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Chapter 17

Memory: Normative development of memory systems

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Abstract

During the past decades, abundant behavioral, clinical, and neuroimaging data have shown several memory systems in the brain. A memory system is a type of memory that processes a particular type of information, using specific mechanisms, with distinct neural correlates. What we call memory is therefore not a unitary capacity but a collection of distinct systems. From a developmental perspective, each memory system has its own developmental course. This explains the heterogeneity of children's mnemonic competencies: for example, 3-year-olds learn many new words and concepts every day but have trouble recalling in detail an event that happened the week before. In this chapter, we sum up major findings regarding the development from infancy to early adulthood of the main memory systems. Specifically, we report recent data regarding the development of declarative memory (i.e., episodic and semantic memory), and the relationship between the maturation of their neural correlates and the phenomena of infantile and childhood amnesia. We conclude by indicating some of the possible avenues for future research.

INTRODUCTION

Memory is essential to the tremendous amount of learning that takes place during childhood. Learning how to walk, talk, perform arithmetic operations, and navigate through the norms of the social world all rely partly on the brain's ability to retain information. Abundant behavioral and neuroimaging data have demonstrated that "memory" is not a unitary capacity. These works referred to "memory systems" as encompassing a collection of related abilities. This plurality of mnemonic competencies is observable in behavior. Remembering how to ride a bike feels like a "childhood memory experience" different from recalling the name of the president of the United States, or recalling what has just been read. Crucially, differences at the neural level, which are often dissociable according to the different memory systems, correspond to these behavioral differences (e.g., Squire, 2004, 2009; Cabeza and Moscovitch, 2013; Squire and Dede, 2015).

From a developmental perspective, each memory system has its own developmental course. This explains the heterogeneity of children's mnemonic abilities: for example, 3-year-olds learn many new words and concepts every day, but have trouble recalling in detail an event that happened the week before. This chapter sums up major findings regarding the development of distinct memory systems from infancy to early adulthood and concludes by indicating some of the possible avenues for future research. Following the influential taxonomy of Squire and Zola (1996), Squire (2004, 2009), and Squire and Dede (2015) (see Fig. 17.1), the first distinction is between short-term memory, which refers to retention of information over short time spans limited in capacity, and long-term memory, which is theoretically unlimited in capacity and can retain information over the course of a lifetime. Long-term memory is moreover divided into nondeclarative (implicit) memory, i.e., unconscious mechanisms of information retention, and

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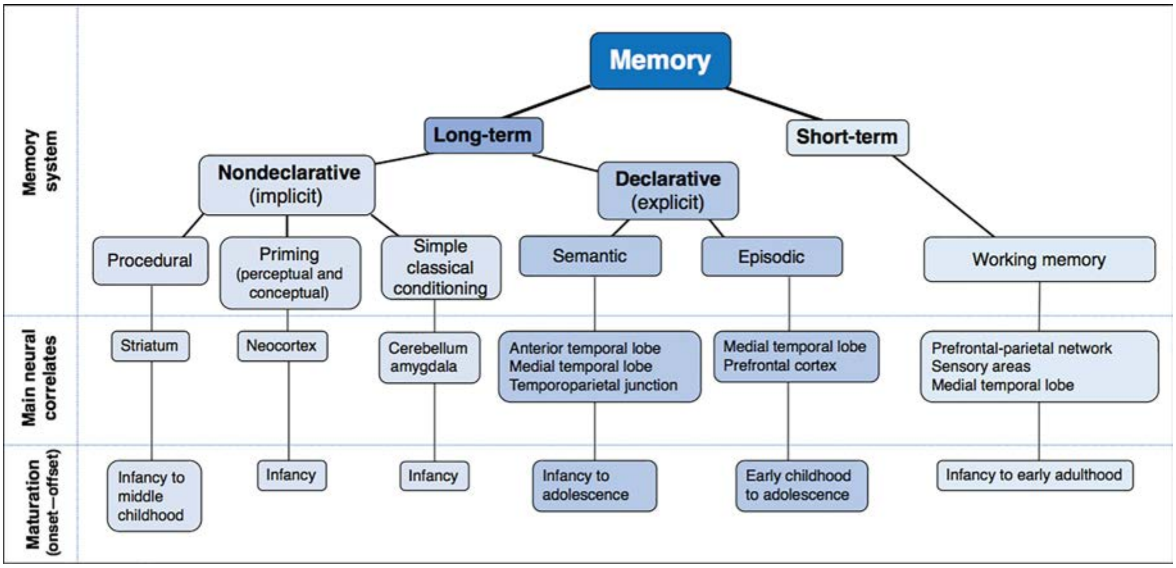

Fig. 17.1. A taxonomy of memory. The main neural correlates and the putative maturational onset and offset are indicated for each memory system. These figures are original work from the authors. This taxonomy of memory is modified from Squire, L. R., Zola, S.M., 1996. Structure and function of declarative and nondeclarative memory systems. *Proc Natl Acad Sci* 93, 13515–13522.

declarative (explicit) memory, i.e., mechanisms of voluntary encoding and recall of information. Finally, long-term declarative memory is split into two separate entities: semantic memory (world knowledge) and episodic memory (memories of specific events).

