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Review

Memory updating and the structure of event representations

Christopher N. Wahlheim[1,3,*] and Jeffrey M. Zacks[2,3,*]

People form memories of specific events and use those memories to make predictions about similar new experiences. Living in a dynamic environment presents a challenge: How does one represent valid prior events in memory while encoding new experiences when things change? There is evidence for two seemingly contradictory classes of mechanism: One differentiates outdated event features by making them less similar or less accessible than updated event features. The other integrates updated features of new events with outdated memories, and the relationship between them, into a structured representation. Integrative encoding may occur when changed events trigger inaccurate predictions based on remembered prior events. We propose that this promotes subsequent recollection of events and their order, enabling adaptation to environmental changes.

Highlights

To effectively guide behavior, the memory system needs to update in response to changes in the environment.

Recent behavioral, neurophysiological, and computational research has focused on mechanisms that reduce the accessibility of outdated information or render outdated information more distinctive from current information.

An alternative mechanism, which accounts for the structured and dynamic nature of event representations, proposes that memory updating can construct new representations that integrate outdated and current activity. Such representations are *recursive* in that they include information about retrieval of the outdated information in the representation of encoding the new information.

Studies using neuroimaging, eye tracking, and overt prediction and memory judgments support this proposal.

A fork in the path

We both enjoy hiking. On a recent outing, the more avid hiker of us got just a little lost. He returned to a trail that he had enjoyed hiking the previous year, and came to a hillside climb where the path became hard to follow. Since his initial visit, the trail was rerouted due to erosion. At first, he missed the turn for the new route, instead following the previous path. He then backtracked and found the new trail easily. What might happen on his next visit to this trail? If his memory serves him, he will recall taking a wrong path before, watch the trail carefully when approaching the climb, and take the correct turn.

We suggest that situations like this are an important reason why episodic memory evolved: to register environmental changes, adapt current behaviors, and thereby improve outcomes. This example illustrates the importance of **memory updating** (see Glossary) – the process of memory systems adjusting to changes in experience. Successful updating requires navigating a balance between maintaining stable, experienced-based representations of the world and flexibly updating those representations when events change. When a memory system fails to update, it suffers from **proactive interference**: Outdated memories impair retrieval of recent events. However, earlier events sometimes become relevant again. When this occurs, it is important to remember both the earlier and recent events as well as the changes between them. Navigating the balance between stability and updating may become especially important in later life, when habits and routines become rigid and unexpected changes are less well accommodated [1,2]. Here, we review the proposed mechanisms of episodic memory updating and present a theory of how episodic memories can be updated based on a single new learning experience. (The updating of semantic memory is another important topic [3], but not one we take on here.)

What to do with outdated memories – push them away or hold them close?

How do humans beat proactive interference? There would seem to be two solutions that are both intuitive but are contradictory. The first is to distance outdated memories from recent memories of similar events. The second is to integrate outdated memories with the recent memories.

[1]Department of Psychology, The University of North Carolina at Greensboro, Greensboro, NC 27402, USA
[2]Department of Psychological & Brain Sciences, Washington University in Saint Louis, Saint Louis, MO 63130, USA
[3]The two authors contributed equally.

*Correspondence:
cnwahlhe@uncg.edu (C.N. Wahlheim) and jzacks@wustl.edu (J.M. Zacks).

Outdated memories may be distanced by weakening their accessibility after retrieval, intentionally forgetting them, or distorting their representations to make them less similar to recent memories. All of these mechanisms reduce the influence of memories on perceptions, thus mitigating interference. In contrast, integrating the memory of a previous event into the experience of a new one can prevent interference by helping to encode or retrieve the features that distinguish the two events or by encoding the fact that features have been superseded.

Updating by reducing access to outdated memories

One class of memory updating mechanism reduces access to outdated memories. Repeating a stimulus sequence creates a memory that leads to a **prediction error** if the end of the sequence is changed during a later experience [4,5]. Prediction errors may serve as triggers to weaken memory representations of the previous ending; this would be adaptive because those unstable aspects of the world are likely to be less relevant in the future. Importantly, whether this type of prediction error weakens an outdated memory may vary based on the strength and quality of the mnemonic basis; we return to this issue later. Weakening of previous memories may also be under deliberate control: Asking people to disregard an earlier event – an instruction called **directed forgetting** – can reduce its accessibility and improve memory for a subsequent event [6,7]. This reduction may be accomplished via cognitive mechanisms such as terminating rehearsal of studied items or creating mental context changes that create distances among competing memories. Directed forgetting studies using pattern-based functional magnetic imaging (fMRI) suggest that trying to forget can also reduce the accessibility of outdated memories by decreasing neural **reactivation** [8,9]. Although these studies collectively suggest that the accessibility of outdated memories can be decreased in several ways, the mechanisms have not been directly compared to determine if they modify memory representations differently.

