

Schemas, reinforcement learning, and the medial prefrontal cortex.

Oded Bein^{1} & Yael Niv^{1,2}*

Affiliations

¹Princeton Neuroscience Institute and ²Psychology Department,
Princeton University, Princeton, NJ, 08540, USA.

*Correspondence: oded.bein@princeton.edu

Key words:

Schema, reinforcement learning, orbitofrontal cortex, medial prefrontal cortex, learning, memory

Abstract

Schemas are rich and complex knowledge structures about the typical unfolding of events in a context. For example, a schema of a lovely dinner at a restaurant. Schemas are central in psychology and neuroscience. Here, we suggest that reinforcement learning (RL), a computational theory of learning the structure of the world and relevant goal-oriented behavior, underlies schema learning. We synthesize literature about schemas and RL to offer that three RL principles might govern the learning of schemas: learning via prediction errors, constructing hierarchical knowledge using hierarchical RL, and dimensionality reduction through learning a simplified and abstract representation of the world. We then suggest that the orbito-medial prefrontal cortex is involved in both schemas and RL due to its involvement in dimensionality reduction and in guiding memory reactivation through interactions with posterior brain regions. Finally, we hypothesize that the amount of dimensionality reduction might underlie gradients of involvement along the ventral-dorsal and posterior-anterior axes of the orbito-medial prefrontal cortex. More specific and detailed representations might engage the ventral and posterior parts, while abstraction might shift representations toward the dorsal and anterior parts of the medial prefrontal cortex.

Introduction

Imagine entering a restaurant. You immediately know the likely sequence of occurrences and the relevant set of behaviors. You will be seated at a table and given a menu. After placing your order, you will receive a delicious meal, and maybe a glass of fine wine. This will be followed by paying the bill and leaving the restaurant. The general knowledge of what typically occurs in an event and in what order, as well as the appropriate behavior, is referred to as the “schema” of the event^{1–4}. While schemas are widely used in psychology and, more recently, in neuroscience, they also remain notoriously elusive and ill-defined^{2,5}. Importantly, we still lack a satisfying computational account of how schemas are learned through experience and with respect to goals, how schemas guide behavior, and how they influence perception, attention, learning, and memory.

Reinforcement learning (RL) offers a computational theory of how we learn the structure of our environment and the relevant behaviors through experience⁶. RL algorithms have been powerful in accounting for behavioral and neural findings in simplified environments^{7,8}. However, these algorithms suffer from a “curse of dimensionality:” they scale poorly to rich high-dimensional everyday life events^{6,9}. Thus, RL and schemas can be thought of as two ends of a spectrum: at the one end, highly rich and ecological knowledge structures that lack a satisfying computational account. At the other end, a detailed account that is dissatisfying in the complexity of the phenomena it explains. Here we bring these seemingly disparate fields of research together.

We are motivated by recent neuroscientific research that has emphasized the importance of the medial prefrontal cortex (mPFC) and orbitofrontal cortex (OFC) for both schemas and RL. Within the RL framework, the medial orbitofrontal cortex and ventral part of the medial prefrontal cortex (mOFC/vmPFC) are thought to represent a “cognitive map” of the current task^{1 13–17}. In RL, this map partitions the task into specific contexts termed “states,” each including information relevant to guiding behavior in that context. In parallel, memory research on schemas suggests that the mPFC (which includes the mOFC/vmPFC) represents

¹ Another prominent view within the RL literature proposes that the mOFC/vmPFC represents economic value that guides decisions^{10,11}; for additional theories about these brain areas, see e.g.,¹².

schemas and mediates the influence of schemas on memory (e.g.,^{5,18–22}). This co-localization prompted us to explore common mechanisms that might underly RL and schemas.

Below, we synthesize research on schemas and RL to propose that RL (and complementary algorithms) may provide a computational framework for learning schemas. We focus on three core computational principles that could underly schemas: (1) learning a summary of the environment through prediction errors, (2) grouping of states through hierarchical RL and latent cause inference, and (3) dimensionality reduction through learning of abstract state representations. We begin with a brief description of schemas and RL mechanisms, and show how these are related. We then postulate that the mPFC is involved in both RL and schemas as it mediates dimensionality reduction and guides memory retrieval through communicating with posterior brain regions. We conclude by postulating that graded recruitment along the ventral-dorsal and anterior-posterior axes of the mPFC might reflect the amount of dimensionality reduction required in a current situation.

A (very) brief introduction to schemas

Schemas are learned knowledge structures that organize knowledge of what typically occurs in a context^{2,4,23–25}, including associative knowledge of relationships and co-occurrences between units (e.g., menu and food in a restaurant). They contain knowledge of commonalities extracted over multiple experiences,² and as such, are by definition devoid of details of specific episodes. Here, we predominantly discuss schemas that are extended in time (similar to the notion of ‘scripts’³ or ‘event schemas’²⁶) and thus include knowledge of the *temporal structure* of an event.

Schemas can guide behavior as they include knowledge of context-appropriate actions. For example, the knowledge that upon receiving a menu, one should read it and place an order. Finally, schemas can be thought of as hierarchically organized “modules” that can be recombined: both the restaurant schema and that of having dinner at home can include a module of sitting at the table and eating, and the schema of an airport can include a restaurant as a module. Thus, schemas can be a part of other schemas, as well as include other schemas.

Despite decades of research on the influence of schemas on cognition^{1,4,5,25}, it is not

completely clear how schemas are learned and how they influence perception, action, learning, and memory^{22,27,28}. Computational models of semantic networks, concepts and category learning^{24,29–35}, characterize some aspects of extracting general knowledge about the co-occurrence of entities and the hierarchical structure of conceptual knowledge, but do not seem to capture fully the scope and richness of schemas. Particularly relevant is the fact that schemas are learned through experience that is dynamic in time. For this, we turn to the framework of RL.

A brief introduction to reinforcement learning

Reinforcement learning (RL) provides a set of algorithms for goal-oriented learning and behavior. The goal is typically conceptualized as maximizing reward while minimizing costs or punishments⁶. Through trial and error over multiple instances, an RL agent learns the sequence of actions most suitable for achieving maximal reward in an environment.

In RL theory, tasks are divided into a series of discrete time points or contexts, termed “states”. For instance, a visit to a restaurant can be divided into the states of standing at the entrance, sitting down, having a menu in hand, etc. Each state has an associated action policy – the probability of taking each action at that state. A state (or state-action pair) can also be associated with a value, which denotes the (possibly discounted) sum of future rewards expected when in that state (and, for state-action pairs, taking that action). Tasks can be divided into states at different levels of coarseness, and similarly, policies can be defined as single actions or high-level action groupings (see below).

In addition to learning what actions lead to long-term reward in each state, in a sequential task that extends over time, the agent can learn the probability of transitioning between different states contingent on different actions, that is, the probabilities of different sequences of states^{36–38}. Generally, learning in RL occurs when one encounters a prediction error: a situation in which the actual outcome is different from the predicted one^{39–41}. Prediction errors include both reward prediction errors, which refer to obtaining more or less reward than expected, and state prediction errors, which refer to transitioning to a different state than expected. When encountering a prediction error, the agent adaptively updates their

expectations so that these align better with the observed outcome. In this way, through experience, the agent can learn a world model, which includes the representation of states, transitions between them, and the distribution of rewards in each state, and mentally simulate actions within the learned world model to determine which action is best in what situation (termed “model-based RL”³⁶). Alternatively, in “model-free RL,” the agent can learn the optimal policy directly from trial and error using reward prediction errors, without learning a world model.

From this description, it is already clear how schemas might be mapped to a representation of a task in model-based RL, including the world model and the policy. In what follows, we unpack that mapping (Figure 1).

Schema

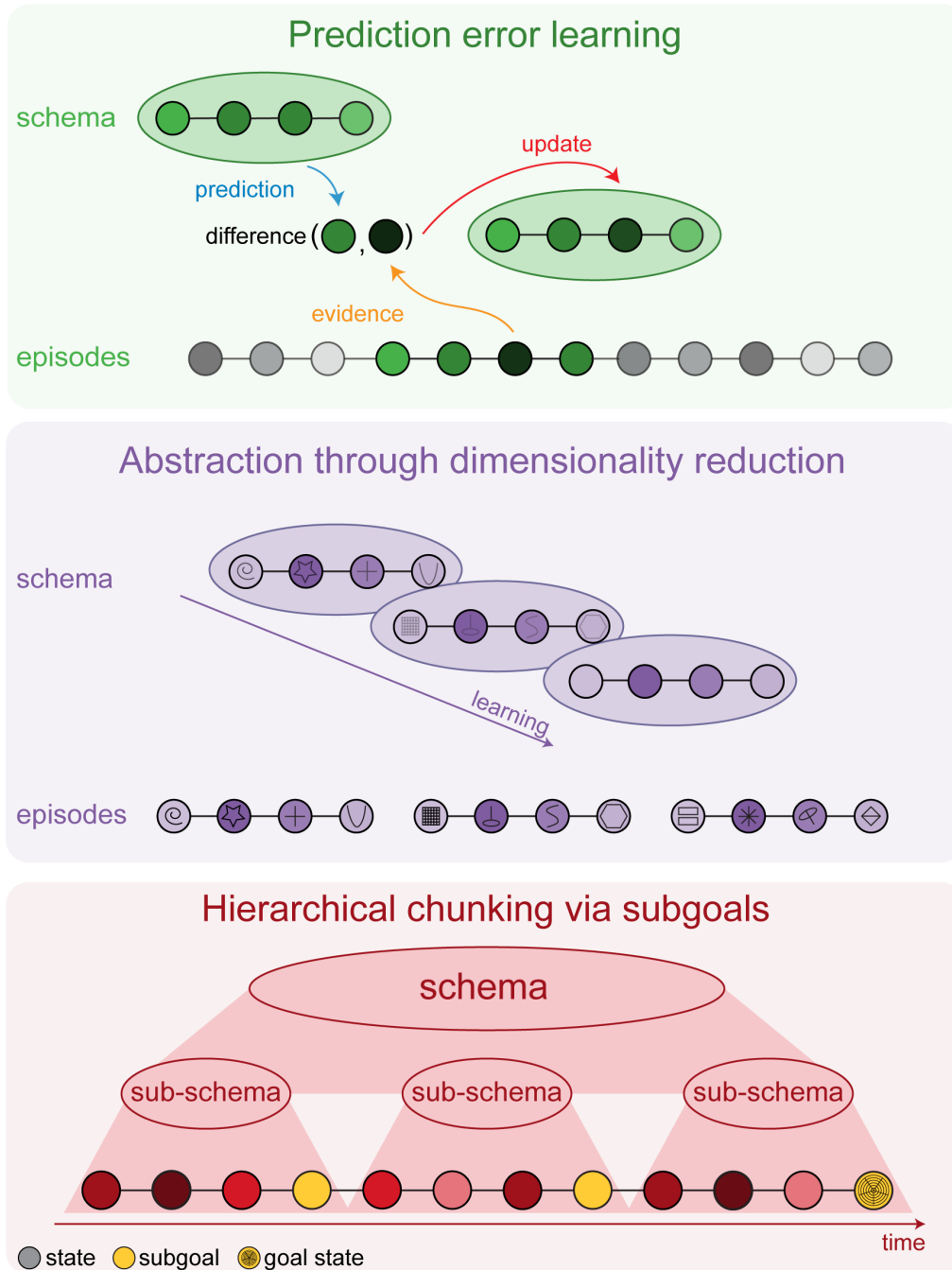


Figure 1. Three reinforcement learning principles contribute to schema learning. Circles represent states/time points in the schema or the episode, with different shades and colors representing different features of states. **Top:** Prediction errors, namely, the difference between the schema-based predictions (top) and the evidence from a specific episode (bottom), drive schema update (middle). This eventually converges to the typical unfolding of events. The episode and schemas to be updated are selected through latent cause inference, illustrated by the green circles 'selected' from the grey ones in the stream of experience. **Middle:** dimensionality reduction, implemented via schema-guided attention, mediates the elimination of episodic details that differ across episodes (symbols), and the inclusion of goal-relevant information as well as repeating, but not necessarily goal-relevant information (purple shades). **Bottom:** the hierarchical structure of schemas is learned via identifying subgoals (yellow) that chunk sub-schemas.