DEVELOPMENT OF SHORT-TERM AND WORKING MEMORY

As the constructs of short-term memory and working memory are closely related, confusion between the two is not uncommon. The working memory system was initially popularized by Baddeley and Hitch (1974), who demonstrated that visuospatial and verbal information could be held simultaneously in short-term memory with limited impact on their respective retention. In other words, the combined quantity of verbal and visuospatial information that one can memorize over short-term delays greatly exceeds the quantity of only verbal or only visuospatial information that one can memorize over an equivalent delay. To account for this specialization in short-term memory, Baddeley and Hitch proposed a model that comprises two modules for short-term retention of information: one dedicated to verbal-phonologic stimuli (the phonologic loop), and another dedicated to visuospatial stimuli (the visuospatial sketchpad). These two modules are managed by a third one, the central executive, which controls short-term memory modules by maintaining, for example, the stored information or manipulating its relevant features. Numerous models of working memory have been proposed since this original account (e.g., Cowan, 1998; Miyake and Shah, 1999; Baddeley, 2000; for a review, see Cowan, 2010, 2016), sometimes adding new components (e.g., Baddeley's (2000) episodic buffer mediating short-term and long-term memory processes). However, all agree that working memory is multifaceted, involving short-term storage and executive control.

Working memory in infants

Here we refer to the maturation of working memory as describing the maturation of the capacity to store information over short-term spans and the maturation of the ability to maintain and manipulate this information.

Working memory abilities become evident around 6 months of age and increase dramatically between 6 and 9 months (Reznick, 2009). Preferences-to-novelty paradigms are typically used to investigate visual working memory in infants. They infer retention of information indirectly, based on differences in gaze duration of infants presented with either new stimuli or previously seen stimuli; the underlying assumption is that infants prefer to look at novel stimuli as compared to those already seen. Studies using variations of this paradigm demonstrated that 6-month-old infants remember the characteristics of a single visual item over short-term delays, and that 9-month-old infants can maintain the representation of 3–4 visual items simultaneously in the dedicated short-term module (Káldy and Leslie, 2003, 2005; Ross-Sheehy et al., 2003; Oakes et al., 2006, 2011). The dramatic increase in working memory capacity between 6 and 9 months of age surprisingly suggests adult-like capacities of 3–4 different "memory slots" available to store short-term representations (Cowan, 2010). However, the infant's working memory is far from reaching maturation. One of the main processes that allows a volume of information to be maintained in memory while still using a few available memory slots is the ability to mentally reorganize information in order to store representations not just of individual items, but also of groups, or "chunks." This strategy is commonly used by older children and adults, but not infants, unless they are provided with specific cues (Moher et al., 2012). This suggests that the ability to "chunk" items together starts to be observable in infancy without specific training and is strongly related to improvements of working memory capacities further in the lifespan (Rosenberg and Feigenson, 2013).

The neural correlates of working memory in school-aged children and adults are well known and imply a prefrontal-parietal network that supports executive processes (Courtney et al., 1997; Klingberg et al., 2002; Kwon et al., 2002; Nagy et al., 2004; Klingberg, 2006). Retention of information occurs in sensory regions in a modality-specific manner, as the regions involved in the perceptive processing of an object are also involved in the retention of the representation of that object in short-term memory (D'esposito and Postle, 2015; Eriksson et al., 2015). There is also evidence that medial temporal lobe regions, which are typically associated with long-term memory, are involved in working memory as well (Ranganath and Blumenfeld, 2005; Axmacher et al., 2007; Baddeley et al., 2011). Because neuroimaging methods suited to infants (such as EEG) do not have a high spatial resolution, it is unclear if the correlates of working memory during infancy considerably differ from those observed in children and adults. However, there is evidence that improvement of working memory during infancy is correlated to the maturation of white matter tracts that connect parts of the frontal, prefrontal, parietal, and temporal cortices, suggesting similar neural correlates to those observed in later development (Short et al., 2013). The cerebral bases of working memory are hence likely online early in development and their maturation supports later improvements in the lifespan.