Updating by differentiating outdated memories

Another mechanism that keeps outdated memories at bay is **differentiation** (also referred to as **repulsion**), which makes two representations more distinctive from each other. Theories have proposed that when moderately similar representations compete for retrieval, synaptic changes occur in the hippocampus and elsewhere that reduce the similarity between them [10]. This proposal has been supported by studies showing shifts in remembered features of outdated memories and in the neural reactivation associated with those memories, which push them away from features and reactivation patterns associated with potentially competing memories [11–13]. This mechanism leads outdated memories to be distorted to appear more distinctive from the competition, but their accessibility is not necessarily diminished by this process.

Updating by integrating and facilitating memory for changed events

In contrast to keeping competing memories apart, integration mechanisms can update memories by incorporating relationships to previous experiences into the encoding of new experiences. Integration generally enhances access to prior memories rather than diminishing them. However, integration incorporates the original event features and the new event features into a composite memory, together with the relations between them, thus overcoming proactive interference. For example, one might read a piece of misinformation and later retrieve that information when reading a true social media post with conflicting details. According to the aforementioned accounts, retrieving the misinformation when reading the true post would lead to changes that reduce access to the misinformation. However, there is mounting evidence that the opposite occurs. In particular, being reminded of misinformation when reading a true post can enhance memory for (i) the true information, (ii) the previously encoded false information, and (iii) the fact that the true information corrected the previous false information [14].

Glossary

Association: degree to which two representations tend to activate or inhibit each other is referred to as the strength of their association. If two representations have a strong positive association strength, activation of one will tend to activate the other; if they have a strong negative association strength, activation of one will tend to inactivate (inhibit) the other.

CA1/CA3 fields, dentate gyrus: four subdivisions of the hippocampus. CA refers to cornu Ammonis (Ammon's horn), a Latin name for the hippocampus.

Complementary learning systems: proposal that the hippocampus and associated structures are specialized for one-shot learning of novel associations, whereas the cortex is specialized for slow learning. Fast learning in the hippocampus can capture associations that can then be consolidated in the cortex through replay.

Consolidation: the transitioning of a representation from a vulnerable state upon initial encoding to a stable state that is resistant to modification.

Differentiation (repulsion): when neural representations are distorted to render them less similar.

Directed forgetting: phenomenon in which people are told to forget just-presented information and often are successful in doing so, as indexed by subsequent testing.

Event memory retrieval and comparison (EMRC) theory: proposed mechanism for memory updating, in which retrieving a related previous instance leads to predictions about what will happen next, and, when these predictions fail, a new integrated representation of the changed information is formed.

Event segmentation theory: theory proposing that prediction failures lead to updating event representations. It forms a component of the EMRC theory.

Memory updating: process of the memory system adjusting to changes in experience.

Memory-for-change framework: theory proposing that memory updating can be implemented by forming a recursive representation of the old information, the changed information, and the relationship between the two. It forms a component of the EMRC theory.

Nonmonotonic plasticity hypothesis: proposal that high levels of

Relatedly, in the associative inference paradigm, people are able to link successive events to form new representations of inferred relationships [15]. For example, if one sees a new neighbor walking a small gray dog and then later sees a different person walking the same dog, one might form a representation that links the two people together as likely co-owners of the dog. In this case, two pieces of presumptively true information are being integrated, rather than integrating misinformation with a correction. Associative inference in memory has been shown to depend on the medial temporal lobes.

Evidence for integrative encoding has been shown in classic studies of memory updating focused on interference effects (Box 1). These studies suggest that when event features change, whether interference or facilitation is produced depends on how the changed event is encoded. More evidence that the consequences of changes depend on how they are encoded comes from neuroimaging studies, which have shown that activity in the hippocampus and prefrontal cortex is central to whether outdated memories are retrieved during current events and integrated with those events (Box 2). Collectively, these studies suggest that the coactivation of outdated features retrieved from memory together with current features from perception allows for associative encoding of the events within the same mental context. This may increase their associative strength while at the same time encoding relationships that keep the differences between the events distinct. This cascade of processes should then lead to enhanced memory accuracy, whereas the absence of such encoding could lead to interference.

One computational framework that could support integrative encoding is **complementary learning systems**: the proposal that the hippocampal system supports rapid encoding and retrieval of specific episodes that enables integration with knowledge established more slowly by the cortical system [16]. Within the hippocampal system, computational accounts propose that a **pattern separation** process supports the encoding of distinctive features, whereas a **pattern completion** process supports the retrieval of outdated memories triggered by the features that similar perceptions share with outdated memories [17,18].

Box 1. Historical antecedents

Current conceptions of memory updating have their roots in the verbal learning tradition of the 1940s-1970s, which in turn grew out of behaviorism. A focus of this literature is on interference between memories. If word A is presented with word B, and then with a different word C, we can describe this in terms of **retroactive interference** and proactive interference. Retroactive interference describes the finding that recall of A–B is worse after experiencing A–C. Proactive interference describes the finding that a prior A–B pairing reduces recall of a subsequent A–C pairing. Verbal learning theorists proposed at least three mechanisms for these effects [76]. First, learning A–C might extinguish the A–B association, which is related to current conceptions of reduced access [4,5]. Second, the A–B and A–C associations may compete during memory retrieval. Third, the learner may form an association between A and C that is mediated through B (i.e., A–B–C). When C was closely related to B, researchers observed retroactive facilitation rather than interference, consistent with the memory benefits of forming a unitized A–B–C complex [76,77]. Later work showed that restudying an A–B pair while learning a new A–C pair reduced proactive interference for A–C [78]. This could also be explained in terms of mediation, but the authors argued that a better explanation was that the two representations could become differentiated. This fourth cognitive mechanism is similar to modern notions of neural differentiation. However, it was proposed before the technology was available to show that differentiated memories can become adaptively distorted in representational space [10,79].

