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Neural Development of Memory and Metamemory in Childhood and Adolescence: Toward an Integrative Model of the Development of Episodic Recollection

Simona Ghetti¹ and Yana Fandakova²

¹Department of Psychology and Center for Mind and Brain, University of California, Davis, California 95618, USA; email: sghetti@ucdavis.edu

²Center for Lifespan Psychology, Max Planck Institute for Human Development, 14195 Berlin, Germany

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Keywords

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Abstract

Memory and metamemory processes are essential to retrieve detailed memories and appreciate the phenomenological experience of recollection. Developmental cognitive neuroscience has made strides in revealing the neural changes associated with improvements in memory and metamemory during childhood and adolescence. We argue that hippocampal changes, in concert with surrounding cortical regions, support developmental improvements in the precision, complexity, and flexibility of memory representations. In contrast, changes in frontoparietal regions promote efficient encoding and retrieval strategies. A smaller body of literature on the neural substrates of metamemory development suggests that error monitoring processes implemented in the anterior insula and dorsal anterior cingulate cortex trigger, and perhaps support the development of, metacognitive evaluations

in the prefrontal cortex, while developmental changes in the parietal cortex support changes in the phenomenological experience of episodic retrieval. Our conclusions highlight the necessity of integrating these lines of research into a comprehensive model on the neurocognitive development of episodic recollection.

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INTRODUCTION

From the early days of their lives, infants and young children exhibit impressive abilities to remember past events, including after long delays (e.g., Bauer 2007, Bauer et al. 2000, Quas et al. 1999, Simcock & Hayne 2003). This ability continues to improve in childhood and adolescence (e.g., Fandakova et al. 2013; Ghetti & Angelini 2008; Ngo et al. 2018, 2019a; Shing et al. 2010; Schneider et al. 2002). As children become better at recalling detailed memories, they also demonstrate an ability to engage metamemory processes: They increasingly reflect on the content and accuracy of their memories (Ghetti et al. 2011, Piolino et al. 2007) and make decisions on the basis of these assessments (Hembacher & Ghetti 2013). The subfields focusing on the neuroscience of memory and metamemory have been traditionally separated. The former has focused on the neurocognitive mechanisms affording more detailed and durable memory representations, whereas the latter has instead primarily examined mechanisms supporting individuals' abilities to recognize memory uncertainty or experience a sense of vividness about things past. Although it may seem apparent that these two levels of analysis provide complementary information, their integration in models of the development of episodic memory is lacking. In the present review, we first provide an overview of the research to date examining the neural substrates supporting changes in both memory and metamemory. We then identify missing links toward building a comprehensive model of memory development.

NEURAL UNDERPINNINGS OF MEMORY DEVELOPMENT

The development of the ability to remember past episodes reflects the increasingly skilled encoding, retention, and retrieval of complex memory representations that capture the richness of our experiences. Numerous factors may explain the robust memory improvements observed during childhood, including changes in the relational binding mechanisms that afford the formation and reinstatement of those complex representations (Eichenbaum & Cohen 2001) as well as changes in the use of controlled processes, including attentional mechanisms and organizational strategies directed at optimizing learning and strategic retrieval (e.g., Ghetti & Alexander 2004, Ghetti et al. 2010a, Nussenbaum et al. 2019, Ornstein et al. 2006, Paz-Alonso et al. 2009, Schwenck et al. 2007). In this section, we provide an overview of the current state of the art regarding the neural basis of these contributors to memory development.

Developmental Changes in the Medial Temporal Lobes Support Improvements in Memory Representations

To successfully recall our past in detail, our brains ought to process the various aspects of past events and bind them in a way that specifies the spatiotemporal context in which they were encountered. The hippocampus, a structure in the medial temporal lobes, is critical for forming and retrieving bound representations that integrate the diverse aspects of an event (Davachi et al. 2003, Eichenbaum & Cohen 2001, Eichenbaum et al. 2007, Moscovitch et al. 2016) based on input about events from the perirhinal cortex and the context of those events from the posterior parahippocampal gyrus (Diana et al. 2007, Ranganath 2010, Ranganath & Ritchey 2012). These bound representations provide the foundation for our ability to remember minute details, distinguish between similar experiences, and retrieve our memories flexibly from a variety of often nonoptimal cues. Functional magnetic resonance imaging (fMRI) research in adults has suggested a division of labor along the anterior-posterior axis of the hippocampus, with the anterior portion supporting coarser-grained spatiotemporal memory representations and the posterior portion supporting more fine-grained representations (Brunec et al. 2018). This coarse-to-fine spatiotemporal representation along the hippocampal axis is consistent with distinct patterns of connectivity (Ranganath & Ritchey 2012) and the different distributions of dentate gyrus and cornu ammonis 1 (CA1) subfields along this long axis (Malykhin et al. 2010). Together, this evidence suggests that the anterior hippocampus codes for general or global relations among different entities supporting the capacity to identify what is common across experiences and to reinstate memories flexibly from different cues (Chadwick et al. 2010, Chua et al. 2007, Giovanello et al. 2009); in contrast, the posterior hippocampus codes information more precisely (Moscovitch et al. 2016, Poppenk et al. 2013), which may amount to more fixed perceptual representations of the episodic context.

The hippocampus develops rapidly in the first years of life but continues to change into adolescence. With regard to early development, hippocampal volumes have been found to double from birth to the first year, with further increases in the second year of life (Gilmore et al. 2011). After the first few years of life, overall volumetric changes in the hippocampus are relatively limited (Gilmore et al. 2011). This evidence, along with examinations of hippocampal microstructure (e.g., Insausti et al. 2010, Lavenex & Banta Lavenex 2013), has suggested that the hippocampal basic anatomy, including the establishment of a functional trisynaptic circuit, is achieved during infancy and early childhood and provides the foundation for episodic memory and navigation (Bauer 2007, Lavenex & Banta Lavenex 2013).