Development of working memory from childhood to adulthood

Infant studies suggest that 9-month-old infants have a remarkable working memory, being able to maintain four representations simultaneously in a short-term memory module. This performance contrasts with that of 3–4-year-olds, who can only maintain the representation of 2–3 items (Simmering, 2012). This paradoxical apparent decrease of cognitive capacity during the infancy-to-childhood transition was expressed by Keen (2003) in the following words: "Why do infants look so smart and toddlers look so dumb?" As discussed by Cowan (2016), the explanation may be of a methodologic nature. Results obtained in infant and children populations have poor comparability. Children have access to strategies for information retention (like counting) that infants do not possess, thus limiting the use of infants' working memory protocols in young children. Paradigms specific to children are thus much more demanding (verbally or pressing a button, for instance) than those used with infants, in which participants must give their answer actively, and the response is inferred indirectly. Therefore, the contrast between the rapid improvements during infancy and the slower improvements in early childhood may reflect methodologic discrepancies rather than true developmental processes.

The apparent slowed development of working memory abilities during the infancy-to-childhood transition is nonetheless followed by a rapid increase from midchildhood to midadolescence. During this period, the ability to store information during short delays for later processing is augmented considerably, regardless of the type of information to be stored and the executive demands of the task (Gathercole, 1999; Luciana et al., 2005; Gilchrist et al., 2009; Sander et al., 2011; Heyes et al., 2012, 2016). Functional magnetic resonance imagery (fMRI) studies pinpoint that these improvements are related to the functional maturation of the prefrontal and parietal regions (e.g., Casey et al., 1995; Klingberg et al., 2002; Kwon et al., 2002; Crone et al., 2006; Klingberg, 2006). These functional changes are also concomitant to structural maturation, as gray matter volume peaks in the prefrontal and parietal cortices between 10 and 14 years of age, before a later decrease (Lenroot and Giedd, 2006; Kharitonova et al., 2013; Tamnes et al., 2013). Working memory improvements from midchildhood to midadolescence thus likely benefit from increasing executive control abilities. From late adolescence to early adulthood, further, although slower, improvements can be observed in working memory abilities. Evidence from longitudinal fMRI or diffusion tensor imaging (a technique that describes white matter tracts) studies shows these later improvements are related to an increased activity in the sensory regions, but not in the prefrontal or parietal cortex (Darki and Klingberg, 2014; Simmonds et al., 2014, 2017; Ullman et al., 2014). Increases in working memory capacity from adolescence to adulthood could thus be driven by a more efficient storage of short-term representation in modality-specific sensory regions rather than by an improvement of executive control.

DEVELOPMENT OF NONDECLARATIVE MEMORY

Nondeclarative memory (or implicit memory) refers to long-term retention of information occurring in the absence of conscious memory content. It is measured through performance (as an indicator of retention) rather than through recollection, meaning that nondeclarative memories are formed and recalled without the consciousness of forming them or recalling them. As such, nondeclarative memory "provides for myriad unconscious ways of responding to the world" (Squire and Dede, 2015, p. 3). The dissociation between declarative and nondeclarative memory is evident during development. Overall, nondeclarative memory reaches maturity early in life while declarative memory follows a protracted development during childhood. Developmental differences for nondeclarative memory are relatively small compared to a much more important age-related variability in declarative memory (Schneider, 2014). In this section, we classify kinds of nondeclarative memory into four main categories, partly based on Squire and Zola's (1996) taxonomy: simple classic conditioning, procedural memory, perceptual priming, and conceptual priming.

Simple classic conditioning

Simple classic conditioning consists of learning the temporal association between a neutral stimulus (called a conditioned stimulus, CS) presented before an unconditioned stimulus (US) that will trigger an emotional (for example, in fear conditioning) or motor (for example, in eyeblink conditioning) response. After a repeated exposure to the CS–US, the presentation of the CS alone, without being followed by the US, will trigger the emotional or motor response normally caused by the US. Classic conditioning relies on the amygdala for emotional responses and on the cerebellum for motor responses. The cerebellum and the amygdala are both phylogenetically ancient and among the first cerebral structures to mature during ontogeny. They are fully developed in the first months of life (Nelson, 1995), explaining why no age-related improvements are found afterwards.