Over a career that began rooted in the associative verbal learning tradition, Hintzman and colleagues strayed from the associative learning paradigm to investigate how people remember temporal distance and spacing between items in a list [50]. One study showed that people were better at remembering the temporal distance between two appearances of the same word than they were at remembering the distance between two different words [80]. They proposed that features in the environment can spontaneously remind people of related experiences. For example, if one were to see a word pair A–B and then a pair A–C, one might retrieve A–B. One may then encode a recursive representation, in that the experience of remembering A–B is embedded in the representation of experiencing A–C. This idea resembles a neurocomputational implementation of event-cued retrievals that enables coactivation, integration, and generalization of memories via complementary hippocampal and cortical learning systems [81].

reactivation promote strengthening of memories and of associations among features between memories, leading to integration. Conversely, moderate levels of reactivation promote weakening of memories and of associations among features between memories, leading to differentiation. Low levels of reactivation are assumed to have little, if any, effect on memories and their connections.

Pattern completion: process in which the presentation of a partial pattern or similar pattern leads to reinstatement of a pattern representing a previous experience.

Pattern separation: encoding process in which patterns representing two similar experiences are rendered more distinctive.

Prediction error: difference between a predicted feature or value and the subsequently observed feature or value.

Proactive facilitation: see proactive interference.

Proactive interference: when previous experience impairs memory for subsequently presented information. (Note that proactive facilitation can also be observed when previous experience improves memory for subsequently presented information.)

Reactivation: activation is the degree to which a representation is able to influence processing. In theoretical models, activation strength is usually an abstraction intended to correspond to strength of neural finding or to modulation of synaptic connections. Reactivation an increase in activation strength due to memory retrieval.

Reconsolidation: proposed process in which reactivating information leads it to be less stable.

Recursive representation: representation of an experience that includes within it features related to remembering the retrieval of a previous experience.

Retroactive interference: when subsequent experience impairs memory for previously presented information.

Box 2. Neural mechanisms of memory integration in associative learning

Neural evidence that retrieval during study can counteract interference has been shown using variants of classic paired-associate learning protocols. One study [82] used an A–B/A–C design in which participants learned one set of associations (A–B) and then learned new associations to the same cues (A–C). Hippocampal activity during encoding of A–C associations was associated with lower retroactive interference during recall of A–B associations. Similar results have been found using pattern-based fMRI analysis methods, showing that the context of A–B learning is reactivated during A–C experiences [83]. Those results suggest that A–C events can trigger retrieval of A–B events, which amplifies the accessibility of prior memories and provides the opportunity for integrative encoding. However, neither study showed direct evidence for integration. Other studies more directly identified the role of integrative encoding by varying whether participants were instructed to retrieve and integrate A–B associations when encoding changed A–C associations [11,55]. Those instructions led to hippocampal responses during A–C encoding that were associated with reduced interference from A–B associations in behavioral memory measures. The prefrontal cortex was shown to hold prior memories in mind for comparison with current perceptions, which may be necessary for integrative encoding to occur. More generally, these findings are compatible with studies using related A–B/B–C protocols in which participants learn one set of associations (A–B) and then another set with responses that become cues paired with new responses (B–C). Those studies also collectively show roles for the hippocampus and prefrontal cortex in integrative encoding of A–B memories during B–C encoding that leads to inferences about indirect A–C associations mediated by B items [84].

Prediction errors weaken, differentiate, or integrate memories

Reducing access, differentiation, and integration seem like quite distinct mechanisms, yet they can all mitigate potential interference. One possibility is that all these mechanisms can be triggered by prediction errors, as in the case that we described of a change in a learned sequence. The general proposal is that the brain makes predictions about how an activity will unfold [19] and that some predictions are driven by retrieval of related events [20,21]. When predictions lead to errors, this can trigger updating [22], but the specific mechanism of updating depends on additional variables. One variable that may determine which mechanism is triggered is the strength of associative retrieval (reactivation). The **nonmonotonic plasticity hypothesis** proposes that high reactivation strengthens connections between memories, which leads to integration, whereas moderate reactivation weakens connections between memories, which leads to differentiation [23]. Another variable that may be important is semantic congruence between outdated and more recent features [24]; the effects of semantic congruence may interact with current task demands to differentiate related representations [25,26]. Neuroimaging studies suggest that different hippocampal subsystems are selectively responsible for triggering integration or differentiation [27–29]. Importantly, other work has shown that because integration can add new associative features, it can actually lead to neural activation patterns that look like differentiation [30].