Are schemas learned through prediction errors?

Since RL algorithms use prediction-error driven learning, the first question we ask is whether schemas are also learned and updated via prediction errors (Fig. 1, top). The alternative is that a summary of the typical and repeating structure of the world is learned by tracking the frequency of occurrences (termed “unsupervised learning”³²). In this frequency hypothesis, learning does not require a prediction and an update following an error; instead, each experience leads to an update of associations between contiguous events.

The discovery of “blocking”^{42,43} led animal-learning theorists to shift from assuming that contiguity (i.e., co-occurrence) is sufficient for associative learning to considering prediction errors as driving learning. In blocking, a neutral stimulus (e.g., light) previously associated with a motivationally relevant outcome (e.g., an electric shock or food) prevents a co-occurring neutral stimulus (e.g., tone) from also becoming associated with the same outcome. The idea is that because the first stimulus fully predicts the outcome, there is no prediction error when the outcome occurs, and thus learning about the association with the newly added stimulus is “blocked”^{40,41}. In humans, a wealth of research shows that reward prediction errors drive learning^{39,44,45} and facilitate long-term memory^{46–49}.

Since schemas include state-transition probabilities, to establish that prediction errors drive schema learning, one can test whether state prediction errors lead to updating of the schema and to changes in behavior. Recent work in rodents suggests this by showing blocking of learning of simple stimulus-stimulus associations, thereby establishing that learning of “neutral” associations requires prediction errors^{50,51}. Computational models that learn via state prediction errors have been shown to explain choice data of humans and animals in studies that involve frequent changes (reversals) of either transition probabilities or the full state structure^{52–56}. Studies also show that participants trained on state transitions exhibit enhanced memory of items that violated these transitions^{57–61} and reduced memory for items that cued a future state that was (surprisingly) not transitioned to^{62,63}. This is consistent with updating a model of the world through prediction errors.

These studies, which focused on simplified tasks that trained participants on few associations and over a few trials or sessions, provide evidence that initial learning of schemas

might be driven by state prediction errors. In contrast, consolidated and well-learned semantic knowledge is thought to be stable and less amenable to change, largely supported by cortical structures (whereas newly-acquired knowledge is supported by the hippocampus, see Box 1), and more abstract and including fewer specific episodic details.^{64–68} It is therefore not clear that previous findings from simplified tasks generalize to updating of complex and well-learned schemas, as work in humans shows that complex semantic knowledge can both impair and enhance learning and memory of new associations^{69–77}.

One example of this complexity is that in everyday life, cues and outcomes are not as clearly defined as in many of the studies mentioned here, but rather dynamically evolve in time, and span multiple temporal scales^{78–80}. Indeed, viewers of continuous sport games also remembered events that elicited prediction errors better^{81,82}. In another study that directly targeted the updating of memories, Sinclair and colleagues⁸³ used rich movie-clip stimuli to elicit predictions of action outcomes that had been learned over a lifetime of experience, for example, a baseball batter hitting a home run. They then violated these predictions by stopping the movie before the expected outcome and presenting another, semantically related movie clip. In a subsequent memory test of the original clips, participants demonstrated memory intrusions, recalling details from the related clips as if they were in the original clip, and more so for movies that were stopped prematurely during encoding^{83,84}. These intrusions might reflect memory update of the original movie clips that was enhanced by violations of everyday life expectations. Of course, in everyday life, experience never stops. Rather, surprise occurs when events unfold in an unexpected way. In sum, emerging literature suggests that schemas might indeed be learned and updated via prediction errors, similar to learning in RL.

Schema hierarchies might be learned, and instantiated, via hierarchical RL and latent cause inference mechanisms

Schemas are hierarchically organized: each schema can be composed of subschemas and might be a subschema of another, larger schema. Hierarchical RL algorithms^{85–92} might provide a blueprint for how such a schema hierarchy is acquired (Fig. 1, bottom). Learning via RL algorithms can become prohibitively slow in complex environments. Hierarchically grouping

states and actions into larger units can alleviate this scaling problem. In such “temporal abstraction”,^{86,93} a temporally extended task is divided into subunits, called “subtasks”. A subtask is defined by a set of possible start states, a subtask-specific action policy and a set of termination states (also called “subgoals”) in which the subtask will cede control back to the overarching decision policy^{89,91–95}. For example, ‘adding salt’ can be a subtask that starts upon tasting bland food, continues with a policy that includes reaching for the salt shaker, grasping it, and shaking it over the food, and ends when the subgoal is reached: there is salt on the food. Subtasks can be used across tasks^{89,96,97} (e.g., ‘adding salt’ is used by ‘dining at a restaurant’ and ‘eating at home’). The term “subgoal” distinguishes the termination state of the subtask (food is salted) from the overall goal of the task (having a full stomach). In some algorithms, reaching a subgoal leads to a pseudo-reward signal^{89,98,99}. Pseudo-rewards allow standard RL reward-maximizing algorithms to discover the optimal policy for the subtask.

An important question in hierarchical RL is: how are subgoals selected? In terms of schemas, this is the question of how to segment continuous experience into discrete event schemas²⁶. Hierarchical RL offers more than one mechanism^{89,91,92,95}. Some mechanisms rely on exploring an environment while keeping track of sequences of states and actions that co-occur frequently (i.e., statistical learning^{100–104}), and use states right before a transition to another sequence as subgoals^{86,88,105}. Other algorithms introduce Bayesian inference to maximize the discovery of optimal hierarchies given the structure of the environment^{92,95} and the cost of planning⁹¹. These algorithms rely on repeated experience to construct a hierarchical model of the world.

Another idea is that salient events trigger the creation of a subgoal. Salient events create an intrinsic reward signal and engage motivation-related neural systems, much like rewards^{106–112}. Research on event segmentation that focuses on how ongoing and continuous experience is chunked into discrete events^{26,113,114} has shown that salient changes, termed “event boundaries,” cause humans to segment their experiences in memory. For example, events that span a boundary are remembered as happening farther apart in time from each other, and memory of their temporal order is often worse than that of events not separated by a boundary^{115–117}. This suggests that event boundaries, like subgoals, structure our experiences

into discrete, segmented units. Interestingly, this structuring of memories has been shown for reward prediction errors as well¹¹⁸, consistent with salient prediction errors creating subgoals.

A mechanism that relies on salient changes to create subgoals does not require repetition (i.e., statistical learning). A change of context, perceptual details, or internal state, can trigger segmentation even in the first instance^{113,114,116,119}. This discrete event representation can form a base that future instances will join to build an event schema. This proposal resonates with recent behavioral work suggesting that schema memories can be created rapidly¹²⁰ (see Box 1). Such rapid extraction of structure can facilitate goal-oriented learning and behavior in new situations^{96,121,122}, with later learning refining the initial structure^{123,124}.

Latent cause inference might be the computational process by which salient changes trigger the instantiation of an existing (sub)schema or the initiation of a new one. Latent cause inference is a computational theory of how observations are grouped into clusters (“latent causes”) according to similarity^{9,28,96,125}. The latent cause underlying the current observations can be inferred using Bayesian inference by combining prior beliefs about the probability of various latent causes (e.g., the latent cause responsible for recent observations is most likely to underlie the next one) with evidence from current observations. Thus, external observations that are sufficiently different from past ones prompt the creation of a new latent cause^{126,127}. This new latent cause then supports learning a new state-transition model and submodels and their respective policies, potentially through RL mechanisms. Recent theoretical work has begun to explore how salient changes such as event boundaries trigger the inference of a new latent cause^{28,114} or instantiate a relevant event schema²⁸.

Box 1: Rapid learning in the hippocampus shapes new schemas

The idea that event boundaries can become subgoals could mean that first instances of events – in which subgoals are created – might be highly influential in shaping our models of the structure of the world. This is in contrast to the idea that structure is extracted solely through incremental and relatively slow learning^{103,128}. In RL, the initial values with which a model is

initialized bias learning and can be hard to overcome⁶. To avoid this, in many algorithms, the rate of updating (called the learning rate) is high at the beginning of a task and decreases with time. Indeed, Shteingart et al.¹²⁹ showed that the first experience is highly influential on choices in future trials. This behavior was best explained by assuming maximal updating on the first trial (i.e., learning rate of 1). Other studies showed relatively quick learning of regularities^{130–132} and generalization based on such regularities¹²⁰ in a single lab session. The hippocampus, known to be involved in rapid learning^{67,128,133,134} and in event segmentation^{113,135–137}, also mediates learning the structure of the environment^{131,138–149}. Thus, converging behavioral and neural evidence suggest that rapid initial learning largely shapes our schemas.

----- end of Box 1-----

Dimensionality reduction through selective attention might mediate schema learning

Schemas summarize information across multiple multidimensional episodes. One option is that schema learning simply averages across features in all dimensions, such that features that repeat across episodes persist, while features that change average out. Alternatively, schema learning might involve goal-sensitive dimensionality reduction, whereby dimensions that include repeating goal-relevant features (e.g., the prices of dishes) are prioritized, while goal-irrelevant dimensions that include unique episodic features (e.g., the color of the host's shirt) are down-weighted.

In RL, an optimal representation of a state focuses on only goal-relevant information in the environment^{6,150,151}. The process by which an agent learns what dimensions of the environment are important to a given task has been termed “representation learning”⁹, and often involves dimensionality reduction. The idea is that through experience, we can learn what dimensions of our environment are relevant to our goals and therefore should be attended to, and what dimensions are irrelevant and thus can be ignored. Research has shown that indeed learning the relevant (i.e., reward-predicting) dimensions of a state guides attention to these dimensions, which in turn prioritizes learning predictions associated with these dimensions^{9,152–158}. These studies suggest that goal relevance and selective attention might mediate dimensionality reduction during schema learning.

However, repetition of features might result in learning of goal-irrelevant dimensions as well. Indeed, people are faster to identify a stimulus that appears in a location where, in other trials, regularities existed in a stream of symbols^{159–161}, suggesting prioritized attention to that location despite it being goal-irrelevant. Similarly, processing of item pairs that are semantically congruent and encountered repeatedly in daily life (e.g., restaurant and menu) is typically enhanced (reduced reaction times and increased accuracy) compared to incongruent pairs that are rarely encountered (e.g., spinach and train), even if congruency is task irrelevant¹⁶² and pairs are presented only briefly^{163,164}. Task-irrelevant congruence also enhances long-term memory¹⁶⁵. However, the prediction of a feature in a goal-irrelevant but repeating dimension comes at the expense of later memory of unique episodic details^{62,63,166} (see also¹⁶⁷). Together, these findings suggest that attentional mechanisms might prioritize the learning of repeating information, goal-relevant or not, potentially at the expense of down-weighting episodic details. This might be adaptive because it allows flexible behavior when the world changes^{2,153,168} (similar to cognitive maps; Box 2).. For example, learning that in restaurants the cashier is typically next to the bar – even if mostly irrelevant because we usually pay with a server – can be useful if we are ever asked to pay at the cashier.