Procedural memory

Procedural memory refers to cognitive and sensorimotor habits and skills learned through repetition. The repetition of an activity leads to the progressive consolidation of the memory trace of the involved skills, leading to their automatization. It is involved in daily activities such as learning to tie shoes, ride a bike, or drive a car. In the laboratory, procedural memory is typically studied through serial reaction time (SRT) paradigms in which the reaction time in a simple motor task (pressing a button) is measured. Diminution of the reaction time with repetition of trials is an indicator of the procedural learning of the task. There is conflicting data regarding maturation of procedural memory. On the one hand, Meulemans et al. (1988) examined differences in procedural memory performance between children 6 years old and 7 years old and adults with an SRT task; they reported no significant differences in procedural memory performance between the children groups, or between the children and adult groups. In a similar fashion, Finn et al. (2016) compared declarative and procedural memory between 10-year-old children and adults and found age-related improvement of declarative, but not of procedural, memory. On the other hand, Thomas et al. (2004) examined procedural memory performance of children between 7 and 11 years old and procedural memory performance of adults, finding significant differences between children and adults. Lum et al. (2010) used a longitudinal protocol examining both procedural and declarative memory in children 5-and-a-half years old with an SRT task, and then of these same children 1 year later. They found age-related increases for declarative and for procedural memory. However, the magnitude of age-related performance increase was more important for declarative than for procedural memory, suggesting a maturation of the latter through middle childhood, albeit in a modest way. Overall, behavioral and neuroimaging data suggest that procedural memory is relatively stable at least after late childhood. Subtle developmental differences may be observed in procedural memory skills after that point, but these changes are far less important than what is observed in declarative memory. It is not clear, however, at which precise point in development procedural memory's maturation stabilizes. The neural correlates of procedural memory are the basal ganglia, in particular the dorsal striatum (comprising the caudate and the putamen) and the cerebellum. While the cerebellum reaches maturation early in the lifespan (Nelson, 1995), several studies have shown a maturation of the dorsal striatum through adolescence (Larsen and Luna, 2015; Peters and Crone, 2017). Further research is necessary to describe potential age-related changes or invariancy in procedural memory in behavior and its relation to cerebral maturation.

Perceptual priming

Perceptual priming is when the perception of a target stimulus is influenced by the prior perception of a prime stimulus. For instance, in word-stem completion tasks, exposure to a prime (e.g., WO___) facilitates the reading of the target word (e.g., WORD). As formulated by

Squire and Dede (2015, p. 7), the effect of priming "is experienced as part of perception, as perceptual fluency, not as an expression of memory." Evidence of perceptual priming has been found in 6-month-old infants (Webb and Nelson, 2001; see also Vöhringer et al., 2018), showing that this effect appears early in development. Regarding its maturation through development, most studies have concluded that it is developmentally invariant, finding similar perceptual priming responses between younger and older children, and between children and adults (see Lloyd and Newcombe, 2009 for a review). However, as noted by Schneider (2014, Chapter 3), no studies examined perceptual priming from infancy to childhood using a paradigm that would allow comparability of performances across age. It is thus not possible to conclude a true developmental invariancy of perceptual priming in the state of current findings.

Conceptual priming

Conceptual priming is the facilitation of the semantic processing of a word (e.g., access to the meaning of that word) caused by prior exposure to a semantically related word. For instance, it is easier to access the meaning of the word "cat" after having been exposed to the word "dog," as both share the same "animal" semantic category. This is believed to occur because of coactivation mechanisms between words that share the same semantic network. Activation of a word in this semantic network by its presentation to a reader leads to an activation of surrounding words in this network. Hence, subsequent processing of these related words is facilitated. There is evidence of conceptual priming in infants. For example, Arias-Trejo and Plunkett (2009) used an intermodal preferential looking task in which word pairs were used to direct attention to a target picture. The target pictures were either semantically associated with the prime words, or unrelated. As reported, 18-month-old infants looked more at target pictures after they were exposed to related prime words, suggesting an early development of semantic-lexical links between lexical items through a conceptual priming effect. Conceptual priming has also been found using auditory stimuli in infants of 21 months (Willits et al., 2013). The early presence of conceptual priming suggests that it may be the reliable by-product of the cognitive structure of semantic knowledge. Regarding age-related change in conceptual priming effects, Barry (2007) compared perceptual and conceptual priming between 7- and 8-year-olds and college students and found a significant difference only in the conceptual priming task, with facilitation of semantic processing more important for college students than for children. However, several other studies showed no age-related effect on conceptual priming (Anooshian, 1999; Billingsley et al., 2002). Overall, it seems that age-related improvements are observed in conceptual priming when an advanced semantic knowledge base is necessary for succeeding at the task, but not otherwise (Mecklenbräuker et al., 2003; Lloyd and Newcombe, 2009); the mechanism of conceptual priming itself thus appears to be more or less age invariant (see Schneider, 2014).

DEVELOPMENT OF DECLARATIVE MEMORY

Declarative memory (or explicit memory) is a long-term memory system dedicated to the conscious recollection of information. It is divided into semantic and episodic memory, respectively, based on the generality or specificity of the recalled information. Semantic memories are general, as they do not come within the context in which they are formed. Episodic memories are about a specific event and the context in which this event took place. For instance, recalling factual information (e.g., that Paris is the capital of France) or conceptual information (e.g., the definition of the word "capital") are semantic memories; recalling the particular context in which this information was learned (e.g., the moment in the classroom) is an episodic memory.

