (178, 179) and serve as effective retrieval cues to reinstate an event in memory (180).

Importantly, event boundaries can vary in resolution, from fine grained to coarse, segmenting ongoing experience at different levels of granularity (87, 166). The resolution of event boundaries may affect the richness of memory: finer segmentation creates more discrete events, which may preserve detail within each individual event. In contrast, coarser segmentation may integrate more information into a single unit, promoting abstracted, gistlike representations. In line with theories that the hippocampal long axis hierarchically represents information along a detail-to-gist gradient (20, 21, 23, 25, 61, 83, 84), we predict that the posterior hippocampus should segment event structure in a finer manner than the anterior hippocampus. Furthermore, these fine and coarse event boundaries occur concurrently (87), which could provide a neural basis for the concurrent formation of detailed and gistlike memories of the same experience. In mPFC, event boundaries have been observed at transitions between schematic events (e.g., shifts between stages of a restaurant or airport script) (71), consistent with this region's role in representing higher-level knowledge structures. Together, these findings suggest that the resolution of event segmentation during encoding varies hierarchically across brain regions, from detailed in posterior hippocampus, to gistlike in anterior hippocampus, to schematic in mPFC. This hierarchical segmentation may shape memory representations, influencing the balance between detailed and schematic traces.

In addition to bottom-up sensory input, top-down influences such as goal-directed attention and expectations also shape memory encoding. As described above, expectations based on prior experience and attentional goals are often in place before encoding begins. During encoding, these expectations bias sensory representations in visual cortex (181, 182), and attentional goals modulate hippocampal representations, influencing what is later remembered (149). Sustained activation of expectations and attentional templates during encoding may enhance memory formation (149, 183, 184), potentially through connections between mPFC, hippocampus, and sensory regions (**FIGURE 1**; Ref. 142). Although the question of how attentional states at encoding influence the granularity of underlying memory representations is only beginning to be examined, recent work has shown that attention at encoding can differentially influence the formation of detailed versus gistlike memories (185). For example, directing participants' attention toward semantic meaning versus perceptual detail during encoding can bias memory formation toward gistlike representations, supported by activation in the mPFC and anterior hippocampus (186). In this way, expectations and attention influence encoding, thereby shaping the nature of the resulting memory representations.

Therefore, episodic memory encoding is a constructive process in which multiple sources of information, including spatial context, the segmentation of temporally unfolding experience, and attentional goals, are integrated to form a model of the current world at perception, which is then encoded to form a lasting memory trace (**FIGURE 1**).

If encoding itself is constructive, then memory retrieval may be a continuation of an already constructive process. At encoding, scene construction binds event information to spatial context, event segmentation structures experience into meaningful units, and attention filters and interprets incoming information in line with our current goals. As a result, the memories that are later retrieved are not direct recapitulations of past events but rather reconstructions based on multiple interacting representations that are present from encoding. Therefore, from the moment a memory is formed, it can be thought of as a construction, rather than a direct reflection of sensory experience. In light of this, we next turn to how memories are both reconstructed and reproduced at retrieval, focusing on prior knowledge, the passage of time, and task demands in these processes.

4.4. Prior Knowledge Influences Episodic Memories

As described above, Bartlett's (6) foundational study demonstrated that episodic memories are influenced by the congruence between prior knowledge and current experiences, with retrieval errors conforming to existing knowledge. Foundational studies have shown how prior knowledge and interference from related information, even information acquired after the initial experience, readily influence memory retrieval, leading to imprecise and even erroneous recall (6, 40, 121). Such errors are found for emotionally charged memories of real-life events such as 9/11 (187), the explosion of the Challenger spacecraft (188), the O. J. Simpson murder trial (122), President Kennedy's assassination, John Dean's testimony at the Watergate hearings (188), and of both abusing a child and being abused oneself (121). However, prior knowledge also enhances memory formation in day-to-day life, acting as a scaffold for memory encoding and retrieval (10, 155, 189–191). How does prior knowledge drive both reconstruction and reproduction of memories?

According to the contextual averaging model (CAM; Refs. 192, 193), prior knowledge biases memory by influencing the integration of new information with existing schemas, resulting in systemic alterations in the initial memory. When an experience aligns strongly with schematic knowledge, memory retrieval relies more on generalized representations, leading to less precise episodic details and greater conformity to schemas (120, 194, 195). Studies using continuous measures of retrieval accuracy have provided support for this model (196). In these studies, objects are typically encoded in spatial locations or with specific colors. At retrieval, participants are asked to report the location or color of the encoded object, with memory precision measured as the degree of angular error between the encoded and retrieved color or location. Crucially, the stimuli typically *1*) vary in relationship to a prototype or category from preexisting knowledge (124, 197) or *2*) are learned over the course of the experiment, allowing participants to extract commonalities across episodes to promote generalization (99, 198).

Using these continuous memory measures, a wide range of studies have shown systematic influences of prior knowledge on episodic memories (99, 124, 196–199). For example, in one study participants encoded objects in different colors that came from distinct categories (e.g., airplanes, backpacks, etc.). At retrieval, errors in color memory were not random but were biased toward the average color in a given category (124). Similarly, in another study in which participants learned shared and unique features of novel categories, subsequent color memory was biased toward the category's average color, particularly for object features that were shared across category members (198). Such an attraction bias may reflect the integration of related memories (200), which may be stronger for schema-congruent (vs. incongruent) information (28, 189).

In another study, participants learned object-location associations for objects from particular categories, in which category membership predicted location (e.g., birds tended to be clustered in the bottom right corner of the screen). Objects could be typical or atypical members of a given category. Location memory was more accurate for images placed in spatial locations consistent with their category (e.g., birds in the bottom right corner), whereas retrieval of images in inconsistent locations (e.g., birds in the top left corner) was more strongly biased toward the category's center location. This bias was stronger for typical members compared to atypical ones (197). Transcranial magnetic stimulation (TMS) to the anterior temporal lobe (ATL), implicated in category knowledge and semantic memory (201), reduced this category-based bias, particularly for atypical category members (202). These findings are in line with a memory reconstruction account, with prior knowledge influencing episodic memory traces to align with semantic knowledge.

The influence of prior knowledge on episodic memory is also readily apparent in free recall. These experiments, in line with initial demonstrations of memory reconstruction (6), have shown that errors in free recall stem from the influence of semantically related information (203, 204). Foundational studies have revealed that lists composed of schema-related words frequently induce the recall of other schema-congruent words not shown during encoding (205), highlighting how schemas can drive distortions in episodic recall (40). Such schema-related memory distortions are observed immediately, but their influence grows with the passage of time as well (40, 41), highlighting the dynamic interaction between prior knowledge and time on memory representations (see below). Interestingly, patients with vmPFC lesions are less susceptible to these schema-driven influences than healthy control subjects (206), suggesting that the mutual influence of multiple memory representations is not a flaw but an adaptive feature of the memory system. In another experiment, errors in free recall of short video clips conformed to align with other semantically related clips from the same experiment, particularly when coupled with prediction errors (207). This body of work suggests that episodic memories are systematically transformed to align with prior knowledge, either preexisting category or schematic knowledge or knowledge learned over the course of an experiment. Prior knowledge may therefore bias memories toward reconstruction, influencing how details are remembered or altered based on existing schemas and semantic relationships.

It is important to note, however, that typically prior knowledge enhances, rather than impairs, memory fidelity. Indeed, schemas and semantics are well known to enhance accuracy for congruent information (10, 139, 154, 155). Prior knowledge can simultaneously have a beneficial and detrimental influence on episodic recall (194, 196, 208), which may depend on how much new episodic information conflicts with prior knowledge (99, 199). In line with this, recent work has found enhanced memory precision for episodes that are highly schema congruent compared to moderately schema congruent (209).

One possibility for the general enhancement of schema-congruent information is that highly congruent experiences free up attentional resources, which benefits encoding of precise details. Alternatively, schemas may serve as scaffolds to reconstruct accurate details at retrieval, even when episodic details have been forgotten. However, the interplay between memory distortions and enhancements driven by prior knowledge remains an open and dynamic area of research.

4.5. Multiple Memory Representations Underlie the Effects of Prior Knowledge on Episodic Memories

Dynamic interactions between multiple memory representations therefore underpin the influence of prior knowledge on episodic memories. These influences may emerge during the encoding of a new episodic memory, during the consolidation of schema-consistent episodic memories, and during retrieval of these memories. Encoding schema-congruent experiences may activate regions canonically involved in both episodic and schematic memory, including hippocampus and mPFC (**FIGURE 1**, see above; for a review see Ref. 155). As described above, studies have shown that encoding schema-congruent associations activates hippocampus and mPFC (163, 191) and increases their connectivity (163). Studies have further shown that associating new information with prior knowledge leads to their assimilation, such that neural representations of novel stimuli become more similar to prior knowledge representations in the left inferior frontal gyrus (210).

Multiple studies have shown that mPFC involvement during schema-congruent encoding of naturalistic film clips is associated with enhanced free recall (190, 191). Intriguingly, in one study, schematic representations in the mPFC during encoding predicted memory for clip-specific details rather than generalized schematic memories (190). This observation aligns with prior findings showing that mPFC activity during encoding enhances memory for schema-congruent information (211–213). At the same time, episode-specific representations in the posterior hippocampus, thought to support detailed episodic memory (20, 22), also correlated with the accuracy of detailed recall (190). One possibility is that encoding involves the simultaneous influence of both episodic and schematic memory representations, with schematic representations in the mPFC providing a scaffold for episodic ones in the posterior hippocampus. Masís-Obando et al. (190) found that the detailed representations were more strongly expressed at retrieval, but this leaves open the possibility that the gistlike or schematic representations could be more dominantly expressed at retrieval under different task demands or after a delay (see below). Thus, prior knowledge may influence memory from the outset by shaping how schema-congruent information is integrated into episodic memory representations.

In addition, postencoding processes may also transform memories for schema congruent (vs. incongruent) experiences. During postencoding rest, functional connectivity between hippocampus and fusiform face area (FFA) predicted subsequent memory for associations involving famous faces, suggesting that prior knowledge modulates connectivity to enhance memory (214). Furthermore, coupling between anterior hippocampus and mPFC during postencoding rest for schema-congruent associations predicted more gistlike subsequent memories (189). Similarly, anterior hippocampal-mPFC connectivity after learning overlapping associations predicted their integration (215). Interestingly, one study found decreased connectivity between the hippocampus and vmPFC during encoding for congruent versus incongruent schema, but this was negatively correlated with participants' gist memory (155). Together, these findings suggest that the effects of schemas on episodic memories persist after encoding, facilitating integration and generalized memory traces (81), which may bias the memory system toward reconstruction of memories based on schemas at retrieval.

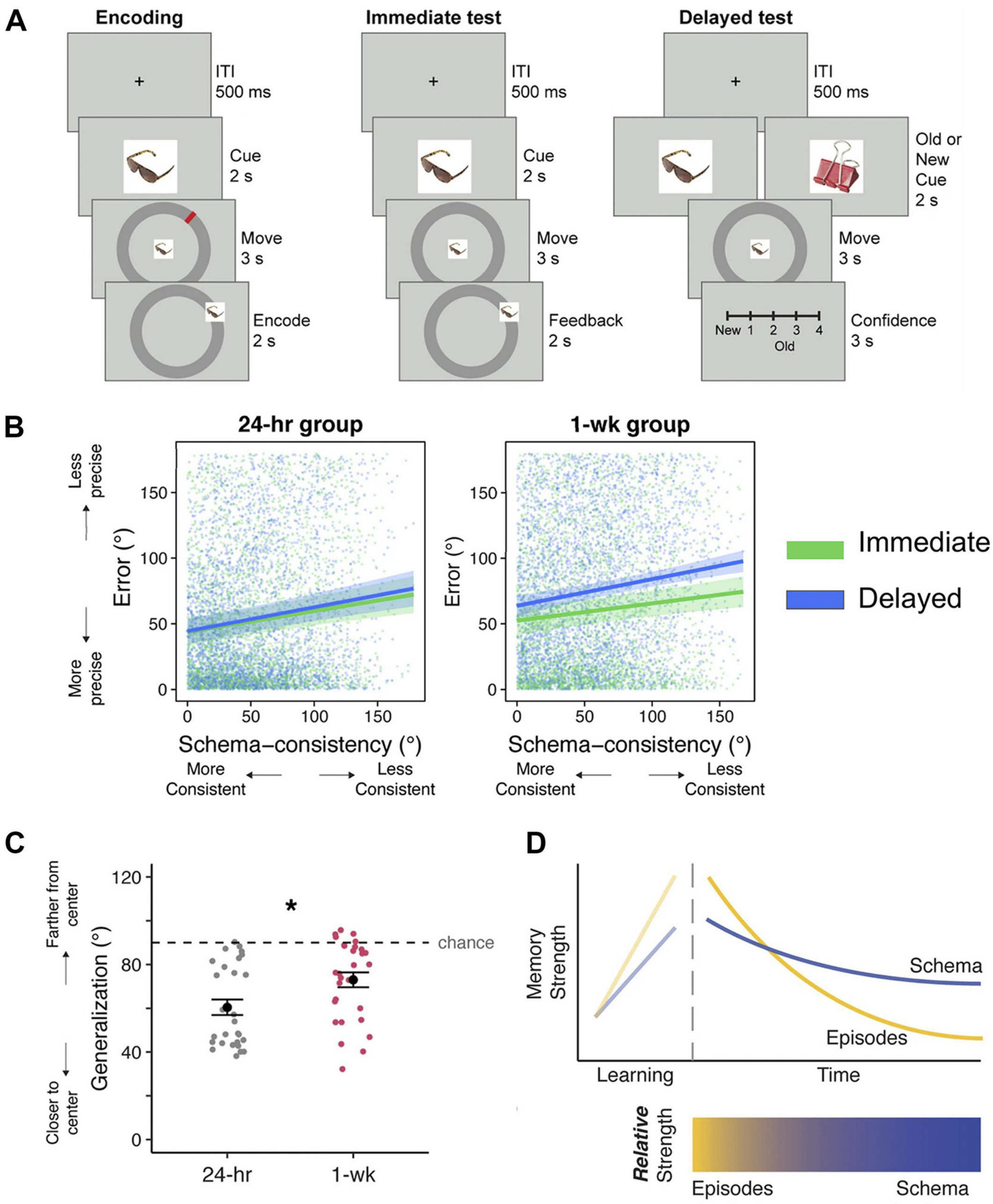
4.6. The Fate of Memories: Transformations in Representations over Time

Memories dynamically change over time, with parallel reorganization in the neural and psychological representations of events (26, 43). Detailed memory representations tend to dominate at recent time points, particularly when memories are not strongly related to prior knowledge, and are supported by posterior hippocampal representations and activity at retrieval (**FIGURE 2**; Ref. 22). Over time, as details of the initial experience weaken, schematic and gistlike representations become more prominent, with the mPFC and anterior hippocampus playing an increasing role in retrieval (**FIGURE 2**; Ref. 22). However, when a memory is strongly related to preexisting schematic knowledge, schemas can guide retrieval immediately, although their influence may continue to grow over time (6, 40, 41). The balance between detailed and schematic memory representations is further influenced by task demands at retrieval, which may emphasize episodic or schematic representations regardless of the time since encoding. Notably, even at remote time points, if detailed memories are retrieved they will continue to engage the posterior hippocampus (98, 131, 216, 217). Thus, the balance between multiple memory representations shifts over time and with task demands. As memories become less detailed, they may shift toward mPFC-mediated reconstructive processes, allowing schematic and gistlike traces to guide behavior.