Box 2: schemas versus cognitive maps

Similarly to schemas, a cognitive map is a representation that organizes aspects of an experience, which can be used to flexibly guide behavior^{168–171}. We suggest that schemas are broader than cognitive maps, and can include additional types of information^{1,24,30,32,140}. Most conceptualizations of cognitive maps represent information through some notion of distance, which can be physical or mental^{169,170}. Indeed, while cognitive maps have been studied extensively in spatial navigation, recent research extended the notion of cognitive maps to non-spatial maps^{130,141,147,172–176}. This work still focused predominantly on relationships that can be mapped to distance measures and used such distances to identify neural correlates. Distance is, by definition, symmetric. However, hierarchical semantic relationships that may be important in schemas are not necessarily symmetric: menus are found in restaurants, but restaurants are not found in menus. Thus, hierarchical information cannot be mapped to a distance measure in

a straightforward way. Interestingly, some frameworks propose that even spatial navigation might rely on strategies or computations that are not based solely on distance^{140,177–180}.

---- end of Box 2 ----

Orbito-medial PFC involvement in schemas and states: dimensionality reduction and the guidance of memory reactivation in posterior brain regions.

There is wide agreement that the orbitofrontal (OFC) and medial prefrontal cortex (mPFC) are involved in both RL and schema-related processes. However, the functions these regions play are a topic of intense debate^{5,11,12,14,16,22,65,181,182}. In this section, we relate the conceptual ideas we laid out above to potential neural substrates, focusing on the medial part of the OFC and ventromedial PFC (mOFC/vmPFC) and the mid-mPFC (the area dorsal to the mOFC/vmPFC on the medial wall, but ventral to the most dorsal part of the mPFC), using “mPFC” to collectively refer to these areas. We summarize evidence that the mPFC represents both states in RL and schemas, offer that low-dimensional representations in the mPFC that can activate detailed memories in posterior brain regions might underlie these representations,²² and postulate that the amount of dimensionality reduction in the mPFC determines the involvement of subparts along its ventral-lateral and anterior-posterior axis.

A prominent theory suggests that the mPFC and OFC represent a map of task states^{14,16,183–186}. Recent work indeed found in the mOFC/vmPFC representations of states and the relationships between them for conceptual spaces^{172,176}, sequential structures^{15,130,187,188}, and social knowledge¹⁷³. Some theories suggest that the mOFC/vmPFC is particularly needed when states cannot be determined based on perceptual input alone but are latent (like latent causes above) and require the retrieval of information from memory^{16,183}. Empirically, multivoxel activation patterns in mOFC/vmPFC are consistent with Bayesian inference of the current (latent) state when this inference requires integrating retrieved prior memories and current observations¹³. Another study successfully classified from mOFC/vmPFC states that included information from the current and the previous trial, and thus relied on memory¹⁵. The mid-mPFC also mediates the retrieval and recombination of memories needed to make choices

about novel stimuli^{189,190}.

Schemas hold knowledge of what typically occurs in an event, and therefore require retrieving information from memory. Consistent with the mPFC representing latent states that rely on memory, it is also involved in mediating schemas^{5,21}. For instance, lesions to the mOFC/vmPFC impair the appropriate deployment of schema knowledge^{20,191–193}. Moreover, recent studies showed that activation patterns in the mid-mPFC were more similar for events that belonged to the same schema (e.g., different examples of visiting a restaurant) compared to different schemas (visiting a restaurant versus an airport), even when similarity was computed across video and audio stimuli, suggesting a schematic representation beyond perceptual features^{18,194–196}. Together with the finding above that mPFC representations follow Bayesian inference¹³, these findings strengthen the proposal that schemas are instantiated via Bayesian latent cause inference²².

The mPFC might represent schemas and states through dimensionality reduction

Studies show dimensionality reduction in the mPFC across paradigms^{18,195} (Fig. 2). For instance, in an RL task, mid-mPFC activation was correlated with predicted rewards computed based on attending to one relevant task dimension out of three available¹⁵⁵ (Fig. 2a). More directly, Mack et al.¹⁹⁷ used a categorization task and principal component analysis (PCA) to extract the number of orthogonal components that account for variance in mOFC/vmPFC multivoxel activity patterns and showed more compression through learning, especially for categorizations that required fewer dimensions (Fig. 2b). Other studies exposed participants to item-scene associations, with some items sharing the same scene^{194,198,199}. After consolidation, the neural representations of items that shared the same scene, but not different scenes, showed stronger similarity to each other in the mid-mPFC, as if specific episodes (each item-scene pair) were grouped based on a shared feature (the scene), while the details of each episode were reduced (Fig. 2c). Similar results were obtained when grouping episodes based on similar attentional goals²⁰⁰. Finally, studies showing a lack of episodic details in the mPFC also suggest dimensionality reduction during schema instantiation (Fig. 2d).^{18,195}

Consistent with our proposal that dimensionality reduction prioritizes both goal-

relevant and repeating but goal-irrelevant dimensions, evidence suggests that the mPFC represents both types of information^{16,183,186,201,202}. In particular the mPFC has been shown to represent task structure even when it is goal-irrelevant^{173,188,202,203}. For example, the mOFC/vmPFC represented a map of a two-dimensional social hierarchy, even in a task that asked participants to make inferences only based on one dimension¹⁷³. In general, mOFC/vmPFC neural representations of items that share a dimension (e.g., the context of learning) are more similar than representations of items that do not share a dimension even when participants perform an unrelated task^{204,205}. The mPFC also showed differential activity during encoding of semantically congruent vs. incongruent information not only when participants were asked to judge congruency,^{206,207} but also when they judged grammatical correctness of word stimuli (i.e., semantic congruency was goal irrelevant).^{208–210}

Interestingly, temporal order seems to be a consistently important dimension in mPFC schematic representations. Indeed, scrambling the order of events in a schema disrupts mPFC representation¹⁸ (Fig 2d). In rodents, lesions to the mPFC impair temporal memory²¹¹. In humans, mPFC lesions specifically impair schema knowledge, while sparing category knowledge²⁰; arguably, the temporal order of events is a critical aspect of the former but not the latter. Representation of sequential order in the mPFC might be supported by strong anatomical connections to the hippocampus^{212–215}, widely thought to represent temporal and sequential information^{123,216–219}, as mPFC-hippocampal functional connectivity supports learning and memory of sequential information^{131,220}. Such representations of temporal order are consistent with representation of schemas because, like the transition probabilities between states in model-based RL, sequence information is an essential part of a schema.

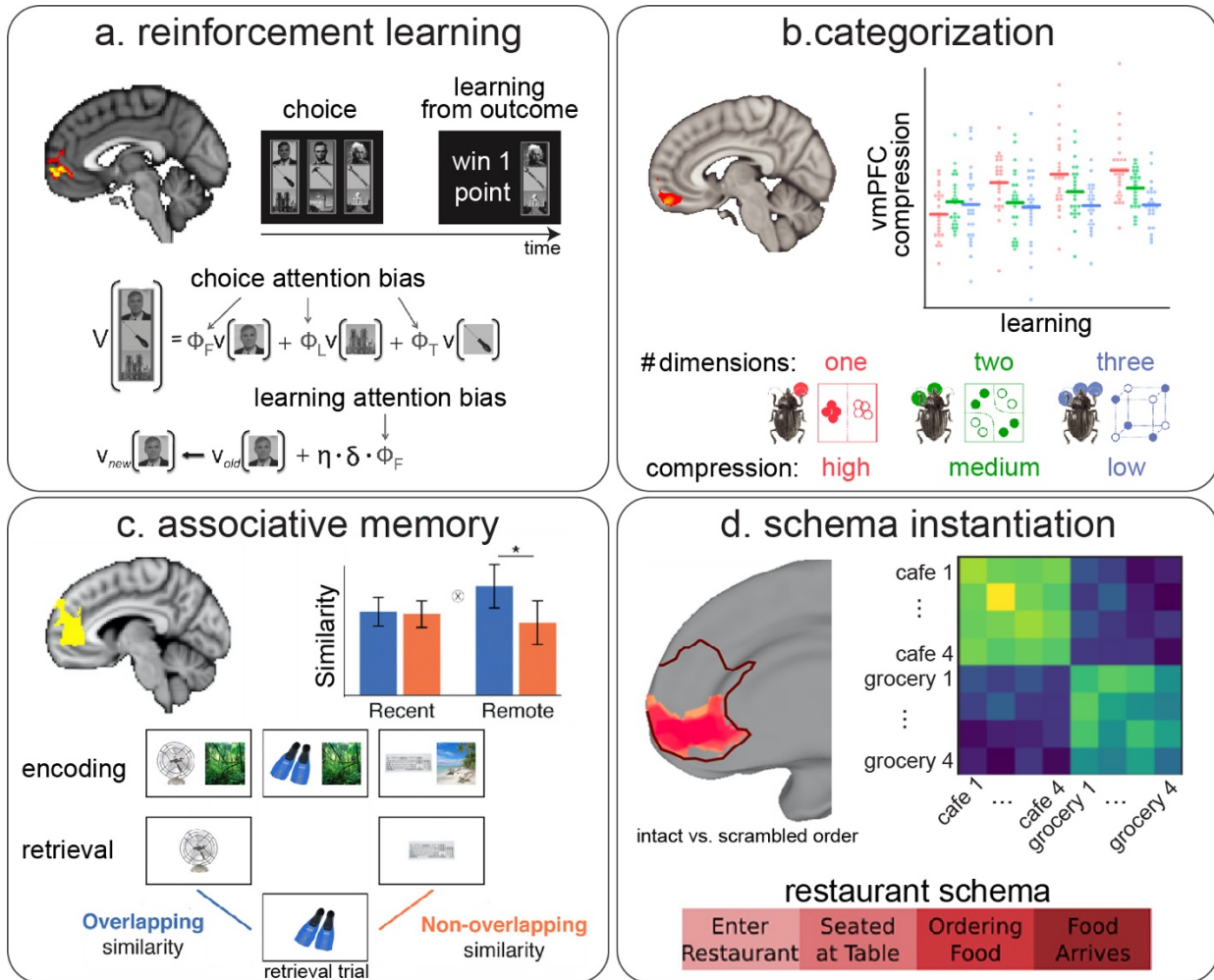


Figure 2. Examples of dimensionality reduction in the mPFC. **a.** Participants learned that one of three category-dimensions is relevant for obtaining reward. A model that biased attention towards that category during choice and learning best explained behavior, suggesting a dimensionality-reduced representation of the task. Activity in the mPFC correlated with values as estimated by that dimensionality reduced representation (adapted from Leong, Radulescu et al., 2017). **b.** Participants categorized bugs based on one, two or three dimensions. PCA was used to extract the dimensions of vmPFC multivoxel activity patterns, and dimensionality reduction ('compression') was quantified as the number of PCA components that explained 90% of the variance in vmPFC activity patterns, with fewer components interpreted as stronger compression. As participants learned the categories, the simpler the categorization the stronger was the compression observed in the vmPFC (top right plot), suggesting that dimensionality reduction in vmPFC tracked the dimensions of the categories (adapted from Mack et al., 2020). **c.** Participants encoded associations between trial-unique objects and several shared scenes. During retrieval, greater neural similarity was observed in the mPFC between objects that had appeared with the same scene compared to those that appeared with different scenes during encoding. This similarity only emerged following a period of consolidation ("remote"), and potentially reflects loss of distinct details (adapted from Tomparry and Davachi, 2017). **d.** Participants watched movie clips showing different instances of schemas. MPFC representations generalized across instances of schemas (e.g., all café clips), as indicated by increased similarity within the same schema compared to across schemas (top right, adapted from Reagh et al., 2023). This suggests reduced dimensions and lack of specific details of each instance in the mPFC. Similar representations were also found across visual vs. auditory modalities, but not when the order of events was compromised (left, adapted from Baldassano et al., 2018), suggesting the modality dimension is reduced in mPFC schema representations while sequential information is preserved.