The original definition of episodic memory by Tulving (1972, 1985, 2002) focuses on personal/autobiographic events. It defines episodic memory as the memory for events in one's personal past and stresses that the possibility to reexperience these events mentally is one of its defining features. Since Tulving's account, episodic memory has been more broadly defined as the ability to recall specific and contextual information that can be personal or not. Protocols used in the laboratory typically involve the retention of impersonal information (like recognizing visual items after a varying delay) and often focus on describing specific episodic memory processes, like binding information into a unique representation (relational memory) or recalling the source of learned information (source memory) (e.g., see Newcombe et al., 2007; Olson and Newcombe, 2013; Keresztes et al., 2018). In all cases, a consensual definition of an episodic memory can be formulated as follows: it is a long-term mnemonic representation of a unique event that binds together different kinds of information, which can be factual (what happened), perceptual (what was perceived), spatial (where it took place), temporal (when it took place), cognitive (what one thought), and so on.

In this section, we present evidence regarding early development of declarative memory and discuss the development of the semantic and episodic memory systems.

Early declarative memory abilities

A few days after birth, infants are able to recognize highly familiar stimuli, such as the voice or the face of their mother, showing that they can compare sensory data with representations stored in long-term memory (DeCasper and Fifer, 1980; Bushneil et al., 1989; Mullally and Maguire, 2014). Around the end of the first year of life, there is evidence of a stark increase in the infant's capacity to memorize new information over long-term delays. Deferred imitation paradigms are good nonverbal tests of declarative memory, and, as such, are typically used to test declarative memory early in the lifespan (e.g., Carver and Bauer, 2001; Bauer et al., 2003). They consist of showing novel sequences of actions, enacted by props, to infants. Infants are provided with these props after a varying delay; if they recreate the sequence of actions, they are thought to have recalled the event. While half of 6-month-old infants can recall a sequence of events after a 24h delay, most 9-month-old infants can recall it after 1 month, and 10-month-old infants after a delay of up to 6 months (Carver, 1999; Carver and Bauer, 2001; Bauer et al., 2003). Therefore, as for working memory, a strong increase in declarative memory competencies is observed between 6 and 9 months of age, approximately.

Declarative memories are formed by infants, but it is not clear if they are semantic or episodic. Infants' success at deferred imitation tasks could be explained either by their recall of the moment they watched the sequence of actions (an episodic memory), or by a general feeling of knowing how to perform the sequence of actions with the props they are provided (a semantic memory) (Mandler, 2004; Raj and Bell, 2010). To some authors, early declarative memory is most likely semantic (Mandler, 2004), a claim that is supported by evidence that infants and young children have superior abilities for recalling general factual information than for recalling the specific features of an event (for a discussion, see Keresztes et al., 2018). On the contrary, other authors consider that nonverbal paradigms show evidence of episodic-like memories among infants in their second year of life (Lukowski et al., 2011; Bauer, 2015a). In all cases, it is later in development, after the acquisition of language, that it becomes possible to distinguish without ambiguity the episodic or semantic nature of these declarative memories, i.e., to assess their specific or general character.

Development of semantic memory

Tremendous numbers of facts and concepts are learned during the first years of life (Newcombe et al., 2007). Early semantic knowledge is robust: toddlers do not forget highly familiar semantic information, like their name, where they live, who their parents are; and they are extremely good at memorizing novel semantic knowledge, as illustrated by the acquisition of language. Semantic knowledge is highly organized in the cognitive system: facts and concepts are parts of networks in which they can be related to each other based on thematic relations (cooccurrence in events or scenarios) or taxonomic relations (sharing of semantic features). For instance, the words "leash," "bone," and "dog" are thematically related (they cooccur frequently in representations of dogs), while "whale," "pigeon," and "dog" are taxonomically related (they are part of the same "animal" category) (Mirman et al., 2017). A 2-year-old can explicitly make thematic relations between different items, and taxonomic relations are observable around 3 years old (Fenson et al., 1989). Although there are conflicting findings in the literature, it seems that children have an overall preference for thematic relations, while taxonomic relations are more common in later development (Smiley and Brown, 1979; Murphy, 2001; Favarotto et al., 2014). In adults, there is moderate evidence that these two kinds of relations might have distinct neural correlates, namely the temporoparietal cortex for thematic relations and the anterior temporal lobe for taxonomic relations (Lewis et al., 2015; Mirman et al., 2017). These regions might act as "hubs" responsible for relating, either thematically or taxonomically, distinct semantic fact and concepts, which are known to be widely distributed across the brain (Martin and Chao, 2001; Price et al., 2015). Studies in adults also identified the importance of the prefrontal cortex for monitoring the encoding and retrieval of semantic information (e.g., Prince et al., 2007). Surprisingly, in children, the cerebral bases of semantic memory have not been a major topic of interest in the scientific literature. The overall paucity of data regarding developmental differences of the neural correlates of semantic memory may suggest limited changes, but this claim remains putative in the absence of more research. In particular, it is unclear how cerebral maturation is related to the multiplication of more complex (i.e., taxonomic) semantic relations through development.

