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Review

The development of neural correlates for memory formation

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ABSTRACT

A growing body of literature considers the development of episodic memory systems in the brain; the majority are neuroimaging studies conducted during memory encoding in order to explore developmental trajectories in memory formation. This review considers evidence from behavioral studies of memory development, neural correlates of memory formation in adults, and structural brain development, all of which form the foundation of a developmental cognitive neuroscience approach to memory development. I then aim to integrate the current evidence from developmental functional neuroimaging studies of memory formation with respect to three hypotheses. First, memory development reflects the development in the use of memory strategies, linked to prefrontal cortex. Second, developmental effects within the medial temporal lobes are more complex, and correspond to current notions about the nature in which the MTL support the formation of memory. Third, neurocognitive changes in content representation influence memory. Open issues and current directions are discussed.

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1. Introduction

Memory is not a unitary entity; rather, behavioral, neuropsychological, and neuroimaging data from adults and children support the notion that memory is comprised of a number of distinct systems, including declarative (concerned with experiences and facts) and procedural (concerned with skills, or 'how to') memory systems (Squire, 1987). Within declarative memory, Tulving introduced and developed a distinction between the episodic memory system, concerned with awareness of an earlier experience in a certain situation at a certain time, and the semantic memory system, concerned with factual knowledge about the world (Tulving, 1983, 1993, 2002). It is accepted that episodic memory develops throughout infancy and childhood (Bauer, 2005; Nelson, 1993; Perner and Ruffman, 1995; Tulving, 1983; Wheeler et al., 1997). It is not clear, however, at what age children acquire a mature, functioning, episodic memory system, and whether the episodic memory system continues to evolve through middle childhood and adolescence (Brown, 1975). A central question to the development of memory is *what is memory development the development of?* Among the key players suggested in the behavioral literature are the development of strategies for deliberate remembering and the growth in one's knowledge base (Bjorkland et al., 2009; Chi and Ceci, 1987; Flavell, 1970; Kee and Davies, 1990; see Brown, 1975; DeMarie and Ferron, 2003; Ornstein et al., 2004; Schneider and Pressley, 1989 for reviews of additional factors).

Brain imaging has offered a unique window to explore the neural correlates of memory. The neural correlates of episodic memory were extensively examined in adults (Kim, 2011; Spaniol et al., 2009). Recent years brought intense interest in understanding brain development and its relation to cognitive development (Casey et al., 2005). Specifically, there is a growing use of functional magnetic resonance imaging (fMRI) in pediatric populations, though due to difficulty of these procedures, typically the youngest children are 7 or 8 years old. In this review I present the main findings of several recent studies that used fMRI to examine the correspondence between memory and functional brain development from middle childhood into young adulthood (Chai et al., 2010; Chiu et al., 2006; Ghetti et al., 2010; Maril et al., 2011, 2010; Menon et al., 2005; Ofen et al., 2007; Wendelken et al., 2011). These studies have primarily assessed brain activations during the encoding of information into memory, i.e., during memory formation. As a consequence, this review is focused on memory formation and cannot address potential developmental trends that are specifically manifested during memory retrieval. Collectively, these studies applied a cognitive neuroscience approach to study the development of memory. Such an approach is beginning to provide useful insights to assess the contributions of strategy, mnemonic processes, and growth in knowledge to the development of memory from middle childhood to adulthood.

2. The cognitive neuroscience of the development of episodic memory formation

2.1. Memory development—behavioral evidence

Behavioral evidence suggests that episodic memory develops from childhood through adulthood (Perner and Ruffman, 1995), with substantial qualitative changes in episodic memory happening during infancy and young childhood (Bauer, 2005). In the study of memory development between middle childhood and adulthood, much of the behavioral literature focuses on how encoding, storage, and retrieval of information are influenced by children's use of memory strategies (Bjorkland et al., 2009; Flavell, 1970; Pressley and Hilden, 2007), children's knowledge base (Chi and

Ceci, 1987), and by the manners in which these components interact (Bjorklund, 1987; Kee and Davies, 1990; Ornstein and Naus, 1985; Pressley and Hilden, 2007). Below is a brief consideration of these developmental effects. Children tend to under-perform compared with adults, under conditions that directly test the effect of deliberate use of memory strategies. For example, adults are more accurate than children when old and new pictures are similar and thus the memory distinction is difficult (Brown and Scott, 1971). When minimal use of memory strategies is needed, children could recognize old from new pictures as efficiently as adults (Brown and Scott, 1971), and are as accurate as adults, although slower, on verbal encoding tasks (Ackerman, 1981; Emmerich and Ackerman, 1979). The effect of knowledge on the ability to memorize is well documented by findings that experts out-perform novices in memorizing material within their domain of expertise (Schneider et al., 1989). The basic notion is that with age, increases in knowledge result in improvements in the ability to memorize. As stated by Flavell: "... what the head knows changes enormously in the course of development, and these changes consequently make for changes in memory behavior" (Flavell, 1985, p. 213). Furthermore, when the amount of knowledge between children and adults is controlled, age effects in memory ability are minimized, and under some conditions younger children can even out-perform older children and adults (e.g., Schneider et al., 1989; Chi, 1978). Finally, the interaction between strategy and knowledge is illustrated by the finding that growth of knowledge may allow older children and adults to use additional task-relevant processing of the to-be-learned material that are not available to younger children (Kee and Davies, 1990).