Probing *in vivo* hippocampal function in humans during these early ages is challenging because fMRI, one of the most successful methods for this investigation, cannot be easily implemented with

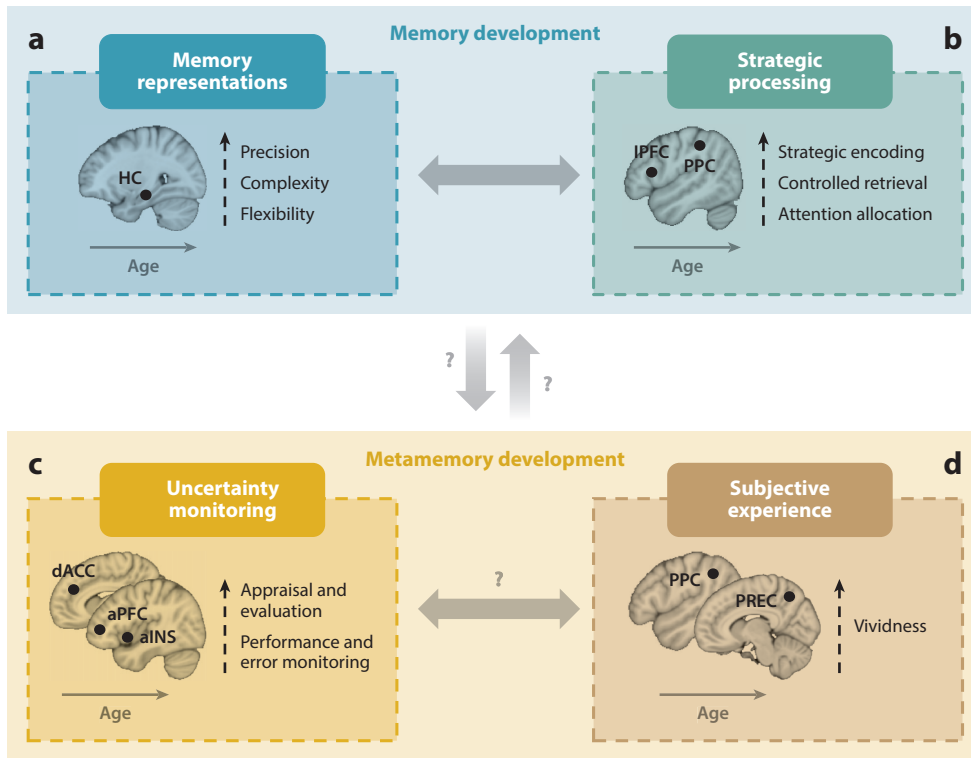


Figure 1

Neural substrates of the development of memory and metamemory organized around four central building blocks: (a) memory representations, (b) strategic processing, (c) uncertainty monitoring, and (d) and subjective experience. Abbreviations: aINS, anterior insula; aPFC, anterior prefrontal cortex; dACC, dorsal anterior cingulate cortex; HC, hippocampus; LPFC, lateral prefrontal cortex; PPC, posterior parietal cortex; PREC, precuneus.

young children. Recent research introduced a new paradigm that capitalizes on memory reactivations during sleep (Prabhakar et al. 2018) to address these difficulties. In this paradigm, laboratory experiences were tagged with songs. When previously learned and novel songs were delivered to two-year-old toddlers during natural nocturnal sleep, hippocampal activation was stronger for the learned song compared to the novel song, regardless of whether the learned song was played intact or presented backward. Moreover, children's memory for where the song had been learned was positively associated with hippocampal activation associated with the intact song. These results establish that hippocampal activation, at least in the third year of life, reflects past experiences and bolster the account that early memories are supported by hippocampal processes and not solely by cortically mediated learning (Gómez & Edgin 2016). These findings are also in line with the long-held view that hippocampal function is foundational for the emergence and early development of episodic memory (e.g., Newcombe et al. 2007). Over the past decade, research has begun to demonstrate that changes in hippocampal structure and function continue well beyond early childhood (Gogtay et al. 2006), with direct implications for improvements in memory precision, complexity, and flexibility into adolescence (e.g., Daugherty et al. 2017; Lee et al. 2014, 2020; Tamnes et al. 2014) (**Figure 1a**).

Precision. Optimal memory representations capture the unique aspects of an experience despite its likely similarities with other experiences. It is therefore reasonable to hypothesize that developmental improvements in memory representations depend in part on mechanisms affording an increased ability to discriminate among similar memories despite their overlapping content. One such mechanism is hippocampal pattern separation, which supports discrimination among similar memories through sparse recruitment of distinct populations of neurons in the dentate gyrus (e.g., Norman & O'Reilly 2003). The investigation of pattern separation has been pursued with behavioral tasks in which participants are required to make fine discriminations between target and similar distracters (e.g., Yassa & Stark 2011).

This approach has helped establish a link between the ability to discriminate between targets and similar distracters and hippocampal structure in children. For example, in a series of studies comparing 4-year-olds, 6-year-olds, and adults, younger children showed a disproportionately greater tendency to mistakenly recognize similar distracters as studied items, above what would be expected as a result of failure to recognize studied items (e.g., Ngo et al. 2018); this pattern may be even stronger when children ought to discriminate between similar spatial contexts as opposed to similar objects (Ngo et al. 2019b). In other words, compared to older children, younger children do not simply fail to recognize individual items, but they seem instead to have difficulty forming or retrieving sufficiently precise memory representations to support memory discriminability. Additionally, individual differences in memory discrimination between 4 and 8 years of age were associated with volumetric variations in the dentate gyrus (combined with subfields CA2, CA3, and CA4) (Canada et al. 2018), consistent with the possibility that these tasks capture pattern separation.

In contrast to the increasing body of research in early childhood, substantially fewer studies have examined development of memory precision in older children and adolescents. Although a handful of studies have reported associations between volume of the dentate gyrus and episodic memory in children and adolescents (Daugherty et al. 2017, Lee et al. 2014, Tamnes et al. 2014), none of these studies have manipulated precision or discriminability. One study examining age-related differences in memory discriminability into adolescence reported positive associations with a global index of structural maturity in the hippocampus as opposed to more specific associations with the dentate gyrus (Keresztes et al. 2017).