Recent research has examined time-dependent interactions between episodic memories and schematic representations (99, 199, 218, 219), inspired by work in rodents studying emergent schematic representations using a modified Morris water maze task (see below, Ref. 70). Similar to the studies using continuous measures of retrieval described above, in one study participants learned object-location associations where object categories followed a normal distribution, allowing participants to learn regularities during encoding (**FIGURE 3**; Ref. 99). To test how schematic and episodic memories changed with time, location memory was assessed immediately, after 1 day, and after 1 wk. Participants recalled the locations of previously learned objects and, crucially, estimated locations of novel objects from the same categories, isolating schematic knowledge from episodic memories (**FIGURE 3**). Objects closer to the category center were remembered with greater precision, particularly when location memory was assessed after a delay, suggesting a time-dependent increase in the influence of schematic structure on episodic memories (**FIGURE 3**). However, schema precision, measured as generalization to novel objects, declined over longer delays (**FIGURE 3**). This suggests that schemas are rapidly formed and used when episodic details are unavailable, through either lack of experience or forgetting (99). Similar findings reveal that spatial gist representations emerge quickly (220) but become less precise over time (218, 219, 221). Nonetheless, gist memories may persist longer than item-specific memories, influencing memory retrieval over a delay (221). These findings align with a reconstruction account of memory, highlighting the dynamic interplay between episodic and schematic systems, with shifting contributions from multiple representations over time. Episodic memories initially dominate, but, as they fade, schematic representations are more likely to guide behavior (**FIGURE 3**). Importantly, task demands can modulate this balance, leading to the expression of schemas shortly after encoding if no episodic memory is available (99). Furthermore, the reverse can also occur, with reminders reviving previously inaccessible perceptual details and leading to their dominance over schematic representations even at long delays (102).

Other studies have shown that memory for structure in the environment is maintained, or even strengthened, with time and sleep (222–227). For instance, consolidation has been shown to promote the abstraction of regularities from learned experiences, enabling the enhancement of representations that reflects temporal or categorical structure (222, 223, 227). At the same time, memory for perceptual details tends to decline over time (222, 223, 228), consistent with the idea that episodic details are more vulnerable to forgetting. This enhancement in environmental structure representations may adaptively prioritize information to guide future behavior at the cost of perceptual details from encoding (222).

Neural evidence further supports this time-dependent shift from episodic to schematic representations. As mentioned above, studies have investigated memories for short narratives, showing faster forgetting of peripheral details compared to central, gistlike ones (228). These changes toward gistlike memory representations for narratives have been associated both with hippocampal activity at event boundaries during encoding (229) and by decreasing posterior hippocampal activity and increasing mPFC activity over time (98). Such an increase in schema-related mPFC activity has been observed after long delays of up to 10 mo (230). Another



Adapted from Tompary et al., 2020

FIGURE 3. Memory reconstruction shifts with time and task demands. *A*: at encoding, participants learned object-location associations where object categories followed a normal distribution, allowing participants to learn a location schema over the course of encoding. They were tested on objects' locations immediately and after a 24-h or 1-wk delay. In the delayed test, they were also asked to estimate the location of novel objects from the same category, to isolate the influence of schematic and episodic representations. ITI, intertrial interval. *B*: objects that were more consistent with their category distributions were more precisely retrieved. The influence of schemas on episodic memory increased over time, particularly after a 1-wk delay. *C*: generalization of the schema to new objects decreased over time. *D*: proposed model of schema and episodic memory over time. During learning, schemas and episodic memories are formed, but schemas are only expressed if required by task demands. Over time, episodic memories are forgotten faster than schemas, leading to the dominance of schematic memories in a time-dependent manner. Adapted from Tompary et al. (99); used with permission under CC-BY license.

study showed that mPFC and hippocampus represent overlapping experiences more similarly, but only after a delay (63). Integrated representations in mPFC support the behavioral ability to generalize across experiences (72, 80), particularly over time (231). However, episodic details, when preserved, continue to engage the hippocampus (92, 98). Together, these findings suggest that mPFC and hippocampus represent memories at differing levels of granularity, with their relative strength changing over time but the correspondence between the psychological and neural representations staying stable regardless of time since encoding (26). Such a representational shift can support the extraction and maintenance of information used to guide adaptive future behavior, while forgetting less relevant details.

In addition to the emergence of structured knowledge over the course of an experiment, preexisting schemas can aid in the time-dependent transformation of new episodic memories. In one recent study, participants studied object-scene associations that could be schema congruent (e.g., toaster and kitchen) or schema incongruent (e.g., elephant and kitchen). After a 72-h delay, schema-congruent memories became coarser, such that context-specific details from encoding were forgotten. These memory changes were supported by more integrated representations in mPFC (**FIGURE 4**; Ref. 189). In contrast, the posterior hippocampus came to represent detailed information about object-scene associations, whereas the anterior hippocampus represented more gistlike aspects of the associations (189), consistent with a posterior-anterior hippocampal hierarchy. Furthermore, as described above, schema-congruent memories tend to engage the mPFC, with this contribution increasing over long delays, even for memories that maintain detail over time (155, 191). Such enhancement and integration of schema-congruent memories allows us to use prior knowledge to guide adaptive future behavior (232). Together, this suggests that preexisting schemas act as a scaffold to aid in the delay-dependent transformation of new, congruent episodic memories, resulting in integration and generalization over time.

As noted above, however, when memories retain detail with time there is a simultaneous preservation of posterior hippocampal activity (98, 191). Indeed, a growing body of work suggests that the time-dependent reorganization of memory representations need not result in decreased fidelity. In one study, participants experienced complex, naturalistic events followed by free recall tests. As expected, the quantity of freely recalled episodic details decreased over time. However, the details that were recalled were highly accurate (13). In another study, administration of a noradrenergic agonist after encoding attenuated forgetting, increased hippocampal activity and multivariate similarity between encoding and retrieval, and decreased neocortical involvement after a delay of 28 days (131). This study, however, did not differentiate between posterior and anterior hippocampus. This suggests that detailed memories can be reproduced with high accuracy even at long delays.

Sleep can also protect episodic memories from interference, leading to better memory after sleep compared to a comparable interval of wakefulness (233–235). In one recent study, sleep improved memory for unique details of category exemplars while reducing memory for shared features (236). This suggests that consolidation does not always aid the generalization of shared features (37). Instead, time-dependent changes in memory representations may still support the reproduction of specific memories with high accuracy. The factors underlying the varying effects of sleep are still under investigation, with recent theories suggesting that changes in memory representations may depend on task demands and goals from encoding (26, 132).

Mechanistically, how do time-dependent changes in memory representations occur? Foundational theories propose that memory reactivation during repeated experience, sleep, or rest supports the extraction of commonalities across experiences, gradually forming cross-episode regularities in the neocortex (237). Reactivating an episodic memory can coactivate related memories, strengthening their connections in hippocampal-cortical circuits and transforming their representations over time. For example, repeated retrieval (vs. restudy) leads to more generalized memories and increases access to semantic features, suggesting that retrieval promotes semanticization (238, 239). Such semanticization has been associated with integrated representations in mPFC during repeated retrieval (238), highlighting how repetition can increase the influence of prior knowledge on memory over time (240). Furthermore, stronger cortical reactivation, including in the mPFC, has been observed for memories encoded multiple times compared to those encoded once (241), suggesting that repetition may enhance the dominance of schematic memory representations. This enhancement may support the integration of memories in the mPFC (63, 72, 80, 189), contributing to the growing dominance of schematic representations over time.

Reactivation of specific memories in the hippocampus during rest has also been shown to enhance memory (241, 242). However, it remains unclear which memories are prioritized for reactivation and how this reactivation influences changes in their representations. Some studies report greater replay for weaker memories (242), others, for stronger memories (243), and some find no difference (241). This suggests that reactivation can sometimes strengthen individual memories for specific experiences.

Indeed, reactivation does not always promote integration. As described above, memory reactivation during sleep can enhance memory for unique, exemplar-specific features but not for shared category features (236). This suggests that reactivation can preserve item-specific details rather than promote generalization under some conditions. This observation aligns with prior work showing that sleep can protect individual memories

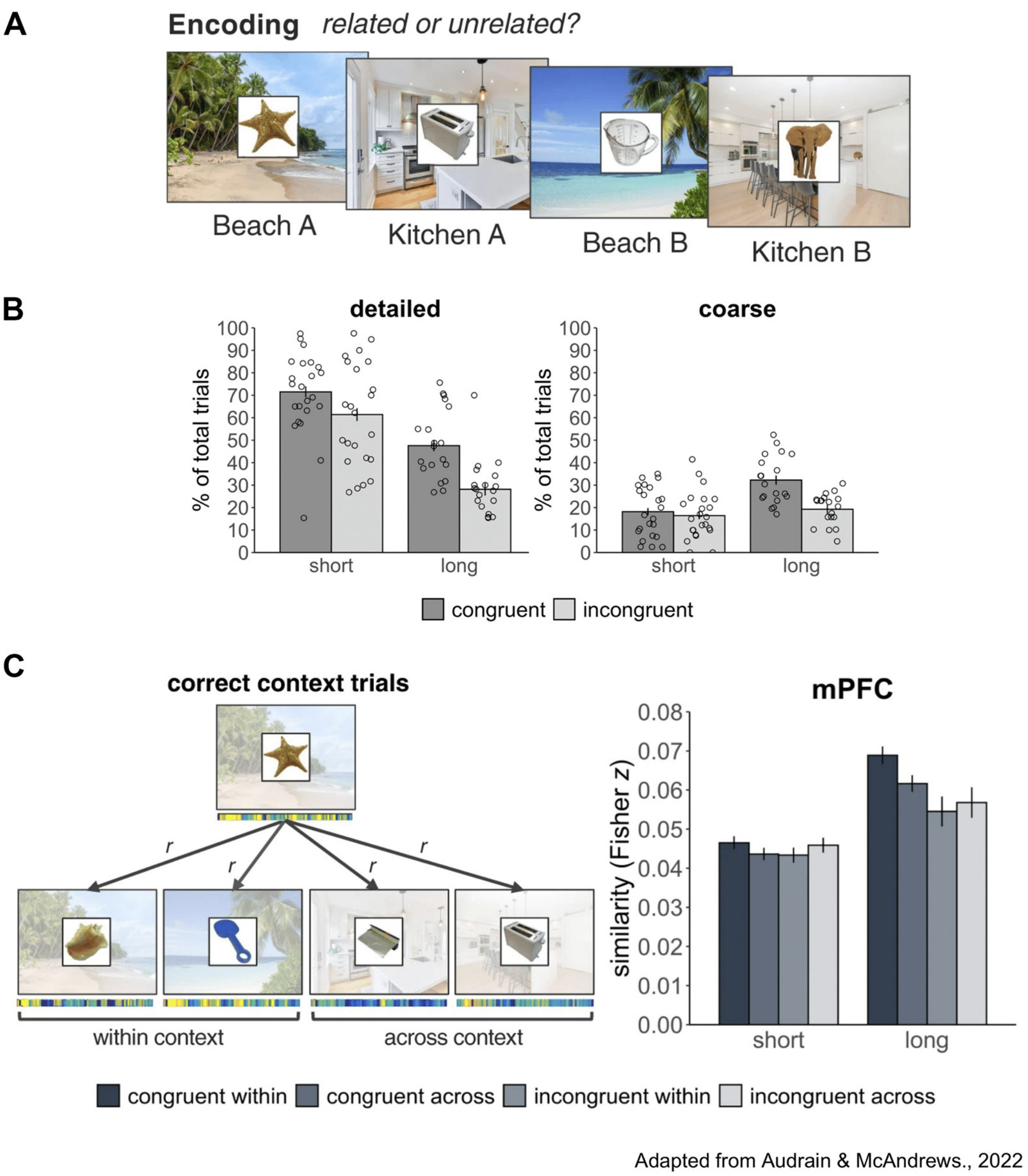


FIGURE 4. Schema-consistent episodic memories become integrated over time. *A*: at encoding, participants learned object-scene associations that could be schema congruent or schema incongruent. Schema-congruent and -incongruent objects were associated with 1 of 2 scenes (e.g., Beach A and Beach B). *B*: memories for the object-scene associations became less detailed over time, such that participants were less likely to remember the specific scene associated with the object at the long delay. Schema-congruent, but not -incongruent, associations became coarser over time, such that participants were more likely to remember the context (beach vs. kitchen) associated with a schema-congruent vs. -incongruent object at the long delay. *C*: multivoxel patterns of brain activity were compared between a given trial and *1*) all other trials from the same context and *2*) all other trials from the different context, separately for schema congruent and incongruent. Patterns of brain activity in medial prefrontal cortex (mPFC) were more similar for congruent compared to incongruent associations at the long delay, suggesting that schema-congruent episodic experiences were integrated into neocortical representations over time. Adapted from Audrain and McAndrews (189); used with permission under CC-BY license: http://creativecommons.org/licenses/by/4.0/.

from interference (233–235). Together, these findings suggest that reactivation can promote semanticization via schema-related representations in the mPFC, particularly over time, while also preserving episodic detail via hippocampal reactivation when task demands require it (132). These processes are not mutually exclusive and may operate in parallel (238), depending on context. A key direction for future research is to determine how hippocampal and mPFC reactivation jointly shape the balance between detailed, gistlike, and schematic memory representations.

One way that reactivation influences memory representations is through the process of reconsolidation. Work in humans and nonhuman animals shows that reactivating a consolidated memory renders it labile, allowing it to be updated with new information. Reconsolidation is a putative mechanism underlying memory reconstruction in the hippocampus (244) and supports adaptive behavior, such as associative inference (80), but also leaves memories susceptible to distortions (207, 244). Such updating depends on hippocampal mechanisms: patients with medial temporal lobe damage can learn initial AB associations but are impaired in forming AC pairs (245), and Ozubko et al. (246) showed that this impairment is specific to memories retrieved via hippocampus-dependent recollection. In rodents, hippocampal lesions impair transfer when individual components of learned pairs are presented separately (247). These findings raise the possibility that, beyond constructing and reconstructing memories, reactivation in the hippocampus may also support deconstruction, fractioning a memory's elements for flexible reuse. We hypothesize that both reconstruction and deconstruction of memories guide flexible behavior, imagination, and the adaptive use of episodic memories.

Taken together, these results suggest that time- and reactivation-dependent changes in memory are best viewed as a shifting balance of multiple memory representations at the neural and psychological levels. The influences of these memory representations dynamically change with time and task demands, with reproduction of details initially dominating, followed by reconstruction as specific details fade (**FIGURE 2**). Reminders and task demands, however, can help recover or preserve the dominance of detailed memories. An important avenue for future work will be to determine how goals and task demands modulate this representational shift over time.