Retrieval-induced reconsolidation in humans

A controversial theory related to the aforementioned accounts is that **consolidation** and **reconsolidation** processes allow humans to establish and then destabilize memories in order to update them [31]. Consolidation refers to the postencoding processes that stabilize memory representations, whereas reconsolidation refers to a process whereby retrieving a memory renders it susceptible to modification by subsequent experiences. In rodent models, evidence for reconsolidation comes primarily from studies in which presenting a cue that was previously paired with a shock while pharmacologically blocking consolidation leads to exaggerated forgetting of the relationship between the cue and the shock [32]. However, other rodent work has shown that reactivation-induced impairment can be eliminated when an amnestic agent administered after reactivation is later reinstated as a retrieval cue on a memory test [33]. This finding can be accounted for by an integration mechanism in which the existing memory is more accessible when the encoded contextual state also serves as a retrieval cue [34,35]. This mixture of effects across studies is challenging for reconsolidation theory.

Despite such challenges, human studies have also been conducted to determine if post-reactivation interventions lead to impairments similar to those in rodents [36–38]. In object-list learning, for example, participants first study a set of objects in one room and then study a second set of objects in another room. Before the second set, participants are either reminded of the first set procedure or not. Reminders often increase second-set intrusions into first-set recall [38,39]. Researchers have also looked for reconsolidation in naturalistic scenarios. In one study, participants watched a television show and then listened to a summary of the show that included misinformation about some of the details [36]. In between, some participants practiced cued recall of show details and others performed an unrelated distractor task. On a final recognition task, the group who practiced retrieval before hearing misinformation had worse recognition of the original details than the control group. These retrieval-induced impairments might be due to reconsolidation, but other accounts of these effects in terms of context changes are supported by computational and functional magnetic resonance imaging (fMRI) studies [40–42]. One translation of the nonhuman findings to human tasks has proposed that reactivating a memory and experiencing a prediction error destabilizes the memory, triggers updating, and leads to intrusions. This account is supported by behavioral and neuroimaging findings [43,44]. However, some studies have found that retrieved memories are enhanced or even unaffected; this inconsistency poses a challenge for human reconsolidation accounts [45]. Overall, some human evidence is compatible with findings from rodent studies that support predictions from reconsolidation theory. However, on balance, the body of evidence does not unequivocally support that account over models proposing roles for standard context- and interference-based cognitive mechanisms.

A theory of event memory updating driven by retrieval and prediction error

Most research on memory updating, including most of the aforementioned work, has used static materials such as words or pictures. This allowed researchers to focus on the effects of variables including repetition, spacing, and semantic **association**. However, a complete account of event memory updating must address a central fact: Memory encoding and retrieval happen in the context of a dynamic environment in which features of an event are related to each other contemporaneously and across time [46–48]. In terms of our hiking example, hearing a woodpecker predicts that one might see the woodpecker, and approaching a hilltop predicts that one will soon experience a new vista. **Event memory retrieval and comparison theory (EMRC)** [49] is an account of how memory updating for ongoing events unfolds within one's dynamic environment. It is grounded in the mechanisms of classical verbal learning, in the recursive reminding [50] hypothesis (Box 1), in modern studies of event perception and memory, and in modern behavioral and neurophysiological studies of memory updating.

EMRC brings together an account of episodic memory updating proposed by the **memory-for-change framework** [51] with an account of the dynamics of comprehension and working memory updating from **event segmentation theory** [52]. EMRC proposes that the brain maintains current working models of what is happening now, which combine current perceptions with information from knowledge and episodic memory (Figure 1). When one encounters a situation similar to a specific prior episode, such as a previously walked stretch of trail on a hike, this may trigger a reminder of that experience, which will influence the current working model. In a stable environment, this usually leads to accurate predictions about how the situation will evolve. However, if something changed, such as the trail being rerouted, episodic retrieval will lead to a prediction error. When this occurs, the retrieved memory and perceived event become co-activated in the working model. This provides the opportunity to form a **recursive representation** in episodic memory: one that incorporates not just the current perceptual features and the retrieved memory, but also the experience of (i) retrieving that memory, (ii) using it to predict, and (iii) experiencing a prediction error. A representation of this sort can be a powerful tool for guiding future behaviors: It includes the features of what happened initially and during the changed event, which helps make both feature sets available. In addition, because a recursive representation includes the reminding of the initial event by the changed event, it

