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Interactive Development of Adaptive Learning and Memory

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Abstract

Across development, interactions between value-based learning and memory processes promote the formation of mental models that enable flexible goal pursuit. Value cues in the environment signal information that may be useful to prioritize in memory; these prioritized memories in turn form the foundation of structured knowledge representations that guide subsequent learning. Critically, neural and cognitive component processes of learning and memory undergo marked shifts from infancy to adulthood, leading to developmental change in the construction of mental models and how they are used to guide goal-directed behavior. This review explores how changes in reciprocal interactions between value-based learning and memory influence adaptive behavior across development and highlights avenues for future research.

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INTRODUCTION

Throughout our lives, we rapidly acquire knowledge through experience. This knowledge is structured—it reflects regularities in our environments such as sequential relations between events, contingencies between actions and outcomes, and similarities across contexts (Tenenbaum et al. 2011). Across development, we exploit this structure to support the flexible pursuit of valued outcomes. The acquisition of structured mental representations relies centrally on memory processes that enable us to remember the specific events and situations we experience and to extract useful regularities across them. While we often think of memory as a record of the past, this record is selective—our memories, and the mental models that they support, tend to reflect the information that is most likely to be useful for guiding future decisions (Anderson & Schooler 2000, Biderman et al. 2020, Shohamy & Adcock 2010).

Value cues in our environments (e.g., rewarding outcomes or their predictors) signal information that is important to remember (Adcock et al. 2006, Castel et al. 2011). This prioritized information forms the foundation of more abstract representations, which are, in turn, harnessed to guide choice (Behrens et al. 2018, Collins 2018). The representations that are formed in memory and used to guide learning are adaptive when they help us bring about beneficial outcomes. Reciprocal interactions between adaptive learning and memory support goal-directed behavior from infancy through adulthood.

Until recently, memory and value-based learning have largely been studied as separate cognitive processes. However, behavioral and neuroscientific evidence has increasingly indicated that learning and memory function as part of an integrated system (Biderman et al. 2020, Gershman & Daw 2017). A growing body of research in adults has examined how the interactive functioning of value-based learning and memory guide behavior (Bornstein et al. 2017, Jang et al. 2019, Rouhani & Niv 2021, Wimmer & Shohamy 2012). In parallel, developmental studies have revealed marked age-related changes in value computations (Bolenz et al. 2017, Nussenbaum & Hartley 2019), memory processes (Ghetti & Fandakova 2020, Ofen 2012, Shing et al. 2010), and decision-making mechanisms (Jacobs & Klaczynski 2002, Raab & Hartley 2018, Rosenbaum & Hartley 2019), pointing to fundamental shifts in interactions between learning and memory across the life span. Nonetheless, we lack a comprehensive understanding of the changing nature of these interactive processes.

In this review, we provide an overview of change in adaptive learning and memory systems, highlighting their interactive development, and point to areas that warrant further investigation. We begin with a brief introduction to the value-based learning framework. We then provide a high-level overview of the neuroscience of value-based learning and memory in adults, emphasizing both the high degree of overlap in their underlying brain circuits and the pronounced changes that occur within these circuits across development. We review findings that highlight the bidirectional interaction of learning and memory through the lens of development. We illustrate the diverse ways in which value signals serve to prioritize what information is retained in long-term memory, and in turn, how memory representations are used to guide the pursuit of valued outcomes. Throughout, we highlight how changes in underlying computations and cognitive processes may alter the nature of these reciprocal interactions over development.

Value-Based Learning

Convergent theoretical frameworks from the fields of animal behavior (Dickinson 1985), artificial intelligence (Sutton & Barto 1998), and decision neuroscience (Rangel et al. 2008) propose that agents' actions are guided by value signals that arise through interactions with their environments. The value of a stimulus or action can stem from its inherently pleasant or unpleasant properties, as with reinforcers such as food, warmth, or pain. Stimuli can also acquire positive or negative value through association with rewarding or punishing stimuli. Beyond extrinsic physical rewards or punishments, experiences such as knowledge gain, agentic choice, and exposure to novelty may also function as reinforcers, with their reward value derived from intrinsic human motivations to learn about and exert control over the environment (Ryan & Deci 2000).

Insights into how the brain computes value have come from the interdisciplinary study of reinforcement learning (Sutton & Barto 1998). Reinforcement learning models formalize the computations through which the values of stimuli or actions are learned through experience. In these algorithms, a value estimate is updated through an incremental learning process driven by a prediction error (PE), or the degree to which an experienced outcome is better or worse than one's expectations. This error signal is then used to update the value estimate, yielding a corresponding upward or downward revision. Reinforcement learning algorithms can assign value to stimuli or actions in multiple ways: Organisms can learn and store recency-weighted estimates of the average rewards brought about by past actions to determine which behaviors merit repeating in the future (Dickinson 1985, Sutton & Barto 1998); action-value computations can leverage knowledge of the structure of the environment to enable the prospective consideration of which actions are currently most likely to yield desired outcomes (Daw & O'Doherty 2014, Doll et al. 2015); retrieved memories of past instances in which actions have been rewarding can also be used as a basis for future action (Lengyel & Dayan 2008); and stimuli that are reliable predictors of valenced events can acquire positive or negative value (Rescorla 1988), eliciting reflexive behavioral responses (e.g., freezing in anticipation of danger) (LeDoux & Daw 2018). Each of these evaluative processes reflects a different way that the organism might determine which action to select in a given decision context.

Further, evidence from a growing body of developmental research suggests that the diverse computations that underlie the valuation of stimuli or actions undergo marked shifts from infancy to young adulthood (Bolenz et al. 2017, Nussenbaum & Hartley 2019).

Neural Systems Supporting Value-Based Learning and Memory

Historically, lasting memory for different types of learned information has been broadly subdivided into declarative memory for events, supported by the medial temporal lobe (MTL) (Davachi 2006, Eichenbaum et al. 2007, Squire 2004), and nondeclarative, implicit memory, supported by several different neural systems (Squire & Dede 2015, Winograd 1975). Nondeclarative memory is often further subdivided into procedural memory, priming, classical conditioning, and nonassociative habituation or sensitization, with these distinct forms of learning supported by circuitry centered around the striatum, the neocortex, the amygdala, and reflexive pathways, respectively (Cohen & Squire 1980, Mishkin et al. 1984, Tulving & Schacter 1990). Despite this historical focus on cognitive and neural dissociations within learning and memory, recent research in adults points to a more integrated system (Biderman et al. 2020, Gershman & Daw 2017). The learning processes engaged in forming long-term memories for useful information, as well as those involved in assigning value to stimuli and guiding adaptive action, all depend on coordinated interaction across the brain systems dissociated within this historical framework. Below, we present evidence highlighting the overlapping and integrated nature of the neural systems involved in these adaptive learning and memory processes.