In line with the idea that more global hippocampal measures may capture aspects of developing memory precision comes one of the first demonstrations of age-related differences in hippocampal activation during encoding (Ghetti et al. 2010b). In that study, 8-year-olds, 10-to-11-year-olds, 14-year-olds, and young adults engaged in incidental encoding of a series of object drawings that appeared in either green or red ink. Participants provided semantic judgments that differed based on the color of the item, thereby orienting them to attend to associations between items and their color. Later, participants were asked to provide item recognition judgments on black-ink test items. When they claimed to recognize an item, participants were asked to report the color of the drawing, thereby probing the arbitrary association between an object and the color in which it appeared during the study phase. Group differences in patterns of activation suggested developmental change in hippocampal mechanisms supporting memory precision. Adults and 14-year-olds exhibited increased activation in the hippocampus only when they subsequently remembered the item and its color compared to recognized items whose color was recalled incorrectly or forgotten items; activation levels in these latter two trials did differ from one another. In contrast, 8-year-olds showed stronger hippocampal activation for recognized items regardless of whether the color was correctly recalled (compared to forgotten items), suggesting that hippocampal recruitment during encoding did not afford the same level of precision to support accurate recall of

item-color associations. The 10-to-11-year-olds' profile seemed to reflect a phase of transition, as it showed neither a selective response to precise item-color encoding nor a general response to item recognition. This transition pattern likely transcends memory precision and may depend on more global changes in hippocampal function because it has been also observed in recent cross-sectional and longitudinal studies on hippocampal contributions during episodic retrieval (Sastre et al. 2016, Selmecky et al. 2019).

Precision likely depends at least in part on the quality of the input the hippocampus receives from other regions. For example, Golarai et al. (2007) reported that age-related increases in activation level and cluster size during encoding in high-level visual regions (i.e., fusiform face area for face stimuli, parahippocampal place area for scene stimuli) predicted item recognition. Similarly, activity in the fusiform face area and lateral occipital cortex during encoding was related to better memory for face-object pairs in 6-to-19-year-olds (Rosen et al. 2018). Moreover, a recent application of multivariate analysis techniques revealed that the extent to which regions in the parahippocampal, lateral occipital, and retrosplenial cortices decoded three different scenes during encoding predicted performance not only in the memory task requiring retrieval of the association between one of those scenes and a unique object presented with it, but also in other memory tasks requiring scene processing (Fandakova et al. 2019). This result highlights that multivariate measures represent a promising way to capture development in the general ability to form precise memory representations. Overall, these studies suggest developmental changes in the quality of memory representations in the hippocampus and cortical regions that provide its critical input. However, none of these studies utilized manipulations of memory precision, thereby precluding firm conclusions. The effects of precision manipulations should be examined in future research.

Relational complexity. Optimal memory representations capture the unique aspects of an experience that vary along multiple dimensions, such as space and time. Therefore, in addition to precision, it is reasonable to predict that developmental improvements in memory representations depend in part on the type of information that ought to be retained. Although the capacity to remember specific events increases substantially overall, distinct patterns of age-related differences in memory for spatial, temporal and co-occurring items have been documented in cross-sectional studies (Guillery-Girard et al. 2013, Lee et al. 2016, Picard et al. 2012). This body of research has suggested that memory for spatial relations may be more robust at a younger age compared to memory for temporal relations (Guillery-Girard et al. 2013, Lee et al. 2016, Picard et al. 2012) and item-item relations (Lee et al. 2016); these latter two types of relations are shown to be retained at adult levels later in childhood (i.e., temporal order) and during adolescence (i.e., item-item relations). These distinct behavioral trajectories may emerge in part from division of labor along the anterior-posterior axis of the hippocampal structure (Brunec et al. 2018, Poppenk & Moscovitch 2011). For example, more anterior hippocampal regions may be more critical for memory for item-item relations (Giovanello et al. 2009), whereas posterior hippocampal regions may support item-space relations more strongly (Persson et al. 2018).

Cross-sectional studies examining hippocampal structure also suggest heterogeneous development along the anterior-posterior axis (DeMaster et al. 2014, Lee et al. 2017, Riggins et al. 2018, Schlichting et al. 2017): Whereas the hippocampal head increases in volume up to middle childhood and declines afterwards, the hippocampal body increases in volume after middle childhood. More recently, a large longitudinal study (Lee et al. 2020) of 7-to-11-year-old children across three time points—resulting in assessment of the period between 7 and 15 years of age—confirmed the distinct developmental trajectories of behavioral change in memory for spatial, temporal, and item-item relations identified in cross-sectional studies. This study also showed developmental

decreases in volume of the hippocampal head along with increases in the hippocampal body. Moreover, the longitudinal associations between structural and behavioral change depended on hippocampal subregion and type of relations and were more pronounced among older children, again highlighting the protracted development of hippocampus-dependent memory mechanisms. Volumetric changes in the hippocampal head predicted improvements in item-item relational memory, volumetric changes in the head and body predicted improvements in item-order relational memory, and volume of the right tail predicted improvements in item-space relational memory.

These studies underscore that the various aspects of an episode may be retained with different levels of success across child development. This raises the question of whether younger children experience disproportionate difficulty with retaining coherent representations, especially when it comes to retrieving temporal aspects of events, including the co-occurrence of two events in the same context. From this perspective, partial cues would be less successful in supporting the recovery of entire events in younger compared to older children. Research in adults has demonstrated a considerable retrieval dependency (i.e., holistic recollection), such that there exists a contingency of retrieval success among within-event associations (e.g., Horner & Burgess 2013). Specifically, after studying a series of events, each including an object, a person, and a scene, participants' retrieval of one association (e.g., object-scene) was statistically dependent on their retrieval of other associations from the same event (e.g., person-scene). The development of holistic recollection has rarely been formally examined, but the one study on the topic (Ngo et al. 2019a) demonstrated age-related increases in holistic recollection. Whether these results uniquely depend on difficulty with reinstatement of holistic representation from partial cues, difficulty retrieving certain aspects of the experiences (e.g., item-item associations) (Lee et al. 2020), or both awaits empirical investigation.