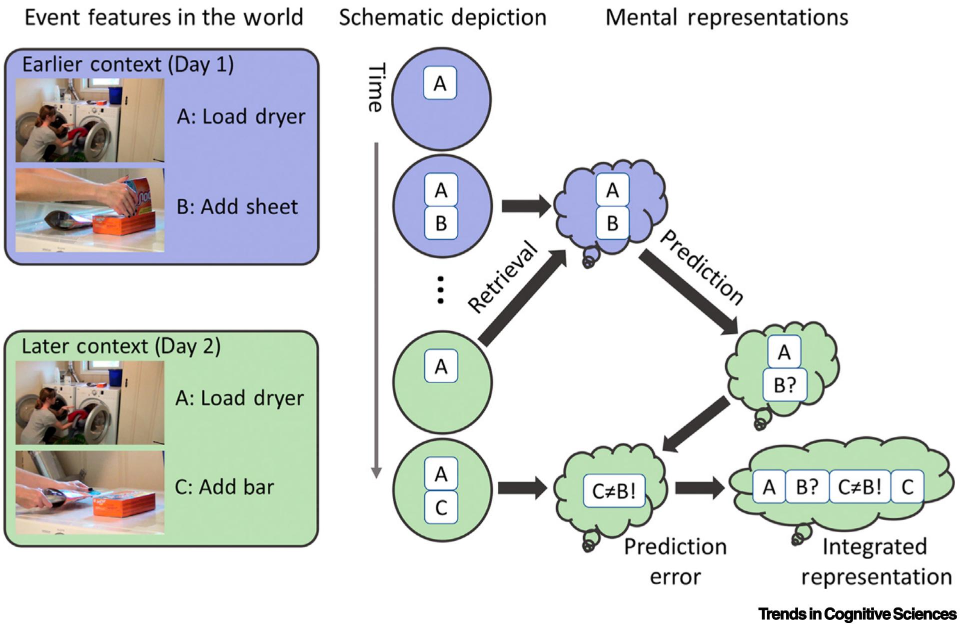

Figure 1. Schematic depiction of the processes in event memory retrieval and comparison theory. The left column depicts two experience contexts: Day 1 (blue) and Day 2 (green). On Day 1, the actor loads the dryer (feature A) and then adds a dryer sheet (feature B). On Day 2, the actor loads the dryer, as in Day 1, but then adds a dryer bar (feature C) rather than a sheet. The middle column schematically depicts how the temporal dynamics evolve: On Day 1, A is followed by B; on Day 2; A is followed by C. The right column depicts some of the mental representations formed during these experiences: During the Day 1 experience, the A-then-B sequence is encoded into long-term memory. In the Day 2 context, encountering A cues retrieval of this sequence, leading to the prediction that B will follow A in the new context (depicted by B?). When C is encountered rather than A, this prediction error may be registered (C≠B!) and a new recursive representation may be formed, including the experience of A, followed by the prediction of B, followed by the prediction error and C (A/B?/C≠B!/C).

preserves the order of those events. Forming and accessing a recursive representation is a clear method of overcoming proactive interference by integrating existing and more recent memories, as well as their temporal order, as we have already discussed.

EMRC makes two core claims about event memory updating. First, integrative encoding of a recursive representation leads to successful updating. Second, successful updating is characterized by a particular dynamic sequence when viewing changed events: retrieving a relevant existing event memory, experiencing a prediction error when noticing a changed outcome, and integrating the perceived change into a recursive memory representation that updates predicted outcomes. This role for prediction error is akin to that observed in sequence learning paradigms [4,5]. EMRC assumes that people can remember experiencing prediction errors, and they can use those memories to distinguish earlier from more recent events.

Moreover, although prior-event retrieval is necessary to form a recursive representation, it is not sufficient. EMRC assumes that when integrative encoding fails, subsequent recollection of events and their temporal contexts is more likely to fail. This explains why perceiving changed events can produce memory enhancement in the form of **proactive facilitation** but also proactive interference. When prior-event retrieval happens but integrative encoding fails, proactive interference can be particularly bad because practicing retrieval of the existing memory tends to strengthen its influence (repetition priming). It is also possible that retrieving can lead to encoding new memories that flexibly recombine features from two related events but bind the wrong features together; this is another route to interference in memory [53,54]. Importantly, different encoding tasks should tend to promote integration differently. Depending on the structure of the learning phase and the relationships among stimuli, retrieving previous memories may be more likely to lead representations of earlier memories to become more integrated [11,55] or to become more differentiated [10,56] or weakened [4].

Evidence for the roles of retrieval and prediction error in memory updating

To test the claims of EMRC about event memory updating, we developed a quasirealistic movie viewing paradigm inspired by classic A–B, A–C protocols [49]. In this task, viewers watch movies of an actor performing everyday activities at her home and work on two separate days in her life. Embedded in each movie are activities that were filmed with the same beginning and two different endings. For example, she might load her dryer and then add a fabric softener sheet on Day 1 in the first movie and a bar on Day 2 in the second movie (Figure 1, left). After watching the two movies, participants' memories for events on both days are tested by cueing with the beginning of an activity and asking about the ending ('What form of fabric softener did the actor use in the dryer?'). This paradigm has been used to establish the mechanisms of event memory updating, and to determine how cognitive differences associated with older adulthood affect these mechanisms.