Although this review is not intended to present a comprehensive survey of behavioral evidence about the development of memory, it is important to note a few influences that, due to space limitations, are largely missing from this review. First, the development of memory is considered to reflect age-related improvements in more 'basic' cognitive functions such as speed of processing, attention, and capacity in working memory (DeMarie and Ferron, 2003; Kail and Salthouse, 1994). Second, there is mounting evidence that metamemory, knowledge about memory, plays a critical role in memory development (Holland Joyner and Kurtz-Costes, 1997; Schneider and Pressley, 1989). It is important to recognize that the relation between memory and other cognitive functions (e.g., attention, problem solving), and the relation between memory and metamemory are inextricably intertwined (Brown, 1975).

When considering the net effects of factors contributing to changes in memory from middle childhood into adulthood, one consistent finding is that developmental effects can be specific to certain aspects of memory, whereas other aspects show little change with age. For example, with age, the quality of memories changes as memories become richer in details. Testing the quality of memory is currently accomplished with a variety of paradigms adapted from adult studies of memory. These include asking participants to reflect on their own memory, using a remember/know judgment (Gardiner and Java, 1993; Gardiner et al., 2002; Squire, 1987), or using a confidence scale (recollection is then derived by plotting receiver operating characteristic methods that link accuracy and confidence) (Yonelinas, 2001b). Alternatively, researchers test recall of specific details of controlled experience with source memory paradigms (Johnson et al., 1993), process-dissociation procedure (Jacoby, 1991), or conjoint recognition (Brainerd et al., 1999, 2001). An important feature in all these paradigms is that they can provide more than one measure of memory, and thus allow a more detailed characterization of memory ability and memory development. For example, in source memory paradigms a series of stimuli (e.g., line drawings) are presented in a distinct context (e.g., line drawings are presented in one of two colors: red or green). In a following recognition memory test, participants are asked about the

identity of the stimuli (have you seen this line drawing?) and also about the context in which each stimulus was presented (was this line drawing presented in red or green?). Source memory refers to the recall of specific details about the context in which a stimulus was presented (e.g., color in the example above). Improvements in source memory related to age are much greater than those for remembering the series of stimuli (Cycowicz et al., 2001; Ghetti et al., 2010). Overall, the developmental evidence that is obtained using the above-mentioned paradigms shows that development is most protracted for memory tasks that demand greater detail in recollection, such as remembering specific details of the context in which information was presented, relative to the information itself (Billingsley et al., 2002; Brainerd et al., 2004; Cycowicz et al., 2001; Dirks and Neisser, 1977; Ghetti and Angelini, 2008; Mandler and Robinson, 1978; Ofen et al., 2007). The developmental distinction between different aspects of recognition memory may reflect two dissociable mnemonic processes in episodic memory: recollection, that includes specific knowledge of the details of the event; and familiarity, that include less contextual details (Jacoby et al., 1993; Yonelinas, 1999, 2001a; Yonelinas and Levy, 2002). Taken together, the behavioral data suggest that familiarity-based memory processes are used early in development, whereas recollection processes show a relatively prolonged maturational course (Ghetti and Angelini, 2008).

2.2. Neural correlates of brain systems supporting memory formation

The neural systems mediating episodic memory in adults have been identified through neuropsychological lesion evidence. Medial temporal lobe (MTL) structures, including the hippocampus and surrounding perirhinal and parahippocampal cortices, are essential for the formation of new declarative memories. Bilateral MTL injury results in global amnesia, defined by an inability to form new declarative memories (Scoville and Milner, 1957; Squire, 1992; Zola-Morgan et al., 1986). The prefrontal cortex is not essential for memory formation, but prefrontal lesions impair declarative memory for contextual details of an experience (source memory) (Janowsky et al., 1989; Schacter et al., 1984). The most common interpretation of the dissociation between intact and impaired episodic memory in patients with frontal-lobe lesions relies on the observation that episodic memory tasks differ in their strategic memory demands, i.e., in how much retrieved memories must be evaluated, manipulated, and transformed. Recognition tests given shortly after study may have minimal strategic demands as participants quickly decide whether or not a particular stimulus had been included in a study list. Tests of free recall, temporal order, and source may have much greater strategic demands as participants have to figure out how they will recall stimuli or at what time or place a familiar stimulus was encountered. It may be that episodic memory tasks with severe strategic memory demands tax the capacity of executive components of working memory that have been associated with frontal cortices.

Convergent evidence to the involvement of the MTL and the prefrontal cortex in memory comes from functional neuroimaging evidence (Kim, 2011; Spaniol et al., 2009). Functional neuroimaging, in addition offers a unique window to directly examine the neural correlates of memory at distinct stages. In a typical fMRI paradigm that tests memory formation, brain imaging is conducted while participants study a series of stimuli. Participants' memory of those stimuli is then tested, and brain activations during encoding of stimuli later remembered are contrasted with brain activations during encoding of stimuli later forgotten (subsequent memory effect). Subsequent memory effects in prefrontal and MTL regions are typically found in adults (Brewer et al., 1998; Buckner et al., 1999; Davachi et al., 2003; Spaniol et al., 2009; Wagner et al.,

1998). Furthermore, recent meta-analysis revealed that the magnitude of subsequent memory effects in MTL, prefrontal, as well as in fusiform and parietal regions, is modulated by the amount of detailed encoding, and by the content of the material (verbal or pictorial) (Kim, 2011).