4.7. Similarities and Differences between Encoding and Retrieval Representations

When we retrieve a memory, we often bring to mind the sensations and thoughts that we experienced initially. In line with the correspondence between psychological and neural representations (26), this reexperiencing of an event has a clear parallel in the brain, where representations that were present at encoding are reactivated during retrieval. Such reactivation is thought to drive behavioral expressions of memory, and recent advances in the field have enabled the detection of activity patterns from encoding that support veridical memory retrieval (16). However, this focus on similarities between encoding and retrieval has potentially overshadowed differences between their representations (248). Examining such differences could provide a window into understanding how memories are reconstructed. Below, we describe similarities and differences between encoding and retrieval representations and propose how these two bodies of work can be reconciled by viewing reactivation from a multiple memory representation perspective.

4.7.1. Similarities between encoding and retrieval.

According to the encoding specificity principle, memory retrieval is most effective when conditions at retrieval resemble those at encoding (249). In line with this, multivariate neuroimaging methods have made it possible to isolate brain activity patterns associated with specific stimuli during memory tasks, revealing convergence between brain activity patterns during encoding and their reactivation during retrieval (i.e., encoding retrieval similarity; see below for a similar discussion in research with rodents). Such similarities have been observed for reinstatement of the general context from encoding (250) and also for specific stimuli, together reflecting the reinstatement of episodic experiences. Indeed, stimulus-specific reactivation of activity patterns from encoding has been shown in cortical regions (111), particularly frontal and parietal regions (16, 251), in hippocampus (17, 18), in the surrounding medial temporal lobe (17, 252), and in early visual regions (253), likely reflecting the reinstatement of sensory details from memory. Furthermore, retrieval-based similarity to encoding patterns is related to successful retrieval (16, 252), suggesting that the reinstatement of episode-specific encoding activity patterns is linked to the fidelity of memory retrieval.

These findings are well aligned with hippocampal indexing theory, which provides a framework for understanding how the hippocampus supports memory reinstatement. The hippocampus is thought to bind distributed cortical activity patterns that represent various aspects of an experience into a cohesive memory trace (42, 45, 46). During encoding, the hippocampus links these cortical representations, enabling the rapid formation and retrieval of episodic memories. At retrieval, the hippocampus reactivates cortical patterns from encoding, thus supporting the retrieval of past experiences. Indeed, this theory aligns with the multivariate neuroimaging studies described above. Similarity between encoding and retrieval in cortical regions during successful memory retrieval is often associated with increased hippocampal activity (16, 251, 252), which may mediate the effects of encoding-retrieval pattern similarity on retrieval success (16). Thus, the hippocampus works in tandem with cortical regions to precisely reactivate encoded representations at retrieval.

In rodents, the advent of optogenetic tools has provided more direct support for the reactivation of episode-specific hippocampal memory traces (i.e., engrams, see below). Neural ensembles in the hippocampus that are active during encoding form memory traces for specific experiences (19). Reactivation of these neural ensembles at retrieval, either naturally or optogenetically, elicits behavioral expressions of memory retrieval

(Ref. 19; see below), providing evidence of the encoding specificity principle in rodents (254). In humans, emerging evidence complements these findings, with studies identifying neurons in the hippocampus that represent specific episodic memories, providing a neural signature of memory retrieval at the single-neuron level (255). Although many studies identifying the engram in rodents have targeted hippocampal neural ensembles (3), cortical engrams also play a role in retrieval, especially for remote memories (256). We return to this topic in more detail below. Together, converging evidence from humans and rodents suggests that activity patterns in coordinated hippocampal-cortical networks are reproduced at retrieval, supporting successful behavioral expression of memories.

Of note, however, despite advances in both human and rodent memory research, a fundamental gap remains in our ability to directly compare episodic memory representations across species. In rodents engram studies allow researchers to identify and causally manipulate memory traces at the cellular level, whereas in humans fMRI studies can only infer memory representations from distributed brain activity patterns but provide a window into representations at the network level. Additionally, rodent studies often rely on fear conditioning paradigms (see below), whereas human research is able to examine memory representations for richer and more complex experiences.

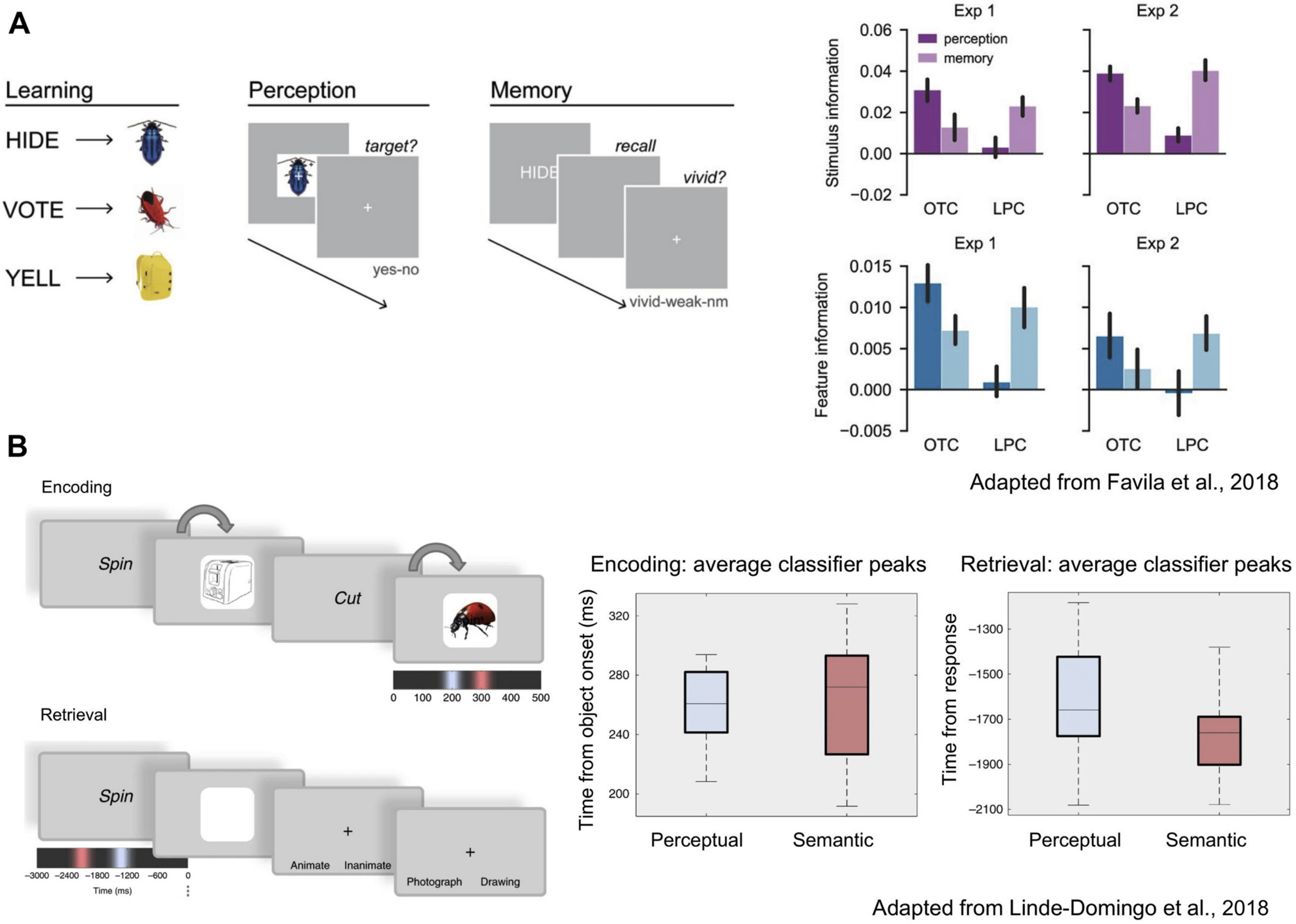
4.7.2. Spatial and temporal transformations between encoding and retrieval.

Encoding a memory involves processing rich sensory input, yet retrieved memories, even when vivid, are not identical to the original sensory experience. Reflecting this psychological distinction, neural representations at retrieval are often transformed compared to encoding, exhibiting spatial localization (248) and temporal differences (**FIGURE 5**; Ref. 258). Whereas early sensory regions may strongly represent ongoing perceptual experience during encoding, memory representations during retrieval tend to be stronger than encoding in frontoparietal regions (257, 259, 260). This shift in the spatial localization of representations is present even when the same perceptual information is on the screen but task demands are to retrieve rather than encode (261). Importantly, parietal representations during retrieval reflect a combination of semantic and episodic information (262) and predict distortions in memory (263), suggesting that encoding-retrieval differences in this region may reflect a reconstructive memory process. In another study, transformations in memory representations reflected the emergence of semantic representations late in encoding, which was associated with better memory for the category of recalled information (264). One possibility is that such representations emerge through coupling between hippocampus, mPFC, and posterior parietal cortex during retrieval (155). Indeed, theories of schema representations suggest that the posterior parietal cortex is important for the recombination and integration of schematic and episodic information (28, 265). Therefore, encoding and retrieval representations differ in their spatial localization within and across regions. These spatial transformations predict distortions in memory precision and the integration of prior knowledge representations with episodic information.

In addition to spatial transformations, there are also differences in the time course of encoding versus retrieval. Visual perception progresses hierarchically through the brain, with low-level features processed in early visual areas before higher-order features, including abstract and conceptual representations, along the ventral visual stream (266). Emerging work suggests that the flow of this perceptual to conceptual processing hierarchy is reversed during memory retrieval, such that conceptual features of a memory are brought to mind during recall before perceptual ones (239, 258, 267, 268). For example, in one study participants encoded or retrieved objects while making conceptual (animate vs. inanimate) or perceptual (photograph vs. line drawing) judgments during EEG recording. A classifier trained to identify perceptual versus conceptual information from patterns of EEG activity found that perceptual processing peaked earlier than conceptual processing during encoding. This pattern was reversed during retrieval, with conceptual processing peaking earlier than perceptual representations (**FIGURE 5**; Ref. 258). Using fMRI-EEG fusion, the authors further found that the temporal reversal from encoding to retrieval was accompanied by increased conceptual representations in parietal cortex during retrieval (269), aligning with spatial transformations between encoding and retrieval (248). Taken together, this emerging body of work suggests that memory retrieval may be underpinned by both spatial and temporal transformations in neural representations, potentially reflecting a neural signature of memory reconstruction.

4.8. Postretrieval Processes Influence Memory Representations

Retrieved memories do not remain static: they are subject to updating, strengthening, or changes depending on postretrieval processing. This postretrieval processing has lingering effects on the fate of those memory representations. Nadel and Moscovitch (92) proposed that memory retrieval, whether occurring online or offline, during rest or sleep, necessarily happens in a



Adapted from Favila et al., 2018

Adapted from Linde-Domingo et al., 2018

FIGURE 5. Spatial and temporal transformations between encoding and retrieval representations. *A*: spatial transformations. In Favila et al. (257), participants learned object-word associations. At retrieval, they were cued with a word and had to recall the object. At encoding, object and feature representations were stronger in occipitotemporal cortex (OTC). At retrieval, recalled object and feature representations were stronger in lateral parietal cortex (LPC). *B*: temporal transformations. In Linde-Domingo et al. (258), participants encoded word-object associations. Objects differed in conceptual (animate vs. inanimate) and perceptual (line drawing vs. photograph) features. At retrieval, participants were cued with a word and were asked to indicate the conceptual or perceptual feature of the associated object during EEG recording. A classifier trained to identify perceptual vs. conceptual information from patterns of EEG activity found that perceptual processing peaked earlier than conceptual processing during encoding. This pattern was reversed during retrieval, with conceptual processing peaking earlier than perceptual representations. *A* adapted from Favila et al. (257) and *B* adapted from Linde-Domingo et al. (258); used with permission under CC-BY license.

context different from the one in which the original memory was formed. This contextual shift leads to the formation of a new trace (270, 271). Relatedly, Antony et al. (240) argued that retrieval acts as a fast track for reorganization and consolidation of memories, by stabilizing memory representations and integrating them to promote semanticization. This phenomenon is linked to the testing effect, in which retrieval (vs. restudy) strengthens memory retention (272). As described above, this process is thought to shift the neural substrates of retrieval. Indeed, repeated retrieval increases reliance on semantic rather than perceptual information, increases multivoxel pattern similarity in mPFC, and decreases hippocampal activity (238, 239), thereby altering hippocampal-neocortical dynamics (238, 240). Furthermore, in line with the role of parietal regions in memory representations, repeated retrieval leads to the rapid emergence of posterior parietal cortex engrams (273) and of semantic representations based on category structure (238). These studies provide further evidence that semanticized information comes to be represented in the posterior parietal cortex during retrieval, in line with its proposed role in integrating schema-consistent information (28), and highlight the continually transformative nature of memory representations at retrieval.

One way that repeated retrieval may lead to semanticization is through fuzzy, imperfect reinstatement of memory representations, along with coactivation of related information (240). Because memory retrieval is often imperfect, we rely on other postretrieval processes, monitoring and verification, to assess the accuracy and relevance of retrieved memories. These processes are thought to rely on various regions in prefrontal cortex, including the subgenual, orbitofrontal, dorsolateral, and ventromedial PFC (274–276). Indeed, damage to the vmPFC leads to confabulation, in which individuals unintentionally generate false memories while believing them to be true. Patients with vmPFC lesions frequently fail to identify errors in their recollections, leading to erroneous yet confident memories (276). We speculate that damage to the vmPFC leads to deficits in schema reinstatement and instantiation that help initiate and guide memory search. Because the schemas serve as a template against which retrieved memories can be compared, damage to vmPFC can also lead to deficits in memory monitoring and verification (274). Together, these findings underscore how postretrieval processes influence the quality of memory representations. Repeated retrieval leads to semanticization and the transformation of memory representations, and monitoring and verification processes allow us to select goal-relevant and accurate memories. Damage to the vmPFC disrupts these processes, leading to impairments in both retrieval and the ability to detect and correct memory errors.

4.9. Reconstruction and Reproduction from a Multiple Memory Representation Perspective

Building on our previous theoretical work and the evidence reviewed above, we propose that multiple representations of experiences coexist at different levels of granularity and interact to drive both reconstruction and reproduction of memory traces. As described above, at encoding detailed, gist, and schematic representations are formed simultaneously, supported by distinct brain regions (26, 43). At retrieval, which memory representation is expressed depends on various factors, including relatedness to prior knowledge, task demands, and the passage of time. The expression of detailed representations at retrieval, underpinning the faithful reproduction of episodic memories, may rely on precise neural activity patterns and hippocampal processes that recapitulate encoding-related activity (16, 18, 19). In contrast, spatial (248) and temporal (258) transformations between encoding and retrieval may facilitate the dominance of abstract, conceptual representations, contributing to memory reconstruction.