EMRC proposes that encountering a previously seen feature in a new context induces associative retrieval of prior events, and this enables event memory updating. This proposal has been tested using pattern-based fMRI [57]. During MRI scanning, participants watched two movies including both repeated (A–B) and changed (A–C) activities. During the second movie, participants were periodically asked to use their memory of the previous movie to predict what would happen next. Patterns of brain activity were recorded during the presentation of each activity's ending in the first movie and during retrieval in the second movie. Analyses focused on the medial temporal lobe (MTL) and posterior medial cortex (PMC); these are key regions in a network associated with the retrieval of event-specific associations [58–60]. Both areas (and many other cortical regions) showed strong evidence of retrieval (i.e., pattern completion). In both areas, the strength of neural retrieval from the first movie during viewing of the second movie was associated with the subsequent recall of the changed activity endings (Figure 2, top).

To test the proposal that memory-guided prediction errors contribute to event memory updating, another study asked viewers to make overt predictions of event endings during the second movie [57,61]. When viewers predicted the ending that they had previously seen, they updated their memory more successfully: On a subsequent test, they better recalled the changed endings and were better able to remember that the activity ending had changed as well as the details of the earlier ending (for a boundary condition on this effect, see [62]).

To assay predictive processing without interrupting ongoing comprehension, eye gaze was used as an indirect assay of memory-based predictions [63]. Viewers' gaze was tracked as they watched the actor perform activities in which she contacted objects in different spatial locations, as in the dryer sheet and bar (Figure 1). Prior work showed that viewers look ahead to where actors will contact objects in goal-directed activities [64–67]. Similarly, when viewing the beginning of a previously seen activity during the second movie, viewers looked ahead to the object that the actor would contact. Figure 2 (middle) shows that more predictive looking to the outdated object (i.e., prediction error) was associated with better subsequent recollection of that an event ending had changed. The fact that participants were better able to reject the outdated object after trials on which they made a prediction error could be accounted for by pattern separation of the outdated and updated features; however, the fact that participants can relate the outdated and updated information correctly requires an additional integration mechanism.

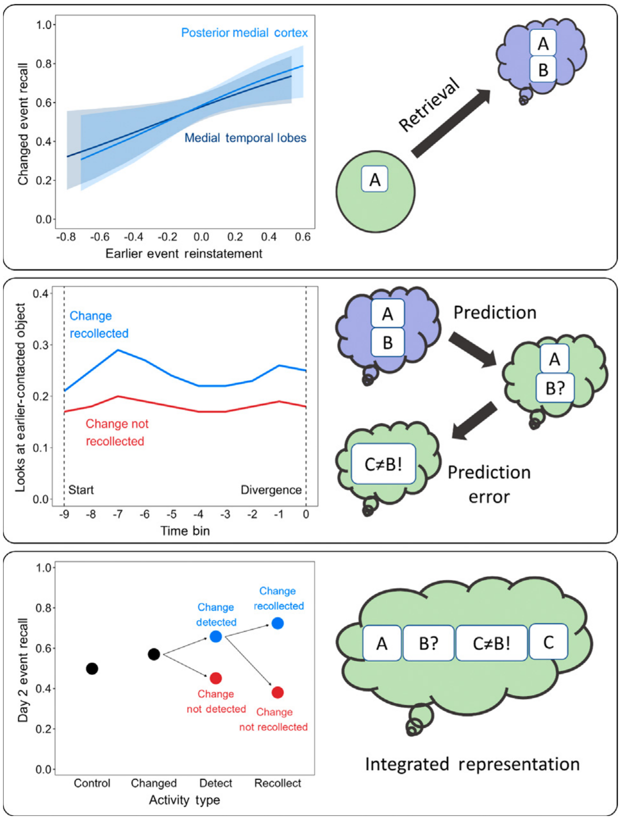

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Figure 2. Empirical support for event memory retrieval and comparison theory. In all studies, younger adult participants first viewed a movie depicting a day in an actor's life (Day 1) and then viewed a second movie (Day 2) that included repeated events and events with changed endings, and in some cases control activities that only appeared on Day 2. The left column shows select findings from those studies, and the right column shows the hypothesized processes from Figure 1. Top: in a functional neuroimaging study [36], participants who showed greater reinstatement of Day 1 activities (earlier events) in the posterior medial cortex and medial temporal lobes had better memory for changed events. Middle: in an eye-tracking study [40], looks to the changed object and looks to the earlier-contacted object were tracked during Day 2 viewing. Looks to the earlier object are predictive looking errors; making these errors was associated with better subsequent recollection that the ending had changed. Bottom: in a behavioral experiment [32], participants attempted to detect changes during Day 2 viewing (Detect above) and, at test, were asked to recollect if events had changed, which entailed both identifying events as changed and recalling the changed feature from Day 1 (Recollect above). Surprisingly, changed events were recalled better than control events overall, showing proactive facilitation. Successful detection and recollection of changes were associated with proactive facilitation (blue points), whereas failure of either change detection or change recollection (following successful change detection) was associated with proactive interference (red points). This pattern is consistent with the formation of an integrated representation, in which experiencing a prediction error is encoded together with updated event features.