Gradients of dimensionality reduction and memory reactivation along mPFC axes

One potential role of schema and state representations in the mPFC is to guide the retrieval of knowledge via memory reactivation in posterior brain regions^{5,22,153}. For instance, mPFC neural activity precedes hippocampal and ventral-temporal activity during memory retrieval^{221–224}. Mid-mPFC activity also correlates with the persistence (across time) of ventral-temporal and hippocampal representations of items experienced within the same context²²⁵. More directly, a recent study showed that the extent of schema representation in the mPFC correlated with the strength of the representation of specific instances of that schema (i.e., a specific movie belonging to that schema) in a posterior medial cortical region¹⁹⁶. Lesion studies demonstrate causality: in a rodent reversal-learning task that required resolving interference to infer the correct state, mPFC lesions impaired hippocampal representations that mediated interference resolution²²⁶. In humans, mOFC/vmPFC lesions impair the evaluation of retrieved memories^{227,228}, which can result in confabulation – retrieval of memories that are irrelevant to a specific context or schema^{192,229}. Additionally, the mPFC might route the involvement of cortical vs. hippocampal systems based on how memories relate to the current schema^{5,21}: connectivity with posterior cortical regions mediates memory of schema-consistent information, while connectivity with the hippocampus mediates memory of schema-inconsistent information^{19,21,23,206,207,230–234}.

The findings reviewed above were reported in different loci in the mPFC. Here, we hypothesize that the level of dimensionality reduction, or the degree to which memories are schematized and lack specific details, might underlie the gradual involvement of subregions along the anterior to posterior and the ventral to dorsal axes of the mPFC². Our proposal is motivated by gradual changes in the anatomical structure and connectivity along the mPFC. There is a wide agreement on a gradual transition from agranular to granular cortex along the posterior-anterior axis of the mPFC^{235–237}. Along the ventral-dorsal axis, studies in humans and monkeys generally show different connectivity profile of mid-mPFC vs. mOFC/vmPFC^{212–215} (more below), and a recent study found that these changes are gradual²³⁸.

² The medial to lateral axis in the OFC, with some focus on the lateral OFC, has been discussed elsewhere, suggesting that while vmPFC/mOFC is involved in latent states that require memory retrieval, the lateral OFC is involved in representing states based on observable information^{16,182,201}

We thus propose that abstract representations might recruit more anterior parts of the mPFC, while detailed memories might recruit the posterior mPFC and its connectivity with the hippocampus. Research suggests that the anterior part of the PFC is involved in representing future or counterfactual states and actions, but not current ones^{239–243}. Studies on prospective planning and predictions also show a gradient of predictions in mPFC, whereby predictions of the far future are represented more anteriorly and predictions of the near future are represented more posteriorly^{78,80}. Potentially, the farther we prospect to the future, the more abstract and less concrete and detailed are our thoughts^{244–246}, and therefore they are represented more anteriorly. This might be true also for counterfactual thoughts compared to actions and events that have materialized. Finally, studies reporting dimensionality reduction in abstract tasks in the mOFC/vmPFC find a more anterior cluster of voxels^{155,197} compared to studies addressing retrieval of autobiographic memories of specific events²⁴⁷. This aligns with the connectivity of the more posterior (and ventral) part of the mPFC and the hippocampus,^{212–215} which is critical for the encoding and retrieval of detailed memories, potentially through the allocation of distinct representations that serve to disambiguate similar stimuli^{248–252} and states^{253–255}.

Specificity versus abstraction might also underlie graded involvement from ventral to dorsal mPFC, supported by differences in functional connectivity. For instance, identity-specific expected value representations have been found ventral to general (scalar) expected value representations in the mPFC^{256,257}. Further, while retrieval of specific autobiographical memories tends to involve a ventral cluster of voxels²⁴⁷, a study addressing rule learning that required abstraction across multiple episodes showed a mid-mPFC activation²⁵⁸. While the mOFC/vmPFC is connected to the hippocampus (important for detailed memories), the mid-mPFC is connected with the posterior medial cortex,^{215,238,259} which has been shown to represent events over large timescales, potentially abstracting away more specific details^{196,260–262}. Of note, the studies mentioned here employed a variety of learning protocols and stimuli, so they are not all directly comparable. Nevertheless, they are in line with our proposal that the extent of dimensionality reduction underlies differential involvement of mPFC subregions, and the change in connectivity patterns along mPFC axes.

Other proposals for mPFC function include the evaluation of retrieved memories²²⁸, representing confidence^{228,263}, or signaling the match between prior schemas and perceptual information²¹. In our view, recent studies that examined multivoxel activity patterns support state or schema representations, because these studies show different representations for memories retrieved with similar levels of confidence, values, or match to prior memories^{15,196,199,256,264}. Potentially, multiple codes exist in the mPFC: different populations of neurons might represent different states and schemas, that in turn activate memories represented by different neuron populations in posterior brain regions^{21,65}, whereas the overall level of activity in the neurons can signal value, match with prior memories or other monitoring signals.

Conclusion

We outlined how reinforcement learning, state representations, and event schemas might be related. We proposed that schemas might be learned via reinforcement-learning related mechanisms such as prediction errors, hierarchical decomposition of tasks, and dimensionality reduction. We then hypothesized that dimensionality reduction might underlie the involvement of the medial prefrontal cortex in both schemas and reinforcement learning and postulated that the extent of abstraction might determine the locus of involvement along medial prefrontal axes. Broadly, we hope to facilitate better integration of the fields of learning and memory^{46,265,266} that will advance our understanding of human cognition and the brain.

References

1. Alba, J. W. & Hasher, L. Is memory schematic? *Psychol. Bull.* **93**, 203–231 (1983).
2. Ghosh, V. E. & Gilboa, A. What is a memory schema? A historical perspective on current neuroscience literature. *Neuropsychologia* **53**, 104–114 (2014).
3. Schank, R. & Abelson, R. Scripts. in *Scripts Plans Goals and Understanding: an inquiry into human knowledge structures* 36–68 (1977). doi:10.1515/9789048536825-005.
4. Bartlett, F. C. *Remembering: A Study in Experimental and Social Psychology*. (Cambridge University Press, Cambridge, UK, 1932).
5. Gilboa, A. & Marlatte, H. Neurobiology of Schemas and Schema-Mediated Memory. *Trends Cogn. Sci.* **xx**, 1–14 (2017).
6. Sutton, R. S. & Barto, A. G. *Reinforcement Learning: An Introduction*. (MIT press, Cambridge, MA, 2018). doi:10.1016/S0140-6736(51)92942-X.
7. Dayan, P. & Niv, Y. Reinforcement learning: the good, the bad and the ugly. *Curr Opin Neurobiol* **18**, 185–196 (2008).
8. Schultz, W., Dayan, P. & Montague, P. R. A neural substrate of prediction and reward. *Science* **275**, 1593–1599 (1997).
9. Niv, Y. Learning task-state representations. *Nat. Neurosci.* **22**, 1544–1553 (2019).
10. Levy, D. J. & Glimcher, P. W. The root of all value: A neural common currency for choice. *Curr. Opin. Neurobiol.* **22**, 1027–1038 (2012).
11. Padoa-Schioppa, C. & Conen, K. E. Orbitofrontal Cortex: A Neural Circuit for Economic Decisions. *Neuron* **96**, 736–754 (2017).

12. Delgado, M. R. *et al.* Viewpoints: Dialogues on the functional role of the ventromedial prefrontal cortex. *Nat Neurosci* **19**, 1545–1552 (2016).
13. Chan, S. C. Y., Niv, Y. & Norman, K. A. A Probability Distribution over Latent Causes, in the Orbitofrontal Cortex. *J Neurosci* **36**, 7817–7828 (2016).
14. Klein-Flügge, M. C., Bongioanni, A. & Rushworth, M. F. S. Medial and orbital frontal cortex in decision-making and flexible behavior. *Neuron* S0896627322004639 (2022) doi:10.1016/j.neuron.2022.05.022.
15. Schuck, N. W. *et al.* Human Orbitofrontal Cortex Represents a Cognitive Map of State Space Article Human Orbitofrontal Cortex Represents a Cognitive Map of State Space. *Neuron* **91**, 1402–1412 (2016).
16. Wilson, R. C., Takahashi, Y. K., Schoenbaum, G. & Niv, Y. Orbitofrontal cortex as a cognitive map of task space. *Neuron* **81**, 267–279 (2014).
17. Zhou, J. *et al.* Evolving schema representations in orbitofrontal ensembles during learning. *Nature* **590**, 606–611 (2020).
18. Baldassano, C., Hasson, U. & Norman, K. A. Representation of real-world event schemas during narrative perception. *J. Neurosci.* **38**, 9689–9699 (2018).
19. Bonasia, K. *et al.* Prior knowledge modulates the neural substrates of encoding and retrieving naturalistic events at short and long delays. *Neurobiol Learn Mem* **153**, 26–39 (2018).
20. Giuliano, A. E., Bonasia, K., Ghosh, V. E., Moscovitch, M. & Gilboa, A. Differential influence of ventromedial prefrontal cortex lesions on neural representations of schema and semantic category knowledge. *J Cogn Neurosci* 1–28 (2021) doi:10.1162/jocn_a_01746.

21. van Kesteren, M. T. R., Ruiter, D. J., Fernández, G. & Henson, R. N. How schema and novelty augment memory formation. *Trends Neurosci* **35**, 211–219 (2012).
22. Varga, N., Morton, N. & Preston, A. Schema, Inference, and Memory. in *The Oxford Handbook of Human Memory* (eds. Kahana, M. J. & Wagner, A. D.) (Oxford University Press, 2022). doi:10.31234/osf.io/m9adb.
23. Preston, A. R. & Eichenbaum, H. Interplay of hippocampus and prefrontal cortex in memory. *Curr Biol* **23**, R764–73 (2013).
24. Rumelhart, D. E. & Ortony, A. The Representation of Knowledge in Memory. *Sch. Acquis. Knowl.* 99–135 (1977) doi:10.4324/9781315271644-10.
25. Piaget, J. *The Origins of Intelligence in Children*. (International Universities Press, New York, NY, 1952).
26. Zacks, J. M. Event Perception and Memory. *Annu. Rev. Psychol.* **71**, 165–191 (2020).
27. Elman, J. L. & McRae, K. A model of event knowledge. *Psychol Rev* **126**, 252–291 (2019).
28. Franklin, N. T., Norman, K. A., Ranganath, C., Zacks, J. M. & Gershman, S. J. Structured Event Memory: A neuro-symbolic model of event cognition. *Psychol Rev* **127**, 327–361 (2020).
29. Collins, A. M. & Loftus, E. F. Spreading activation theory of semantic processing. *Psychol. Rev.* **82**, 407–428 (1975).
30. Collins, A. M. & Quillian, M. R. Retrieval time from semantic memory. *J. Verbal Learn. Verbal Behav.* **8**, 240–247 (1969).