When there is limited prior knowledge available to scaffold new learning and influence retrieval, detailed representations are often expressed immediately after encoding, unless task demands favor schematic representations (99). As episodic detail fades or schemas are formed through repeated learning or reactivation, schematic representations may become more influential over time, leading to reconstruction of memories and concomitant changes to neural representations between encoding and retrieval. When a well-formed schema is already available, schematic representations can influence encoding immediately, leading to reconstruction and divergence between encoding and retrieval representations even without a delay. However, even in these cases, the influence of schematic representations may increase over time as episodic details fade. This dynamic shift in memory representations likely contributes to changes in reproduction versus reconstruction observed with time and prior knowledge. Crucially, when episodic memories are remembered with specificity even at long delays (10, 11, 13) they will continue to engage the hippocampus regardless of the passage of time (98).

Viewing both reconstruction and reproduction through the lens of multiple memory representations leads to a number of testable hypotheses. For instance, divergence between encoding and retrieval activity patterns should increase with greater reliance on prior knowledge or with the passage of time. When episodic memories lack strong links to preexisting knowledge and are tested immediately, high similarity between encoding and retrieval should be observed, consistent with reproduction. Over time, as episodic details fade, schematic representations may become more dominant, resulting in greater divergence between encoding and retrieval patterns, favoring reconstruction. In contrast, when memories are strongly linked to prior knowledge, such divergence may emerge even at recent time points and continue to increase over time. Critically, differences in encoding-retrieval similarity should correlate with schema-based memory distortions. Additionally, the temporal trajectory of memory retrieval, particularly for heavily reconstructed memories, should progress from schema-based representations to gist-level representations and finally to episodic detail, mirroring the conceptual-to-perceptual continuum. Finally, manipulating task demands to emphasize episode- or schema-based retrieval should modulate the balance between reproduction and reconstruction, with concomitant changes in neural pattern similarity between encoding and retrieval.

Going forward, we believe that focusing on *1*) the correspondence between representations underlying psychological and neural representations, *2*) how these representations transform with prior knowledge, time, and task demands, and *3*) the differences between encoding and retrieval representations will be crucial for uncovering the dynamic interplay between memory stability and flexibility, as well as their mutual influences on adaptive behavior. We return to these ideas in sect. 7.

5. INDIVIDUAL DIFFERENCES AND MNEMONIC REPRESENTATIONS

Thus far, we have proposed that multiple memory representations support the balance between reproduction and reconstruction, exhibiting a relatively consistent pattern across individuals. However, people differ. Although this may be a truism, the vast majority of behavioral and neuroimaging research in memory and cognition, including that described above, is designed to test mechanisms that apply to the general population. Interindividual variability is treated as noise, inflating the denominator in effect size calculations and masking experimental effects.

In contrast to this nomothetic approach, the idiographic approach treats interindividual differences as independent variables rather than noise (277). Although the idiographic approach is associated with clinical or personality research, there is a robust literature on individual differences for working memory, attention, and executive control (278–280) processes that entail distributed connectivity between central core processing circuits to heteromodal association cortex, which is where neurodevelopmental variability is most likely to give rise to meaningful cognitive profiles (281). To the extent that memory tasks reviewed above also draw upon such distributed processes, individual differences on these tasks carry signal and not just noise. Taking these differences into consideration could therefore improve the precision of hypothesis testing and prediction over and above the treatment of samples as homogeneous.

Imagine being asked how well a friend or family member remembers past events. In answering this question, most people would reflect on the person's ability to remember events from days, weeks, and years ago rather than from minutes or hours ago. As noted above, memory transformations, including forgetting of episodic details and reliance on gist, increase with the passage of time. Extrapolating to populations, interindividual differences in memory for remote events (relative to the typical timescales assessed in laboratory studies) carry potentially meaningful signals about memory transformation, in addition to the search, retrieval, and verification operations associated with recovery of remote details.

Testing at timescales beyond minutes or hours, however, poses methodological challenges, especially given the need for larger samples when analyzing individual differences (282). Autobiographical cues (e.g., lifetime periods) are commonly used to elicit personally experienced, remote events occurring at a unique time and place (108). Although such approaches have advanced our understanding of memory transformation (283, 284), cued remote events lack control over prior reactivation or rehearsal. Indeed, these cued events are, by definition, accessible and likely highly rehearsed. This limitation can be partially overcome by selecting relatively unrehearsed events (e.g., harvested from others or via photo albums or diaries) or with staged events, where the encoding context and delay intervals can be controlled and responses can be verified against the ground truth (13, 223, 285). Alternatively, questionnaires can be used to probe the quantity and quality of mnemonic retrieval or related processes or mnemonic traits (i.e., how one remembers events in general as opposed to performance on an isolated test). Despite the limitations of self-report, questionnaires enable rapid assessment across large samples that are required for individual differences analyses yet cannot be obtained with detailed behavioral testing. Moreover, self-report is required to estimate the subjective, autonoetic quality of mnemonic experience.

There is good evidence that the tendency to vividly reexperience events (vs. experiencing them in a gistlike manner) can be assessed as a stable individual difference (286–288). Autobiographical recollection is dominated by visual imagery (90, 289), also a stable individual difference (290, 291). Moreover, the tendency to vividly reexperience images and details from past events is independent from spatial navigation, spatial schematic imagery, and spatial transformations (286, 290, 292, 293). The subjective vividness of the experience can even be dissociated from memory for the observable details that form its content, with subjective aspects of the experience linked to posterior parietal cortex (69). As we shall see, similar dissociations can be found in people at the extremes of the continuum of episodic autobiographical memory capacities.

The degree to which one fluently recovers visual, sensory, or other episodic contents when recollecting past events moderates their reliance on schema, prior knowledge, and other nonepisodic processes in memory and cognition. When recalling visual details from film clips, people endorsing strong visual imagery were susceptible to concomitant experimental visual interference (i.e., dynamic visual noise on a screen) due to difficulty with visual reinstatement, whereas those with low visual imagery and presumably better developed nonvisual schematic processes were unaffected by visual interference (294). During free recall of a staged event, quantified episodic (but not nonepisodic) details were related to saccadic eye movements that reinstated the visual scene (295), but only for people with high trait autobiographical memory; those with lower trait autobiographical memory generated episodic details using alternative (likely nonvisual) processes (95). These findings provide behavioral evidence that ostensibly equivalent memory performance can be produced via different mechanisms, depending on a person's trait capacity for visualization. Furthermore, they suggest that individuals differ in the extent to which they encode detailed versus schematic representations, predicting that memory reconstruction is more prevalent in those who rely more on semantic and schematic processing than in individuals with strong imagery-based memory.

These observations are supported by neural data. In an fMRI study, individuals with high trait autobiographical memory show increased resting-state connectivity between the medial temporal lobes and posterior (visual) regions, whereas those reporting high factual/semantic memory showed increased connectivity between the medial temporal lobes and prefrontal regions involved in organization and integrating conceptual information (296) (**FIGURE 6**). These same patterns were associated with perceptual and gist-based processing, respectively, when applied to large-scale imaging data from the Human Connectome Project (HCP) (299).

Similar findings are evident in group studies of healthy individuals with extreme neurodevelopmental variants. Severely deficient autobiographical memory (SDAM) is a nonpathological extreme variant developmental condition [like developmental prosopagnosia (300)] defined by reduced event recollection for visual details of remote events (301, 302), with corresponding reductions in engagement in the brain's distributed autobiographical memory network when presented with autobiographical retrieval cues (301–303). Individuals with extremely low mental imagery abilities, or aphantasia, also show reduced episodic recollection (304). Neither SDAM nor aphantasia is associated with everyday functional impairment.

Reduced integrity of the fornix in SDAM suggests degraded outflow from the posterior hippocampus such that distributed activity required for recollection is not engaged, even though recognition is intact (301, 305). These findings are confirmatory in that they are consistent with self-reported low autobiographical memory, yet they do not speak to preserved everyday function in SDAM. One possibility is that people with SDAM compensate for their low episodic AM with strong nonepisodic processes such as schematic or implicational reasoning, speaking to the adaptive nature of these memory representations (see Ref. 304 for a similar observation in the related syndrome of aphantasia).

Using fMRI, Bone and colleagues (14, 306) demonstrated that normal adults' recognition of visual details from previously encoded images was associated with reinstatement of low-level visual features in the primary visual cortex in conjunction with posterior hippocampal activity. People with SDAM, however, relied upon higher-level semantic features of the images in conjunction with anterior hippocampal activity (298) (**FIGURE 6**). This finding provides objective correspondence to the subjective reports of people with SDAM that they make inferences based on higher-level schematic or semantic processes, as opposed to detailed visual representations. Parallel findings are seen in aphantasia (307, 308). Such evidence is consistent with our hypothesis that individuals who rely more on schemas and semantics are more prone to memory reconstruction than reproduction.

These advanced inferential abilities support normal everyday function, which is why SDAM is regarded as an exceptionality rather than a pathology. Indeed, this exceptionality appears to confer advantages despite these participants' self-reported mnemonic deficit. These include overrepresentation in science, technology, engineering, and mathematics (STEM) (especially computational) professions involving schematic reasoning skills (309) and protection from age-related functional decline due to well-developed compensatory abilities (310). In other words, people with SDAM draw upon inferential logic and schema rather than episodes to solve problems, further highlighting the adaptive nature of multiple memory representations.

Vivid memories are an asset for a rich inner life and everyday activities, fostering positive states of reminiscence, imagination, and creativity, but they can be maladaptive under some circumstances. After exposure to trauma, vivid memories or flashbacks of a distressing event can be seen and felt as if they are being relived, even when the objective threat has passed. Such intrusive memories disrupt schemata pertaining to one's sense of safety, and they are considered hallmark symptoms of posttraumatic stress disorder (PTSD) (311, 312). Accordingly, the structural integrity of the brain's visual system predicts outcomes following trauma exposure (313), as well as higher resting-state activity in primary visual regions (V1/V2) in treatment-naive individuals with PTSD (314).

In 936 participants who had been exposed to significant trauma, self-rated richness of visual imagery [Object-Spatial Imagery Questionnaire (OSIQ-Object)] was positively correlated with PTSD symptoms. Conversely, measures of spatial-schematic processing (OSIQ-Spatial) were negatively correlated with PTSD symptoms (297) (**FIGURE 6**). We also found that PTSD symptoms were negatively correlated with reasoning abilities, but not working memory and attention, corresponding with the nonvisual, implicational processes we hypothesize to be protective in PTSD.

These findings are consistent with models of connectivity-based competitive processing (see Ref. 281), which hold that ostensible developmental weaknesses, such as low imagery and autobiographical memory, may be associated with complementary strengths, such as high

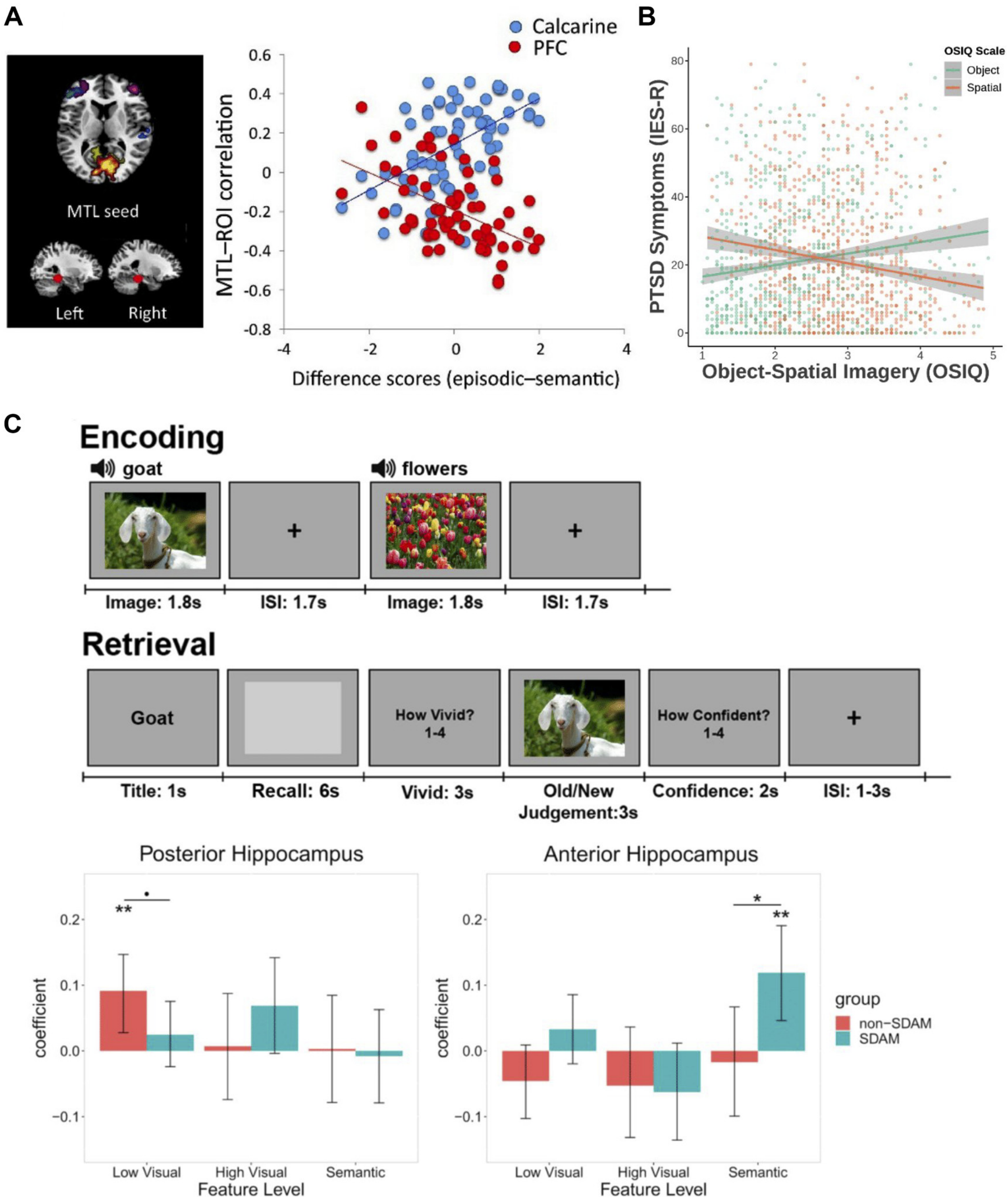


FIGURE 6. Individual differences in episodic vs. schematic representations: relation to brain networks and psychopathology. *A*: individual differences in trait episodic vs. semantic autobiographical memory [measured with the Survey of Autobiographical Memory (SAM)] are associated with medial temporal lobe (MTL) connectivity. Warm colors depict the connectivity pattern that was positively associated with episodic scores, and cool colors depict the pattern that was positively associated with semantic scores. The scatterplot depicts regions of interest (ROIs) demonstrating these patterns, including the calcarine and lateral prefrontal cortex (PFC). *B*: vivid object imagery as rated by the Object-Spatial Imagery Questionnaire (OSIQ) is associated with posttraumatic stress disorder (PTSD) symptoms in trauma-exposed adults, $r(918) = 0.15$, whereas spatial imagery abilities are negatively associated with PTSD symptoms, $r(918) = -0.15$. *C*: visual imagery paradigm employed by Bone et al. *Top*: during encoding, participants performed a 1-back task while viewing a sequence of color photographs accompanied by matching auditory labels. During retrieval, participants retrieved and maintained a mental image of the associated photograph over a 6-s delay in response to the visually presented label, followed by ratings. *Bottom*: feature-specific informational connectivity (FSIC) between the hippocampus and visual cortex during recall in matched groups ($N = 14$) with and without severely deficient autobiographical memory (SDAM). As previously demonstrated, people without SDAM had significant low-level visual connectivity between the early visual cortex and the posterior hippocampus (*left*), whereas SDAM participants had significant semantic connectivity between the early visual cortex and the anterior hippocampus (*right*). Thus, in visual recall, people with SDAM engage semantic representations mediated by anterior hippocampal-visual cortical connectivity instead of relying on low-level visual features mediated by posterior hippocampal-visual cortical connectivity, as is the case in people without SDAM. $\cdot P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$. *A* adapted from Palombo et al. (287). Copyright 2018 by Elsevier. Reproduced with permission. *B* adapted from Yeung et al. (297). Copyright 2025 by Sage Publications. Reproduced with permission. *C* adapted from Bone et al. (298). Copyright 2025 by MIT Press Journals. Reproduced with permission.

logical or schematic reasoning (see also Refs. 304, 315–317). Individual profiles of strengths and weaknesses in mnemonic traits promote alternative routes to event retrieval (287, 318, 319), with implications for both occupation and clinical outcomes.