EMRC proposes that memory updating depends on registering the discrepancy between a predicted and actual outcome and storing a representation of that prediction error. To test this proposal, one study asked viewers, while watching the second movie, to judge whether each activity changed from the first movie [49]. If a recursive representation has been formed, one should be able to report that an activity changed, identify which feature changed, and describe what it previously had been. As predicted by EMRC, Figure 2 (bottom) shows that being able to detect a changed activity ending during viewing and later remember that the ending had changed was associated with proactive facilitation in retrieval of what feature had changed. In contrast, when changes were detected but not later remembered (or not detected at all), there was proactive interference. These results suggest that the same operations that promote awareness of changes may promote event memory updating. Consistent with this, directing viewers' attention to changed features was found to improve event memory updating [68].

These results are opposite to the pattern predicted by accounts proposing that prediction errors weaken outdated memories. EMRC proposes that reinstatement should strengthen the outdated memory, rather than weaken it, which weakening accounts propose would increase proactive interference. Moreover, weakening accounts propose that remembering the changed ending entails forgetting of the outdated ending; in contrast, when people remembered the changed ending, they also tended to remember the original ending.

Age differences in memory retrieval and prediction-based updating

The ability to update episodic memories is crucial for flexible adaptation to changes. With age, cognitive flexibility diminishes. This may be inconsequential in stable environments but can be devasting in new environments. The mechanisms of memory retrieval, prediction, and comparison inherent to EMRC may help explain such age differences in memory updating. In some situations, older adults experience more proactive interference and update memories less well than younger adults [69–71]. EMRC proposes that updating differences could arise at several points along the processing chain: encoding of earlier events, associative retrieval of those events, prediction generation, change detection, and remembering changes. Older adults experience changes in attention control, episodic memory, and predictive processing [72,73] that could lead to breakdowns at each point. Since breakdowns in earlier points impact downstream processes, it can be challenging to isolate them.

Studies have begun to identify specific factors that could be at play. Older adults have weaker associations between PMC and MTL reinstatement of earlier events and memory updating than younger adults [57]. In older adults, making overt memory-based predictions before viewing changed events was associated less strongly with successful memory updating [61]; instead, it was associated with more intrusions of outdated activity features. However, some of the mechanisms proposed by EMRC appear to function similarly in younger and older adults: In both groups, being able to remember that an activity changed was associated with successful memory updating [32], and directing attention to changed endings facilitated memory updating equally [68]. Together, these results suggest that aging primarily impairs both the encoding and retrieval processes that lead to prediction errors and trigger memory updating. This possibility is consistent with findings that older adults show larger memory differences in conditions that require endogenous regulation of encoding and retrieval mechanisms [74].

Concluding remarks and future directions

Clearly, memory can be updated in multiple ways. Updating can render representations less or more accessible, and it can change the similarity of representations. One helpful way to think about these processes has been by conceptualizing the representation of an experience as a singular atomic ‘item,’ and describing memory updating in terms of making an item more or less active or by modulating the association strength between two items. This conceptualization underlies classical verbal learning theory, as well as current theories of pattern separation, pattern completion, and reconsolidation.

Box 3. Atomic versus structured representations

Classic verbal learning theories of memory treat representations of isolated experiences as self-contained and undifferentiated atomic units [85], which are associated with other units. The units are sometimes modeled as bare labels or as points in a feature space. This view is often illustrated with network drawings in which memories are represented as nodes and associations as edges. On this view, memory effects must be accounted for by the activation of item features and contextual information in a representation or by one representation’s associations with other representations. This approach is natural for experiments in which the memoranda are lists of familiar words or pictures. This venerable way of thinking about memory representations is still very much alive in modern theories of word list learning [86–89] and memory updating in human and nonhuman species [90,91]. However, it is important to note that an event one experiences has a lot of structure; a spatial and temporal context, entities, objects, interactions, affective tone, traces of cognitive operations such as memory retrieval and inference, and so on. Starting with Minsky’s work on frames in the 1960s [92], researchers in some areas of cognitive science and cognitive neuroscience have modeled event memories as structured complexes that explicitly represent spatial and temporal parts, entities, objects, and other subcomponents. Moving from undifferentiated atomic units to richly structured event representations enables a vastly richer catalog of potential interactions among representations. Thus, one broad and important distinction between theories of memory updating is between those that are cast in terms of activation and association strength [89,93–95], and those that are cast in terms of structured representations with multiple kinds of interactions between memory representations [96–101]. Both approaches have advantages and disadvantages.

Outstanding questions

How do different components of the medial temporal lobe memory system, in particular subfields of the hippocampus presumed to support pattern completion and pattern separation, contribute to memory updating for dynamic events?

How does memory updating relate to event segmentation? When a change in the environment leads to a prediction error, does this lead to an event boundary as well as the formation of an integrated memory representation?

How do semantic and episodic memory interact in guiding predictions? When viewing everyday events, do scripts or schemas based on similar experiences lead to variations in priors that determine the strength of predictions and frequency of errors?

How does the influence of semantic and episodic event representations change over the course of learning about a class of events? Recursive representations become noisier as the chain of reminding gets longer, but at the same time, the brain is forming schemas that capture environmental regularities; how is the balance between these navigated?