2.2.1. Subsequent memory effects in prefrontal cortex

Subsequent memory effects are stronger for verbal, compared with pictorial, material in the inferior frontal cortex (Golby et al., 2001), a region implicated in organization, selection and retrieval of verbal information (Blumenfeld and Ranganath, 2007; Thompson-Schill, 2003; Thompson-Schill et al., 1997; Wagner et al., 2001). Furthermore, subsequent memory effects for verbal information in the inferior frontal cortex are stronger when encoding detailed, associative information, compared to non-detailed information (Kim, 2011). Taken together, the inferior frontal cortex may contribute to memory formation of verbal material through its role in organization, selection, and maintenance of verbal material. In contrast, subsequent memory effects for pictorial material more strongly engage the fusiform gyrus and occipital cortex, regions implicated in high-level perceptual processing (Garoff et al., 2005; Kanwisher et al., 1997). Thus, fMRI evidence in adults highlights the involvement of the prefrontal cortex in memory formation and suggests that differential modulation of these regions is linked to the richness and specific content of subsequent memory.

2.2.2. Subsequent memory effects in the MTL

Although the MTL is strongly associated with episodic memory formation, there is considerable debate about the specific nature in which the MTL supports the formation of episodic memory. First, one line of research explores whether certain structures within the MTL have specialized role in memory formation. Most notably, there is a debate whether the hippocampus plays a specific role in the formation of detailed, recollected memory (Brown and Aggleton, 2001; Davachi, 2006; Diana et al., 2007), or whether it plays a role both in the formation of recollection and familiarity-based memories (Gold et al., 2006; Wixted and Squire, 2011). Results of a recent meta-analysis show that the MTL is equally involved in associative and item memory formation (Kim, 2011), in line with suggestions that the MTL is important in both familiarity and recollection (Squire et al., 2007; Wixted and Squire, 2011). A second line of research explores the degree to which familiarity influences activations along the long axis of the MTL (Lepage et al., 1998). Anterior portions of the MTL are more responsive to novel events and contexts, whereas posterior portions respond strongly to repeated materials (Gonsalves et al., 2005; Habib et al., 2003; Lepage et al., 1998). The novelty-encoding hypothesis asserts that novel material is more memorable as novelty detection and assessment may be an early stage of encoding by which adaptively significant events are identified for additional processing, while redundant (familiar) information is filtered (Tulving et al., 1996). Thus, anterior parts of the MTL may provide operations to support both familiarity (reduction in activation for previously seen items) and memory encoding, optimally allocating limited encoding resources away from already familiar information and towards novel information (Fernandez and Tendolkar, 2006). Challenges to the notion that novel material is more memorable come from findings that increasing familiarity, through repetition, enhances episodic memory formation of scenes (Poppenk et al., 2010). Nonetheless, there seems to be a specialization in subsequent memory activations along the long axis of the MTL; activations in anterior portions of the MTL (right hippocampus and right amygdala) predict memory for novel scenes, whereas activations in posterior hippocampi predict memory for repeated scenes (Poppenk et al., 2010). A third line of research explores content-sensitive effects in the MTL. Subsequent memory

effects in the MTL are more robust and more bilateral for pictorial materials, compared with verbal materials that are weaker and left lateralized (Golby et al., 2001; Kim, 2011). The degree to which certain structures within the MTL, such as the hippocampus, support content-general memory processes and whether specific content is represented along the long axis of the MTL is less clear (Preston et al., 2009).

2.2.3. Subsequent memory effects in parietal and premotor cortex

Functional neuroimaging evidence also implicates the involvement of lateral, parietal, and premotor cortices (Kim, 2011), regions associated with allocation of attention and cognitive control processes (Raz, 2004), in memory formation. The role of the parietal cortex in memory has been the focus of intense investigation, motivated by its ubiquitous activation in neuroimaging studies of memory (Cabeza, 2008; Ciaramelli et al., 2008; Vilberg and Rugg, 2008; Wagner et al., 2005) and by the minimal neuropsychological evidence for a critical role of parietal cortex in memory (Haramati et al., 2008). The involvement of parietal cortex in memory may, at least partially, reflect the involvement of attentional or controlled processes in successful memory performance (O'Connor et al., 2010).

2.3. Brain development

Late childhood and adolescence is a period of robust change in the structure and function of the brain. Post-mortem and structural imaging evidence indicates that the brain continues to mature during development and that this maturation is most prolonged in prefrontal and parietal regions (Giedd et al., 1999; Gogtay et al., 2004, 2006; Huttenlocher, 1979; Sowell et al., 2003, 2004). Structures in the MTL do not show robust structural changes with development, but some evidence suggests continued development of certain MTL regions in the human brain (Abraham et al., 2010; Giedd et al., 1996; Gogtay et al., 2006; Sowell and Jernigan, 1998; Sowell et al., 2002). These anatomical findings support the idea that prefrontal memory functions develop more slowly than MTL memory functions in the human brain, but also raise the possibility that functional development may occur in the MTL between mid-childhood and young adulthood.