PTSD therapies focus on dampening vivid recollections (e.g., through exposure or extinction) or boosting schematic safety narratives (312, 320–322). In social anxiety, the schema-congruent and -incongruent learning (SCIL) model draws upon the same distinctions within autobiographical memory to foster conceptual rescripting of anxiety-inducing autobiographical memories (323).

The foregoing evidence supports our hypothesis that multiple representations of an experience are laid down in memory and suggest that individual differences play an important role in which representations dominate during retrieval. Although evidence from studies of individual differences generally support our view that episodic memory is adaptive, they also call our attention to the fact that some of the very qualities that make episodic memory adaptive in most circumstances may be maladaptive in others (7), even leading to pathology. The dissociation of subjective components (i.e., self-reported reexperiencing) of episodic memory from memory accuracy, at the level of both brain responses and real-life outcomes, points to the importance of considering subjectivity along with objective memory test responses in considering the adaptive functions of episodic memory.

5.1. Individual Differences in Nonhumans?

Many of the challenges inherent to the study of remote memory in humans can be easily circumvented in nonhuman samples. Encoding characteristics can be exquisitely controlled, and testing can occur at precise time points relative to the organism's lifespan. There is far more flexibility in the application of naturalistic stimuli, including traumatic stimuli, in nonhumans, where ethical constraints preclude causal inferences (324). Moreover, as described above, nonhuman preparations provide a comprehensive set of tools for mechanistic hypothesis testing at the circuit and cellular levels.

The text above in sect. 5 describes emerging research on individual differences in humans in the context of dominant experimental methodologies. In nonhuman research, however, the idiographic approach is even less popular. If humans' individual differences are biologically meaningful, it is unlikely that they developed anew in human evolution. It should therefore be possible to test the effects of these differences in nonhuman samples (for example, see Ref. 325).

6. EPISODIC MEMORY IN NONHUMAN ANIMALS

Animal models offer the advantage of studying the neural underpinnings of memory processing at the cellular, molecular, and genetic levels, offering a level of mechanistic granularity that is not possible in humans, but the limitations in probing complex cognitive processes and subtle facets of memory processing with animal models are considerable. Generally, when attempting to assign human constructs such as cognitive states, motivation, or intention to overt behavioral expression in animals, we apply "-like" to describe the behavior. We can objectively assess the behavioral output of the what-where-when components during a task, and from this we infer recollection of the event previously experienced by the animal (326–328). This egocentric view ignores the reality that animals are not tiny models of human behavior (329). We should use caution in applying our human notions to describe observed behavior and be sensitive to the biological preparedness of each taxa when attempting to understand their behavior and how the memory functions of each species have evolved to allow them to learn and survive (330–333).

6.1. How Have Different Taxa Evolved to Process Memory Formation and Retrieval?

Lower-order invertebrate taxa with simple nervous systems such as gastropods (*Aplysia*), arthropods (*Drosophila*), and nematodes (*Caenorhabditis elegans*) are common neurobiological models used to study the molecular basis of learning and memory. Landmark studies in *Aplysia californica* demonstrated that sea slugs are capable of forming an associative memory for the connection between a light touch of the siphon and an aversive shock, resulting in a long-lasting conditioned siphon and gill withdrawal response (334). Through this simple association, Kandel and his team were able to identify the molecular basis of learning and memory, representing a massive step forward in the field's understanding of the physiological substrate of a memory (335). This reductionist approach permits the isolation of cellular and molecular plasticity mechanisms supporting this "what" association in sensory and motor neurons but lacks the hallmarks of what is considered episodic memory, including the "where" and "when" components. The simple nervous system of invertebrates lacks higher-order brain structures that would permit the formation of these episodic properties. The processing of complex sensory, perceptual, contextual information within an episodic memory requires coordinated interconnection between thalamic regions, the hippocampus, and prefrontal cortex and cannot occur in lower-order taxa lacking these structures. Fortunately for the slug, it has evolved in a way that does not require the combination of such complex spatiotemporal elements to survive in its natural environment.

The evolutionary point at which episodic memory processing abilities emerged is debated (336), although the homology between hippocampal and prefrontal cortical brain structures in humans, nonhuman mammals, and some birds suggests that episodic-like abilities are possible in other species (337). For the purposes of our argument, we limit our discussion of episodic memory to mammals and some birds. The mammalian brain's hippocampus and association cortices with higher-order sensory, affective, and cognitive function add richly detailed, multisensory associations to experienced event memories. The anatomy of the hippocampus is remarkably conserved across mammalian species, with humans, monkeys, and rats having homologous hippocampal subfields, though with differences in relative size and complexity (337, 338). Functional and morphological differences in the structure and connectivity of the nervous system will change how complex event memories may be formed. As described above, the structural and functional connectivity between the hippocampus and mPFC in the mammalian brain (particularly humans and rodents) facilitates the interplay between the perceptually detailed elements of an episodic or event experience and the schematic elements (98). This interplay guides behavior by contextualizing episodic details within previous experiences or semantic knowledge associated with the retrieval cue (339, 340). Taxa that lack such connectivity, or lack these structures, will likely have less supporting information coactivated in response to a memory cue, making it more likely that they will experience a reproductive replay of the associated event memory triggered by the cue (330, 337). The way in which memory is tested will strongly influence interpretations of the memory capabilities of a given species. The stimulus used to trigger a response will determine the type of behavior expressed, such that tasks employing simple, discrete cues will trigger a basic conditioned stimulus-response memory, whereas more complex naturalistic cues may trigger competing memory representations and result in more varied responses depending on the time since acquisition, prior related experiences, the cues attended to, and even the internal state of the animal at the time of testing.

6.2. How Is Episodic Memory Evaluated in Nonhuman Animals?

Over the past two decades, numerous clever experimental designs have successfully demonstrated that behavioral output of the "what," "where," and "when" components of a retrieved discrete event can be exhibited by rodents (rats, mice) (341–345) and birds (scrub jays, magpies, hummingbirds, black-capped chickadees) (326, 346–350). If an additional hallmark of episodic memory is that it is based on a single unique experience, then many typical assessments of episodic-like behavior used in animal models that use multiple trials are not true measures of episodic memory. The majority of behavioral tasks used to assess episodic-like memory in animals use multiple trials over several days. This repeated experience may solidify a reproductive memory of the event, or it may facilitate the formation of a generalized memory based on repeated similar experience (multiple trials) over the course of training (240). Nonepisodic alternative explanations for apparent episodic memory expression are important considerations when interpreting animal behavior (348, 351, 352). It has been argued that familiarity-based memory, or memory lacking precise spatial-temporal context, can support what appears to be an expression of episodic memory by using a familiar cue to trigger recall (353).

6.3. When Is Memory Reconstruction or Generalization Adaptive in Animals?

As discussed above, both detailed and generalized memories may be used to guide adaptive and flexible behavior. Given the different demands on humans and animals, when applying notions of human episodic memory to animal models we should consider how event-specific or event-general schematized expressions of memory, and the ability to flexibly update memories, may benefit different aspects of the animal's behavior. Additionally, for each animal model, understanding what the animal has evolved to do for survival is a critical component to understanding how specific or generalized memories promote survival in the animal's natural environment.

Capitalizing on the rat's innate feeding behavior, the "social transmission of food preference" task exposes an observer rat to a demonstrator conspecific that has recently consumed a sample food flavor (e.g., cocoa or cinnamon) (354–357). When the observer rat is given a choice between consuming cinnamon- or cocoa-flavored food in the same context in which the olfactory transmission event occurred, it will favor the sample flavor previously consumed by the demonstrator rat. If 1 wk elapses between the transmission event and the food selection, however, the observer rat will favor the novel flavor in the same context but the familiar sample flavor in a different context (358). Although this change in preference might be interpreted as the rat forgetting the sampled food in the original context, there is an alternate interpretation from an evolutionary perspective that accounts for the spatiotemporal components of this food-based memory task. Context-dependent memory would discourage selection of the sample food in the same environment where it may not be biologically adaptive to persist with that response after a long delay, whereas generalized, context-independent memory, which evokes a less precise representation of the environment, would favor selection of a previously experienced, familiar food (358). These observations reflect those discussed above in humans, where multiple memory representations (detailed vs. schematic) can be differentially adaptive in the immediate versus long term.

These findings also mirror the landmark findings of Clayton and Dickinson (326), who showed that, when given the choice of searching locations for previously cached perishable worms or nonperishable nuts, Western scrub jays will selectively search the location of the preferred worms after several hours but will avoid the worms and search for the nuts after a delay of several days. Scrub jays also use knowledge about the rate of decay of crickets to guide their search and foraging behavior in response to caches of crickets or nuts made after varying intervals and are capable of updating this knowledge in response to new decay rate information (346). The birds initially searched the cricket-baited locations after 1 day but not after 4 days, when the crickets would have decayed and perished, showing evidence of spatial-temporal memory. When the crickets' rate of decay was changed during the retention interval, the jays were able to update their cricket location cache memory accordingly based on the new information and proceeded to seek out the preferred cricket-baited locations at the 4 day interval. This updating of the food cache event memory shows strong support for flexibility, updating, and reconstruction of the what-where-when components of the event memory. Likewise when caching food, the jay will pretend to cache if the jay believes another jay is observing, especially if the caching jay had itself pilfered food in the past (359), potentially suggesting the subjective use of theory of mind.

6.4. *Reconstructive Memory in the Wild*

An animal's ability to incorporate episodic and schematic elements into its spatial navigation and foraging behavior likely beneficially influences the animal's decisions and behavior in a way that promotes survival (360). In the wild, there is evidence that primates use episodic information and knowledge related to recently experienced weather events to influence their food searching behaviors. After several days of warm weather, monkeys were more likely to revisit trees containing previously unripe fruit but avoided revisiting trees that previously lacked fruit, suggesting that they recollected the location of available food and used knowledge of recent weather patterns and the effect of warm weather in accelerating fruit ripening to guide their foraging behavior (361). The consideration of the "what" (what fruit was previously unripe), "where" (where the previously unripe fruit was located), and "when" (how many days of warm weather had recently passed) with the integration of knowledge for the effect of weather patterns on rates of fruit ripening suggests a sophisticated reconstructive memory process that is updated based on changing environmental conditions.

Multimodal environmental stimuli and memory for past experiences undoubtedly shape an animal's behavior in its natural environment. Important considerations when using nonhuman animal models of memory include the unnatural conditions under which subjects are reared and their behaviors are assessed or measured. A rodent's ability to forage and navigate its natural environment and its evolved ability to form complex cognitive maps, or mental representations of a spatial environment (362), based on experience will shape the updating of the cognitive map in response to prior aversive (presence of threat) and appetitive (presence of food or mate) events experienced over months and years. The animal's natural activity levels and food-seeking behavior at any given time will also be informed by circadian and circannual variables including time of day and annual seasons, which do not strongly translate to conditions in a laboratory environment using tightly controlled 12-h light cycles year round (363–365). Within the confines of the experimental conditions used to assess spatial memory in the laboratory, subjects are deprived of these prior experiences and stimuli that would naturally guide their behavior. The expressed behavior in response to a memory cue is therefore limited to a discrete, experimentally produced experience and likely to be more of a reproductive memory expression. This paucity of prior experience is useful in allowing researchers to restrict potential confounding elements that may guide behavior in response to a cue but likely results in an impoverished representation of the types of memory a rodent might naturally experience outside of the restricted laboratory environment.

A further consideration in interpreting an animal's natural behavior in response to a cue is the contributions of attentional or task demands. Although we interpret behaviors expressed in response to a memory cue as indices of memory retrieval or expression, we cannot conclude that this is the only explanation for the animal's behavior and should not discount the influence of motivation, attention, or the animal's "inner state" (329, 332).

One can imagine that a rodent's current internal state (e.g., hunger or thirst) will influence its behavior, but objectively studying these intervening variables remains a limitation to animal models of memory. Although staunch behaviorists will likely bristle at the suggestion of considering the influence of internal, subjective variables and experiences in guiding memory construction, reconstruction, and expression in animals, growing evidence supports their involvement. The inability of nonhuman animals to self-report subjective states seems to pose an insurmountable barrier to the assessment of subjectivity [but see Ref. 328 for a demonstration of receiver operating characteristic (ROC) curves in rats that correspond to recollection and familiarity in humans]. On the other hand, the contention that nonhuman animals do not have inner lives that guide their responses on mnemonic or other tasks cannot withstand observation (366, 367). The subjective states we hold dear, such as the self, social engagement, or future goals, did not arise anew in humans. In addition to the objectively assessed what-where-when criteria, the inner state of nonhuman animals can be experimentally manipulated to test hypotheses concerning unobservable inner states. Additionally, to the extent that the neural correlates of subjective states (e.g., mnemonic vividness) can be reliably measured in humans and be related to, yet dissociable from, objective neural measures, it should be possible to interrogate conserved versions of these states in nonhuman animals (328, 344, 368).