Do changes in the similarity of event memories in representational space depend on conscious awareness of changes between past experiences and current perceptions?

What happens to the neural patterns associated with event components that trigger retrieval and the subsequent event components that conflict with a previous memory? For both, does the memory integration lead to more similar multivariate brain activity or to differentiation?

How does aging affect memory updating in naturalistic experience, including allocation of attention, event segmentation, reactivation of prior events, making predictions, and using prediction error as a control signal to update structured event representations?

We suggest that another helpful way to think about memory updating is in terms of structured event representations [75] (Box 3). An event representation generally has components representing entities and objects related in a spatiotemporal framework. It may also include relational features such as causes and goals. It has intrinsic dynamical structure, such that activating a representation should not just tend to activate related representations, but should do so over time in accord with the temporal order encoded in the representation. Thinking about event memory in terms of structured representations allows us to consider not just whether a representation might be rendered more or less active or more or less strongly associated with another representation; we can also consider that the relations amongst components of a representation might reconfigure. Further, activating an event representation might not only spread activation to other representations, but might do so with structured dynamics. Consider again our hiking example. The original experience would have included particular companions, time of day and year, weather, sunlight and wind conditions, and a temporal sequence of turns, vistas, and climbs. The new experience might have different companions and weather, but would likely include traces of the objects, vistas, and turns that remained the same. These relations are important for modeling event memory; they embed the spatial and temporal structure of the experience, and they cannot be reduced to similarity.

Importantly, some targets of relations are features of one's mental state. For memory updating, features of the experience of retrieval during comprehension can be crucial. A new representation formed when hiking a changed trail might incorporate features of the external terrain, people, and objects, but it may also include features generated by the retrieval process during the second hike: a prediction about what the next turn will be and the conflict between that prediction and the new turn of the trail. We think of this as metadata (a term borrowed from software engineering)

Box 4. Pattern completion and pattern separation in event memory updating

Event memories are represented throughout the brain [58,60,102–104]. However, episodic memory research has focused intensively on encoding and retrieval operations supported by areas within the medial temporal lobes, with an emphasis on the hippocampus [105–107]. Computational models propose that hippocampal subfields are specialized for reinstating memories from partial cues and encoding new events uniquely from similar memories [16,108]. Recent human studies have suggested that the **dentate gyrus** of the hippocampus is optimized for pattern separation, whereas the **CA3** field is optimized for pattern completion [109–111]. **CA1** may also be critical for detecting novelty and supporting the comparison processes that enable the integration of pattern completed memories with new perceptual inputs [112]. These subfields are assumed to interact with other structures in the medial temporal lobes and broader cortical regions to promote integration and differentiation of memories [113]. In addition, there is evidence that cortical inputs to the medial temporal lobes carry some of the computational load of separating potentially conflicting patterns [114,115]. However, an alternative proposal is that the dentate gyrus and CA3 bind elements of events into complexes [116]. One possibility is that the reorganization of event complexes represented in the dentate gyrus and CA3 forms a basis for integrated representations of changed events. The success of memory updating may depend on the extent to which overlapping event features are pattern completed (retrieved) while the distinct features are pattern separated (encoded distinctively).

Studies examining the interplay between pattern completion and separation have mostly used static stimuli such as paired associates, pictures, or scenes, in which the degree of feature overlap is varied [117], but see [118] for an example of a mnemonic discrimination task using naturalistic events]. However, it is difficult to distinguish pattern completion from pattern separation under these approaches because the simultaneous appearance of shared and distinctive features evokes both pattern completion and separation. The roles of these processes in memory updating may be better isolated using everyday changes protocols with dynamic unfolding events. These protocols have the advantage of temporally varying feature overlap, such that repeated event beginnings should evoke more pattern completion, whereas changed event endings should evoke more pattern separation. This approach would be ideally used with high-resolution fMRI methods capable of separating CA3, DG, and other key subfields while maintaining high-resolution imaging of cortical regions. The representational similarity in those subfields along with frontal, parietal, and ventral visual cortices [114] during temporal segments of events could then be compared. This would characterize more fully how pattern separation and completion throughout the brain, which may interact to support integrative encoding and/or neural differentiation, support memory updating as events unfold.

about the cognitive operations during the second experience. Such metadata can be a powerful basis for adaptive memory updating.

This perspective may help resolve current controversies about the role of the medial temporal lobe memory system in pattern separation and pattern completion (Box 4). The prevailing view is that patterns are separated to reduce interference and are completed from partial cues in memory reinstatement, and that these have different neural mechanisms within the hippocampus. Pattern completion may reflect memory-guided prediction, while pattern separation can result from the features added when a prediction error is registered (see Outstanding questions).

We believe that this approach to memory updating gives an inclusive and productive view of how memories are created, accessed, and used. It can be a basis for formal models of memory updating, and it can provide tools for neurophysiological and behavioral investigations. Like the process of memory updating itself, the field of memory updating brings together a rich past with a dynamic present, oriented to a future yet to unfold.

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Declaration of interests

No interests are declared.

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