Retrieval flexibility. Our memories are arguably most helpful when they can be recovered flexibly through a variety of retrieval clues. Memory retrieval is more demanding under conditions that do not reinstate aspects of the encoding context (e.g., Smith & Vela 2001, Tulving & Thomson 1973), and this may be particularly true for children (Levy-Gigi & Vakil 2010, Paz-Alonso et al. 2009). The evidence of hippocampal involvement in flexible retrieval in adults (e.g., Giovanello et al. 2009, Zeithamova & Preston 2010) suggests a link between hippocampal development and developmental change in retrieval flexibility. Evidence consistent with this possibility was found by DeMaster et al. (2016). In their study, 8-year-olds failed to recruit the hippocampus when there was a change between encoding and retrieval conditions in an associative recognition test (e.g., pairs of studied items switched their location on the screen compared to during encoding). In contrast, 8-year-olds were more likely to recruit the hippocampus than adults when there was a match between encoding and retrieval conditions (i.e., the studied pairs were presented in the same location as during encoding). An individual difference analysis across children and adults showed that greater hippocampal activation during switched trials predicted better performance in a creativity task requiring participants to generate novel uses of known objects. This result suggests that the functional implications of hippocampal contributions to retrieval flexibility may extend beyond the memory domain to support various forms of flexible cognition, including the ability to simulate future events (Ghetti & Coughlin 2018, Schacter et al. 2017). Taken together, these studies show that continued development of the hippocampus plays an instrumental role in memory development during childhood because it is linked to improvements in the precision, complexity, and flexibility of memory representations.

While continued memory improvements supported by hippocampal maturation in early and middle childhood have been demonstrated in recent years, memory changes during the transition to adolescence have been more inconsistent. Although some studies showed similar

neural and behavioral profiles between adolescents and adults (e.g., Ghatti et al. 2010b, Shing et al. 2008), others demonstrated protracted development during adolescence (e.g., Keresztes et al. 2017, Tamnes et al. 2014). These discrepancies are not surprising considering abundant research in other cognitive domains suggesting that adolescent development is best characterized as refinements in the specificity and consistency with which neural mechanisms support cognitive operations (Luna et al. 2015). Thus, it is less likely that large global changes in memory would occur during adolescence, but rather, subtler changes emerge in particular contexts, such as those that capture adolescents' presumed increased sensitivity to rewards (van Duijvenvoorde et al. 2016). Initial evidence suggests that this increased sensitivity may result in greater memory benefits for adolescents compared to adults when memoranda are associated with subsequent, surprisingly large rewards (Davidow et al. 2016; see also Fandakova & Gruber 2019 for similar effects of intrinsic motivation). Davidow et al. (2016) showed that enhanced memory in the adolescent group was related to greater prediction-error activity in the hippocampus and increased connectivity between the hippocampus and the striatum, a brain structure that plays a prominent role in reward processing. Future research is needed to elucidate the developmental trajectory of these processes and to disentangle reward and motivation effects on the precision, complexity, and flexibility of hippocampal representations.

An understanding of adolescent memory also requires a characterization of hippocampal plasticity in relation to pubertal onset. At the start of puberty, increasing gonadal hormone release initiates the development of secondary sexual characteristics between 8 and 15 years of age (e.g., Shirliff et al. 2009). The hippocampus is characterized by a high density of sex steroid hormone receptors (Sarkey et al. 2008) and may be particularly sensitive to pubertal changes in hormone levels. Accordingly, one longitudinal study with children and adolescents between 8 and 14 years found that children who were initially older and showed greater pubertal changes over time also showed a greater increase in precision of hippocampal activation during the correct retrieval of object-scene associations (Selmezy et al. 2019). Notably, pubertal hormones modulate the neurobiological mechanisms regulating plasticity of the hippocampus in animal studies, indicating that the entry into puberty may lead to differential memory malleability in peripubertal children compared to prepubertal children and adults (Laube et al. 2020). Overall, future research in adolescence will have most discovery potential if it identifies contexts that might moderate memory function and provides a full account of the effects of pubertal changes in hippocampal structure and function.

Developmental Changes in Frontoparietal Regions Support Improvements in Controlled Memory Encoding and Retrieval

The capacity to form and retrieve bound representations is guided and supported by cortical mechanisms in the prefrontal cortex (PFC) and posterior parietal cortex (PPC) that afford the ability to allocate attention and engage in strategic processing to form and retrieve these representations (e.g., Badre & Wagner 2007, Blumenfeld & Ranganath 2007, Cabeza et al. 2008, Wagner et al. 2005). To date, the development of the PFC and its contributions to children's increasing memory ability have received substantially more attention than other cortical regions, such as the PPC.

The large behavioral literature indicating that developmental improvements in memory are largest when strategies and other controlled processes are required (e.g., Bjorklund et al. 2009) has directed researchers' attention to how the PFC contributes to memory development (**Figure 1b**). Changes in PFC thickness and volume have been documented throughout adolescence (e.g., Giedd 2004, Gogtay et al. 2004, Paus et al. 1999, Sowell et al. 2001), and early investigations

with small cross-sectional samples provided initial support for the proposal that better memory performance in children was associated with cortical thinning in the PFC (e.g., Østby et al. 2012, Sowell et al. 2004). More recent studies have provided further support for this idea. For example, Yu et al. (2018) showed that semantic clustering during verbal recall, which is indicative of organized recall strategies, increased between 5 and 25 years of age. This increase was negatively associated with volume in the lateral PFC, consistent with the hypothesis that PFC pruning during development contributes to successful strategy use (Petanjek et al. 2011).