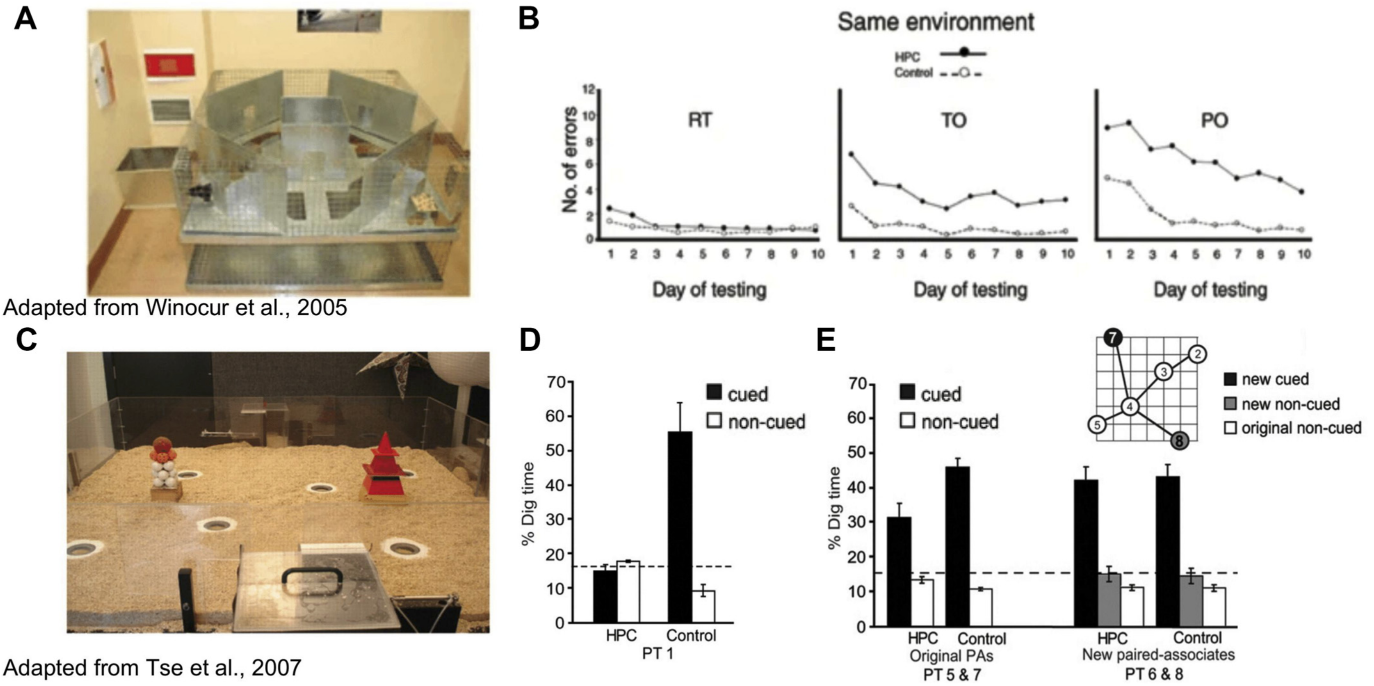
Studying memory under naturalistic conditions has obvious limitations and lacks control. If the purpose of a memory assessment is to identify how the brain can form a memory trace at the structural, molecular, or genetic level, then modern engram studies do a beautiful job of capturing the "physiological footprint" of a discrete event memory experience. If, however, the goal is to understand when overt expression of memory retrieval is a reproductive or reconstructive process, regardless of species, we should consider how both time and repeated experiences influence the formation and transformation of a memory trace and its content, and why changes to the memory representation are adaptive in guiding future behavior (125, 340).

6.5. *Spatial Memory Transformation*

The expansive literature on cognitive maps and spatial place fields (362, 369) could also be discussed in terms of spatial memory reproduction and reconstruction, but its relevance to memory updating and schemas is only touched upon briefly here. Spatial schemas are thought to form through repeated navigation within an environment, where recurring patterns of spatial relations among key elements of the environment are learned and a general allocentric representation of the environment is formed (370–374). The hippocampus and related MTL regions are known to play a critical role in spatial memory acquisition and retrieval (375–377). Like episodic memories, the mPFC emerges as a key extrahippocampal region supporting well-learned remote spatial memory and spatial schemas (29, 30, 70, 378, 379).

When an established spatial schema exists, new information in that environment can be rapidly integrated through accelerated memory reorganization in the mPFC, potentially through fast mapping (28, 380–382). In a series of influential studies, Tse and colleagues (29, 30) trained rats on a hippocampus-dependent paired-associates memory task in which they learned the spatial arrangement of flavor-place paired associations within a spatial arena. After rats had established this spatial schema, they were presented with new paired associates followed by hippocampal lesions either 3 h or 48 h later. Lesions made 3 h after acquisition abolished the memory for the new paired associates, suggesting early reliance on the hippocampus, whereas memory was unimpaired when lesions were made 48 h after acquisition. The retention of both the original and the new paired associates locations indicates that the existing spatial schema supported the rapid integration of this new, related, spatial information into an mPFC-mediated representation. In follow-up studies, they identified strong connectivity between the hippocampus and midline neocortical regions (prelimbic cortex, anterior cingulate cortex) and AMPA receptor- and NMDA receptor-mediated activity as critical for encoding new paired associates into existing schemas (30, 383) (**FIGURE 7**). Further evidence for the time-dependent emergence of schematic representations comes from a study in which rodents completed an adapted Morris water maze task, where platform locations followed a normal distribution (70). Rodents could rely on episodic memories of specific platform locations or an emergent schematic representation of the platform distribution, learned across multiple episodes, to guide their search after 1 day or 30 days. After 30 days, rodents were better at using the schematic representation of the platform distribution. Furthermore, conflicts between the learned distribution and new platforms were reduced by pharmacological inhibition of the mPFC, but only after 30 days (70).

This evidence suggests that the ability to rapidly assimilate new information into a spatial schema is a beneficial reconstructive process that facilitates the updating of memory for one's general environment in response to ongoing changes. When new experiences align with existing spatial schemas, they are efficiently integrated into cortical networks (29, 30, 70, 383–385).



Adapted from Winocur et al., 2005

Adapted from Tse et al., 2007

FIGURE 7. Spatial schemas become hippocampus (HPC) independent with time and experience. *A*: village environment. In Winocur et al. (374), rats were reared in the village for 3 mo (RT) or given only preoperative training (TO) or postoperative spatial location training (PO). All rats were trained to find a food or water goal in the village. *B*: RT rats (*left*) retained robust spatial memory for the reward locations, indicating that the spatial memory had become hippocampus independent after extensive premorbid experience in the village environment. TO rats with limited prelesion village experience (*center*) exhibited significant spatial memory impairment, indicating that the recently acquired retrograde spatial memory was still hippocampus dependent. PO rats with only postlesion spatial training experience (*right*) exhibited significant spatial learning impairment. Subsequent probing on the nature of the retained spatial representation in hippocampally lesioned RT rats indicated that they were relying on a simplified schematic spatial representation of the environment that was insufficient to support updating and remapping of the spatial environment. *C*: spatial arena for paired-associates learning, where Tse et al. (29) trained rats to associate flavor-location pairs. *D*: hippocampal lesions performed before paired-associate (PA) training impaired the rats' ability to form the flavor-location memory. *E*: hippocampal lesions performed after the spatial schema had been well learned no longer impaired the rats' ability to recall the original flavor-location PAs (*left*) or to learn new PAs (*right*) in the arena, demonstrating a rapid assimilation of new spatial information that is consistent with a preexisting spatial schema. *A* and *B* adapted from Winocur et al. (374), *Nature Neuroscience* 8: 273–275, 2005, © Springer Nature. Reproduced with permission. *C–E* adapted from Tse et al. (29), *Science* 316:76–82, 2007. © 2007 American Association for the Advancement of Science. Reproduced with permission.

If a new experience deviates significantly from an established spatial schema, it will be processed as a unique memory, again requiring engagement of the hippocampus (270, 374, 383). A demonstration of this dissociation was observed in rats given prolonged experience of living in a complex spatial "village" environment, allowing them to form a robust spatial memory for the naturalistic spatial environment. Hippocampal lesions made after 3 mo of continual exposure to the village environment did not impair the rats' ability to successfully navigate the highly familiar routes, indicating that the spatial map had become hippocampus independent. Rats given limited prelesion experience in the environment, however, did not retain memory for the spatial locations, nor were naive rats capable of learning the spatial layout when exposed to the village environment after hippocampal lesions. The retained spatial memory in hippocampus-lesioned rats was a schematic representation of the environment. When minor spatial cues were altered in the village, rats were unimpaired in their navigation. When major spatial cues were reconfigured, or when previous familiar routes were blocked, lesioned rats displayed significant spatial memory impairment (374) (**FIGURE 7**). These findings suggest that lesioned rats with extensive premorbid experience in the village were using major, stable geometric cues to guide their navigation, relying on this simplified schematic spatial representation of the environment rather than a detailed allocentric representation that would allow them to update and cognitively remap the altered environment. These findings suggest that spatial memories develop both schematic and contextually detailed representations, with shifts in their balance over time, similar to what is observed with episodic memory reorganization. It should be noted that similar patterns of hippocampus-independent generalized spatial memory for highly familiar environments have been observed in humans (283, 386–389). The ability to rely on schematized spatial representations, rather than retrieving context-specific representations of each unique experience, likely offers adaptive advantages. Such a strategy may enhance an animal's ability to rapidly make decisions in unfamiliar situations such as foraging or safety seeking, increasing the likelihood of its survival.

6.6. Fear Memory Transformation

As reviewed above, schemas reflect the extraction of commonalities across multiple event exposures. Fear conditioning assessed weeks after a single exposure elicits a different kind of transformation, referred to here as generalization (98, 358, 390).

Cued and context fear conditioning, in which animals acquire a long-lasting memory for a discrete, single trial event, are among the most common methods used to assess the neural basis of episodic-like memory in rodent models (391–393). Freezing behavior, a species-specific defensive response, is a standard measure of memory expression in these paradigms (391). Expression of the fear-based memory appears to be both reproductive and reconstructive, depending on the age of the memory and the cues guiding memory retrieval. After contextual fear conditioning, rodents will exhibit context-specific freezing 1 day after conditioning, but 1 mo later they will exhibit generalized freezing in both the original conditioning context as well as a novel context sharing general features of the original experience (98, 358, 390, 394, 395).

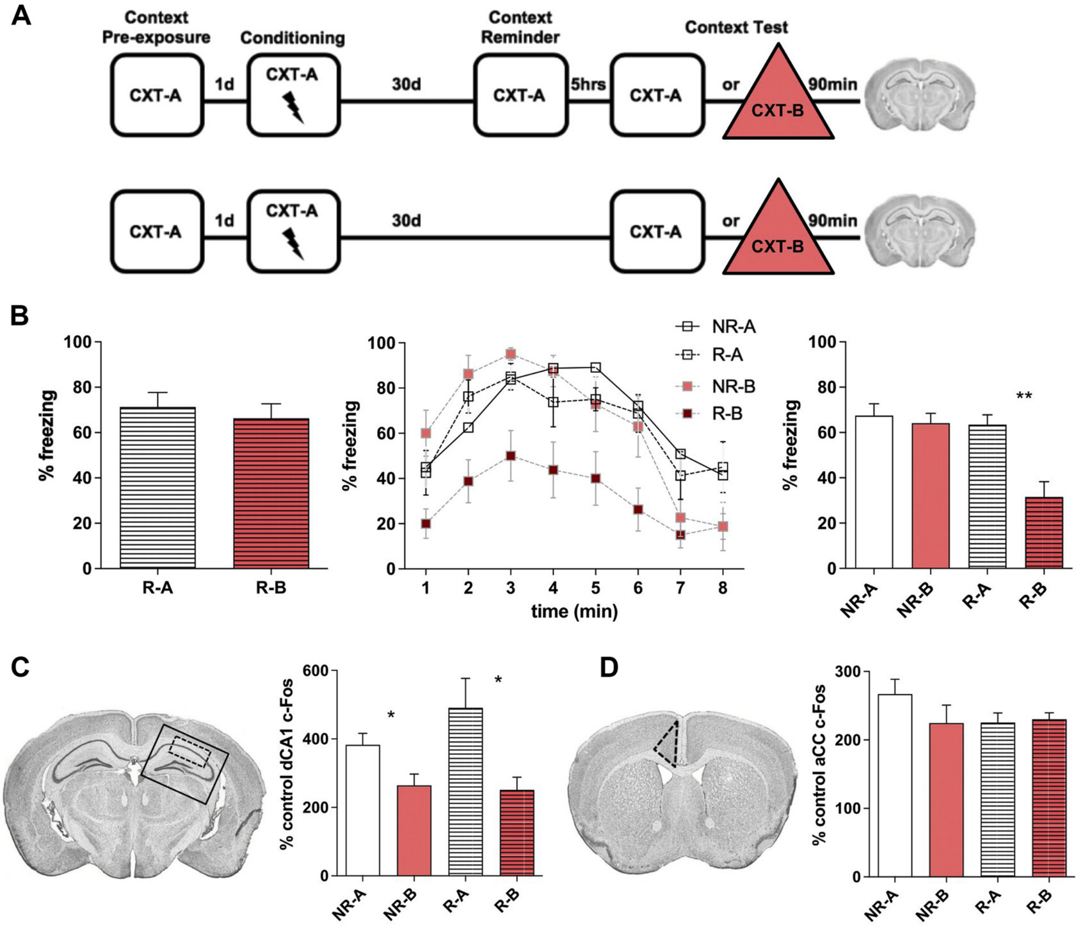
Immediate-early gene expression of c-Fos in the hippocampus and mPFC provides insight into the neural trace supporting context-specific and context-general retrieval. If the hippocampus is primarily involved in processing the contextual elements associated with the fear conditioning event, then the high hippocampal c-Fos expression during freezing in the original context at both recent (1 day) and remote (1 mo) delays suggests that the match between the encoding and retrieval context is engaging hippocampally mediated reproductive recollection at both time points. If the animal is relying on the use of more general, context-independent cues over time, then increased mPFC c-Fos expression at the remote time points observed during freezing in both the original and novel contexts would support the interpretation that familiarity is guiding recall based on memory reconstruction (101) (**FIGURE 8**). Whether this memory generalization reflects time-dependent forgetting or the establishment of a reconstructive memory trace is an important distinction. Active forgetting is a beneficial process that involves the pruning of weak or infrequently used synaptic connections, leading to a more efficient and refined neural network (396). This selective loss helps optimize memory storage and retrieval by removing outdated or irrelevant information. Memory reconstruction, on the other hand, permits an updated version of the relevant memory based on newly encountered information (395). Reminding the animal of the original context cues is sufficient to reinstate the context specificity to the remote memory and to reactivate the hippocampus-dependent memory trace as the memory reconsolidates (100, 101, 397).

Memory reconsolidation is one putative process supporting memory reconstruction, where previously stable memories can be reactivated and returned to a labile state in which they are susceptible to change and updating if new information is presented within the reconsolidation window (244, 398, 399). The ability of a context reminder to reactivate and reinstate the context-specific version of the expressed memory suggests that, in the absence of a reminder cue, expression of the generalized context fear memory over time is the default representation. In the intact brain, there is evidence that both the hippocampus-dependent context-specific memory trace and a more general, context-independent mPFC-dependent memory trace can coexist, and the cues at the time of retrieval will dictate which version is activated and expressed. Lesioning or inactivating the hippocampus at this remote time point may still allow the cortically mediated version of the memory to support memory retrieval in both the original and novel contexts (100, 358).

Why might this generalization occur? Ultimately, this transition from context-specific to generalized memory serves an evolutionary function. For a rodent placed in an inescapable environment, freezing as a defense is highly adaptive (391). If that environment has previously been paired with a shock, the threat associated with the context is high. If memory's contextual specificity fades over time, then exhibiting a generalized freezing response when placed in a similar situation will increase the chances of the rodent's survival. Thus, memory generalization, guided by network remodeling and active forgetting, is not a failure of memory but a strategic, adaptive feature of it (7, 118, 120).