31. Kenett, Y. N., Levi, E., Anaki, D. & Faust, M. *The Semantic Distance Task: Quantifying Semantic Distance With Semantic Network Path Length. Journal of Experimental Psychology: Learning, Memory, and Cognition* (2017). doi:10.1037/xlm0000391.
32. Kumar, A. A. *Semantic Memory: A Review of Methods, Models, and Current Challenges. Psychonomic Bulletin and Review* vol. 28 (Psychonomic Bulletin & Review, 2021).
33. Love, B. C., Medin, D. L. & Gureckis, T. M. SUSTAIN: A Network Model of Category Learning. *Psychol. Rev.* **111**, 309–332 (2004).
34. McClelland, J. L., McNaughton, B. L. & Oreilly, R. C. Why there are complementary learning-systems in the hippocampus and neocortex – insights from the success and failures of connectionist models of learning and memory. *Psychol. Rev.* **102**, 419–457 (1995).
35. Murphy, G. L. *The Big Book of Concepts*. (MIT press, 2004).
36. Daw, N. D., Niv, Y. & Dayan, P. Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nat. Neurosci.* **8**, 1704–11 (2005).
37. Daw, N. D., Gershman, S. J., Seymour, B., Dayan, P. & Dolan, R. J. Model-based influences on humans' choices and striatal prediction errors. *Neuron* **69**, 1204–1215 (2011).
38. Doya, K., Samejima, K., Katagiri, K. & Kawato, M. Multiple Model-Based Reinforcement Learning. **1369**, 1347–1369 (2002).
39. Niv, Y. & Schoenbaum, G. Dialogues on prediction errors. *Trends Cogn. Sci.* **12**, 265–272 (2008).
40. Rescorla, R. A. Pavlovian conditioning. It's not what you think it is. *Am. Psychol.* **43**, 151–160 (1988).

41. Rescorla, R. A. & Wagner, A. R. A theory of Pavlovian conditioning. *Classical conditioning II current research and theory* 497 Preprint at <https://doi.org/10.1101/gr.110528.110> (1972).
42. Kamin, L. J. Predictability, surprise, attention, and conditioning. in *Punishment and Aversive Behavior* (eds. Campbell, B. A. & Church, R. M.) 279–296 (Appleton-Century-Crofts, New York, 1969).
43. Kamin, L. J. “Attention-like” processes in classical conditioning. in *Miami Symposium on the Prediction of Behavior, 1967: Aversive Stimulation* (ed. Jones, M. R.) 9–31 (University of Miami Press, Coral Gables, Florida, 1968).
44. d’Acremont, M., Schultz, W. & Bossaerts, P. The human brain encodes event frequencies while forming subjective beliefs. *J Neurosci* **33**, 10887–10897 (2013).
45. Niv, Y. & Langdon, A. Reinforcement learning with Marr. *Curr. Opin. Behav. Sci.* **11**, 67–73 (2016).
46. Ergo, K., De Loof, E. & Verguts, T. Reward Prediction Error and Declarative Memory. *Trends Cogn Sci* **24**, 388–397 (2020).
47. Greve, A., Cooper, E., Tibon, R. & Henson, R. N. Knowledge is power: Prior knowledge aids memory for both congruent and incongruent events, but in different ways. *J. Exp. Psychol. Gen.* **148**, 325–341 (2019).
48. Rouhani, N., Norman, K. A. & Niv, Y. Dissociable effects of surprising rewards on learning and memory. *J Exp Psychol Learn Mem Cogn* **44**, 1430–1443 (2018).
49. Rouhani, N. & Niv, Y. Signed and unsigned reward prediction errors dynamically enhance learning and memory. *Elife* **10**, (2021).

50. Sharpe, M. J. *et al.* Dopamine transients are sufficient and necessary for acquisition of model-based associations. *Nat Neurosci* **20**, 735–742 (2017).
51. Sharpe, M. J. *et al.* Dopamine transients do not act as model-free prediction errors during associative learning. *Nat. Commun.* **11**, 106 (2020).
52. Momennejad, I. *et al.* The successor representation in human reinforcement learning. *Nat Hum Behav* **1**, 680–692 (2017).
53. Sharp, P. B., Dolan, R. J. & Eldar, E. Disrupted state transition learning as a computational marker of compulsivity. *Psychol. Med.* 1–11 (2021) doi:10.1017/S0033291721003846.
54. Sharp, P. B., Russek, E. M., Huys, Q. J., Dolan, R. J. & Eldar, E. Humans persevere on punishment avoidance goals in multigoal reinforcement learning. *eLife* **11**, e74402 (2022).
55. Akam, T. *et al.* The Anterior Cingulate Cortex Predicts Future States to Mediate Model-Based Action Selection. *Neuron* **109**, 149–163.e7 (2021).
56. Bartolo, R. & Averbeck, B. B. Prefrontal Cortex Predicts State Switches during Reversal Learning. *Neuron* **106**, 1044–1054.e4 (2020).
57. Bein, O., Plotkin, N. A. & Davachi, L. Mnemonic prediction errors promote detailed memories. *Learn Mem* **28**, 422–434 (2021).
58. Greve, A., Cooper, E., Kaula, A., Anderson, M. C. & Henson, R. Does prediction error drive one-shot declarative learning? *J. Mem. Lang.* **94**, 149–165 (2017).
59. Kafkas, A. & Montaldi, D. Expectation affects learning and modulates memory experience at retrieval. *Cognition* **180**, 123–134 (2018).
60. Henson, R. N. & Gagnepain, P. Predictive, interactive multiple memory systems. *Hippocampus* **20**, 1315–1326 (2010).

61. Quent, J. A., Henson, R. N. & Greve, A. A predictive account of how novelty influences declarative memory. *Neurobiol Learn Mem* **179**, 107382 (2021).
62. Kim, G., Lewis-Peacock, J. A., Norman, K. A. & Turk-Browne, N. B. Pruning of memories by context-based prediction error. *Proc. Natl. Acad. Sci.* **111**, 8997–9002 (2014).
63. Kim, H., Schlichting, M. L., Preston, A. R. & Lewis-Peacock, J. A. Predictability Changes What We Remember in Familiar Temporal Contexts. *J. Cogn. Neurosci.* **32**, 124–140 (2020).
64. Antony, J. W. & Schapiro, A. C. Active and effective replay: systems consolidation reconsidered again. *Nat. Rev. Neurosci.* **20**, 506–507 (2019).
65. Frankland, P. W. & Bontempi, B. The organization of recent and remote memories. *Nat Rev Neurosci* **6**, 119–130 (2005).
66. Gilboa, A. & Moscovitch, M. No consolidation without representation: Correspondence between neural and psychological representations in recent and remote memory. *Neuron* **109**, 2239–2255 (2021).
67. Moscovitch, M., Cabeza, R., Winocur, G. & Nadel, L. Episodic Memory and Beyond: The Hippocampus and Neocortex in Transformation. *Annu Rev Psychol* **67**, 105–134 (2016).
68. Squire, L. R. & Alvarez, P. Retrograde amnesia and memory consolidation: a neurobiological perspective. *Curr Opin Neurobiol* **5**, 169–177 (1995).
69. Anderson, J. R. & Reder, L. M. The fan effect: New results and new theories. *J. Exp. Psychol. Gen.* **128**, 186–197 (1999).
70. Bein, O., Trzewik, M. & Maril, A. The role of prior knowledge in incremental associative learning: An empirical and computational approach. *J Mem Lang* **107**, 1–24 (2019).

71. Bein, O., Gasser, C., Amer, T., Maril, A. & Davachi, L. Predictions transform memories: How expected versus unexpected events are integrated or separated in memory. *Neurosci. Biobehav. Rev.* **153**, 105368 (2023).
72. Bellana, B., Mansour, R., Ladyka-Wojcik, N., Grady, C. L. & Moscovitch, M. The influence of prior knowledge on the formation of detailed and durable memories. *J Mem Lang* **121**, 104264 (2021).
73. Gasser, C. & Davachi, L. *Cross-Modal Facilitation of Memory through Actions*. <https://www.researchsquare.com/article/rs-1466467/v1> (2022) doi:10.21203/rs.3.rs-1466467/v1.
74. Hemmer, P. & Steyvers, M. Integrating episodic memories and prior knowledge at multiple levels of abstraction. *Psychon. Bull. Rev.* **16**, 80–87 (2009).
75. Lee, W.-T., Hazeltine, E. & Jiang, J. Interference and integration in hierarchical task learning. *J. Exp. Psychol. Gen.* **151**, 3028–3044 (2022).
76. Reder, L. M., Paynter, C., Diana, R. A., Ngiam, J. & Dickison, D. Experience is a Double-Edged Sword: A Computational Model of The Encoding/Retrieval Trade-Off With Familiarity. in *Psychology of Learning and Motivation* vol. 48 271–312 (Elsevier, 2007).
77. Tompary, A. & Thompson-Schill, S. L. Semantic influences on episodic memory distortions. *J Exp Psychol Gen* (2021) doi:10.1037/xge0001017.
78. Brunec, I. K. & Momennejad, I. Predictive Representations in Hippocampal and Prefrontal Hierarchies. *J. Neurosci.* **42**, 299–312 (2022).
79. Gravina, M. T. & Sederberg, P. B. The neural architecture of prediction over a continuum of spatiotemporal scales. *Curr. Opin. Behav. Sci.* **17**, 194–202 (2017).

80. Lee, C. S., Aly, M. & Baldassano, C. Anticipation of temporally structured events in the brain. *Elife* **10**, (2021).
81. Antony, J. W. *et al.* Behavioral, Physiological, and Neural Signatures of Surprise during Naturalistic Sports Viewing. *Neuron* 1–14 (2020) doi:10.1016/j.neuron.2020.10.029.
82. Antony, J. W., Van Dam, J., Massey, J. R., Barnett, A. J. & Bennion, K. A. Long-term, multi-event surprise correlates with enhanced autobiographical memory. *Nat. Hum. Behav.* (2023) doi:10.1038/s41562-023-01631-8.
83. Sinclair, A. H. & Barense, M. D. Surprise and destabilize: prediction error influences episodic memory reconsolidation. *Learn. Mem.* **25**, 369–381 (2018).
84. Sinclair, A. H., Manalili, G. M., Brunec, I. K., Adcock, R. A. & Barense, M. D. Prediction errors disrupt hippocampal representations and update episodic memories. *Proc. Natl. Acad. Sci.* **118**, e2117625118 (2021).
85. Badre, D. Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends Cogn Sci* **12**, 193–200 (2008).
86. Barto, A. G. & Mahadevan, S. Recent Advances in Hierarchical Reinforcement Learning. *Discrete Event Dyn Syst Theory Appl* **13**, 41–77 (2003).
87. Botvinick, M. M. Hierarchical models of behavior and prefrontal function. *Trends Cogn Sci* **12**, 201–208 (2008).
88. Botvinick, M. M. Hierarchical reinforcement learning and decision making. *Curr Opin Neurobiol* **22**, 956–962 (2012).
89. Botvinick, M. M., Niv, Y. & Barto, A. G. Hierarchically organized behavior and its neural foundations: a reinforcement learning perspective. *Cognition* **113**, 262–280 (2009).