These results converge with a growing body of work using fMRI methods. Studies examining brain activations during encoding have consistently reported age differences in the extent to which activation in the lateral PFC, especially the dorsolateral PFC (DLPFC), predicts subsequent memory (Ghetti et al. 2010b, Ofen et al. 2007, Shing et al. 2016). A factor that might modulate the extent of age differences observed across studies is the degree of participants' engagement in effortful encoding processes. Indeed, age differences appeared to be more robust or to extend into adolescence when participants were instructed to do their best to remember (Ofen et al. 2007) or to assess how successful their encoding processes were (Shing et al. 2016), and these differences were restricted to late childhood when incidental encoding procedures were used (Ghetti et al. 2010b).

Although most studies have focused on increased activation during encoding predicting subsequent memory in the lateral PFC, one recent study highlighted that these effects are complemented by deactivations predicting subsequent memory in other frontal regions, including the superior PFC (Tang et al. 2018); this result has been interpreted as reflecting more efficient regulation of attentional processes in the service of memory encoding. Behavioral improvements in strategic encoding co-occur with development in the maintenance and manipulation of new information, which is associated with increased and more selective recruitment of the PFC, particularly in the DLPFC (Crone et al. 2006). Relatedly, Wendelken et al. (2011) found that the extent to which the lateral PFC selectively encoded task-relevant versus task-irrelevant information differed between 8-to-13-year-olds and adults. Overall, improvements in working memory abilities likely account in part for the age differences observed in encoding-related activation. However, manipulations of working memory demands to probe the neural substrates of the development of long-term memory encoding have not been systematically employed.

Not surprisingly, age differences in PFC recruitment are also observed during successful retrieval, along with age differences in parietal activations (e.g., Amlen et al. 2018, Brod et al. 2017, DeMaster & Ghetti 2013, Fynes-Clinton et al. 2019, Ofen et al. 2012, Selmecky et al. 2019). Despite converging evidence on age differences, most studies have focused on inferring developmental change from differences in memory-related contrasts (e.g., activation for successfully retrieved items greater than activation for forgotten items). Differences across PFC subregions that vary in their contributions to memory retrieval (Simons & Spiers 2003) and in structural development across childhood (Gogtay et al. 2004) have not been explored, with very few exceptions. For example, Brod et al. (2017) recognized that the examination of the role of knowledge structures in memory has been conducted predominantly in the context of encoding operations (e.g., Maril et al. 2011); thus, Brod et al. (2017) manipulated the extent to which children and adults were probed to retrieve schema-congruent or schema-incongruent events. As predicted, medial PFC activations were less pronounced in children than adults, consistent with developing schemas represented in this region.

To date, most studies have not systematically manipulated factors that might explain age-related differences in retrieval and that are known to modulate PFC activation in adults, including improvements in the generation of effective cues (Dobbins et al. 2002), engagement in decision operations (Scimeca et al. 2016), and assessment of current goals (Tarder-Stoll et al. 2020). Thus,

many questions remain about the relative role of these processes and associated PFC substrates for the development of memory retrieval.

Many questions also remain about the contribution of the parietal cortex, especially the PPC, to the development of memory. Numerous roles in memory retrieval have been proposed for this region, including that it might serve as an episodic buffer to maintain the episodic signal available for further assessment (e.g., Vilberg & Rugg 2008), an accumulator of mnemonic evidence to provide the basis for the assessment of memory signals (Wagner et al. 2005), or a hub for attentional processes driven by contextual reinstatements or to drive internally generated retrieval (e.g., Cabeza et al. 2008).

Similar to what has been observed in the PFC, research has documented developmental differences in PPC involvement during memory retrieval but has not elucidated the processes underlying these differences. For example, DeMaster & Ghetti (2013) reported increased activity in the PPC during retrieval for items that were successfully recollected with contextual detail in 8-to-11-year-old children, whereas in adults, this region was recruited for recognized items regardless of whether contextual details were correctly retrieved. This result may be consistent with proposals that the ventral PPC responds to detail recollection irrespective of accuracy (Vilberg & Rugg 2008) following a bottom-up attentional capture (Cabeza et al. 2008). From this perspective, only the signal associated with the retrieval of accurate details would be strong enough to activate this region in children. However, the lack of direct manipulations of relevant processes in this and other studies prevents firm conclusions regarding the contribution of PPC regions to the development of memory retrieval.

Structural and Functional Changes in Memory-Related Networks Predict Behavioral Improvements

Changes in hippocampal, medial temporal, prefrontal, and parietal regions can contribute to memory development only to the extent that they can communicate efficiently with each other. We cannot do justice to this literature here because we focused our discussion on specific memory processes that are more readily tied to regional specialization. Nevertheless, an increasing body of work using diffusion-weighted MRI has reported consistent development from early childhood throughout adolescence in most white matter tracts involved in memory (Krogsrud et al. 2016, Lebel & Beaulieu 2011, Lynch et al. 2020), including the uncinate fasciculus, connecting the anterior hippocampus with the lateral and orbitofrontal PFC (Petrides & Pandya 1988); the cingulum bundle, connecting the posterior hippocampus with the parietal cortex, among others (Mufson & Pandya 1984); and the superior longitudinal fasciculus, connecting PFC and parietal regions. Associations have been reported between memory performance in children and variations in structural integrity in these developing tracts (Mabbott et al. 2009, Ngo et al. 2017, Wendelken et al. 2014) as well as in the fornix (Wendelken et al. 2014), which appears to be age invariant and connects the hippocampus with subcortical structures such as thalamus and mammillary bodies (Amaral & Insausti 1990).

Structural changes in white matter tracts may affect the reorganization of functional networks involving the hippocampus and cortical regions contributing to memory (Paz-Alonzo et al. 2013, Riggins et al. 2016, Tang et al. 2018). For example, Paz-Alonso et al. (2013) demonstrated that successful recognition of semantically related words was associated with increased connectivity between the hippocampus and DLPFC and between the hippocampus and PPC in adults but not in 8-to-9-year-olds. Using resting state fMRI, Sherman et al. (2014) found that the left hippocampus and left orbitofrontal cortex were connected to the posteromedial cortex at age 13 years but not at age 10 years in a longitudinal sample. These results suggest that adolescence may be

particularly important for more efficient network integration between the hippocampus and frontoparietal regions (see also Calabro et al. 2019, Murty et al. 2016).