2.4. Components in the cognitive neuroscience of memory development: integrating evidence from behavior, functional, and structural brain imaging

Developmental cognitive neuroscience hypotheses about memory development proposed here stem from integrating behavioral evidence about the development of memory (Section 2.1), with evidence of the neural correlates of memory formation in adults (Section 2.2), and evidence about brain structural maturation (Section 2.3). The first hypothesis is that developments in encoding strategies (how material is evaluated, manipulated, and transformed to memory), contribute to the improvement of memory, and are subserved by the prefrontal cortex. Considering the critical role of the MTL in memory and the small structural developmental change in the MTL between middle childhood and adulthood, a second hypothesis is that during development, the MTL contribute primarily to those aspects of memory that change little with age. As will be considered below, the current data, however, suggest that the link between memory development and developmental changes in the MTL is complex.

These two hypotheses are consistent with a recent account that proposes dissociable developmental trajectories between two components of memory: (i) a strategic component that specifies the role of cognitive control via frontal-parietal networks that undergo protracted maturation and (ii) an associative component

that specifies the role of binding processes via regions in the MTL which mature early (Shing et al., 2010, 2008). Current imaging studies on memory development (reviewed in Section 3) did not manipulate a direct measure of an associative component (e.g., item-item associations), and thus there is currently no direct support in the neuroimaging data for this proposal.

Finally, the behavioral literature highlights the influence of the growth in knowledge on memory (Chi and Ceci, 1987; Lindberg, 1980; Ornstein and Naus, 1985). In parallel, neuroimaging evidence reveals prolonged functional maturation in regions that are specialized for processing materials of specific domains (such as faces or scenes) (Golarai et al., 2007). I further speculate that functional changes in brain regions that are specialized for processing material of specific domains may relate to developmental changes in knowledge within these domains. Piecing these notions together, a third hypothesis is proposed that age-related changes in brain regions specialized for processing specific materials act to influence age-related changes in memory formation.

The three hypotheses presented above form the basis for an initial framework for a cognitive neuroscience approach to memory development. In the sections below I present the current evidence and discuss each hypothesis in detail. The development of memory is likely to be better conceptualized by the combined effect of the three hypotheses proposed above. An attempt to distinguish the contributions of these hypotheses is, however, useful for informing a better understanding of the typical development of memory.

3. Current fMRI evidence of the development of memory formation

Compared to the large amount of knowledge gained using fMRI to examine the neural correlates of memory formation in adults, only a few studies examined the normal development of episodic memory formation from childhood through adulthood (Chai et al., 2010; Chiu et al., 2006; Ghetti et al., 2010; Maril et al., 2011, 2010; Menon et al., 2005; Ofen et al., 2007; Wendelken et al., 2011). Below, I survey studies examining developmental trajectories in the neural correlates of memory formation. Those studies used pictorial, verbal, or a combination of pictorial and verbal materials. The youngest participants in these studies are typically 7 or 8 years old, and they were all conducted as cross-sectional designs, comparing age effects between participants.

3.1. Pictorial material

The neural correlates of the development of memory formation were tested with pictorial materials in four studies. First, comparing the encoding of novel scenes to the repeated presentation of a single scene, Menon et al. (2005) found reductions in left MTL activations and increases in functional connectivity between left MTL and left prefrontal cortex between the ages of 11–19 years. Menon et al. (2005), however, used a block design, which precluded a direct examination of the relation between the magnitude of activation and memory formation on a trial-by-trial basis. Second, using an event-related design, Ofen et al. (2007) found increases in subsequent detailed recollection (assessed by subjective 'remember' response) in the prefrontal cortex, but not in the MTL, between the ages of 8 and 24. Furthermore, activations in the prefrontal cortex, but not the MTL, correlated with developmental gains in memory for details of experiences, assessed by a source memory paradigm (Ofen et al., 2007). In contrast, developmental increases in activations in a posterior portion of the MTL are found for the subsequent detailed recollection of complex scenes, but not for simple ones (Chai et al., 2010). These results suggest that regions in the prefrontal cortex that are important for the formation of

detailed memories for experiences have a prolonged maturational trajectory, whereas the MTL demonstrates a more complex pattern of developmental effects. Third, Wendelken et al. (2011) examined the effects of attention on short-term and long-term memory. In that study, children (8–13 years) and adults viewed series of four stimuli in the following order: face-scene-face-scene and were instructed to attend the scenes, or the faces. When children were instructed to attend the scenes, there were age-related increases in activations in scene-selective regions that were correlated with better memory. A limitation of the Wendelken et al. (2011) study is that increases in activation in scene-sensitive regions were not linked to memory on a trial-by-trial basis. Nonetheless, the Wendelken et al. (2011) findings are consistent with the findings from Chai et al. (2010), which demonstrate developmental effects in posterior parts of the MTL that are linked to better memory for scenes.