6.7. Are Modern Neurobiological Engrams a Representation of Memory Reproduction?

Theories of memory consolidation long considered memories to become stable and "fixed" over time, through the unidirectional process of systems consolidation. One such theory, the complementary learning systems (CLS) framework, proposes that the hippocampus enables rapid, interference-resistant encoding of episodic memories, whereas the neocortex supports slower, structured learning by extracting regularities across experiences (237, 400). This dual-system network is thought to reduce interference via hippocampal maintenance of distinct episodic traces through



Adapted from Sekeres et al., 2020

FIGURE 8. Context fear memory generalizes over time, but context specificity can be reinstated by memory reactivation. *A*: context fear conditioning paradigm with remote memory reactivation using a context reminder. *B*: Sekeres et al. (101) demonstrated that reactivating (R) a remote context memory in the original conditioning context induces robust freezing (*left*). One day later, rats that had undergone memory reactivation displayed context-specific memory, with high freezing in the original context (R-A) but not a novel context (R-B). In the absence of a remote preretrieval reminder, rats display generalized freezing in both the original (NR-A) and novel (NR-B) contexts (*right*). *C*: c-Fos expression is sensitive to retrieval context in the dorsal hippocampus but insensitive to context and reminder in the anterior cingulate cortex (aCC) (*left*) Mean c-Fos expression levels in dorsal (d)CA1 were significantly higher after testing in context A than in context B and did not differ between the reminded (R) and non-reminded (NR) groups (*right*). *D*: mean c-Fos expression levels in aCC did not differ between context A and context B test conditions, regardless of reminder condition. $^*P < 0.05$, $^{**}P < 0.001$. Adapted from Sekeres et al. (101); used with permission under CC-BY license.

sparse coding and pattern separation while the neocortex gradually forms generalized representations over time.

We now know that memories are dynamic, with both the neural representation and qualitative content of a memory changing through time and experience, prompting a reconsideration of how the field discusses and considers the process of memory consolidation and reorganization (22, 26, 43). For example, the reactivation of hippocampally dependent, event-specific memories even after those memories have been represented cortically cannot be accommodated by earlier frameworks (see Ref. 43 for discussion). The interplay between the hippocampus and mPFC in supporting memory expression over time can be seen at the network level in rodents, with the hippocampal representation dominating early on and the mPFC representation becoming increasingly necessary over time (98, 101, 270, 358, 379, 394, 401–405). As this hippocampal-mPFC shift in dominance occurs, there is a corresponding transformation in the quality of the memory, shifting from highly detailed and context specific to a more gistlike or generalized version lacking precise detail (26, 406, 407).

The precise memory trace supporting episodic memory formation and retrieval can be identified at the cellular level. As touched upon above, the neuronal assembly active in response to the encoding of a discrete event forms an enduring representation of the memory trace, referred to as the memory engram (1–3, 19, 408, 409). Engram cells active during the encoding of a single context fear event are distributed across the brain, including robust activation of neurons in the hippocampus, amygdala, and cortex (410). It is possible to bias neurons for allocation to a memory engram, notably through overexpression of the transcription factor cyclic AMP-responsive element-binding protein (CREB) and increasing neuronal excitability (411–413). The stable engram theory holds that reactivation of this precise neural assembly may lead to memory expression driven by reproductive recall of the event memory (19, 408). Consistent with the "encoding specificity hypothesis" (249), when the cues (both external contextual cues and internal physiological states) at the time of retrieval closely match the cues present during encoding, the highest degree of engram reactivation is observed (254). Influential studies found that artificially stimulating memory engram cells is also sufficient to induce memory retrieval (410, 414–420) and artificially inhibiting engram cells at the time of memory retrieval prevents expression of a fear memory (411, 421). These studies are among the foundational engram investigations demonstrating a high degree of control over memory expression via manipulation of the neural assembly active during the initial memory encoding process.

Although engram neuronal assemblies form in a distributed network throughout the brain (410), most studies seeking to artificially manipulate or interrogate the engram target only a very small ensemble of the network (410, 416, 417, 419, 420). Greater activation of the engram assembly, or the unified engram complex, is associated with stronger memory expression (410).

When only a small part of the engram complex is artificially activated, memory expression may differ significantly because key elements supported by inactive engram neurons are left out. In other words, the neurons that remain silent during artificial activation could contribute essential components of the memory, and their absence may fundamentally alter how the memory is expressed. Hippocampal engram neurons can also become silent with time and may not be active during retrieval in response to natural cues, yet they can be artificially activated in response to optogenetic stimulation (422). This finding raises an important issue in how we understand the natural process of memory transformation and reorganization that occurs with time. If an engram's neuronal assembly and corresponding memory are artificially activated (i.e., optogenetically stimulated), it would seem to be an expression of episodic memory reproduction (423).

Observations of engram changes with time and experience (395, 424) suggest that memory reconstruction, rather than reproduction, is the default process that dominates under normal retrieval conditions as a memory ages. In considering what makes a particular memory representation "strong" or "dominant," recent evidence highlights hippocampal network stability and neuronal excitability as key mechanisms supporting the persistence of specific memory representations. Behaviorally, the dominant memory is the one expressed at retrieval, influenced by both external and internal cues as well as the physiological state of the memory network. Physiologically, hippocampal engram network stability favors the expression of context-specific memories, whereas ongoing reorganization within hippocampal networks reduces the probability of reactivation and memory retrieval (425) (**FIGURE 9**).

6.8. Dynamic Engrams and Memory Reconstruction

6.8.1. Representational drift and network instability.

The memory engram is not as stable as early modern engram studies would support (426). Memory linking, memory updating through new learning, reconsolidation,

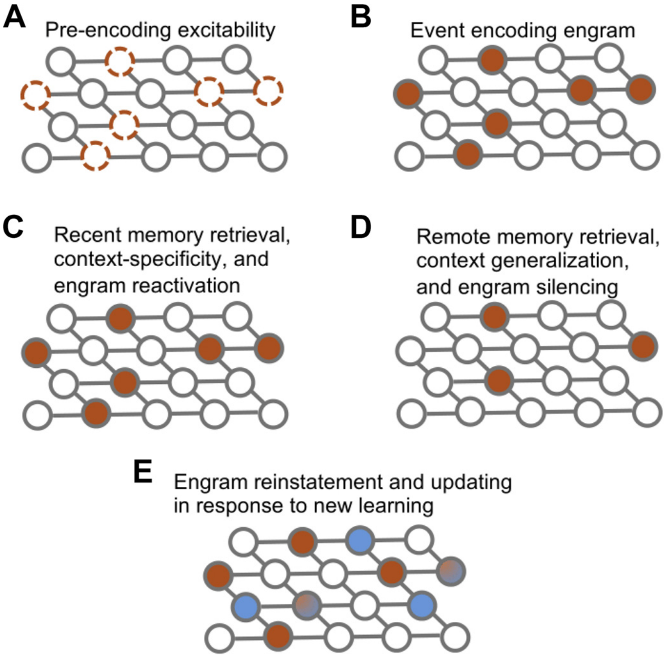


FIGURE 9. Hippocampal engrams flexibly reconstruct with time and experience. *A*: preencoding excitability primes neurons for allocation to engram neural assemblies. *B*: event encoding results in memory construction and engram formation (orange circles). *C*: retrieval of the context-specific event memory shortly after encoding reactivates the original engram trace (reproductive memory). *D*: with time, hippocampal engram neurons become silent and increasingly supported by medial prefrontal cortex (mPFC) neural assemblies as the event memory loses context specificity. *E*: reactivation of the remote context memory and the introduction of new, related information results in hippocampal engram reinstatement and updating (blue circles), supporting memory reconstruction.

schema formation, and active forgetting are among the processes that contribute to the representational drift of memory engrams over time and experience (395, 396, 408, 427–429). The flexibility and dynamic nature of the memory trace allows memories to be updated and reconstructed in response to new, relevant information and experiences (395). Activation of the original engram may support retrieval of the original, context-specific or episodically detailed (reproductive) memory event, but partial activation of the "drifted" memory trace is sufficient to support memory expression of the event's general framework (430). Place fields within dorsal hippocampal place cell assemblies exhibit both passive drift with time (431–433) and active remapping in response to experience (434, 435). Notably, remapping can occur within short temporal windows as short as 3 h, when driven by novel or changing experiences. In contrast, when experiences are fixed, place field representations remain stable over this same time period (435), highlighting the experience dependence of rapid remapping. Over longer timescales spanning several weeks, changes in place cell activity have been observed following the passage of time alone, whereas intervening experiences induce remapping of the place fields (434). These findings suggest that both time and experience differentially contribute to representational drift by modulating network excitability and specificity and collectively shape the transformation of memory representations to reflect updating of networks.

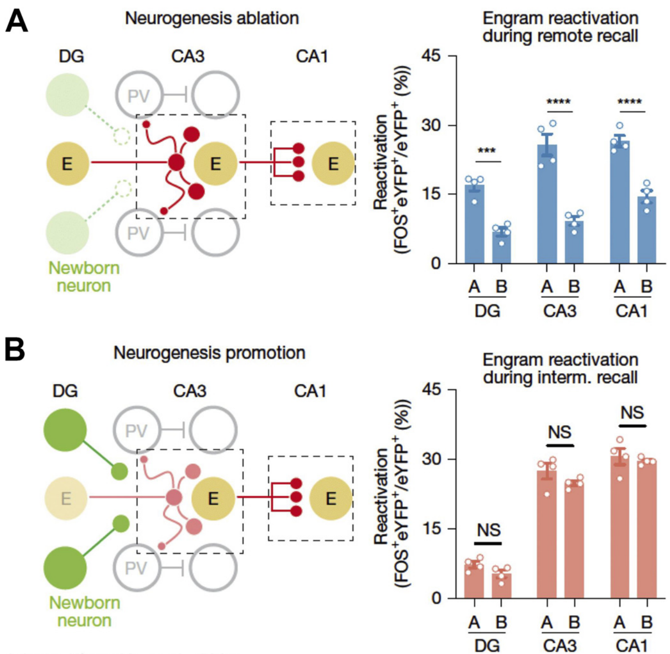
A computational model put forth by Antony and colleagues (436) proposes that hippocampal representations gradually reorganize over time through decontextualization and corresponding memory drift. According to this model, this decontextualization can occur within the hippocampus itself, enabling memory representations to be flexibly used in situations that differ from the original encoding context. When experiences are separated in time but share overlapping contextual features, the model predicts that repeated elements will be strengthened, while incidental or nonrepeated elements will weaken, contributing to representational drift and adaptive generalization of the memory trace (436). A similar proposal has been made in which hippocampal engram traces that are infrequently reactivated may lead to adaptive, natural forgetting that allows the network to deprioritize the retention of outdated or no longer relevant information (437).

A long-standing view holds that memory generalization primarily depends on systems-level network transformation between the hippocampus and mPFC. However, accumulating evidence indicates that intrahippocampal reorganization also contributes to the gradual shift from detailed, event-specific memories to more generalized gistlike representations over time (22, 26, 436). A recent study by Ko et al. (425) has identified key physiological mechanisms within the hippocampus that underlie this transformation. By visualizing tagged engram neurons across hippocampal subregions [dentate gyrus (DG) → CA3 → CA1] during contextual fear conditioning, they identified robust engram reactivation during recent memory recall in the original conditioning context, but not in a novel one. However, 1 mo later, when memory had generalized, engram neurons in CA1 and CA3 were promiscuously coactivated during retrieval in both the conditioned and novel contexts, indicating a loss of engram specificity over time. This generalization was accompanied by a time-dependent reduction in filopodial contacts between DG engram cells and parvalbumin-positive (PV+) inhibitory interneurons in the CA3 stratum lucidum and an increase in excitatory synaptic density between CA3 and CA1 engram neurons. These findings provide compelling evidence for two physiological mechanisms of memory transformation: *1*) reduced feedforward inhibition from DG engram cells and *2*) enhanced excitatory synaptic clustering among active CA1 engram neurons. Together, these changes may mediate the shift from specific to generalized memory representations by promoting nonspecific engram activation within the hippocampus. Additionally, the study implicates hippocampal neurogenesis as a further contributor to engram network reorganization and memory transformation over time (425).

The hippocampal network remains structurally dynamic in the mature brain because of ongoing neurogenesis in the subgranular zone of the DG. Newborn neurons gradually mature, integrate into existing circuits within the granule cell layer, and extend mossy fiber projections to synapse onto CA3 pyramidal neurons (438). Although this process supports the encoding of new, precise memories, it can paradoxically disrupt existing ones. According to the neurogenic hypothesis of retrograde forgetting, the integration of adult-born neurons destabilizes previously established memory circuits by displacing existing synaptic connections and altering network architecture (439). Recent findings by Ko et al. (425) provide direct evidence that neurogenesis contributes to memory generalization by disrupting the stability of hippocampal engram networks over time. Specifically, axonal projections from adult-born DG neurons formed new synaptic contacts within previously established CA3 engram circuits. CA3 engram neurons receiving these inputs were more likely to fire nonspecifically during remote memory retrieval, consistent with a loss of contextual specificity. Ablation of adult neurogenesis through hippocampal irradiation (∼80% reduction in new neuron formation) attenuated this effect. Irradiated mice exhibited reduced nonspecific engram reactivation in DG, CA3, and CA1 during retrieval in a novel context, preserved PV+ interneuron feedforward inhibition from DG, and maintained stable synaptic clustering between CA3 and

CA1 engram neurons. This intervention effectively stabilized the memory network, preserving the fidelity of the original context-specific memory and preventing the typical transformation to a generalized memory trace. Conversely, increasing rates of neurogenesis accelerated hippocampal network reorganization and excitability across hippocampal subregions, promoting faster memory generalization (Ref. 425; **FIGURE 10**).

Extending this work, Golbabaei et al. (440) examined engram specificity in the DG and prelimbic (PrL) region of the mPFC. DG engrams were initially high fidelity but lost fidelity with time, whereas PrL engrams were persistently low fidelity. Suppression of neurogenesis preserved DG engram specificity at remote time points but had no effect on PrL engram activation, suggesting that neurogenesis selectively modulates intrahippocampal transformation without directly influencing hippocampal-mPFC network reorganization. Similar displays of time-dependent emergence of mPFC traces representing commonalities or overlapping properties from experienced objects emerge within single-cell recordings of the mPFC (441), supporting the emergence of low-fidelity mPFC memory traces for common events in rodents (407). These findings also fit with observations of low-fidelity vmPFC activation observed in humans during event memory construction (23, 65).