A large neuroscientific literature in the past two decades has begun to characterize the neural circuitry involved in value-based learning (Balleine & O'Doherty 2009, Daw & O'Doherty 2014). Studies across species have demonstrated that the activity of dopamine neurons corresponds closely to the reward PE signal within these models (Glimcher 2011, Schultz et al. 1997). Computational analyses of human functional magnetic resonance imaging data also suggest a central role for the dopaminergic system in value computation (Bartra et al. 2013). These studies commonly observe that activation within the ventral striatum, a brain region densely innervated by dopaminergic neurons, correlates with reward PE signals, whereas activation within the ventromedial prefrontal cortex (vmPFC), a region with reciprocal projections to and from the striatum (Haber & Knutson 2009), correlates with subjective value estimates (Bartra et al. 2013). Interactions between the amygdala, ventral striatum, and prefrontal cortex (PFC) support the assignment of positive or negative value to environmental stimuli (Cardinal et al. 2002, LeDoux & Daw 2018). A broader neural circuitry is implicated in the computation of action values (Balleine & O'Doherty 2009), with greater engagement of the hippocampus and orbitofrontal cortex (OFC)—regions proposed to encode information about the relational structure of the environment (Behrens et al. 2018, Wilson et al. 2014b)—typically observed when such structured knowledge is recruited in service of goal-directed action (Balleine & O'Doherty 2009).

Cross-species evidence has shown that the MTL plays a crucial role in general memory formation processes that also support the storage of valuable information (Eichenbaum et al. 2007, Squire 2004). In humans, cortical MTL areas, including the perirhinal and parahippocampal cortices, are thought to relay information about items and context to the hippocampus (Davachi 2006). The hippocampus has been widely implicated in encoding memories and in binding item and context information to create episodic memories (Eichenbaum et al. 2007, Squire 2004). Paralleling the crucial role of the dopaminergic system in value-based learning, studies carried out in adult rodents have demonstrated that dopamine-dependent plasticity in the hippocampus is critical for memory formation (Lisman & Grace 2005). Additionally, research in humans and rodents suggests that memory for affectively salient or rewarding information can involve interactions between the amygdala, dopaminergic midbrain, and hippocampus (Adcock et al.

2006, McGaugh et al. 1996, Yonelinas & Ritchey 2015). Memories are thought to initially be stored in neural ensembles within the hippocampus (Eichenbaum et al. 2007, Squire 2004). Although there is evidence that memory representations in the hippocampus persist (Nadel et al. 2000, Yonelinas et al. 2019), systems consolidation theories posit that over time, memories are also supported by distributed representations across cortical brain areas (Simons & Spiers 2003, Tonegawa et al. 2018). These distributed representations are thought to stabilize long-term memories and facilitate their use to guide future behavior (Rissman & Wagner 2012).

Using memories to guide action relies not only on memories for specific events but also on the extraction and accumulation of information across different events. The vmPFC and OFC have been specifically implicated in memory generalization processes and the formation of schemas (Gilboa & Marlatte 2017, Tse et al. 2007, Zeithamova & Bowman 2020). Consistent with systems consolidation theories that propose cortical representations of generalized knowledge, several studies suggest that individuals with hippocampal damage are able to perform generalization tasks (Knowlton & Squire 1993, O'Connell et al. 2016). However, recent work suggests that the hippocampus itself can support memory abstraction and generalization (Mack et al. 2018, Zeithamova & Bowman 2020). Thus, there may be multiple mechanisms for generalizing across experiences that rely on different brain systems.

Models of neurobiological development suggest that there are asymmetries in the developmental trajectories of the subcortical and cortical brain systems centrally implicated in adaptive learning and memory and posit that information exchange between these brain systems exhibits continued changes throughout adolescence (Casey et al. 2019, Murty et al. 2016). The hippocampus and PFC, in particular, undergo protracted structural and functional development into and throughout adolescence (Calabro et al. 2019; Gogtay et al. 2004, 2006; Lee et al. 2014a; Sowell et al. 2004). The continued maturation of these neural systems suggests that there may be corresponding, dynamic changes in adaptive learning and memory processes across development.

FORMING ADAPTIVE REPRESENTATIONS IN MEMORY

The ubiquity of new experiences and opportunities for learning during development raises an important question about the function of adaptive memory systems: What should be prioritized in memory? Memory representations are adaptive if they prioritize information that is likely to be useful for making future decisions. The structure of our environments, including the reward statistics involved in value computations, may influence memory formation by signaling information that is useful to remember. For example, we might remember a new lunch spot with exceptionally tasty—or exceptionally terrible—food. Additionally, frequently needed and goal-relevant information may also be prioritized. For example, we may preferentially encode the name of a person we often bump into or the central concepts we think will help us ace a test in school. In this section, we discuss factors that can lead us to prioritize information in memory and existing evidence for how memory prioritization changes over the course of development.

Goal-Directed Encoding

Knowing ahead of time that information will be useful to remember can help us prioritize it in memory. A number of studies conducted in adults have demonstrated that information that is incentivized or might be useful for earning rewards in the future is more readily encoded (Shohamy & Adcock 2010). This form of goal-directed encoding is thought to be driven by top-down attentional and cognitive control mechanisms involving prefrontal and parietal cortical systems that undergo protracted development throughout childhood and adolescence (Blumenfeld & Ranganath 2007, Cabeza et al. 2008, Gogtay et al. 2004, Mills et al. 2016). Behavioral evidence aligns with this neurobiological account. Recall for incentivized information has been found to improve across childhood and adolescence (Hanten et al. 2007). Additionally, adults show more selective memory for high-value information relative to children and adolescents (Castel et al. 2011). Thus, the ability to intentionally prioritize high-value information in memory seems to improve with increasing age.

Explicit cues signaling the value of remembering information that are typically included in experimental tasks are not often present in the real-world environments in which we encode new information in our daily lives. However, the future utility of information may be signaled by statistical regularities in the environment (Anderson & Schooler 2000). For example, information that is encountered more frequently may be more important to remember (Anderson & Schooler 1991). Recent work with individuals ages 7 to 25 years old indicates that the ability to prioritize information in memory based on the relative frequency with which information can be used to gain later rewards improves with age (Nussenbaum et al. 2020a). Moreover, this ability was related to explicit knowledge about the statistics of the environment. Furthermore, memory prioritization based on learned value signals was associated with increased activity in the striatum and PFC, which have been implicated in value-based learning and cognitive control processes. Consistent with theoretical accounts of motivated memory encoding (Shohamy & Adcock 2010), activity in the PFC, but not the striatum, mediated the relation between age and value-based memory selectivity (Nussenbaum & Hartley 2021). Taken together, these results suggest that continued development of prefrontal cortical systems contributes to age-related changes in goal-directed encoding.