The robustness of semantic memory during childhood contrasts with the fragility of early episodic memories, as specific details of events are rapidly forgotten by young children (see section on episodic memory infra). This leads to the question regarding the interaction between these two kinds of declarative memory: does episodic memory maturation rely on that of semantic memory, or do both develop simultaneously, building on each other? The dissociation between the semantic and episodic memory systems is observable early in the lifespan. Developmental amnesia is a pediatric condition in which hippocampal damage causes a severe impairment of episodic memory but leaves semantic memory competencies intact (Elward and Vargha-Khadem, 2018). As discussed by Newcombe et al. (2007), even when hippocampal damage occurs at birth, patients can normally learn factual knowledge during infancy, so that memory impairments become noticeable only when they reach school age. This suggests that semantic memory likely develops before episodic memory. This time-lag between episodic memory and semantic memory development could be developmentally advantageous, as early semantic memory competencies would allow children to learn regularities and patterns (as semantic knowledge is often general and context-less) before being able to recall specific details of events (for an in-depth discussion, see Keresztes et al., 2018). Evidence also exists that episodic memory performance depends on semantic memory competence in children. Robertson and Köhler (2007) showed that 4–6-year-old children's episodic memory performance is predicted by their semantic competency, regardless of the need to access semantic information at retrieval. Overall, it is likely that episodic memory maturation relies, at least partly, on the development of semantic memory.

Development of episodic memory

Evidence suggests that the cognitive development of episodic memory is multistepped: improvements are not linear but delineate distinct periods separated by qualitative transitions (see Newcombe et al., 2007). The most striking evidence for a multistepped development of episodic memory comes from infantile and childhood amnesia. Infantile amnesia refers to the absence of recall, by adults, of personal memories that occurred before the age of 2. Childhood amnesia refers to the scarcity of personal memories that occurred between the ages of 2 and 6 that can be recalled by adults. These phenomena have been known for a long time (e.g., Strachey, 1953) and were demonstrated experimentally by studies asking participants to recall personal memories, regardless of their age at the time of the event: the temporal distribution of thousands of memories recalled by hundreds of participants showed that very few occurred between the ages of 2–6 years old (childhood amnesia), and that none occurred prior to the age of 2 (infantile amnesia) (Rubin, 2000; Newcombe et al., 2007; Bauer, 2015b). The exact causes of infantile and childhood amnesia are not known and the similarity between the underlying mechanisms of these phenomena is unclear. Infantile amnesia could be explained by an absence of an episodic-like memory system during infancy. If the infant's early declarative memories are more semantic than episodic, then there are no specific memories to recall. Childhood amnesia, however, concerns a period during which children have rudimentary episodic memory abilities. In young children, the temporal distribution of recalled memories is explained by an exponential function, meaning that memories are forgotten exponentially as time passes. In older children and adults, "*equal ratios of time result in equal ratios of recall*" (Bauer and Larkina, 2014), meaning that memories are forgotten progressively according to the passage of time. Childhood amnesia is hence characterized by the rapid forgetting of early memories (Bauer, 2015a,b), while later in development, more robust and long-lasting memories are formed and recalled.

The multistepped development of episodic memory suggested by infantile and childhood amnesia is mirrored by several laboratory findings. As discussed, there is little evidence that infant's declarative memories are episodic, as they could lack the specificity that defines an episodic memory (see, however, Bauer, 2015a). At the age of 2, children can distinguish between two highly similar locations based on context, showing that they can form specific representations of a place, but perform poorly if they are not provided with cues (Newcombe et al., 2014). Three-year-olds can recall the factual (what happened), temporal (when it happened), and spatial (where it happened) details of an event after a brief retention interval (Hayne and Imuta, 2011; Scarf et al., 2013), but fail to recall temporal and spatial details after 24 h (Scarf et al., 2013). Important improvements of episodic memory competencies occur between 2 and 6 years old. Around age 6, some episodic memory abilities like recognizing single items, factual details, or simple relationships between items reach maturity (Newcombe et al., 2007; Picard et al., 2012; Ngo et al., 2018). After that point, more complex episodic memory abilities continue to improve until late childhood to adolescence, particularly memory for contextual details (e.g., location, temporal order, context) (Gulya et al., 2002; Picard et al., 2012; Guillery-Girard et al., 2013; Lee et al., 2016), or the ability to discriminate similar events (Yim et al., 2013). It hence seems that episodic memory is implemented in the cognitive system until age 6, and strengthens more slowly after that point, as the "building blocks" (Lee et al., 2016) of episodic memory are present but have not yet fully reached maturation (see Newcombe et al., 2007).