3.2. Verbal and verbal-pictorial material

Developmental effects in the neural correlates of memory formation were tested with verbal or verbal-pictorial materials in four studies. In the first study, using a block design, Chiu et al. (2006) found that activations in the MTL (including the hippocampus) and the prefrontal cortex are associated with recognition of sentences in older (ages 10–18), but not in younger (ages 7–8) children (Chiu et al., 2006). Three recent studies examined verbal or verbal-pictorial memory formation using event-related designs (Ghetti et al., 2010; Maril et al., 2011, 2010). One study examined incidental episodic memory formation of verbal information by children (ages 7–19 years old) and adults (Maril et al., 2010). Participants heard two words, one after the other, and were instructed to create a new word by replacing the first sound (roughly corresponding to the first letter) in the second word with that of the first word (e.g., ‘pen’ followed by ‘tool’, the participant will create the word ‘pool’). Participants were given a surprise recognition test for their subsequent memory of the newly formed words (e.g., ‘pool’). The prefrontal cortex showed subsequent memory activations in adults but not in children. Within the MTL, subsequent memory activations reduced with age in the left hippocampus. Thus, the results of this study are consistent with memory formation reliance on MTL activations earlier in childhood and protracted functional contribution of the prefrontal cortex. A second study examined incidental episodic memory formation for item (line-drawings of common objects) and an associated detail (color) in four groups of participants; 8 years old, 10 years old, 14 years old, and adults (Ghetti et al., 2010). This study focused on the difference, within the MTL, between activations for subsequent memory of a line-drawing and its original color (source memory), and activations for subsequent memory of the line-drawing without memory of its color (item-only memory). The authors report developmental trends such as that source memory was higher than item-only memory in older participants, but not younger participants; in younger participants, activations for source memory were as high as those for item-only memories. Based on these results, the authors proposed a change in the functional organization of the MTL between middle childhood and adulthood. A third study tested the effect of event congruency on episodic encoding in children (ages 8–11) and young adults (Maril et al., 2011). Participants were asked to imagine objects (presented as printed nouns) in one of five different colors, and then make a congruency judgment for each object/color combination. Subsequent memory for the objects was associated with activations in the prefrontal cortex and in occipital regions in both children and adults. Adults, however, showed greater subsequent memory effects than children in prefrontal, occipital, and parietal regions. Children showed greater subsequent memory effects in lateral,

temporal, and posterior occipital regions. Furthermore, Maril et al. (2011) identified that those regions that showed both congruency and subsequent memory effects (that is, instances where congruency presumably aids memory) largely differed between children and adults. The interpretation of these results is further discussed in Section 6. Taken together, using verbal materials, researchers identified age-related increases in the involvement of prefrontal cortex in memory formation, whereas developmental trends in the MTL were less clear.

3.3. Summary of main findings

Taken together, these studies reveal robust developmental changes in prefrontal cortex contributions to subsequent memory formation. Increased activation in the prefrontal cortex likely relates to the more extensive use of appropriate strategies and cognitive control in older children. This notion will be further explored in Section 4. Developmental trends in MTL activation for successful memory formation are less clear. MTL activations associated with memory formation reduced with age during the encoding of scenes (Menon et al., 2005) and of verbal-pictorial memories (Maril et al., 2010). No change in MTL activations was found for the subsequent familiarity (Ofen et al., 2007), or recollection of simple scenes (Chai et al., 2010), though there were increases in activations in the posterior portion of the MTL for the subsequent recollection of complex scenes (Chai et al., 2010), and in hippocampus and parahippocampal gyrus for subsequent detailed recollection of line-drawings (Ghetti et al., 2010). Taken together, these findings suggest protracted maturation in some, but not all, MTL functions related to memory. Section 5 will explore these inconsistencies with respect to current knowledge about principles that determine MTL involvement in memory formation. Section 6 will explore whether developmental changes in content-sensitive regions of the brain may influence memory formation.

4. Developmental effects in prefrontal cortex and use of strategy

Perhaps the most documented contributor to the development of memory is the increase in flexible use of deliberate strategies such as rehearsal (Flavell et al., 1966), elaboration (Pressley, 1982) and organization (Bjorkland et al., 2009; Flavell, 1970; Kee and Bell, 1981). Following Pressley and colleagues (Pressley et al., 1985; Pressley and Hilden, 2007) in this review, I adopt a working definition for strategy as “composed of cognitive operations over and above the processes that are natural consequences of carrying out the task, . . . to achieve cognitive purposes that are *potentially* conscious and controllable activities” (Pressley et al., 1985, p. 4). Using this definition allows both deliberate and non-deliberate task-relevant cognitive operations, such as attentional processes and memory monitoring, to be considered when discussing the neural correlates of memory development. Furthermore, adopting this somewhat imprecise definition rather than adopting a more specific definition of strategy that focuses only on deliberate, conscious operations seem appropriate given the limited availability of neuroimaging data that examined the development of memory.

In Section 2.2 I suggested that the most common interpretation of the dissociation between intact and impaired episodic memory in patients with frontal-lobe lesions (Janowsky et al., 1989; Schacter et al., 1984) relies on the observation that episodic memory tasks differ in their strategic memory demands. Tasks with severe strategic memory demands tax the capacity of executive components of working memory that have been associated with frontal cortices.

Strategic demands are explicit when participants are instructed to actively memorize (intentional memory instructions), compared

with when participants are not expecting to be tested for their memory of experiences (incidental memory). Intentional memory instruction, however, would promote the use of strategies only if children are capable of using appropriate self-selected strategies efficiently. Incidental memory, in contrast, does not depend on engaging in self-selected strategies. Instead, memory outcome is constrained by the type of encoding participants are using. Overwhelming behavioral and neuroimaging evidence suggests that the type of encoding, deep (e.g., semantic) versus shallow (e.g., non-semantic), but not the intention to encode, is strongly related to encoding success (Craig and Tulving, 1975). Encouraging children to use deep (e.g., semantic) encoding promotes the efficient use of an appropriate strategy and maximizes the opportunity for children to recruit appropriate brain regions for encoding and maximizing later recognition (Baddeley, 1982; Pressley, 1982). Indeed, children's memory performance is better, and sometimes even equal to that of adults, following incidental semantic encoding, as compared to intentional encoding or non-semantic incidental encoding (Ackerman, 1981, 1985; Ackerman and Rust-Kahl, 1982; Ghatala and Levin, 1981; Sykes, 1976).