90. Collins, A. G. E. Chapter 5 - Learning Structures Through Reinforcement. in *Goal-Directed Decision Making* (eds. Morris, R., Bornstein, A. & Shenhav, A.) 105–123 (Academic Press, 2018). doi:10.1016/B978-0-12-812098-9.00005-X.
91. Correa, C. G., Ho, M. K., Callaway, F., Daw, N. D. & Griffiths, T. L. Humans decompose tasks by trading off utility and computational cost. Preprint at <http://arxiv.org/abs/2211.03890> (2022).
92. Tomov, M. S., Yagati, S., Kumar, A., Yang, W. & Gershman, S. J. Discovery of hierarchical representations for efficient planning. *PLoS Comput Biol* **16**, e1007594 (2020).
93. Sutton, R. S., Precup, D. & Singh, S. Between MDPs and semi-MDPs: A framework for temporal abstraction in reinforcement learning. *Artif. Intell.* **112**, 181–211 (1999).
94. Holroyd, C. B. & Yeung, N. Motivation of extended behaviors by anterior cingulate cortex. *Trends Cogn. Sci.* **16**, 122–128 (2012).
95. Solway, A. *et al.* Optimal behavioral hierarchy. *PLoS Comput Biol* **10**, e1003779 (2014).
96. Collins, A. G. E. & Frank, M. J. Cognitive control over learning: creating, clustering, and generalizing task-set structure. *Psychol Rev* **120**, 190–229 (2013).
97. Liu, R. G. & Frank, M. J. Hierarchical clustering optimizes the tradeoff between compositionality and expressivity of task structures for flexible reinforcement learning. *Artif. Intell.* **312**, 103770 (2022).
98. Diuk, C., Tsai, K., Wallis, J., Botvinick, M. & Niv, Y. Hierarchical learning induces two simultaneous, but separable, prediction errors in human basal ganglia. *J Neurosci* **33**, 5797–5805 (2013).

99. Ribas-Fernandes, J. J. F. *et al.* A neural signature of hierarchical reinforcement learning. *Neuron* **71**, 370–379 (2011).
100. Frost, R., Armstrong, B. C., Siegelman, N. & Christiansen, M. H. Domain generality versus modality specificity: the paradox of statistical learning. *Trends Cogn. Sci.* **19**, 117–125 (2015).
101. Saffran, J. R., Aslin, R. N. & Newport, E. L. Statistical learning by 8-month-old infants. *Science* **274**, 1926–1928 (1996).
102. Saffran, J. R. & Wilson, D. P. From syllables to syntax: Multilevel statistical learning by 12-month-old infants. *Infancy* **4**, 273–284 (2003).
103. Schapiro, A. C. & Turk-Browne, N. Statistical Learning. *Brain Mapp. Encycl. Ref.* **3**, 501–506 (2015).
104. Turk-Browne, N. B., Jungé, J. & Scholl, B. J. The automaticity of visual statistical learning. *J. Exp. Psychol. Gen.* **134**, 552–64 (2005).
105. Balaguer, J., Spiers, H., Hassabis, D. & Summerfield, C. Neural Mechanisms of Hierarchical Planning in a Virtual Subway Network. *Neuron* **90**, 893–903 (2016).
106. Bunzeck, N., Dayan, P., Dolan, R. J. & Düzel, E. A common mechanism for adaptive scaling of reward and novelty. *Hum Brain Mapp* **31**, 1380–1394 (2010).
107. Bunzeck, N. & Düzel, E. Absolute coding of stimulus novelty in the human substantia nigra/VTa. *Neuron* **51**, 369–379 (2006).
108. Cowan, E. T., Schapiro, A. C., Dunsmoor, J. E. & Murty, V. P. Memory consolidation as an adaptive process. *Psychon Bull Rev* (2021) doi:10.3758/s13423-021-01978-x.

109. Düzel, E., Bunzeck, N., Guitart-Masip, M. & Düzel, S. NOvelty-related motivation of anticipation and exploration by dopamine (NOMAD): implications for healthy aging. *Neurosci Biobehav Rev* **34**, 660–669 (2010).
110. Kamiński, J. *et al.* Novelty-Sensitive Dopaminergic Neurons in the Human Substantia Nigra Predict Success of Declarative Memory Formation. *Curr Biol* **28**, 1333-1343.e4 (2018).
111. Murty, V. P. & Adcock, R. A. Enriched encoding: reward motivation organizes cortical networks for hippocampal detection of unexpected events. *Cereb Cortex* **24**, 2160–2168 (2014).
112. Wittmann, B. C., Bunzeck, N., Dolan, R. J. & Düzel, E. Anticipation of novelty recruits reward system and hippocampus while promoting recollection. *Neuroimage* **38**, 194–202 (2007).
113. Clewett, D., DuBrow, S. & Davachi, L. Transcending time in the brain: How event memories are constructed from experience. *Hippocampus* **29**, 162–183 (2019).
114. Shin, Y. S. & DuBrow, S. Structuring Memory Through Inference-Based Event Segmentation. *Top Cogn Sci* **13**, 106–127 (2021).
115. Clewett, D., Gasser, C. & Davachi, L. Pupil-linked arousal signals track the temporal organization of events in memory. *Nat. Commun.* **11**, 1–14 (2020).
116. DuBrow, S. & Davachi, L. The influence of context boundaries on memory for the sequential order of events. *J. Exp. Psychol. Gen.* **142**, 1277–1286 (2013).
117. Ezzyat, Y. & Davachi, L. Similarity breeds proximity: Pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron* **81**, 1179–1189 (2014).

118. Rouhani, N., Norman, K. A., Niv, Y. & Bornstein, A. M. Reward prediction errors create event boundaries in memory. *Cognition* **203**, 104269 (2020).
119. DuBrow, S., Rouhani, N., Niv, Y. & Norman, K. A. Does mental context drift or shift? *Curr Opin Behav Sci* **17**, 141–146 (2017).
120. Tompary, A., Zhou, W. & Davachi, L. Schematic memories develop quickly, but are not expressed unless necessary. *Sci Rep* **10**, 16968 (2020).
121. Collins, A. G. E. & Frank, M. J. Neural signature of hierarchically structured expectations predicts clustering and transfer of rule sets in reinforcement learning. *Cognition* **152**, 160–169 (2016).
122. Eckstein, M. K. & Collins, A. G. E. Computational evidence for hierarchically structured reinforcement learning in humans. *Proc Natl Acad Sci U A* **117**, 29381–29389 (2020).
123. Davachi, L. & DuBrow, S. How the hippocampus preserves order: the role of prediction and context. *Trends Cogn Sci* **19**, 92–99 (2015).
124. Éltető, N., Nemeth, D., Janacsek, K. & Dayan, P. Tracking human skill learning with a hierarchical Bayesian sequence model. *PLOS Comput. Biol.* **18**, e1009866 (2022).
125. Gershman, S. J. & Niv, Y. Learning latent structure: carving nature at its joints. *Curr Opin Neurobiol* **20**, 251–256 (2010).
126. Gershman, S. J. A Unifying Probabilistic View of Associative Learning. *PLoS Comput Biol* **11**, e1004567 (2015).
127. Gershman, S. J., Monfils, M.-H., Norman, K. A. & Niv, Y. The computational nature of memory modification. *Elife* **6**, (2017).

128. McClelland, J. L., McNaughton, B. L. & O'Reilly, R. C. Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* **102**, 419–457 (1995).
129. Shteingart, H., Neiman, T. & Loewenstein, Y. The role of first impression in operant learning. *J. Exp. Psychol. Gen.* **142**, 476–488 (2013).
130. Schapiro, A. C., Rogers, T. T., Cordova, N. I., Turk-Browne, N. B. & Botvinick, M. M. Neural representations of events arise from temporal community structure. *Nat Neurosci* **16**, 486–492 (2013).
131. Schapiro, A. C., Turk-Browne, N. B., Norman, K. A. & Botvinick, M. M. Statistical learning of temporal community structure in the hippocampus. *Hippocampus* **26**, 3–8 (2016).
132. Sherman, B. E. *et al.* Intracranial Entrainment Reveals Statistical Learning across Levels of Abstraction. *J. Cogn. Neurosci.* **35**, 1312–1328 (2023).
133. Eichenbaum, H. Hippocampus: cognitive processes and neural representations that underlie declarative memory. *Neuron* **44**, 109–120 (2004).
134. Norman, K. A. & O'Reilly, R. C. Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychol. Rev.* **110**, 611–646 (2003).
135. Barnett, A. J. *et al.* Hippocampal-cortical interactions during event boundaries support retention of complex narrative events. *Neuron* S0896627323007663 (2023)
doi:10.1016/j.neuron.2023.10.010.

136. Ben-Yakov, A. & Dudai, Y. Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *J Neurosci* **31**, 9032–9042 (2011).
137. Ben-Yakov, A. & Henson, R. N. The Hippocampal Film Editor: Sensitivity and Specificity to Event Boundaries in Continuous Experience. *J Neurosci* **38**, 10057–10068 (2018).
138. Baraduc, P., Duhamel, J.-R. & Wirth, S. Schema cells in the macaque hippocampus. *Science* **363**, 635–639 (2019).
139. Crivelli-Decker, J. Goal-oriented representations in the human hippocampus during planning and navigation. *Nat. Commun.* (2023).
140. Farzanfar, D., Spiers, H. J., Moscovitch, M. & Rosenbaum, R. S. From cognitive maps to spatial schemas. *Nat. Rev. Neurosci.* (2022) doi:10.1038/s41583-022-00655-9.
141. Garvert, M. M., Dolan, R. J. & Behrens, T. E. J. A map of abstract relational knowledge in the human hippocampal–entorhinal cortex. *Elife* **6**, e17086 (2017).
142. Garvert, M. M., Saanum, T., Schulz, E., Schuck, N. W. & Doeller, C. F. Hippocampal spatio-predictive cognitive maps adaptively guide reward generalization. *Nat. Neurosci.* **26**, 615–626 (2023).
143. Kumaran, D., Summerfield, J. J., Hassabis, D. & Maguire, E. A. Tracking the Emergence of Conceptual Knowledge during Human Decision Making. *Neuron* **63**, 889–901 (2009).
144. McKenzie, S. *et al.* Hippocampal representation of related and opposing memories develop within distinct, hierarchically organized neural schemas. *Neuron* **83**, 202–215 (2014).

145. Schapiro, A. C., Gregory, E., Landau, B., McCloskey, M. & Turk-Browne, N. B. The necessity of the medial temporal lobe for statistical learning. *J Cogn Neurosci* **26**, 1736–1747 (2014).
146. Shohamy, D. & Turk-Browne, N. B. Mechanisms for widespread hippocampal involvement in cognition. *J Exp Psychol Gen* **142**, 1159–1170 (2013).
147. Theves, S., Fernandez, G. & Doeller, C. F. The Hippocampus Encodes Distances in Multidimensional Feature Space. *Curr. Biol.* **29**, 1226-1231.e3 (2019).
148. Theves, S., Neville, D., Fernández, G. & Doeller, C. F. Learning and Representation of Hierarchical Concepts in Hippocampus and Prefrontal Cortex. *J Neurosci* **41**, 7675–7686 (2021).
149. Schapiro, A. C., Turk-Browne, N. B., Botvinick, M. M. & Norman, K. A. Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning. *Philos Trans R Soc Lond B Biol Sci* **372**, 20160049 (2017).
150. Schuck, N. W., Wilson, R. & Niv, Y. *A State Representation for Reinforcement Learning and Decision-Making in the Orbitofrontal Cortex. Goal-Directed Decision Making: Computations and Neural Circuits* (Elsevier Inc., 2018). doi:10.1016/B978-0-12-812098-9.00012-7.
151. Langdon, A. J., Song, M. & Niv, Y. Uncovering the ‘state’: Tracing the hidden state representations that structure learning and decision-making. *Behav. Processes* **167**, 103891 (2019).
152. Daniel, R., Radulescu, A. & Niv, Y. Intact Reinforcement Learning But Impaired Attentional Control During Multidimensional Probabilistic Learning in Older Adults. *J. Neurosci.* **40**, 1084–1096 (2020).