The hippocampus is crucial to episodic memory, as demonstrated by patients with hippocampal damage causing episodic memory impairments (Scoville and Milner, 1957; Tulving, 2002; Squire, 2009). It is the neural correlate of several episodic memory key processes, such as binding different contextual details into a single representation, or discriminating between similar representations (e.g., a typical day at school) to create novel and specific memories (Davachi, 2006;

Ranganath, 2010; Yassa and Stark, 2011; Olson and Newcombe, 2013; Keresztes et al., 2018). This structure is divided into several subfields (the subiculum, the dentate gyrus, and the cornu ammonis (CA) 1–4) that perform distinct neural computations for mnemonic function (Yassa and Stark, 2011; Keresztes et al., 2017, 2018; Schapiro et al., 2017). Because the distribution of these subfields is not similar between the anterior and posterior parts of the hippocampus (Gogtay et al., 2006), functional specialization and structural heterogeneity of the hippocampus are also observed along its anterior–posterior axis (Fanselow and Dong, 2010; Poppenk et al., 2013; Strange et al., 2014). Several studies showed that the volume of the anterior and posterior parts of the hippocampus follow distinct developmental trajectories from early childhood to adolescence, correlated with age-related improvements of episodic memory (DeMaster et al., 2013; Lee et al., 2014; Riggins et al., 2015, 2018; Keresztes et al., 2017; Canada et al., 2018; Tamnes et al., 2018). Most of these structural changes occur prior to the age of 6, suggesting a clear relation between hippocampal maturation and the emergence of episodic memory (Newcombe et al., 2007; Olson and Newcombe, 2013). Considering the multistepped development of episodic memory, infantile and childhood amnesia are likely related to hippocampal immaturity. Early episodic memories could be rapidly forgotten because the hippocampus is too immature to efficiently form, store, and recall them (e.g., Bauer, 2007; Newcombe et al., 2007). Another possibility is that early memories are still present in the brain but stored in an inaccessible form because of retrieval failure (Li et al., 2014). This claim is based on evidence that reexperience of an event by the proxy of cues consolidates mnemonic traces in animal models of early development. Finally, some authors propose a combination of the first two accounts, suggesting that early memories are inherently fragile because of hippocampal immaturity, leading to rapid forgetting, but are stored over the long term in a latent form (Alberini and Travaglia, 2017; see also Bauer, 2015b for a two-processes account).

Regarding the functional maturation of episodic memory, resting-state functional connectivity studies (Riggins et al., 2016; Blankenship et al., 2017) described an increasing integration of the hippocampus to neocortical regions during early childhood, in relation to memory performance (Riggins et al., 2016). Some task-based fMRI studies in children and adolescents found age-related increases of hippocampal activation and surrounding medial temporal lobe cortices during episodic encoding or retrieval (Ghetti et al., 2010; DeMaster and Ghetti, 2013; Pinabiaux et al., 2013; Sastre III et al., 2016; Bauer et al., 2017). However, most task-based fMRI studies converge to stress an increasingly important role of the prefrontal cortex (dorsolateral and ventrolateral regions) and the parietal cortex (posterior parietal cortex and precuneus) in episodic memory processes from midchildhood to adolescence (Gulya et al., 2002; Ofen et al., 2007; Paz-Alonso et al., 2008, 2009; for a review, see Ghetti and Bunge, 2012). Developmental changes in hippocampal-neocortical functional connectivity are also seen during this period in relation with memory development (Menon et al., 2005; Paz-Alonso et al., 2013; Qin et al., 2014). This likely reflects an increasing importance of top-down executive and attentional processes for encoding and retrieval of information, supported by the prefrontal and parietal cortices. These top-down processes are the main drivers of episodic memory maturation in its later development (Ghetti and Bunge, 2012).

Overall, behavioral and neuroimaging data suggest that the development of episodic memory follows three main steps (Fig. 17.2). Prior to the age of 2, there is no evidence of episodic memory abilities in the strict sense (infantile amnesia). From approximately 2–6 years of age, episodic memory starts to be evident but formed memories are forgotten rapidly (childhood amnesia). During this period, rapid hippocampal maturation drives the emergence of the building blocks of episodic memory. The hippocampus also starts to be more integrated to functional networks comprising neocortical regions. Then, from 6 years old to adolescence, the protracted maturation of the hippocampus and its increasing integration with hippocampo-neocortical networks (comprising medial temporal lobe, prefrontal, and parietal regions) drive the ability to form and recall episodic memories of increasing specificity over long-term delays.

CONCLUSIONS AND FUTURE DIRECTIONS

We would like to conclude this chapter by indicating some possible avenues for future research regarding the normative development of the memory systems.