None of the current developmental studies that examined the neural correlates of memory formation contrasted intentional memory instructions with incidental encoding. Across studies, however, one can compare subsequent memory activations during intentional encoding (Ofen et al., 2007), to those achieved during incidental encoding that encourages (Ghetti et al., 2010) or discourages (Maril et al., 2010) deep semantic encoding. Indeed, under intentional encoding, Ofen et al. (2007) found age-related increases in subsequent memory activations in the prefrontal cortex. In contrast, Ghetti et al. (2010) used constrained incidental encoding that encourage deep semantic encoding (deciding whether line drawing is of an object that can be found in a house or not), and found only modest age-related effects in the prefrontal cortex. These findings support the notion that constrained, deep, incidental encoding minimizes age-related differences in the neural correlates associated with the use of strategy. These findings are consistent with findings that older adults, when compared with young adults, show reduced subsequent memory activations in left frontal regions during intentional encoding (left BA 45/47) (Logan et al., 2002). During constrained, deep, incidental encoding, however, older adults showed activation in the same brain region that were at least as great as in young adults.

Constraining the way by which children and adults encode to-be-learned information may not fully alleviate age-related effects, as indicated by the findings of a study that directly contrasted deep and shallow encoding tasks in adolescents and young adults (ages 14–28 years) (McAuley et al., 2007). Deep, compared to shallow, encoding of verbal material in that study was associated with age-related increases in activations in the inferior frontal gyrus (McAuley et al., 2007). Thus, even when incidental encoding instructions are constrained, deep, semantic, encoding is associated with developmental effects in recruitment of the prefrontal cortex, suggesting prolonged maturation of operations relying on deep, semantic, encoding. Evidence that constrained encoding does not alleviate all age effects is also given in the study of Wendelken et al. (2011) that used attentional modulation instructions on pictorial material with children (ages 8–13). Together, McAuley et al. (2007) and Wendelken et al. (2011) provide evidence that supports the idea that children are less able to exert strategic control even when provided with constrained encoding instructions. Critically, these effects are associated with reduced modulation by the prefrontal cortex in children. The evidence that constraining (deep) encoding does not fully alleviate all age differences raises questions about the processes underlying developmental constraints. It is possible that this observation relates to the utilization deficiency phenomenon in the behavioral literature (Bjorklund et al., 1994), according to

which a given strategy does not facilitate memory performance even though it is available.

It is important to note that comparisons across studies are complicated by the nature of encoding and retrieval tasks and by the different age ranges of the participants. Further studies, ideally using longitudinal designs, are needed to fully characterize developmental trends in the use of strategy and the role of constrained encoding on the neural correlates of memory development.

5. Developmental effects in MTL and non-strategic mnemonic processes

Neuroimaging data from adults reviewed in Section 2.2 suggest three principles for MTL involvements in memory formation. First, the MTL may be specifically involved in detailed, associative memory (Diana et al., 2007). Second, there may be an anterior–posterior distinction along the long axis of the MTL with respect to familiarity (Fernandez and Tendolkar, 2006; Lepage et al., 2003). Third, certain content effects influence MTL involvement in memory formation (Golby et al., 2001; Kim, 2011; Preston et al., 2009). As summarized in Section 3.3, the findings regarding developmental changes in activations in the MTL are inconsistent. In this section I will consider the developmental findings with respect to these three principles in an attempt to address some of the inconsistencies across studies.

First, the principle of MTL specificity in the formation of detailed memory can address some of the inconsistent MTL developmental findings. In a source memory paradigm, activations associated with the formation of detailed memories are higher compared to those associated with non-detailed memory in older children and adults (Ghetti et al., 2010), whereas in younger children, activations associated with the formation of detailed memory were as high as those for non-detailed memory. In another verbal-pictorial memory paradigm, activations in the MTL associated with the formation of memories rated as confident were higher in young, compared with older, children (Maril et al., 2010). The apparent inconsistency regarding developmental findings in the MTL can diminish when taking into account that across studies, activations associated with memory were defined by different memory contrasts. Age-related decreases in MTL activation are reported when contrasting hits with misses (Maril et al., 2010). Age-related increases are reported when making a more specific contrast, between detailed hits and non-detailed hits (Ghetti et al., 2010). The contrast of non-detailed hits versus misses in Ghetti et al. (2010) can be taken to reflect age-related reduction in MTL activations, as activation for non-detailed hits are greater than activations for misses in children, but not in adults. This latter contrast (non-detailed hits > misses) is somewhat similar to the contrast in Maril et al. (2010) that compared hits (high confidence, but for which the amount of detail in memory was not assessed) versus misses (Maril et al., 2010). These comparisons allude to the importance of considering specific memory contrasts when drawing conclusions regarding developmental trends. Thus, reports of age-related reductions in MTL activations may arise in paradigms that do not directly assess the specificity of memory formation (Maril et al., 2010; Menon et al., 2005). Furthermore, if indeed contrasts that tap memory selectivity show age-related increases in MTL activations, and contrasts that tap a more general, less selective memory process show age-related decreases in MTL activations, contrasts that combine selective and less selective memory effects may not show any measurable age-related effects (Ofen et al., 2007). The evidence to support the suggestion above is, however, still limited. Future explorations will provide valuable insight about whether developmental effects in the MTL play a specific role in the creation of detailed memories.