Strengthening of the network that supports episodic memory may result from regional changes in the hippocampus, PFC, or PPC, along with dynamic influences among these regions over time. For example, development of strategic processes implemented by the lateral PFC might lead to enhanced connectivity with the medial temporal lobe, resulting in developmental improvement in hippocampal function. This functional change may in turn promote connectivity and enhancements of the quality of the hippocampal input to cortical regions. Similarly, developmental increases in the precision and flexibility of hippocampal representations may facilitate PFC and PPC engagement in the efficient use of encoding strategies and goal-directed retrieval. Future research testing dynamic regional interactions over time can help shed light on the modulation of connectivity between the hippocampus, medial temporal and posterior brain regions, and frontoparietal networks in the service of memory.

NEURODEVELOPMENT OF METAMEMORY AND SUBJECTIVE MEMORY EXPERIENCES

The capacity to remember the past would not be complete without the capacity to reexperience past events as phenomenologically clear and vivid. Indeed, Tulving (1985) argued that episodic retrieval is associated with a mental time travel affording individuals an *autonoetic* (i.e., self-knowing) experience of remembering, as opposed to a *noetic* (i.e., knowing) experience of familiarity.

Initial developmental studies focused on children's conceptual understanding of the origin of memory experiences drawing from the theory of mind tradition (e.g., Perner & Ruffinan 1995). From this perspective, at least two conceptual prerequisites are necessary for reexperiencing the past: namely, the understanding that memories are mental representations of a past reality and that these representations are generated by one's own past experiences (Perner et al. 2007). However, evidence that children can assess some phenomenological aspects of retrieved memories at early ages (e.g., Hembacher & Ghetti 2014) has suggested that these conceptual prerequisites may not be necessary for children to reflect on their memories, even though they may contribute to children's appreciation of the nature of their mental states (Perner et al. 2007). Instead, the subjective experience associated with episodic memory may be an emerging property of retrieval operations that reflect the degree of access to memory representations and the ability to report on their content and quality.

Most of the work on the development of subjective experiences of remembering has therefore taken approaches grounded in metamemory research and has investigated the neurocognitive mechanisms underlying children's emerging subjective experiences during memory retrieval. For example, children as young as 4 or 5 years can monitor varying degrees of memory strength, as indicated by confidence ratings (e.g., Hembacher & Ghetti 2014, Ghetti et al. 2002, Roebbers et al. 2004). Nevertheless, it is clear that the capacity to assess memory representations improves during middle and late childhood. Indeed, most research has focused on this developmental period, during which confidence ratings become more calibrated to memory accuracy and align with finer changes in memory states, such as differences among imagined actions or verbal materials that may evoke less sensory vividness (e.g., Ghetti et al. 2008).

In addition to increased calibration between accuracy and confidence, there are also developmental changes in the informational basis of subjective recollection. For example, 6-to-7-year-olds were more likely to claim to experience recollection when they correctly remembered the color of the items they had studied but not when they correctly remembered the semantic judgment

they had been asked to produce during encoding; the importance of remembering semantic judgments as a basis for recollection emerged later in childhood (Hembacher & Ghetti 2013) or was observed only in young adults (Ghetti et al. 2011). These findings suggest two lines of related inquiry that can help characterize the neural development underlying children's ability to appreciate their memory states.

On the one hand, it is important to characterize the neural substrates affording children's ability to assess their confidence, recognize their uncertainty, and utilize memory states as a basis for decision making. On the other hand, it is relevant to ask about developmental differences in the neural mechanisms that give rise to the subjective experience of vividness, potentially deriving from different types of information (Ghetti et al. 2011). We review these lines of research in turn below. However, the integration of these two levels of analysis still poses challenges in developmental cognitive neuroscience.

Development of Frontal Mechanisms Support Children's Capacity to Recognize If They Can Trust Their Memories

In adults, fMRI research has identified regions within the medial, lateral frontal, and parietal cortex that are modulated by confidence judgments across domains (e.g., Bang & Fleming 2018; Baird et al. 2013; Chua et al. 2006, 2009; Grimaldi et al. 2015; Kim & Cabeza 2009; Morales et al. 2018). Individual differences in anterior PFC volume and connectivity have been consistently correlated with individual differences in uncertainty monitoring (i.e., confidence ratings that discriminate between accurate and inaccurate responses) (Baird et al. 2013, Fleming et al. 2010, McCurdy et al. 2013). Furthermore, a cingulo-opercular network, including the dorsal anterior cingulate cortex (dACC) and the anterior insula/opercular cortex, has been implicated in signaling confidence along with response accuracy across memory and perceptual tasks (e.g., Fleck et al. 2006, Morales et al. 2018, Stolyarova et al. 2019). The contributions of the anterior insula and the dACC to metamemory are consistent with the role of these regions in error and performance monitoring (Boldt & Yeung 2015, Ullsperger et al. 2010) and suggest that they might provide input for metamemory appraisal (Vaccaro & Fleming 2018) (**Figure 1c**).

Research examining the neural basis of metamemory development is still quite rare. However, the majority of the brain regions that have been implicated in uncertainty monitoring in adults exhibit protracted development in childhood and adolescence (e.g., Giedd 2004). It can therefore be expected that developmental changes in these brain regions contribute to the development of children's metamemory. This prediction was tested by Fandakova et al. (2017), who reported change in memory uncertainty monitoring in a longitudinal sample of 7-to-15-year-olds, as well as in its longitudinal relation to structural changes in selected brain regions identified in adults. Interestingly, these brain regions showed distinct patterns of developmental change. Whereas change in the anterior insula follows a roughly linear trajectory of cortical thinning starting earlier in childhood (e.g., Vandekar et al. 2015), lateral and medial PFC regions typically display an initial increase in cortical thickness until around 9–10 years of age, followed by thinning into early adulthood (e.g., Shaw et al. 2008). In line with these distinct trajectories of change, thinning in the anterior insula and thickening in the medial PFC were associated with more pronounced improvements in uncertainty monitoring between 7 and 15 years of age. These findings call into question the possibility that the degree of cortical thinning in and of itself predicts behavioral improvement and suggest instead that regional contributions to metamemory development reflect the unique direction of developmental change in the corresponding brain regions. Consistent with these results, Filevich et al. (2020) found that medial PFC volume in 5- and 6-year-olds—an age period during which the medial PFC increases in thickness and volume—was positively associated with

children's ability to correctly identify their own states of ignorance. Taken together, this research suggests that developmental improvements in metamemory continue well into adolescence and emerge as a function of the specific trajectories of regional cortical change.