Working memory

A major question concerns the infancy-to-childhood transition, as methodologic differences between paradigms suited to infants and young children do not allow a description of the developmental course of working memory during the toddler period. Research would benefit from behavioral paradigms tailored to measure working memory performances in these two populations by controlling the potential confounding factors that could explain young children's, but not infant's, performances, and conversely.

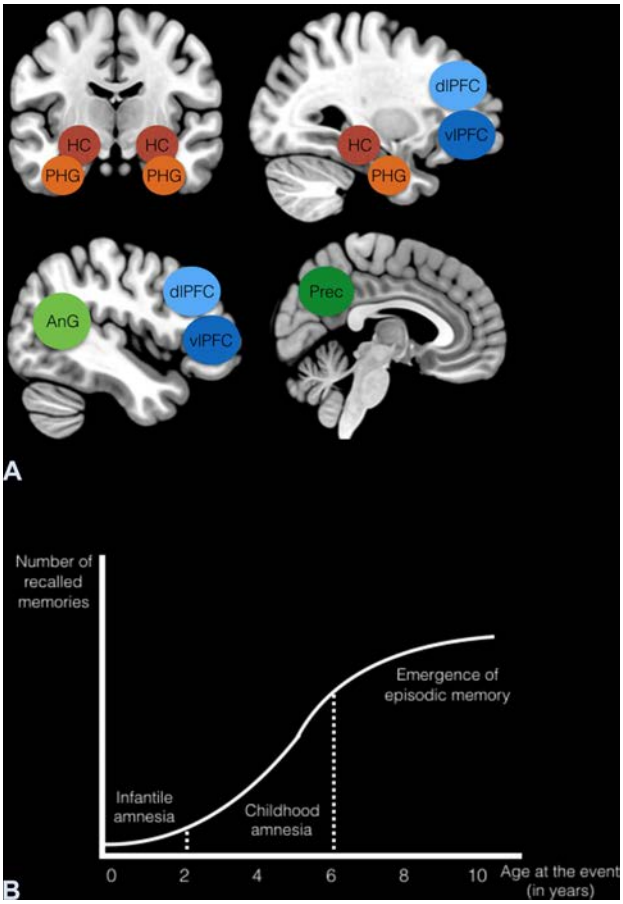

Fig. 17.2. (A) Main neural correlates of episodic memory. *HC*, hippocampus; *PHG*, parahippocampal gyrus, comprising the entorhinal, perirhinal, and parahippocampal cortices. The HC and PHC are both part of the medial temporal lobe. *dlPFC*, dorsolateral prefrontal cortex; *vlPFC*, ventrolateral prefrontal cortex; *Prec*, precuneus; *AnG*, angular gyrus. (B) Distribution of childhood memories recalled at adulthood. The distribution of childhood memories delineates three periods of episodic memory development: an absence of memories prior to 2 years old (infantile amnesia); a scarcity of memories occurring between the ages of 2 and 6 years (childhood amnesia); an adult-like number of recalled memories explained by the passage of time (emergence of the "building blocks" of episodic memory after 6 years old). These figures are original work from the authors. Panel B is a substantially modified version of a figure from Rubin, D.C., 2000. The distribution of early childhood memories. *Memory* 8, 265–269.

Nondeclarative memory

Further research is needed to describe the exact developmental courses of the distinct kinds of nondeclarative memory and the relation between what is observed at the behavioral and neural levels. In particular, the age at which procedural memory stops improving remains unclear.

Declarative memory

In adults, substantial evidence suggests that the episodic and semantic memory systems closely interact with each other. For example, recall of meaningful words is better than of nonmeaningful pseudowords, as the former undergo both episodic and semantic processing (Takashima et al., 2017). The current findings suggest that semantic memory develops earlier than episodic memory, but the relation between these two systems during the early years of life remains unclear. A better understanding of these relations would shed light on how early memories are formed. A related topic concerns infantile and childhood amnesia, whose underlying mechanisms are poorly understood. In the future, a combination of molecular/cellular (e.g., Li et al., 2014; Travaglia et al., 2016), psychologic/cognitive (e.g., Newcombe et al., 2007; Bauer and Larkina, 2014; Bauer, 2015b), and neuroimaging approaches (e.g., Bauer et al., 2017) could lead to a better understanding of these phenomena.

Interaction between memory systems

An important point of research concerns the relation between short-term and long-term memory, both episodic and semantic. Classic models of memory consolidation rely on the idea that representations in short-term memory are progressively consolidated to become long-term memories. However, recent data obtained in animal models suggest that long-term memory representations may, in fact, be formed shortly after an event but remain in a silent state for a few weeks (Kitamura et al., 2017). It is likely that models of memory consolidation over the coming years will be challenged in an exciting way. As such, an outstanding question concerns the relation between short- and long-term memory formation during early development.

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