Second, the role of novelty versus familiarity along the long axis of the MTL may also be relevant in the context of interpreting

developmental findings. There are clear age-related increases in the involvement of posterior portions of the MTL in memory formation (Chai et al., 2010; Wendelken et al., 2011). Thus the differential maturational trajectories shown in structural imaging data (Gogtay et al., 2006) may have functional relevance. Future studies can explore whether there are different developmental effects in anterior versus posterior portions of the MTL during memory formation.

Third, the effect of specific materials on developmental effects in MTL contributions to memory formation has not been tested directly. Comparisons across studies indicate that this dimension does not explain the inconsistent developmental trends in the MTL; a decline of MTL activations associated with memory formation was found for encoding of both pictorial-verbal (Maril et al., 2010) and pictorial (Menon et al., 2005) materials. An open question is to what extent developmental effects may be accounted for by varying levels of pre-experimental familiarity with these materials.

6. Developmental effects in content-sensitive brain regions and growth in knowledge

Memory processes do not exist in isolation; rather, they operate on a person's knowledge structures, and the effects of knowledge on memory performance have been extensively considered in the past (Chi and Ceci, 1987; Lindberg, 1980; Ornstein and Naus, 1985). In the domain of semantic knowledge, for example, more elaborate semantic associative networks may contribute to improvement in memory with age. Thus, limited knowledge or an immature network that represents knowledge may limit children's use of knowledge when compared with adults (Chi and Ceci, 1987). Applying a developmental cognitive neuroscience approach allows the examination of how age-related changes in knowledge influence memory formation. The following assumptions are needed for utilizing a developmental cognitive neuroscience approach to test the influence on knowledge on memory. The first assumption is that the neural correlates of knowledge may be associated with activations in brain regions that are known to be sensitive to specific content. The second assumption is that developmental changes in activations in content-sensitive brain regions may be seen as the neural correlate of growth in knowledge. By accepting these assumptions, one may examine the link between developmental changes in knowledge (as measured by activations in content-sensitive brain regions) and developmental changes in memory formation (as measured by subsequent memory effects). If the representation of certain types of knowledge in a child's brain is limited compared with that of an adult, it may lead to reduced ability to form memories of such knowledge; conversely, if children and adults have the same knowledge representation, they may have equal ability to form new episodic memories that build on that knowledge. Two recent studies demonstrate the potential of applying this approach to test the interaction between growth in knowledge base and memory (Chai et al., 2010; Maril et al., 2011).

Memory for high-level visual stimuli such as natural scenes and faces grows from childhood through adolescence into young adulthood (Diamond and Carey, 1977; Mandler and Robinson, 1978), and this development of memory ability has been associated with the development of cortical areas that are specialized for visual perception of scenes and faces (Chai et al., 2010; Golarai et al., 2007). Specifically, functionally defined scene-selective posterior parahippocampal gyrus (PHG) known as the 'parahippocampal place area' (Epstein and Kanwisher, 1998) grows in size from childhood through adulthood, and this growth in size correlates with recognition memory for scenes. We recently showed that complex scenes (scenes that depict more than four unique item categories), are remembered better by adults compared to children, and that

this development is linked to age-related increases in the functional representation of complex scenes in the posterior PHG. Critically, age-related increases in subsequent memory activations in the same posterior PHG region show age-related increases in the functional representation of scene complexity (Chai et al., 2010). These age-related increases in subsequent memory activations are specific for detailed memories of complex scenes, as there are no age-related changes associated with detailed memory of low-complexity scenes, or either detailed or non-detailed memory of simple scenes. The relation between prolonged maturation of detailed memory for complex scenes and prolonged maturation of high-level representation in the brain support the notion that limited knowledge representation in a child's brain can lead to reductions in memory formation. The selectivity of these results for complex, detailed memory further supports the notion that if children and adults have the same knowledge representation they form equal memories. The nature of age-related increases in the knowledge representation of complex scenes (Chai et al., 2010) can reflect increased accessibility of detailed representations or improved processing of the spatial relations among the objects.

Maril et al. (2011) provide another elegant example of using a cognitive neuroscience approach to investigate the influence of knowledge on memory. These authors used an encoding task that taps semantic knowledge structures and found that for successful encoding, adults rely on frontal and parietal structures, whereas children depend more on posterior perceptual systems. Based on these findings, the authors suggest that children encode a detailed visual representation of the to-be-remembered information, whereas adults use their extensive semantic knowledge base to encode an a-modal conceptual representation of the information. Such inventive designs are informative in elucidating possible underlying mechanisms that contribute to the development of memory.

Both studies capitalize on a link between specific knowledge representations in the brain and subsequent memory effects for this knowledge. A common assumption in these studies is that changes in knowledge base may have a 'physical' signature in the neural correlates of a specific knowledge type. The neural correlates of scene complexity or semantic congruency are certainly not a direct measure of knowledge and do not directly reflect the developmental growth in knowledge base. However, these findings illustrate a first step in utilizing a cognitive neuroscience approach towards understanding how the growth in knowledge through development is an important factor in boosting memory ability.

Sections 4 and 6 separately considered effects of growth in the use of strategy and growth in knowledge without considering the important interaction between these factors. Neuroimaging may offer a unique way to test these possibilities. For example, advances in methods of imaging the brain's functional connectivity may be useful for delineating the developmental trajectories of cooperation between the prefrontal cortex, content-sensitive brain regions, and the MTL.