153. De Martino, B. & Cortese, A. Goals, usefulness and abstraction in value-based choice. *Trends Cogn. Sci.* **27**, 65–80 (2023).
154. Farashahi, S., Rowe, K., Aslami, Z., Lee, D. & Soltani, A. Feature-based learning improves adaptability without compromising precision. *Nat Commun* **8**, 1768 (2017).
155. Leong, Y. C., Radulescu, A., Daniel, R., DeWoskin, V. & Niv, Y. Dynamic Interaction between Reinforcement Learning and Attention in Multidimensional Environments. *Neuron* **93**, 451–463 (2017).
156. Niv, Y. *et al.* Reinforcement learning in multidimensional environments relies on attention mechanisms. *J. Neurosci.* **35**, 8145–8157 (2015).
157. Radulescu, A., Daniel, R. & Niv, Y. The effects of aging on the interaction between reinforcement learning and attention. *Psychol. Aging* **31**, 747–757 (2016).
158. Radulescu, A., Niv, Y. & Ballard, I. Holistic Reinforcement Learning : The Role of Structure and Attention. *Trends Cogn. Sci.* **23**, 278–292 (2019).
159. Conway, C. M. How does the brain learn environmental structure? Ten core principles for understanding the neurocognitive mechanisms of statistical learning. *Neurosci Biobehav Rev* **112**, 279–299 (2020).
160. Forest, T. A., Siegelman, N. & Finn, A. S. Attention Shifts to More Complex Structures With Experience. *Psychol. Sci.* **33**, 2059–2072 (2022).
161. Zhao, J., Al-Aidroos, N. & Turk-Browne, N. B. Attention is spontaneously biased toward regularities. *Psychol. Sci.* **24**, 667–677 (2013).
162. Bein, O. *et al.* Delineating the effect of semantic congruency on episodic memory: The role of integration and relatedness. *PLoS ONE* **10**, e0115624 (2015).

163. Gronau, N. To Grasp the World at a Glance: The Role of Attention in Visual and Semantic Associative Processing. *J Imaging Sci Technol* **7**, (2021).
164. Gronau, N., Neta, M. & Bar, M. Integrated Contextual Representation for Objects' Identities and Their Locations. *J. Cogn. Neurosci.* **20**, 371–388 (2008).
165. Gronau, N. & Shachar, M. Contextual consistency facilitates long-term memory of perceptual detail in barely seen images. *J. Exp. Psychol. Hum. Percept. Perform.* **41**, 1095–1111 (2015).
166. Sherman, B. E. & Turk-Browne, N. B. Statistical prediction of the future impairs episodic encoding of the present. *Proc. Natl. Acad. Sci.* (2020) doi:10.1101/851147.
167. Melega, G. & Sheldon, S. Conceptual relatedness promotes memory generalization at the cost of detailed recollection. *Sci. Rep.* **13**, 15575 (2023).
168. Tolman, E. C. Cognitive maps in rats and men. *Psychol. Rev.* **55**, 189–208 (1948).
169. Behrens, T. E. J. *et al.* What Is a Cognitive Map? Organizing Knowledge for Flexible Behavior. *Neuron* **100**, 490–509 (2018).
170. Bellmund, J. L. S., Gärdenfors, P., Moser, E. I. & Doeller, C. F. Navigating cognition: Spatial codes for human thinking. *Science* **362**, (2018).
171. Schiller, D. *et al.* Memory and space: Towards an understanding of the cognitive map. *J. Neurosci.* **35**, 13904–13911 (2015).
172. Constantinescu, A. O., O'Reilly, J. X. & Behrens, T. E. J. Organizing conceptual knowledge in humans with a gridlike code. *Science* **352**, 1464–1467 (2016).
173. Park, S. A., Miller, D. S., Nili, H., Ranganath, C. & Boorman, E. D. Map Making: Constructing, Combining, and Inferring on Abstract Cognitive Maps. *Neuron* **107**, 1226–1238. (2020).

174. Tavares, R. M. *et al.* A Map for Social Navigation in the Human Brain. *Neuron* **87**, 231–243 (2015).
175. Theves, S., Fernández, G. & Doeller, C. F. The hippocampus maps concept space, not feature space. *J. Neurosci.* **40**, 7318–7325 (2020).
176. Viganò, S. & Piazza, M. Distance and Direction Codes Underlie Navigation of a Novel Semantic Space in the Human Brain. *J Neurosci* **40**, 2727–2736 (2020).
177. Brunec, I. K., Moscovitch, M. & Barense, M. D. Boundaries Shape Cognitive Representations of Spaces and Events. *Trends Cogn Sci* **22**, 637–650 (2018).
178. Ekstrom, A. D., Harootonian, S. K. & Huffman, D. J. Grid coding, spatial representation, and navigation: Should we assume an isomorphism? *Hippocampus* **30**, 422–432 (2020).
179. Warren, W. H. Non-Euclidean navigation. *J. Exp. Biol.* **222**, (2019).
180. Peer, M., Brunec, I. K., Newcombe, N. S. & Epstein, R. A. Structuring Knowledge with Cognitive Maps and Cognitive Graphs. *Trends Cogn Sci* **25**, 37–54 (2021).
181. Knudsen, E. B. & Wallis, J. D. Taking stock of value in the orbitofrontal cortex. *Nat. Rev. Neurosci.* **23**, 428–438 (2022).
182. Stalnaker, T. A., Cooch, N. K. & Schoenbaum, G. What the orbitofrontal cortex does not do. *Nat Neurosci* **18**, 620–627 (2015).
183. Boorman, E. D., Witkowski, P. P., Zhang, Y. & Park, S. A. The orbital frontal cortex, task structure, and inference. *Behav Neurosci* **135**, 291–300 (2021).
184. Möhring, L. & Gläscher, J. Prediction errors drive dynamic changes in neural patterns that guide behavior. *Cell Rep.* **42**, 112931 (2023).

185. Vaidya, A. R. & Badre, D. Abstract task representations for inference and control. *Trends Cogn. Sci.* **26**, 484–498 (2022).
186. Zhou, J., Gardner, M. P. H. & Schoenbaum, G. Is the core function of orbitofrontal cortex to signal values or make predictions? *Curr Opin Behav Sci* **41**, 1–9 (2021).
187. Baram, A. B., Muller, T. H., Nili, H., Garvert, M. M. & Behrens, T. E. J. Entorhinal and ventromedial prefrontal cortices abstract and generalize the structure of reinforcement learning problems. *Neuron* **109**, 713-723.e7 (2021).
188. Klein-Flügge, M. C., Wittmann, M. K., Shpektor, A., Jensen, D. E. A. & Rushworth, M. F. S. Multiple associative structures created by reinforcement and incidental statistical learning mechanisms. *Nat. Commun.* **10**, 4835 (2019).
189. Barron, H. C., Dolan, R. J. & Behrens, T. E. J. Online evaluation of novel choices by simultaneous representation of multiple memories. *Nat Neurosci* **16**, 1492–1498 (2013).
190. Bongioanni, A. *et al.* Activation and disruption of a neural mechanism for novel choice in monkeys. *Nature* **591**, 270–274 (2021).
191. Ghosh, V. E., Moscovitch, M., Melo Colella, B. & Gilboa, A. Schema representation in patients with ventromedial PFC lesions. *J Neurosci* **34**, 12057–12070 (2014).
192. Gilboa, A. Strategic retrieval, confabulations, and delusions: theory and data. *Cogn Neuropsychiatry* **15**, 145–180 (2010).
193. Spalding, K. N., Jones, S. H., Duff, M. C., Tranel, D. & Warren, D. E. Investigating the Neural Correlates of Schemas: Ventromedial Prefrontal Cortex Is Necessary for Normal Schematic Influence on Memory. *J Neurosci* **35**, 15746–15751 (2015).

194. Zheng, L., Gao, Z., McAvan, A. S., Isham, E. A. & Ekstrom, A. D. Partially overlapping spatial environments trigger reinstatement in hippocampus and schema representations in prefrontal cortex. *Nat Commun* **12**, 6231 (2021).
195. Reagh, Z. M. & Ranganath, C. Flexible reuse of cortico-hippocampal representations during encoding and recall of naturalistic events. *Nat. Commun.* **14**, 1279 (2023).
196. Masís-Obando, R., Norman, K. A. & Baldassano, C. Schema representations in distinct brain networks support narrative memory during encoding and retrieval. *eLife* **11**, e70445 (2022).
197. Mack, M. L., Preston, A. R. & Love, B. C. Ventromedial prefrontal cortex compression during concept learning. *Nat Commun* **11**, 46 (2020).
198. Audrain, S. & McAndrews, M. P. Schemas provide a scaffold for neocortical integration of new memories over time. *Nat. Commun.* **13**, 5795 (2022).
199. Tompary, A. & Davachi, L. Consolidation Promotes the Emergence of Representational Overlap in the Hippocampus and Medial Prefrontal Cortex. *Neuron* **96**, 228–241 (2017).
200. Günseli, E. & Aly, M. Preparation for upcoming attentional states in the hippocampus and medial prefrontal cortex. *Elife* **9**, (2020).
201. Rushworth, M. F. S., Noonan, M. P., Boorman, E. D., Walton, M. E. & Behrens, T. E. Frontal cortex and reward-guided learning and decision-making. *Neuron* **70**, 1054–1069 (2011).
202. Moneta, N., Garvert, M. M., Heekeren, H. R. & Schuck, N. W. Task state representations in vmPFC mediate relevant and irrelevant value signals and their behavioral influence. *Nat. Commun.* **14**, 3156 (2023).

203. Lebreton, M., Jorge, S., Michel, V., Thirion, B. & Pessiglione, M. An Automatic Valuation System in the Human Brain: Evidence from Functional Neuroimaging. *Neuron* **64**, 431–439 (2009).
204. Cowan, E. *et al.* Sleep Spindles Promote the Restructuring of Memory Representations in Ventromedial Prefrontal Cortex through Enhanced Hippocampal-Cortical Functional Connectivity. *J Neurosci* **40**, 1909–1919 (2020).
205. Schlichting, M. L., Mumford, J. A. & Preston, A. R. Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. *Nat. Commun.* **6**, 1–10 (2015).
206. Bein, O., Reggev, N. & Maril, A. Prior knowledge influences on hippocampus and medial prefrontal cortex interactions in subsequent memory. *Neuropsychologia* **64**, 320–330 (2014).
207. van Kesteren, M. T. R. *et al.* Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: from congruent to incongruent. *Neuropsychologia* **51**, 2352–2359 (2013).
208. Reggev, N., Bein, O. & Maril, A. Distinct Neural Suppression and Encoding Effects for Conceptual Novelty and Familiarity. *J Cogn Neurosci* **28**, 1455–1470 (2016).
209. Yacoby, A., Reggev, N. & Maril, A. Examining the transition of novel information toward familiarity. *Neuropsychologia* **161**, 107993 (2021).
210. Yacoby, A., Reggev, N. & Maril, A. Lack of source memory as a potential marker of early assimilation of novel items into current knowledge. *Neuropsychologia* **185**, 108569 (2023).