One prediction resulting from the developmental heterogeneity of the brain regions supporting metamemory is that processes supported by earlier developing brain regions, such as error processing in the anterior insula and dACC, may constitute the building blocks for the later development of PFC regions supporting the capacity to reflect on one's memories. Consistent with the idea of early developing error and performance monitoring mechanisms, Goupil & Kouider (2016) used eye-movement indices to suggest that 12- and 18-month-old infants' visual explorations reflect error monitoring and nascent decision processes. Of note, infants in this study, similar to older children and adults, demonstrated an EEG component that resembled the error-related negativity (ERN) after their gaze was directed to a distractor instead of a target. The ERN is typically observed when participants commit an error and is thought to originate in the dACC. These results suggest that the core neural mechanisms of error and performance monitoring may be present in infancy and may drive later metamemory development. Accordingly, the ERN and its putative generator in the dACC continue to develop in childhood and adolescence (for a review, see Tamnes et al. 2013).

To directly test the prediction that earlier developing error monitoring processes drive the development of the ability to reflect on one's memory over time, Fandakova et al. (2018) examined the neural substrates of the ability to recognize uncertainty in the retrieval of episodic detail. A sample of 8-to-9-year-olds, 10-to-12-year-olds, and adults was assessed, and children were examined longitudinally at two time points about 1.5 years apart. Participants studied a series of pictures of concrete objects that appeared on one of three background scenes. During retrieval, participants were presented with a series of objects, which either had been studied or were novel. Participants were instructed to either recognize the object as new (by pressing the novel button with the left hand) or report either the scene it was paired with or that they were uncertain about what scene the object had been paired with (by pressing one of four buttons corresponding to the selection and available to the right hand). Results showed that children across ages and adults engaged the anterior insula more strongly during inaccurate or uncertain responses compared to accurate responses. In contrast, only older children and adults recruited the anterior PFC more strongly for decisions to report uncertainty (i.e., greater activation for uncertain responses compared to both accurate and inaccurate responses). Interestingly, younger children who exhibited greater activation of the anterior insula at the first assessment showed greater increases in anterior PFC activation for uncertain responses over time, and both of those signals were associated with greater memory improvements over time. Together, these results suggest that variations in structure and function of brain regions associated with error monitoring might promote the engagement of processes that support more efficient metacognitive development, and they highlight the importance of metamemory for the development of episodic memory.

While research has started to elucidate developmental changes in the neural mechanisms supporting children's increasing ability to monitor and reflect on their memories, at present, it is unclear how vividness signals or signals about the quality of memory representations are integrated with uncertainty monitoring during development. Furthermore, feedback plays a critical role in improving confidence judgments in adults (Carpenter et al. 2019). Given increasing sensitivity to feedback and reward in the transition from childhood to adolescence (e.g., Peters & Crone 2017), an intriguing question for future research concerns the degree to which PFC-based metamemory appraisal and its interactions with error and performance monitoring processes in the insula and dACC are modulated by enhanced striatal responses to feedback and rewards at the transition to or during adolescence.

Developmental Changes in Parietal Cortices Might Support the Development of Subjective Vividness

Above, we described behavioral results showing age-related differences in the informational basis of the subjective experience of recollection (Ghetti et al. 2011, Hembacher & Ghetti 2013), which underscores that there may be developmental differences in the type of information that provides more subjectively compelling evidence of episodic memory. The finding that younger children are more inclined to track their memory for color over memory for semantic judgments suggests that visual vividness may be an earlier emerging basis for recollection. This idea has been proposed before. For example, Harris (1995) argued that mental representations that are more visually vivid are more likely to be noticed, evaluated, and reported on than mental representations that are less visually vivid.

This is intriguing because one account concerning feelings of vividness associated with recollection has to do with mechanisms in the parietal cortex orienting attention to memory states (Cabeza et al. 2008). This account suggests that dorsal parietal regions are involved in the allocation of attentional resources in line with current goals and task demands during retrieval, whereas ventral parietal areas, including the precuneus and the angular gyrus, are implicated in bottom-up attention to memory, or the allocation of attention to relevant memory cues or (spontaneously) retrieved memory representations. In line with this account, memories associated with high subjective confidence judgments are typically associated with faster retrieval of higher-quality representations, thus drawing bottom-up attention and engaging ventral parietal regions. Other accounts have implicated the parietal cortex as an accumulator of information in the service of memory decisions (Wagner et al. 2005; see also Bonnici et al. 2016). However, the role of the parietal cortex may go beyond supporting successful retrieval and may rather be concerned with the subjective experience of one's own episodic memory (Yazar et al. 2012) (**Figure 1d**). For example, patients with parietal lesions in the angular gyrus did not show any deficits with respect to memory accuracy, but reported lower vividness and confidence in their memories relative to controls (Berryhill et al. 2007, Simons et al. 2010). In line with these results, Richter et al. (2016) demonstrated a dissociation between the precision of retrieved memory representations, which was associated with the angular gyrus, and subjective vividness, which was uniquely associated with activity in the precuneus (see also Tibon et al. 2019).