In addition to attention and cognitive control, another cognitive process that is likely critical for the intentional prioritization of information in memory is metacognition (Metcalfe 2017). Specifically, metamemory monitoring, or the ability to reflect on one's own memory accuracy, may contribute to reliable deployment of attentional and cognitive control mechanisms that facilitate motivated memory (Ghetti & Fandakova 2020). Metamemory monitoring has been shown to improve across childhood and into adolescence. Improvements in this ability were related to increased thickness in the vmPFC and cortical thinning in the anterior insula, providing further evidence for the crucial role of cortical brain areas implicated in higher-order cognition in supporting strategic memory (Fandakova et al. 2017). Still, more research is needed to map the developmental trajectories of different forms of goal-directed encoding and their underlying neural mechanisms.

Value Signals During Learning

Events associated with positive and negative outcomes are often prioritized in memory. Multiple memory systems accounts suggest that emotional learning and memory systems, centered around the amygdala, are functional early in development (Hartley & Lee 2015, Stanton 2000). Indeed, children as young as 4 years old have shown enhanced memory specificity for items presented alongside positive and negative outcomes relative to those studied under neutral conditions (Ngo et al. 2019b). Adolescents have also demonstrated episodic memory enhancements, similar to those of adults, for items associated with aversive relative to neutral outcomes (Cohen et al. 2019). Thus, valenced outcomes can lead to the prioritization of events in memory across development.

The computations involved in learning to predict valued outcomes can also signal what information may be useful to remember. Experiences that are better or worse than we expect generate PEs. While the role of PEs in updating value estimates has been well characterized (Daw & O'Doherty 2014, Glimcher 2011, Schultz et al. 1997), the influence of PEs on memory formation is less well understood. Dopamine release associated with reward PEs may modulate memory due to dopamine-dependent plasticity in the hippocampus (Lisman & Grace 2005). In line with this possible memory prioritization mechanism, research in adults suggests that PEs can modulate subsequent memory for events encountered during learning. However, studies have found varying associations between PEs and memory, observing heterogeneous effects of PE valence and magnitude (Jang et al. 2019, Rouhani & Niv 2021).

Emerging evidence suggests that developmental change in value-learning mechanisms may influence what information is prioritized in memory. One study revealed that adolescents showed better reinforcement learning and memory for events associated with large, positive PEs relative to adults (Davidow et al. 2016). Adolescents showed PE-related activity in both the striatum and the hippocampus, as well as an association between hippocampal-striatal connectivity and enhanced memory for positively reinforced events. In line with prior research demonstrating heightened sensitivity to rewards during adolescence (Doremus-Fitzwater & Spear 2016, Galván 2013), these results suggest that hippocampal and striatal learning and memory systems may be uniquely tuned to respond to large, unexpectedly rewarding events during adolescence. Moreover, as past studies suggest that reinforcement learning also changes across development (Bolenz et al. 2017, Nussenbaum & Hartley 2019), shifts in both learning computations and the effects of these computations on subsequent memory may give rise to different patterns of memory prioritization across age.

Individual differences in sensitivity to positive and negative outcomes may also contribute to the heterogeneity in findings that link learning signals to memory. For example, individuals who place greater weight on negative outcomes in their value computations may prioritize negative events in memory, while those who are more sensitive to positive information may prioritize positive events in memory. Recent work examining reinforcement learning and subsequent memory for stimuli associated with valenced outcomes in individuals ages 8 to 27 years old suggests that this indeed might be the case (Rosenbaum et al. 2020). Across all ages, individuals who showed negative valence biases during learning demonstrated better memory for worse-than-expected outcomes and those who showed positive valence biases demonstrated better memory for better-than-expected outcomes. Accounting for individual differences in sensitivity to valenced outcomes may be key to understanding the cognitive and neural mechanisms that underlie the influence of value-learning signals on memory prioritization across age.

Intrinsic Reinforcement During Encoding

Value signals that drive memory prioritization are not solely derived from external sources but can also come from intrinsic goals and motivations such as the drives to learn about or exert control over our environments. For example, interest in a topic has been shown to facilitate word learning in young children (Ackermann et al. 2020). In addition, curiosity has been shown to enhance memory for answers to trivia questions in children, adolescents (Fandakova & Gruber 2021), and adults (Gruber et al. 2014). Paralleling previous research examining reward PEs, one study found that finding trivia answers more interesting than expected also enhanced memory, an effect that was stronger in adolescents than in children (Fandakova & Gruber 2021). Different age-related patterns in the influence of curiosity versus curiosity PEs on memory may arise from differences in the timing of these motivational signals—while interest in a question precedes to-be-remembered information, surprise over unexpectedly interesting answers co-occurs with its presentation.

The opportunity to actively control our environments also influences the information that is prioritized in memory. Opportunities to explore and make choices about what information to learn have been shown to result in improved memory for experiences in childhood and adulthood (Feldman & Acredolo 1979, Gureckis & Markant 2012, McComas et al. 1997). Fewer studies have focused on how the influence of active control on memory changes with age. In one study, children, adolescents, and adults all demonstrated similar memory benefits for information presented at the time of choice outcomes when they had the opportunity to make consequential decisions (Katzman & Hartley 2020). In another study, the memory benefit that stemmed from active decisions about what memoranda to study increased from early to late childhood (Ruggeri et al. 2019). Differences in individuals' goals when exerting active control (e.g., seeking reward versus remembering information) as well as the opportunities they have to adjust mnemonic strategies accordingly (e.g., allocating more study time to certain memoranda) may modulate patterns of age-related change in the memory benefits of intrinsic motivation.

Learning about or exerting control over our environments has been proposed to be intrinsically rewarding (DuBrow et al. 2019, Leotti & Delgado 2011). Research in adults has shown that neural mechanisms underlying the influence of curiosity and control on memory overlap with those associated with reward-motivated memory. Increased activity in the nucleus accumbens and ventral tegmental area/substantia nigra and connectivity with the hippocampus during anticipatory states of curiosity have been associated with curiosity-related memory enhancements (Gruber et al. 2014). High anticipatory activity in the striatum and increased striatal-hippocampal connectivity have also been associated with choice-related memory enhancements (Murty et al. 2015). These results suggest that curiosity and control over choices may both act as reward signals that can modulate memory formation across development. However, further research on the neurocognitive mechanisms underlying effects of intrinsic motivation on subsequent memory across development is needed.