211. Chiba, A. A., Kesner, R. P. & Gibson, C. J. Memory for temporal order of new and familiar spatial location sequences: role of the medial prefrontal cortex. *Learn. Mem.* **4**, 311–317 (1997).
212. Barbas, H. & Blatt, G. J. Topographically specific hippocampal projections target functionally distinct prefrontal areas in the rhesus monkey. *Hippocampus* **5**, 511–533 (1995).
213. Cavada, C., Compañy, T., Tejedor, J., Cruz-Rizzolo, R. J. & Reinoso-Suárez, F. The Anatomical Connections of the Macaque Monkey Orbitofrontal Cortex. A Review. *Cereb. Cortex* **10**, 220–242 (2000).
214. Öngür, D. & Price, J. L. The Organization of Networks within the Orbital and Medial Prefrontal Cortex of Rats, Monkeys and Humans. *Cereb Cortex* **10**, 206–219 (2000).
215. Price, J. L. Definition of the orbital cortex in relation to specific connections with limbic and visceral structures and other cortical regions. *Ann N Acad Sci* **1121**, 54–71 (2007).
216. Eichenbaum, H. Time cells in the hippocampus: a new dimension for mapping memories. *Nat. Rev. Neurosci.* **15**, 732–744 (2014).
217. Ranganath, C. & Hsieh, L.-T. The hippocampus: a special place for time. *Ann N Acad Sci* **1369**, 93–110 (2016).
218. Kesner, R. P. & Hunsaker, M. R. The temporal attributes of episodic memory. *Behav. Brain Res.* **11** (2010).
219. Buzsáki, G. & Tingley, D. Space and Time: The Hippocampus as a Sequence Generator. *Trends Cogn Sci* **22**, 853–869 (2018).

220. DuBrow, S. & Davachi, L. Temporal binding within and across events. *Neurobiol Learn Mem* **134 Pt A**, 107–114 (2016).
221. Place, R., Farovik, A., Brockmann, M. & Eichenbaum, H. Bidirectional prefrontal-hippocampal interactions support context-guided memory. *Nat Neurosci* **19**, 992–994 (2016).
222. McCormick, C., Barry, D. N., Jafarian, A., Barnes, G. R. & Maguire, E. A. vmPFC Drives Hippocampal Processing during Autobiographical Memory Recall Regardless of Remoteness. *Cereb. Cortex* **30**, 5972–5987 (2020).
223. Bar, M. *et al.* Top-down facilitation of visual recognition. *Proc. Natl. Acad. Sci.* **103**, 449–454 (2006).
224. Bar, M. The proactive brain: memory for predictions. *Philos Trans R Soc Lond B Biol Sci* **364**, 1235–1243 (2009).
225. Ezzyat, Y. & Davachi, L. Neural Evidence for Representational Persistence Within Events. *J. Neurosci.* **41**, 7909–7920 (2021).
226. Guise, K. G. & Shapiro, M. L. Medial Prefrontal Cortex Reduces Memory Interference by Modifying Hippocampal Encoding. *Neuron* **94**, 183–192.e8 (2017).
227. Hebscher, M., Barkan-Abramski, M., Goldsmith, M., Aharon-Peretz, J. & Gilboa, A. Memory, Decision-Making, and the Ventromedial Prefrontal Cortex (vmPFC): The Roles of Subcallosal and Posterior Orbitofrontal Cortices in Monitoring and Control Processes. *Cereb. Cortex* **26**, 4590–4601 (2016).
228. Hebscher, M. & Gilboa, A. A boost of confidence: The role of the ventromedial prefrontal cortex in memory, decision-making, and schemas. *Neuropsychologia* **90**, 46–58 (2016).

229. Gilboa, A., Alain, C., He, Y., Stuss, D. T. & Moscovitch, M. Ventromedial prefrontal cortex lesions produce early functional alterations during remote memory retrieval. *J Neurosci* **29**, 4871–4881 (2009).
230. Alonso, A., van der Meij, J., Tse, D. & Genzel, L. Naïve to expert: Considering the role of previous knowledge in memory. *Brain Neurosci. Adv.* **4**, 239821282094868 (2020).
231. Sommer, T. The Emergence of Knowledge and How it Supports the Memory for Novel Related Information. *Cereb Cortex* **27**, 1906–1921 (2017).
232. Sommer, T., Hennies, N., Lewis, P. A. & Alink, A. The assimilation of novel information into schemata and its efficient consolidation. *J. Neurosci.* **42**, 5916–5929 (2022).
233. van Kesteren, M. T. R., Fernández, G., Norris, D. G. & Hermans, E. J. Persistent schema-dependent hippocampal-neocortical connectivity during memory encoding and postencoding rest in humans. *Proc Natl Acad Sci U A* **107**, 7550–7555 (2010).
234. van Kesteren, M. T. R., Rijpkema, M., Ruiter, D. J. & Fernández, G. Retrieval of associative information congruent with prior knowledge is related to increased medial prefrontal activity and connectivity. *J Neurosci* **30**, 15888–15894 (2010).
235. Mackey, S. & Petrides, M. Quantitative demonstration of comparable architectonic areas within the ventromedial and lateral orbital frontal cortex in the human and the macaque monkey brains. *Eur J Neurosci* **32**, 1940–1950 (2010).
236. Mackey, S. & Petrides, M. Architecture and morphology of the human ventromedial prefrontal cortex. *Eur J Neurosci* **40**, 2777–2796 (2014).

237. Uylings, H. B. M. *et al.* 3-D Cytoarchitectonic parcellation of human orbitofrontal cortex: Correlation with postmortem MRI Author links open overlay panel. *Psychiatry Res. Neuroimaging* **183**, 1–20 (2010).
238. Jackson, R. L., Bajada, C. J., Lambon Ralph, M. A. & Cloutman, L. L. The Graded Change in Connectivity across the Ventromedial Prefrontal Cortex Reveals Distinct Subregions. *Cereb Cortex* **30**, 165–180 (2020).
239. Boorman, E. D., Behrens, T. E. J., Woolrich, M. W. & Rushworth, M. F. S. How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action. *Neuron* **62**, 733–743 (2009).
240. Boorman, E. D., Behrens, T. E. & Rushworth, M. F. Counterfactual Choice and Learning in a Neural Network Centered on Human Lateral Frontopolar Cortex. *PLoS Biol.* **9**, e1001093 (2011).
241. Haynes, J.-D. *et al.* Reading Hidden Intentions in the Human Brain. *Curr Biol* **17**, 323–328 (2007).
242. Momennejad, I. & Haynes, J.-D. Human anterior prefrontal cortex encodes the ‘what’ and ‘when’ of future intentions. *Neuroimage* **61**, 139–148 (2012).
243. Momennejad, I. & Haynes, J.-D. Encoding of prospective tasks in the human prefrontal cortex under varying task loads. *J Neurosci* **33**, 17342–17349 (2013).
244. Liberman, N., Sagristano, M. D. & Trope, Y. The effect of temporal distance on level of mental construal. *J. Exp. Soc. Psychol.* **12** (2002).
245. Trope, Y. & Liberman, N. Temporal construal. *Psychol. Rev.* **110**, 403–421 (2003).

246. Trope, Y. & Liberman, N. Construal-Level Theory of Psychological Distance. *Psychol. Rev.* **117**, 440–463 (2010).
247. Takashima, A. *et al.* Declarative memory consolidation in humans: a prospective functional magnetic resonance imaging study. *Proc Natl Acad Sci U A* **103**, 756–761 (2006).
248. Baker, S. *et al.* The Human Dentate Gyrus Plays a Necessary Role in Discriminating New Memories. *Curr Biol* **26**, 2629–2634 (2016).
249. Bakker, A., Kirwan, C. B., Miller, M. & Stark, C. E. L. Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science* **319**, 1640–1642 (2008).
250. Berron, D. *et al.* Strong Evidence for Pattern Separation in Human Dentate Gyrus. *J Neurosci* **36**, 7569–7579 (2016).
251. Leutgeb, J. K., Leutgeb, S., Moser, M.-B. & Moser, E. I. Pattern separation in the dentate gyrus and CA3 of the hippocampus. *Science* **315**, 961–966 (2007).
252. Yassa, M. A. & Stark, C. E. L. Pattern separation in the hippocampus. *Trends Neurosci* **34**, 515–525 (2011).
253. Ballard, I. C., Wagner, A. D. & McClure, S. M. Hippocampal pattern separation supports reinforcement learning. *Nat Commun* **10**, 1073 (2019).
254. Jiang, J., Wang, S.-F., Guo, W., Fernandez, C. & Wagner, A. D. Prefrontal reinstatement of contextual task demand is predicted by separable hippocampal patterns. *Nat Commun* **11**, 2053 (2020).
255. Zhou, J. *et al.* Complementary Task Structure Representations in Hippocampus and Orbitofrontal Cortex during an Odor Sequence Task. *Curr Biol* **29**, 3402–3409.e3 (2019).

256. Howard, J. D., Gottfried, J. A., Tobler, P. N. & Kahnt, T. Identity-specific coding of future rewards in the human orbitofrontal cortex. *Proc Natl Acad Sci U A* **112**, 5195–5200 (2015).
257. McNamee, D., Rangel, A. & O'Doherty, J. P. Category-dependent and category-independent goal-value codes in human ventromedial prefrontal cortex. *Nat Neurosci* **16**, 479–485 (2013).
258. Sweegers, C. C. G., Takashima, A., Fernández, G. & Talamini, L. M. Neural mechanisms supporting the extraction of general knowledge across episodic memories. *Neuroimage* **87**, 138–146 (2014).
259. Kahnt, T., Chang, L. J., Park, S. Q., Heinzle, J. & Haynes, J.-D. Connectivity-based parcellation of the human orbitofrontal cortex. *J Neurosci* **32**, 6240–6250 (2012).
260. Baldassano, C. *et al.* Discovering Event Structure in Continuous Narrative Perception and Memory. *Neuron* **95**, 709-721.e5 (2017).
261. Chen, J. *et al.* Shared memories reveal shared structure in neural activity across individuals. *Nat Neurosci* **20**, 115–125 (2017).
262. Hasson, U., Chen, J. & Honey, C. J. Hierarchical process memory: memory as an integral component of information processing. *Trends Cogn Sci* **19**, 304–313 (2015).
263. Barron, H. C., Garvert, M. M. & Behrens, T. E. J. Reassessing VMPFC: full of confidence? *Nat Neurosci* **18**, 1064–1066 (2015).
264. Howard, J. D. & Kahnt, T. To be specific: The role of orbitofrontal cortex in signaling reward identity. *Behav Neurosci* **135**, 210–217 (2021).
265. Biderman, N., Bakkour, A. & Shohamy, D. What Are Memories For? The Hippocampus Bridges Past Experience with Future Decisions. *Trends Cogn. Sci.* **24**, 542–556 (2020).

266. Hartley, C. A., Nussenbaum, K. & Cohen, A. O. Interactive Development of Adaptive Learning and Memory. *Annu Rev Dev Psychol* **3**, 59–85 (2021).