As reviewed above, developmental studies have reported differences in both the precuneus (Amlen et al. 2018) and the angular gyrus (DeMaster & Ghetti 2013) during memory retrieval. However, at present, we cannot draw conclusions regarding the role of the parietal cortex in children's subjective experience of memory because no study has manipulated subjective vividness, the accumulation or integration of retrieved information, or attention to memory demands during retrieval in children. The behavioral studies demonstrating changes in vividness during development suggest the hypothesis that these changes would be, at least to some degree, associated with maturation of ventral parietal regions. Moreover, to the extent that parietal regions provide input to prefrontal regions serving metamemory and decision making, the development of these latter mechanisms may be constrained by information from the parietal cortex.

TOWARD AN INTEGRATIVE MODEL OF NEURAL DEVELOPMENT UNDERLYING EPISODIC RECOLLECTION

The ability to remember past details, experience a vivid sense of recollection, and make decisions on the basis of this experience engages a multitude of neurocognitive processes. Up to this point, we have reviewed these building blocks primarily in isolation. Here, we consider steps to integrate these processes. We focus on retrieval operations as a starting point for this discussion because

the connections between memory signals, subjective recollection, and consequences for decision making may be more readily apparent when individuals attempt to use their retrieved memories in service of their current goals (**Figure 1**).

We have discussed evidence of developmental change in hippocampal processes that may trigger the reinstatement of increasingly more precise, complex, and flexible memory representations (DeMaster et al. 2016, Keresztes et al. 2018, Lee et al. 2020, Ngo et al. 2019b) (**Figure 1a**). Regions in the PPC likely contribute to populating these representations with sensory detail and may respond by evoking a conscious feeling of recollection (Richter et al. 2016) (**Figure 1d**). The degree to which these operations in the PPC are successful likely depends on both the developing hippocampal signal and the increasing refinement of processes in the PPC itself. This proposal generates a series of testable hypotheses capitalizing on manipulations known to affect changes in hippocampal representations, which may reveal developmental differences in parietal response associated with the subjective experience of recollection. One hypothesis is that only more precise or more complex hippocampal representations can successfully trigger PPC engagement in younger compared to older children and adults, offering a mechanism by which developmental changes in hippocampal representations contribute to the subjective experience of recollection. This hypothesis is consistent with evidence that only accurate memories for item-context associations, which are presumably more precise, were associated with activations in the PPC in 8-to-11-year-olds (DeMaster & Ghetti 2013). In adults, the same region responded to both accurate and inaccurate memories. Strong memories may not be critical to trigger parietal mechanisms associated with vivid recollection in adults, given their spontaneous engagement in both bottom-up and top-down memory-related attentional processes (Cabeza et al. 2008). The absence of precision or complexity manipulations in previous developmental fMRI studies prevents firm conclusions about whether strong memories are necessary for children to engage orienting or vividness mechanisms in the PPC; an alternative interpretation of these early findings is that children were overall disproportionately less engaged in the task during inaccurate trials compared to adults. Moreover, to the extent that vivid experiences reflect the integration of different aspects of an event in the PPC (e.g., Bonnici et al. 2016, Wagner et al. 2005), memories may be experienced as more vivid earlier for components that develop earlier, such as space, thereby becoming comparable to adults' experience only later in development, when more complex representations such as item-item relations are developed.

One additional hypothesis is motivated by behavioral studies showing that younger children are more likely to claim subjective recollection when they remember color details compared to when they remember semantic details (despite memories being generally more accurate for semantic details across ages). These results suggest that retrieval of visual details may be more effective to orient attention to memory states in younger children due to continued development of PPC regions that are associated with subjective experiences of vividness. Interestingly, however, age differences in the informational basis of recollection may have to do not only with whether and how feelings of vividness are evoked but also with whether children weigh evidence coming from vision more strongly than from semantic processing, and how that evaluation influences decisions to commit to a memory response. Such evaluative operations are thought to be supported by frontal regions (Fandakova et al. 2017, 2018) (**Figure 1c**). It is therefore an open question whether, even in the face of precise memory representations and successful integration of sensory evidence in the PPC, younger children may show unique developmental difficulties in weighing evidence appropriately and evaluating memory evidence to maximize performance.

Finally, our discussion so far has emphasized the importance of the development of memory representations for the ability to subjectively experience and evaluate those memory representations. However, the evidence that the development of insular-opercular regions and the

PFC (**Figure 1c**), which support confidence assessments, contributes to memory improvements in childhood (Fandakova et al. 2018) implies a complementary process in which metamemory development may support improvements of memory representations. For example, better uncertainty monitoring may promote increases in children's ability to discern what memory feature poses more of a challenge, resulting in regulation of strategic processes during encoding or cue generation during retrieval (**Figure 1b**). Additionally, uncertainty monitoring signals may increase memory precision and tag representations for long-term retention.

Overall, these examples illustrate the necessity of future studies in which putative mechanisms of memory and metamemory development are experimentally manipulated over time and their effects are examined across multiple brain regions to gain new insight into their reciprocal roles and relations.

CONCLUSIONS

The development of memory and metamemory is critical to remember past events in detail, appreciate the phenomenological experience associated with remembering, and plan for appropriate action. Developmental cognitive neuroscience has made strides in providing new insight into how neural changes might support improvements in these processes. We have shown that the development of hippocampal mechanisms, in concert with medial temporal cortices, supports the formation of increasingly precise and complex memory representations that provide the foundation for recalling rich memories. Developing hippocampal mechanisms also support an increasing ability to retrieve memories flexibly, so that children can recall their past even when partial or noisy retrieval cues are available.

We have also underscored the importance of PFC maturation for memory development. However, studies have rarely manipulated specific attentional and strategic processes associated with prefrontal brain areas to examine their contributions to children's increasing encoding and retrieval success. Such designs, along with manipulations targeting processes associated with the PPC, remain to be tested in future research.

Finally, we have argued that a complete understanding of memory development in childhood and adolescence can be achieved only if research on metamemory development is integrated into ongoing research programs. While initial studies have demonstrated the importance of fronto-opercular regions for developing monitoring processes and decision making, future research is needed to investigate how changes in parietal mechanisms that allow children to vividly reexperience the past inform neural mechanisms responsible for guiding decisions and actions.

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