FROM VALUE DRIVING MEMORY TO *MEMORY* DRIVING VALUE-DIRECTED CHOICE

Relations between value and memory are bidirectional; while value signals in our environments influence the information we encode in memory, memories inform how we learn from and pursue valued outcomes (Biderman et al. 2020, Gershman & Daw 2017). By integrating and generalizing across memories of distinct episodes, we begin to form schematic knowledge of the structure of our environments (McClelland et al. 1995). With time and the accumulation of experience, episodes comprise and become situated within abstract, relational structures. For example, mental models of traffic patterns emerge from memories of past commutes to work; representations of workplace hierarchy stem from individual social interactions with colleagues; and knowledge of which parent is more likely to allow an additional hour of video games is built upon multiple, distinct episodes with positive or negative outcomes. As with the influence of value signals on memory prioritization, developmental change in the computations that govern the transformation of past experience into schematic knowledge may give rise to variation in the mental representations that are formed across age. These abstract representations can be used to guide learning across diverse contexts, enabling, for example, the driver to time their commute more optimally or the child to successfully elicit permission from the more lenient parent. In this way, the prioritization of information in memory determines not just what we are able to recall but also how the mental models that enable value-guided action are constructed. Ultimately, interactions between learning and memory guide the choices that individuals make when navigating their environments.

Below, we present an overview of the varied types of environmental regularities that are represented in mental models and used to guide behavior. We briefly discuss findings from the adult literature that provide evidence for the existence of these complex mental representations before delving into the emerging literature on developmental change in model-based behavior.

Abstract Mental Models for Flexible Goal Pursuit

Many learning environments have structural regularities (e.g., hierarchical rules, periodicities in latent states) that can be discovered and exploited to facilitate performance (Collins 2018, Tenenbaum et al. 2011). When higher-order rules govern reward contingencies, acquiring knowledge of these rules enables rapid learning of the optimal action (i.e., learning to learn). For example, in Harlow's (1949) canonical studies of learning sets, a rule that one of two objects, irrespective of its location, is the correct response in each learning epoch can be inferred and applied to rapidly achieve error-free performance in subsequent epochs. In serial reversal learning tasks, knowledge that reward contingencies occasionally reverse can facilitate rapid adaptation after an inferred switch. Abstract relational knowledge acquired at a remote time point, even in the absence of a specific goal, can later be marshalled to inform goal-directed action (e.g., using knowledge of the roads in a city to plan a new route to a desired destination when the usual route is blocked)—a phenomenon referred to as latent learning (Tolman 1948). More generally, schemas that reflect commonalities inferred across many past experiences (e.g., the necessary steps involved in ordering food in a restaurant or crossing the street safely) can be readily generalized to provide cognitive models for action in new contexts.

A rich array of memory representations supports our ability to flexibly pursue our goals. Within the field of animal learning, a goal-directed action is defined by two key properties—it is performed with an expectation about its likely causal effect, and the expected effect is one that is currently valued (Balleine & O'Doherty 2009, Dickinson 1985). Thus, goal-directed behavior depends on structured knowledge about the relations between environmental states and actions. Convergent behavioral and neuroscientific findings provide evidence that organisms form internal models or cognitive maps (Tolman 1948) comprising rich relational knowledge about a current task including learned action-outcome contingencies, sequential relations between events, inferred latent states, and specific sensory properties of outcomes (Behrens et al. 2018, Wilson et al. 2014b). Knowledge about the structure of the environment can be acquired through direct experience or observation, as well as through explicit communication, which adults are readily able to convert into useful task representations (Cole et al. 2013). Once acquired, structured knowledge representations enable greater flexibility in value-guided action.

Cognitive maps can be used to plan multistep actions, evaluate their probable consequences, and determine which choices are most likely to be rewarded. Within the field of reinforcement learning (Sutton & Barto 1998), this type of forward planning is formalized by model-based evaluation algorithms, which use a representation of the transition probabilities between states and actions (the model) to prospectively assign value to a potential action by determining its likely consequences. In contrast, model-free evaluation algorithms compute cached action value estimates based on directly experienced previous rewards, fostering more automatic, but less flexible, reward-guided behavior. The utility of model-based evaluation is most apparent in situations where action-outcome contingencies or the value of specific outcomes change—for example, when a bus route unexpectedly changes. A model-free evaluation process, which only maintains a summary statistic of how good or bad an action is, cannot rapidly adapt its stored action values, yielding perseverative errors. In contrast, by revising a mental model to reflect such changes in transition probabilities or outcome values, this updated representation can be used to plan alternative courses of action.

Sequential decision-making tasks can be used to differentiate the degree to which individuals' choices are better captured by model-free or model-based evaluative processes. In the widely used two-step task (Daw et al. 2011), participants first make a choice between two stimuli, each of which is followed by a probabilistic common or rare transition to one of two second-stage states. In each second-stage state, two choice options each yield rewards with slowly changing probabilities. Whereas model-free learners tend to repeat previously rewarded first-stage choices, model-based learners use knowledge of the task transition structure to navigate to states that they expect to be rewarding. Studies in adults have found that participants who show model-based choice behavior also typically exhibit slower response times following rare versus common transitions (Deserno et al. 2015), consistent with the notion that these rare transitions violate learned expectancies.

In recent years, there has been a surge of interest in providing formal characterization of the formation and use of map-like representations in the brain in adults. In parallel, observations of differences in goal-directed behavior across development have inspired a burgeoning literature that has aimed to characterize age-related changes in the mental representations and decision algorithms that account for these age-related shifts.

Developmental Change in Model-Based Choice Behavior

The use of mental models to support goal-directed behavior is evident in infants and young children. Infants can acquire abstract and hierarchical rules and apply them to novel contexts (Frank et al. 2009, Schonberg et al. 2018, Werchan et al. 2016). Young children can similarly learn to learn, forming response rules that they can apply to novel learning epochs (Harlow 1949). Despite the early emergence of model-based behavior, the use of mental models to guide learning and action selection undergoes pronounced shifts from infancy to adulthood.

Relative to adults, children may rely on less complex mental representations to guide learning and decision-making. Studies have generally observed age-related increases in the influence of task structure knowledge on action selection, with the specific developmental trajectory of this increase depending on the complexity of the task. In one study, for example, young children (1–2 years old) exhibited insensitivity to outcome devaluation, such that they continued to perform previously rewarded actions—pressing a button that makes a video clip play—even when the video was devalued through repeated exposure (Klossek et al. 2008). By age 2.5 children appeared to use their knowledge that the button press would lead to an undesired outcome to select alternative actions. The ability to harness a mental model of the relation between actions, states, and outcomes continues to develop through adolescence. In the two-step task, the use of a model-based learning strategy that exploits knowledge of the task's transition structure increases from middle childhood to early adulthood (Decker et al. 2016, Nussenbaum et al. 2020b, Potter et al. 2017). Moreover, adults harness structural knowledge beyond state transitions—they use mental models of the causal structure of the environment to rationally discount experienced outcomes that they did not cause (Dorfman et al. 2019), they consider environmental reward contingencies to learn from counterfactual information (Palminteri et al. 2016), and they rely on instructions or advice to rapidly construct cognitive maps that bias how they learn from experienced outcomes (Decker et al. 2015, Rodriguez Buritica et al. 2019). In all these cases, the influence of structural knowledge on choice behavior increases with age. Relative to those of adults, children's choices are less influenced by causal knowledge (Cohen et al. 2020), counterfactual reasoning (Palminteri et al. 2016), and instructions or advice (Decker et al. 2015, Rodriguez Buritica et al. 2019).