Adapted from Ko et al., 2025

FIGURE 10. Hippocampal engram stability over time maintains network fidelity. *A*: hippocampal neurogenesis ablation via irradiation stabilizes engram cell firing through inhibition (*left*) and prevents the time-dependent emergence of promiscuous engram neuron reactivity. Engram neurons were selectively reactivated in conditioning context A at a remote delay (*right*). *B*: neurogenesis promotion via running interferes with engram circuitry and stability (*left*). Engram neurons were reactivated in both contexts A and B at an intermediate delay, indicating accelerated hippocampal network reorganization and excitability across hippocampal subregions, promoting faster memory generalization. DG, dentate gyrus; E, engram; eYFP, enhanced yellow fluorescent protein; NS, not significant; PV, parvalbumin. ***$P < 0.001$, ****$P < 0.0001$. Adapted from Ko et al. (425). Copyright 2025 by Springer Nature. Reproduced with permission.

These findings highlight adult hippocampal neurogenesis as a key mechanism underlying the time-dependent transformation of memory. Suppressing neurogenesis preserves the stability of hippocampal engram networks, promoting the long-term retention of high-resolution, context-specific memories. In contrast, under normal neurogenic conditions, the gradual integration of new neurons disrupts existing engram architecture, weakening hippocampal memory traces and facilitating the emergence of generalized representations supported by the mPFC. This shift reflects a broader transformation in memory organization, where dynamic hippocampal network instability driven by ongoing plasticity contributes to representational drift (442).

Under normal conditions, as hippocampal engram cells become increasingly silent during retrieval over time, or lose their fidelity as their firing patterns become less fine tuned (425), mPFC engram neurons become increasingly active during remote memory recall (**FIGURE 11**). Interconnection between hippocampus and mPFC seems to be needed to support this morphological and functional development of the mPFC engram network over time (256, 443, 444). Functionally, mPFC neural assemblies are involved early in the memory formation process, but their involvement is not necessary for memory expression until later in the memory reorganization process (256). At this later stage, inhibition of mPFC engram cells prevents expression of the fear memory, indicating that their involvement is critical for expression of the neocortically based reorganized memory. The mPFC-based remote memory is supported by time-dependent structural remodeling and dendritic spine growth in mPFC neurons, with a corresponding decrease in dendritic spines in the hippocampus (404, 444).

Although hippocampal engram neuron excitability and stability decline with time under endogenous conditions, reactivation of the memory via context cuing can reinstate heightened intrinsic neuronal excitability of those engram cells and reinstate the context memory (397). Presentation of new cues at the time of remote memory reactivation not only reengages hippocampal engram cells but also recruits new neurons in response to the presentation of new information that reconsolidates as an updated memory trace. This updated trace becomes the dominant representation (395), supporting the reconstructive nature of the memory trace with time and with new experiences.

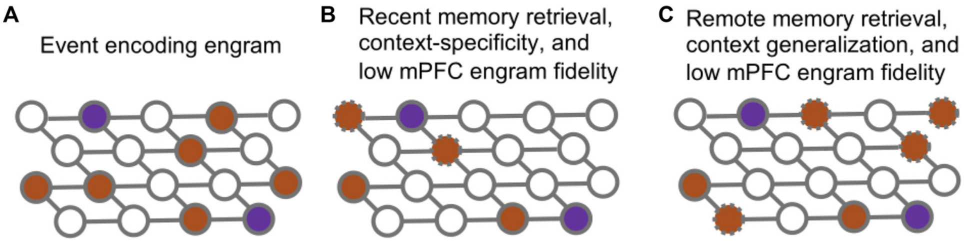


FIGURE 11. Low fidelity of medial prefrontal cortex (mPFC) engrams at recent and remote time points. *A*: event encoding activates a memory trace in the mPFC that includes both event-specific elements (orange circles) and event-general schematic elements (purple circles). *B*: shortly after encoding, retrieval of the event results in weak reactivation of the mPFC engram, indicated by low overlap between encoding and retrieval assemblies, and includes nonspecific activation (dotted circles). *C*: at remote time points, this low overlap persists, with mPFC engram neurons showing nonspecific activation, suggesting continued low fidelity over time. In contrast, schematic elements remain stably expressed regardless of memory age. Unlike in the hippocampus, it is unknown whether biasing mPFC neurons for engram preallocation would enhance the fidelity of mPFC memory engrams.

6.8.2. Memory linking.

Neurons with higher intrinsic excitability are more likely to become activated and allocated into a memory trace (411, 413, 445). The increase in neuronal excitability in response to memory encoding or retrieval is one mechanism thought to bias these same engram neurons to become reactivated in response to subsequent event encoding. If a second event is experienced close in time (∼6 h), a proportion of the *event 1* engram neurons will become reactivated and allocated for representation of the *event 2* engram, owing to the increased intrinsic excitability of the previously active neural assembly (446, 447). This shared neural trace serves to link the memories, where memory for the first event becomes reorganized to include elements related to the second event.

Remarkably, even events separated by several days have been shown to be linked, a process thought to be facilitated by offline hippocampal replay of the first event's engram cells that primes those neurons to become activated during the subsequent event encoding (424) (**FIGURE 12**). Memory reconstruction via event linking is adaptive for survival. Recent findings by Zaki and colleagues (424) found that exposure to an aversive context retroactively updated memory for a neutral context experienced 2 days earlier. When subsequently tested, mice froze in the previously neutral context, but not in a novel context, indicating context-specific memory updating. Notably, if the neutral context was experienced 2 days after the aversive context exposure, the same association was not transferred to the neutral context. It is plausible that the retroactive linking of the neutral and aversive contexts allows the animal to predict the onset of threat, whereas the lack of prospective linking of the two contexts facilitates the separation of dangerous events with new, safe experiences. At the neural level, offline hippocampal replay via calcium dynamics imaging of the shared hippocampal neural ensemble active during both the neutral and aversive contexts was observed, providing a neural mechanism underlying the updating or reconstruction of the retrograde context memory through memory linking.

Over the past 15 years, the engram renaissance has allowed for important advances in the field's understanding of the neurobiological basis of memory networks supporting encoding and retrieval and the influence of time, experience, and internal and external cues on both the physiological activation of a memory trace and the overt expression of a memory. However, a major limitation to modern engram research to date continues to be the ability to monitor the ongoing and dynamic brainwide remodeling and updating of the engram as well as the natural change in memory representation that occurs with time and experience. Advances in in vivo imaging will likely soon overcome this hurdle.

These advances challenge the "tortoise and hare" metaphor of neocortical and hippocampal learning speeds (237) and instead suggest that memory in the two systems develop in parallel, rather than sequentially and flexibly shift their relative influence depending on factors such as time, experience, and structural remodeling of memory networks (425). Updates to models such as CLS consider the rapid cortical integration of new information that is consistent with prior experience (29, 400), and studies such as that of Golbabaei et al. (440) further support the idea that both event-specific and event-general memory traces can form rapidly and concurrently. Over time, and particularly in the absence of salient cues, generalized representations are more likely to be expressed, underscoring the adaptive value of maintaining both types of reproductive and reconstructive memory traces through complementary, coactive systems. It is this dynamic, bidirectional correspondence between schematic or episodic representations, rather than static, unidirectional consolidation, that supports the flexible use of multiple memory representations depending on the conditions and demands at the time of retrieval.

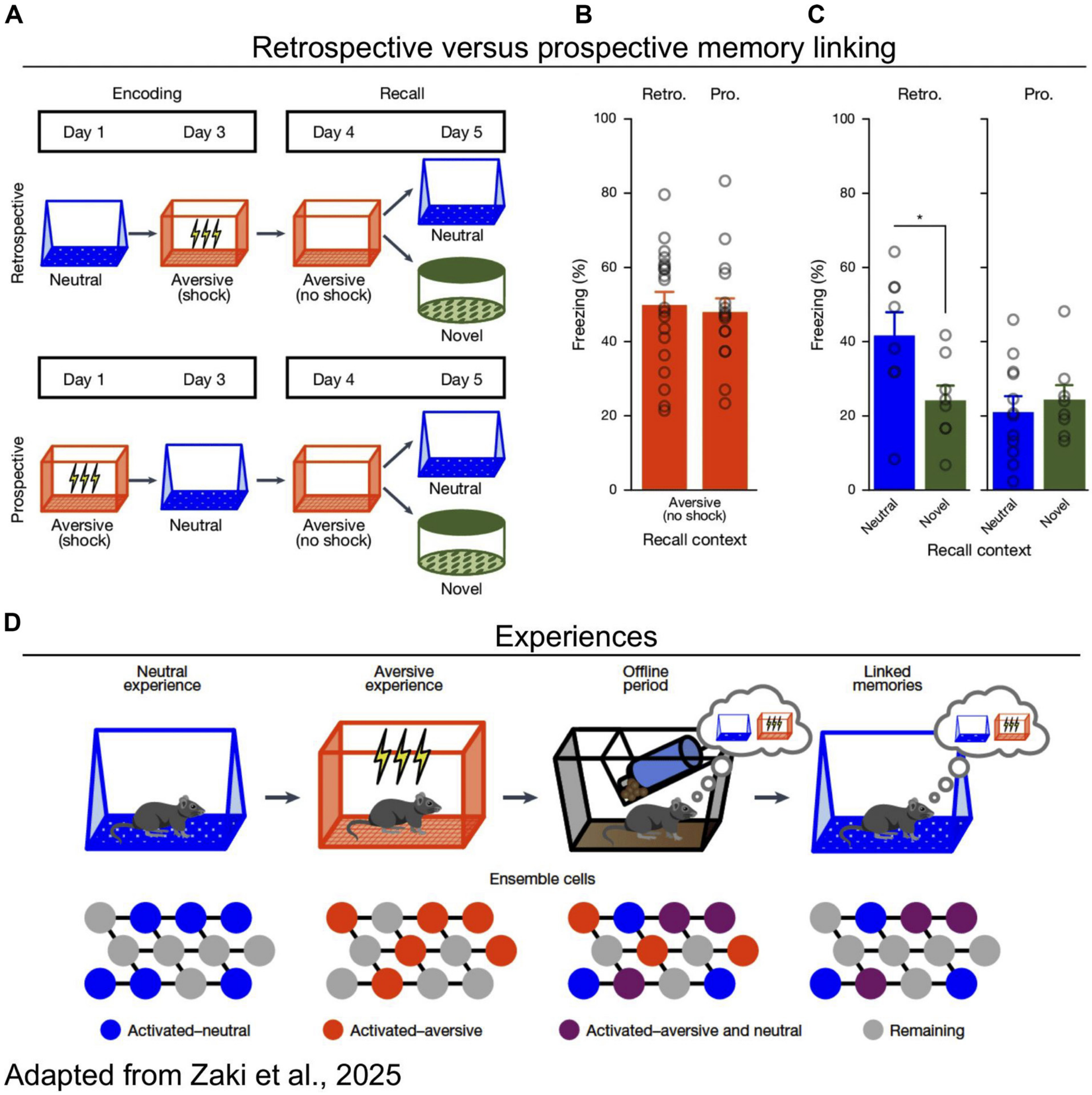


FIGURE 12. Representations of event memories can become linked and retrospectively updated in response to new aversive contextual information. *A*: context fear conditioning paradigm schematic, with retrospective (*top*) and prospective (*bottom*) event linking. *B*: Zaki et al. (424) found that mice exhibited robust freezing during memory testing in the aversive conditioning context (*C*), which became transferred to memory for a previously neutral context in retrospective, but not prospective, direction. *D*: they demonstrated that the previously neutral event engram representation (blue cells) and the subsequent aversive event engram representation (orange cells) became linked (purple cells) via offline hippocampal replay, resulting in an updated, reconstructed memory engram for the previously neutral event that adaptively incorporates new information predicting the safety of an environment. Adapted from Zaki et al. (424); used with permission under CC-BY license: http://creativecommons.org/licenses/by/4.0/.

7. CONCLUSIONS

In this review, we have synthesized research in humans and nonhuman animals to advance our understanding of how memory representations at both neural and psychological levels drive behavior. Drawing on foundational findings across species, we have examined evidence that the representational quality of retrieved episodic memories can range from faithful reproductions of past events, supported by the recapitulation of precise neural representations from encoding, to reconstructed versions of past events, shaped by prior knowledge and time-dependent transformations of neural representations.

By integrating findings across species, we aim to reconcile these perspectives by viewing both reproduction and reconstruction from a multiple memory representation perspective, finding a remarkably consistent pattern of neural and psychological memory representations in humans and nonhuman animals.

We propose that multiple representations of an event are formed at encoding, including detailed, gistlike, and schematic representations. The dominant representation is expressed at retrieval and is shaped by *1*) prior knowledge, *2*) the passage of time, *3*) new experiences that update memories, *4*) task demands, and *5*) individual differences. We argue that shifts in the relative dominance of these representations influence how memory is retrieved. Detailed, hippocampus-dependent representations may support memory reproduction, such as the reinstatement of activity patterns from encoding or an engram from the initially encoded experience (15, 16, 19). In contrast, the dominance of gistlike or schematic representations promotes reconstruction, in which episodic memories are influenced by prior knowledge and schemas at retrieval (15, 16, 19). At the heart of this framework is the correspondence between neural and psychological representations: psychological mnemonic representations depend on concomitant neural representations of an event (26). Consistent with this idea, the hippocampus supports the reinstatement of event-specific memory traces in response to relevant retrieval cues (19, 22, 42, 408), whereas the mPFC is thought to maintain generalized and schematic representations that integrate across experiences (28, 63, 70, 71, 80, 189).

We argue that the coexistence of multiple memory representations, and their shifting balance over time, is adaptive, enabling flexible behavior in response to immediate versus long-term demands on the memory system. Detailed, precise memory representation may be particularly useful in the short term when the context remains relatively stable. Specific memories can also be selectively activated to guide adaptive behavior, such as making future predictions based on context-specific goals at retrieval (85). In contrast, errors in detailed memory that arise from reconstructive processes may reflect a trade-off between precision and generalization, which can be adaptive for long-term goals, such as applying prior knowledge to novel scenarios (70). This dynamic interplay between specific and generalized memory representations enables both stability and flexibility in memory representations, allowing for either reproduction or reconstruction depending on behavioral goals.

Although we believe this framework helps bridge findings in human and nonhuman memory research, a significant gap remains between our understanding of episodic memory across species. The molecular and cellular footprint of memory traces observable in animal models is limited relative to the brainwide network-level memory representations observable in humans. Likewise, the richness of episodic recollection in humans exceeds what can readily be assessed in nonhuman animals. Viewed through the lens of an adaptive memory system, these differences highlight the need to move beyond applying humancentric notions of episodic memory to animal models. Instead, we should consider how the ability to form and use episodic memories serves species-specific needs (330, 360).

Ultimately, the dynamic interaction between multiple memory representations and how they shift with prior knowledge, time, task demands, and individual differences is key to understanding the link between neural representations of memories and their behavioral expression across species. Advances in human and rodent brain imaging techniques have enabled the detection of neural representations with unprecedented precision. Moving forward, we believe important areas of focus will include *1*) the correspondence between psychological and neural representations, within and across species, and *2*) the differences and transformations between encoding and retrieval representations and how they relate to behavioral expressions of memory. Investigating these aspects will be fundamental in elucidating how the balance between stability and flexibility in memory representations supports adaptive behavior.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

H.T.-S., M.J.S., B.L., and M.M. prepared figures; drafted manuscript; edited and revised manuscript; approved final version of manuscript.

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