7. Open questions for future research

In attempt to create a framework for the cognitive neuroscience of memory formation, researchers are building on findings from developmental psychology, cognitive neuroscience of memory, and brain development. The future challenge is how the integration of these efforts will be useful and will produce insights that will further our understanding of the cognitive neuroscience of memory and will provide implications both for education and clinical situations.

7.1. Methodological frontiers

Pediatric neuroimaging is challenging in many respects. A number of feasible goals are yet to be met by future research. First, to date, all studies of the neural correlates of memory development used cross-sectional samples, and thus comparisons across age are also comparisons across individuals who differ from one another not just with respect to age. Testing how a specific child's memory ability changes over the course of development, and how these changes relate to functional and structural changes in that individual's brain, is important not only for increasing the power to detect developmental changes, but in order to dissociate non-developmental factors that differ across children (such as intelligence) from maturational factors. Indeed, the use of longitudinal designs has yielded new insights into typical structural brain development (Gogtay et al., 2006). Future studies will test the utility of a similar approach in functional brain studies of memory development.

A second feasible goal for future research is expanding the age range of participants to include younger children. The current age range of participants tested in fMRI studies is limited (the youngest participants in the studies reviewed here were 7 years old). Robust developmental changes in memory organization and in brain structures assumed to support memory are believed to occur before middle childhood (Bauer, 2008; Nelson et al., 2006; Romine and Reynolds, 2004), suggesting that dramatic developmental changes in the neural correlates of memory formation may be seen when younger children are tested. Evidence from other cognitive domains, such as reading and executive control, suggest that some developmental effects are best characterized as reorganizational changes in the brain's functional networks that support these cognitive domains (Berl et al., 2006). With respect to memory development, the idea that reorganization occurs after middle childhood is supported by the findings of Ghetti et al. (2010). Alternatively, it is possible that developmental changes reflect gradual growth in the magnitude and flexibility in using those systems (Gathercole, 1998). Testing children younger than 7 years old may possibly reveal reorganization that occurs in younger ages. Support for the notion that the organization of memory systems may be flexible and undergo robust changes in younger participants is provided by evidence from developmental amnesia. Patients that suffered an insult to the MTL early in life differ from adult amnesiacs that suffered insult to the MTL later in life. While adult amnesiacs often demonstrate episodic and semantic memory impairments, only episodic memory is impaired in developmental amnesia (Gadian et al., 2000; Vargha-Khadem et al., 2001, 2003). Although the evidence from developmental amnesia suggests that episodic memory requires an intact MTL early in life, the sparing of semantic memory suggest some flexibility in the development of memory systems early in life.

Third, a goal for future research is a better characterization of individual variability in memory abilities. Currently, individual variability is largely ignored as noise in the measurement, as is expected in the initial steps of understanding the neural correlates of memory development. In the future, specific manipulations can test contributions of cognitive processes, including speed of processing, working memory, and other executive control tasks, and the growth in knowledge base by designing experiments that attempt to isolate prior knowledge (introduce a set of previously unknown stimuli) and training (repeated presentation of those stimuli).

7.2. Gaps in understanding multiple aspects of memory

Very little is known about the neurocognitive development of many important aspects that contribute to memory development.

These important aspects include: memory in real-life context such as eyewitness testimonies, and autobiographical memory (Pathman et al., 2011); metamemory, the knowledge about memory functioning, limitations, difficulties and strategies (Brown, 1975; DeMarie and Ferron, 2003); and the influence of social context on remembering (Ornstein et al., 2004). Reviewing the current literature on the neural correlates of memory formation provides little opportunity to address developmental trends in these domains. Further studies are needed to test a cognitive neuroscience approach to investigate the influence of basic (e.g., speed of processing) and more 'higher-order' (e.g., metamemory) cognitive operations on the development of memory. Along these lines, it is important to note that this review is focused on testing memory development in a laboratory-based setting. For a complete understanding, one would have to consider developmental effects in memory of naturalistic experiences as well as memory as assessed in experimental tasks (e.g., lists of words or pictures).

7.3. Network approach to the development of memory formation in the brain

Little is currently known about connectivity within the brain's memory that supports memory formation. Analysis of both functional and structural brain connectivity is an active research program in adults (Kahn et al., 2008). Such exploration is important, considering the mounting evidence documenting developmental trends in functional brain connectivity (Fair et al., 2009, 2007). Current efforts in developmental cognitive neuroscience are addressing network change, rather than a change in single regions, or nodes of such network. This notion is relevant in considerations of memory development. For example, the influence of strategy is likely to be exerted by top-down modulation of mnemonic processes subserved by the MTL.

8. Concluding remarks

Applying a cognitive neuroscience approach to the rich behavioral study of memory development has thus far yielded a number of insights beyond what behavioral methods alone have offered previously. Memory development can now be linked to specific changes in memory systems in the brain. Overall, changes in the prefrontal cortex are related to changes in applying and using strategies efficiently. The developmental changes in mnemonic processes associated with the MTL are more complex, partially due to the debates about the specific nature in which the MTL support memory in the adult literature. Finally, the growth in knowledge base can be related to developmental changes in brain regions that process specific content, and the influence of these can now test how changes in the neural representation of knowledge influence memory. Developmental findings may offer insights to clarify and constrain these debates and further our understanding of the neural underpinnings of memory.

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