Learning and Using Mental Models Across Development

The successful recruitment of mental models to guide choice behavior requires both the formation of an integrated mental representation of a task's structure and the ability to use that representation to guide action. Extensive cognitive developmental research suggests that both components of model-based learning undergo marked shifts across childhood and adolescence. Here, we unpack these varied neurocognitive mechanisms, starting with those that support the transformation of individual episodes into integrated cognitive maps, before moving on to those that enable the proactive and flexible recruitment of those maps during decision-making. Specifically, we review developmental research on statistical learning, generalization, and integration mechanisms that support learning environmental structure and transforming experienced episodes into integrated representations that support value-based decisions. We then examine how working memory, cognitive control, and prospection support the use of these representations to guide action.

Extracting environmental regularities from experience. Across the lifespan, multiple cognitive processes enable individuals to acquire knowledge of the structure of the environment from experience. These processes are supported by a diverse set of neural mechanisms that exhibit distinct trajectories of developmental change.

Statistical learning. From an early age, statistical learning mechanisms promote the acquisition of structured knowledge. Infants display sensitivity to the statistical properties of auditory and visual information, enabling them to parse streams of input into more structured representations (Saffran & Kirkham 2018). Young infants can identify co-occurring syllables embedded within streams of speech sounds (Saffran et al. 1996) and extract ordered sequences of shapes from streams of visual input (Kirkham et al. 2002). These implicit learning mechanisms persist through childhood and remain robust into adulthood, supporting learning across the life span (Amso & Davidow 2012, Meulemans et al. 1998). Further, growing evidence suggests that sensitivity to statistical regularities may improve through childhood and into early adolescence (Schlichting et al. 2017, Shufaniya & Arnon 2018).

Early sensitivity to statistical regularities may serve as a crucial building block for subsequent knowledge formation. While an extensive literature has demonstrated the role of statistical learning in language acquisition (Saffran & Kirkham 2018), the ability to detect patterns of environmental input supports the formation of diverse mental representations, including categories (Younger & Cohen 1986), and causal knowledge (Kushnir & Gopnik 2005). Statistical learning may also promote the construction of mental models through facilitating associative inference (Rmus et al. 2019). In one study, individuals' ability to extract co-occurring triplets from a stream of novel shapes was related to their performance in a separate inference task (Schlichting et al. 2017). Notably, while both individuals' explicit recognition of learned triplets and their inference accuracy improved from childhood to adulthood, performance on the two tasks was correlated even when controlling for age, suggesting that they may be supported by related mechanisms.

Knowledge of the statistics of the environment has also been directly linked to the formation and use of mental models to guide adaptive decision-making. In one study, participants between the ages of 9 and 25 years old completed the two-step task and a separate assay of statistical learning. Both statistical learning and model-based learning increased with age, and individuals with stronger statistical learning abilities also showed increased recruitment of a model-based learning strategy in the two-step task (Potter et al. 2017). Further, statistical learning ability predicted the extent to which individuals demonstrated slower reaction times following rare versus common first-stage transitions, suggesting that individuals who were better at statistical learning also more strongly encoded the task's transition structure.

Statistical learning is supported by a wide network of neural regions, including inferior frontal and superior temporal cortices, as well as the basal ganglia (Finn et al. 2019, Karuza et al. 2013, Schapiro et al. 2013). Although the vast majority of research on the neural mechanisms of statistical learning has been conducted in adults, a few studies of school-aged children have found involvement of similar neural regions during statistical learning tasks. When listening to streams of syllables that contained statistical regularities, children demonstrated increased activity in both the temporal and inferior frontal cortex (McNealy et al. 2010). Further, children who were more sensitive to statistical regularities—as evidenced by stronger increases in superior temporal gyrus activity during structured versus random streams of syllables—were also more successful in extracting novel words (McNealy et al. 2010). In childhood, inferior frontal cortex thickness was associated with better statistical learning ability (Finn et al. 2019), suggesting that structural changes in the frontal cortex may support developmental improvements in statistical learning.

Although traditionally associated with declarative memory, the hippocampus can rapidly represent items within their temporal context and may also play an important role in statistical learning (Schapiro et al. 2014). While the hippocampus may support statistical learning beginning in infancy (Ellis et al. 2021), recent neuroimaging work suggests that the hippocampus undergoes pronounced changes from childhood to adulthood (DeMaster et al. 2014, Riggins et al. 2016). Changes in hippocampal structure and function may contribute to changes in statistical learning across development (Finn et al. 2019, Schlichting et al. 2017). Decreases in hippocampal head volume from childhood to adulthood—potentially reflecting pruning of unneeded connections—may support developmental improvements in statistical learning (Schlichting et al. 2017). Taken together, prior work suggests that developmental change in prefrontal and medial temporal regions supports improvements in the ability to recognize and extract the environmental regularities essential to the construction of mental models.

Transformation of implicit to explicit knowledge. The flexible use of mental models to guide decision-making may require the transformation of implicitly learned statistical regularities into explicit representations of environmental structure (Dienes & Perner 1999). Young children's behavior often reveals a dissociation between these two forms of knowledge—across different domains, children show signs of implicit knowledge before they are able to represent it explicitly or use it to guide behavior (Goldin-Meadow et al. 1993, Karmiloff-Smith 1992). For example, in a balancing blocks task, young children often try to balance blocks on their geometric center prior to being able to explicitly vocalize their balancing strategy (Pine & Messer 2003). Similarly, young children often demonstrate the correct use of relative or possessive pronouns prior to being able to articulate the grammatical rules that guide their behavior (Karmiloff-Smith 1992), suggesting that they have acquired knowledge of key properties of their environment but not yet transformed that knowledge into a model that can be accessed explicitly. These developmental progressions suggest that early sensitivity to the statistical structure of the environment may set the stage for, but not fully enable, the formation of the cognitive maps that support decision-making. Implicitly learned regularities may require further mental transformation to effectively promote flexible, goal-directed action.

While there is mixed evidence for age-related change in implicit learning (Meulemans et al. 1998, Schlichting et al. 2017, Shufaniya & Arnon 2018), there may be more pronounced age-related shifts in the ability to represent learned statistics explicitly (Finn et al. 2016). For example, whereas 10-year-olds perform comparably to adults on probabilistic prediction tasks and artificial grammar learning, they perform significantly worse on explicit tests of declarative memory (Finn et al. 2016).

Generalization. The construction of mental models may also involve abstraction—the extraction of general patterns across diverse episodes or experiences. A recent theoretical proposal suggests that development may be marked by a shift from more abstract to more specific representations, leading to bigger gains in general, schematic knowledge earlier in life, when it may be most critical to construct general-purpose cognitive maps (Keresztes et al. 2018, Ramsaran et al. 2019). Relative to adults, children tend to perform poorly on lab-based tasks of mnemonic discrimination (Ngo et al. 2018, 2019a; Rollins & Cloude 2018). Children's encoding of episodes with less specificity may facilitate the extraction of commonalities across them, promoting abstraction.

Constraints on memory specificity early in life are mirrored by a similar bias in value-based learning. In several developmental studies of aversive conditioning, increases in age were associated with improvements in the discrimination of threat and safety signals, and relative to adolescents and adults, younger children tend to show broader generalization of threat responses to novel stimuli (Glenn et al. 2012, Schiele et al. 2016). This shift from generality to specificity may arise in part due to different developmental trajectories of pattern separation and pattern completion processes in the hippocampus (Keresztes et al. 2018). Through pattern separation, the hippocampus represents overlapping inputs as more distinct, supporting mnemonic discrimination, whereas through pattern completion, the hippocampus reinstates overlapping representations, promoting integration and generalization (Hunsaker & Kesner 2013, Yassa & Stark 2011). An early developmental bias toward pattern completion may thus promote generalization at the expense of the encoding and retrieval of highly detailed memories (Keresztes et al. 2018).

Structural changes in the hippocampus across development may promote the formation of increasingly detailed memories. Different hippocampal subregions continue to mature through late childhood and early adolescence; the hippocampal head decreases in volume in late childhood while the body increases (DeMaster et al. 2014, Lee et al. 2014a, Riggins et al. 2018). These structural changes have been linked to improvements in detailed memory into adolescence (Keresztes et al. 2017). Changes in hippocampal computations may also promote improvements in detailed memory across development. A recent study (Callaghan et al. 2020) found that the distinctiveness of activity patterns within the posterior hippocampus increased across childhood and adolescence and was related to enhanced detailed associative memory after a two-week delay. Still, although mounting evidence points to the formation of more detailed memories with increasing age, it is unclear if these improvements coincide with a developmental shift away from integration and generalization.

Complementary learning systems theory posits that rapid pattern separation processes in the hippocampus enable distinctive representations of specific experiences, while slower neocortical learning processes extract repeated patterns across experiences to promote the acquisition of general, schematic knowledge (McClelland et al. 1995). While some findings suggest that detailed memories and schematic knowledge may compete for expression (Richards et al. 2014), other research suggests that detailed memories support generalization (Tompary et al. 2020). Further work is needed to examine the development of the neurocognitive mechanisms that support the extraction of mental models from more detailed memories of individual experiences.

Integration. While extracting general patterns across disparate memories can promote the formation of general knowledge, existing knowledge itself can facilitate the formation of new memories. Prior knowledge may enhance memory for schema-congruent information by facilitating the formation of richer and more elaborate memory traces (Bransford & Johnson 1972, Craik & Tulving 1975). For example, in one study, both children and adults demonstrated better memory for a tractor paired with a farm than for a tractor paired with an ocean (Brod & Shing 2019). In another study, both child and adult chess experts demonstrated better memory for meaningful chess piece positions relative to random arrangements (Schneider et al. 1993). Interactions between the hippocampus and medial prefrontal cortex (mPFC) may support the use of prior knowledge to guide encoding of new information. Specifically, the hippocampus may represent novel information while the mPFC may instantiate representations of prior schematic knowledge (van Kesteren et al. 2012). The mPFC may exert a top-down influence on hippocampal representations, competitively inhibiting the individuated representation of episodes when they can be integrated into existing schemas (van Kesteren et al. 2012).

The effects of prior knowledge on the encoding and retrieval of new information may change across development, both because prior knowledge itself is in a constant state of flux and because the neurocognitive mechanisms that support schematic integration may themselves change with age and experience (Brod et al. 2013). Several studies have found that relative to adults, children demonstrate weaker memory benefits from semantic congruency (Ghatala et al. 1980, Maril et al. 2011, Stangor & McMillan 1992). This age-related increase in the influence of congruency on memory may arise because adults tend to use more elaborative, semantic encoding strategies relative to children (Brod et al. 2013, Maril et al. 2011). In line with this suggestion, Maril et al. (2011) found that during encoding of word-color combinations, children recruited neural regions more associated with perceptual processing, including the occipital cortex, whereas adults tended to recruit lateral prefrontal regions involved in semantic processing.

A more recent study (Brod et al. 2017) used novel stimuli to control for developmental differences in the strength of prior knowledge. Here, children between the ages of 8 and 12 years demonstrated comparable effects of prior knowledge on encoding relative to young adults, suggesting that age-related change observed in prior studies may in part be due to developmental change in the strength of existing schematic associations. Despite comparable memory performance across age groups, Brod et al. (2017) found that children and adults demonstrated different patterns of neural activity during encoding, such that adults, but not children, more strongly recruited the mPFC when encoding congruent events that were subsequently remembered versus not remembered. Further, the involvement of the mPFC during successful retrieval of congruent events also increased with age. Taken together, prior work suggests that age-related change both in the content of prior knowledge and in the prefrontal mechanisms that support its use contributes to increases in the influence of existing schematic representations on memory across development.

Using mental models to guide decisions. Beyond developmental change in the processes that support the formation of mental models, changes in action selection policies may also stem from differences in the way that mental representations of task structure are used (but see Munakata 2001). For example, in the classic A-not-B task, an experimenter repeatedly hides a toy in location A before switching to hiding it in location B. Infants often reach for location A but look toward location B, indicating that while they have an intact mental representation of the toy's true hiding spot, this representation is not being used to guide their actions (Diamond 1985). Similarly, when preschool-aged children are tasked with sorting cards according to changing rules, they often persist in sorting cards by a previous rule (e.g., by shape) despite being able to explicitly verbalize the rule they should be using (e.g., by color) (Zelazo et al. 1996). With increasing age, young children show increasing competence in using rule representations to guide behavior (Zelazo et al. 1996). The dissociation between knowledge and its use to guide learning persists throughout late childhood and adolescence, particularly as the complexity of the learning environment increases. Relative to adults, children demonstrate decreased use of a model-based decision strategy in the two-step task, but their explicit reports of the task's transition probabilities are equally accurate, and they similarly demonstrate slowed reaction times after rare transitions, suggesting intact knowledge of the task's structure (Decker et al. 2016, Nussenbaum et al. 2020b, Potter et al. 2017). Children also made inferences about the causal source of positive and negative outcomes that were aligned with environmental structure despite not using those inferences to modulate how they learned about the efficacy of their own actions (Cohen et al. 2020). Discrepancies between developmentally invariant reports of task structure and changing decision-making strategies suggest that similar mental models may differentially influence behavior across development.

Further, evidence from adult work suggests that individuals can learn mental models that they flexibly choose whether to use or not use based on the relative costs and benefits of engaging a model-based decision strategy. The cognitive processes that support model-based evaluation are sensitive to speed-accuracy tradeoffs (Keramati et al. 2011) and appear to be modulated by a reliability- and utility-sensitive arbitration process; manipulations that increase the reward value of model-based evaluation or the complexity of the task transition structure respectively increase or decrease the use of a model-based strategy (Kool et al. 2017, Lee et al. 2014b). From childhood to young adulthood, individuals also demonstrate improvements in the flexible arbitration between more model-free and model-based learning strategies based on their relative utility (Bolenz & Eppinger 2020, Smid et al. 2020).

Cognitive control. Model-based evaluations are proposed to arise through a deliberative process of prospectively searching through a mental model of states and potential actions. Consistent with this theoretical proposal, use of model-based evaluation is sensitive to individual differences in cognitive control ability (Otto et al. 2014), working memory (Otto et al. 2013), and information processing speed (Schad 2014). Using mental models to guide learning and decision-making may specifically require proactive cognitive control—or the ability to hold in mind a relevant representation to prepare for an upcoming action (Munakata et al. 2012). Rather than maintaining task-relevant mental representations in working memory, children may rely on reactive cognitive control, in which they instantiate such representations only when needed (Chatham et al. 2009, Munakata et al. 2012). For example, in a task in which participants view sequential stimuli and must make a response to a specific two-stimulus sequence, older children maintain working memory representations of the first target stimulus, whereas younger children retroactively retrieve the preceding stimulus only when they encounter the second target (Chatham et al. 2009, Munakata et al. 2012). In other words, while children may be able to transiently invoke a relevant mental representation when needed, they may not maintain it in working memory in the face of distraction, preventing its flexible and proactive use during decision-making.

Maintaining relevant representations and using them to guide behavior requires gating mechanisms that selectively permit information to enter working memory (Frank et al. 2001) and that selectively permit information maintained in working memory to influence action selection (Chatham et al. 2014). Recent research has revealed pronounced developmental shifts in working memory gating mechanisms. In a task that required the use of complex, hierarchical rules, children, adolescents, and adults all demonstrated similar working memory capacity, but output gating—the ability to select relevant information from working memory to guide behavior—showed stark improvements across childhood and adolescence and into young adulthood (Unger et al. 2016). While maintenance of task-relevant representations depends centrally on the PFC (Miller & Cohen 2001), selective output gating may rely on interactions between the PFC and basal ganglia, supported through cortico-striato-thalamic loops (Chatham et al. 2014). Connectivity between cortical and subcortical circuitry changes through adolescence (Casey et al. 2019, Parr et al. 2021), leading to improvements in the cognitive control processes that support the influence of goal-relevant mental representations on decision-making (Crone & Steinbeis 2017, Luna et al. 2015).

Prospective simulation. The use of mental models to guide decisions may also require the ability to prospectively simulate sequences of actions, states, and outcomes. Corroborating the proposed role of prospective simulation in model-based evaluation, in a neuroimaging study that used a version of the two-step task in which states were represented by neurally decodable object categories, model-based choice was associated with neural evidence of simulation of future trajectories at the decision time point (Doll et al. 2015). Prospection undergoes marked change across childhood and adolescence. Relative to adults, children tend to demonstrate more constrained episodic simulation (Ghetti & Coughlin 2018, Wang et al. 2014), requiring more prompts to generate hypothetical future events they might experience and providing fewer details in their descriptions. Episodic prospection requires the flexible recombination of retrieved episodes into imagined—but possible—futures (Suddendorf & Redshaw 2013). Thus, developmental differences in prospection may arise due to differences in encoding detailed memories, flexibly retrieving and recombining past experiences, or constraining imagined future trajectories to those that are plausible (Ghetti & Coughlin 2018).

In line with adult work (Schacter et al. 2017), across development, the ability to generate detailed, future narratives is tightly coupled to the ability to retrieve details of past experiences, suggesting that common mechanisms underlie episodic memory and prospection (Coughlin et al. 2019). Computations in the hippocampus may support the reinstatement of detailed episodes during both memory retrieval and episodic simulation (Schacter et al. 2017); structural changes in the hippocampus across childhood and adolescence may support increasingly detailed representations during both processes (Callaghan et al. 2020, DeMaster et al. 2014, Lee et al. 2014a). Despite evidence that memory and prospection share common hippocampal mechanisms, children demonstrate more difficulty in constructing hypothetical futures versus recalling the past or creating make-believe narratives, which may reflect the increased demands of constructing imagined futures that are compatible with existing mental models or schemas (Coughlin et al. 2019).

CONCLUSIONS: WHAT'S SPECIAL ABOUT DEVELOPMENT AND WHAT OPEN QUESTIONS REMAIN?

We begin life without extensive knowledge of our environments; over time and with experience, we construct rich and flexible mental models that guide our pursuit of value. The literature featured in this review highlights how, across development, cyclical interactions between learning and memory processes support the acquisition and use of structured knowledge to enable adaptive behavior. We encode experiences, prioritizing valuable information in memory; we transform these prioritized episodes into more integrated and generalizable schemas; and we use these relational knowledge structures to pursue our goals. The choices we make to pursue valued outcomes in turn shape what we experience and what we remember. These learning and memory cycles play out over time, expanding the repertoire of representations used to guide goal-directed behavior across development. Critically, development involves changes in the component processes that compose these reciprocal interactions.

From infancy to adulthood, the learning and memory mechanisms that support the formation of mental models and the cognitive control and prospection processes that enable their use undergo pronounced shifts. Here, we suggest that elucidating the changes in the neurocognitive mechanisms that underpin the development of adaptive learning and memory—and critically, how they interact with and influence one another—is essential to understanding the development of goal-directed behavior. While a growing understanding of the development of adaptive learning and memory is emerging from studies of their component processes, many questions about how these cyclical interactions change across development remain unanswered.

What Is Valued When?

How individuals ascribe value to different types of experiences may change over the course of development. Changes in neurobiology during adolescence are thought to give rise to differential sensitivity to emotional and social inputs from the environment. Accumulating evidence from studies in humans and rodents suggests that adolescents show increased reactivity to emotional, and in particular to rewarding and social, stimuli (Blakemore & Robbins 2012, Casey et al. 2019, Doremus-Fitzwater & Spear 2016). During childhood, parents can buffer behavioral and brain responses to emotional inputs such that parental presence can regulate children's expressions of emotion (Gee et al. 2014, Hostinar et al. 2015). Although incentives used in experimental tasks are often similarly valued across age (Insel et al. 2017, Paulsen et al. 2015), how developmental changes in sensitivity to social and emotional experiences impact individuals' reward functions and what consequences this might have for learning and memory remain unclear.

Early Explorers

The subjective value of different types of information may also change with age. Across the life span, information-seeking promotes the expansion of mental models of the environment (Kidd & Hayden 2015, Loewenstein 1994). Studies of curiosity and exploration have revealed profound developmental shifts in information-seeking behavior. Relative to adults, children may be more exploratory, often making choices that resolve uncertainty at the expense of those likely to lead to immediate reward (Blanco & Sloutsky 2020, Schulz et al. 2019, Sumner et al. 2019). Children also tend to be less strategic in their information-seeking. While adults seek information that is most likely to be useful in the future (Rich & Gureckis 2018, Wilson et al. 2014a), children's exploration demonstrates less sensitivity to information utility (Somerville et al. 2017). Age-related increases in strategic exploration may lead to the formation of mental representations that have greater utility for a particular task, but children's more random sampling behavior, and more diffuse attention, can promote broader knowledge of their environments (Plebanek & Sloutsky 2017, Raab et al. 2020, Sumner et al. 2019). The acquisition of broad knowledge may be particularly beneficial early in life (Gopnik 2020)—relative to adults, children generally have longer time horizons over which to use information. Thus, an early bias toward more random or exploratory behavior may reflect an adaptive latent learning process through which children acquire knowledge that may be useful weeks or months or years later. To date, however, few empirical studies have tested how information encountered early in life influences the construction of the mental models that guide adaptive choice at later developmental time points.

Mapping (in) the Developing Brain

Research on the neural computations that support rodent spatial navigation has provided a foundation for understanding how cognitive maps are represented in the brain. Hippocampal place cells fire in response to particular spatial locations, whereas grid cells in the entorhinal cortex represent relations between locations (Moser et al. 2008). This relational coding scheme appears to be a general system for representing both spatial information and conceptual knowledge (Behrens et al. 2018, Bottini & Doeller 2020). Beyond the entorhinal cortex, the OFC is also proposed to instantiate a map-like representation of the state space of a task, incorporating unobservable features of the environment (e.g., previous state transitions) into its representational code (Schuck et al. 2016, Wilson et al. 2014b). Rapid sequential reinstantiation of experienced states in the hippocampus, known as replay, is proposed to update and strengthen OFC representations. These subcortical-cortical interactions may support the emergence of map-like representations from the accumulation of individual experiences (Schuck & Niv 2019).

Across development, hippocampal-prefrontal connectivity undergoes protracted structural and functional change (Murty et al. 2016), which may alter the processes through which memories for single episodes are transformed into abstract relational knowledge. While a few studies in adults have developed innovative methods for quantifying and decoding the content of temporally compressed replay events (Eldar et al. 2020, Schuck & Niv 2019), no studies to date have examined developmental changes in replay in humans. One study in young rodents found that while the number of replay events was consistent across age, the content of these events changed. With increasing age, replay events shifted from reactivating single previously visited locations to longer spatially extended trajectories (Muessig et al. 2019). However, whether such developmental changes in memory replay occur in humans and how these changes might influence the formation and use of map-like representations are unknown. More broadly, whether the map-like representations observed in both the hippocampus and the OFC serve different functions during goal-directed behavior is not well understood. Future studies should examine whether developmental differences in subcortical versus cortical representations relate to age-related dissociations between the learning of structured knowledge and its use to guide action.

The Power of Sleep

Sleep may play a key role in the transformation of learned regularities to explicit mental models that can be used to guide decisions. In one study, children demonstrated implicit learning of a motor sequence after training (Wilhelm et al. 2013). Explicitly, however, they could report only about half of the transitions within the trained sequence. Notably, after sleep, children's explicit knowledge improved such that not only could they report almost all the transitions but also their explicit performance surpassed that of adults. During sleep, memories of prior experiences and their reward associations are reactivated and consolidated (Paller & Voss 2004, Wilson & McNaughton 1994), leading to enhancements in relational memory and inference (Ellenbogen et al. 2007). Sleep may play a particularly important role in memory consolidation early in development—children sleep more than adults (Ohayon et al. 2004) and similarly demonstrate enhancements in learning and memory following both naps and nighttime sleep (Gómez & Edgin 2015, Johnson et al. 2018, Kurdziel et al. 2018). As in adults, sleep-related memory enhancements in young children may arise from reactivation of hippocampal patterns associated with prior experiences (Johnson et al. 2018). Thus, sleep may play a crucial role in facilitating the memory transformations that underlie cognitive map formation. However, whether there are developmental changes in memory reactivation, or sequential replay, during sleep, and how these changes may influence the formation and use of map-like representations, have received little attention. For example, previous developmental studies of model-based decision-making have required participants to learn task structures within a single day; future research could harness multiday designs to more directly examine the role of sleep in the formation and use of mental models.

Developmental Change as Continuous Adaptation

Throughout this review, we have emphasized how the formation and use of mental models guides goal-directed behavior. One outstanding question, however, is what happens when we form models that do not accurately reflect the structure of our environments? Research in adults suggests that incorrect beliefs about environmental structure can have negative consequences. For example, believing that a changing environment is static (Sumner et al. 2019) or that one's actions are ineffective in an environment that is actually controllable (Raab et al. 2020) can lead to missed opportunities to discover and exploit new sources of reward.

It is adaptive to use mental models when they are accurate, but the construction of accurate mental models often requires gradual accumulation of experience over time. Thus, relying on structured knowledge to a lesser degree early in development—when it may be more prone to inaccuracies—may be adaptive. Less selectivity in attention, working memory, and episodic encoding may enable children to process information unconstrained by prior expectations, enabling more accurate and flexible inferences about environmental structure. Moreover, the protracted development of the component processes that support the use of structured mental representations to guide behavior may prevent the premature harnessing of incorrect beliefs. Thus, rather than promoting the emergence of adaptive cognition, developmental change in learning and memory processes may be continually adaptive in light of changing goals and environmental demands.

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Contents

Errata

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