



# The extended trajectory of hippocampal development: Implications for early memory development and disorder



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## ARTICLE INFO

### Article history:

Received 13 May 2015

Received in revised form 12 August 2015

Accepted 22 August 2015

Available online 25 September 2015

### Keywords:

Memory development

Hippocampus

Cortex

Sleep

Atypical populations

## ABSTRACT

Hippocampus has an extended developmental trajectory, with refinements occurring in the trisynaptic circuit until adolescence. While structural change should suggest a protracted course in behavior, some studies find evidence of precocious hippocampal development in the first postnatal year and continuity in memory processes beyond. However, a number of memory functions, including binding and relational inference, can be cortically supported. Evidence from the animal literature suggests that tasks often associated with hippocampus (visual paired comparison, binding of a visuomotor response) can be mediated by structures external to hippocampus. Thus, a complete examination of memory development will have to rule out cortex as a source of early memory competency. We propose that early memory must show properties associated with full function of the trisynaptic circuit to reflect “adult-like” memory function, mainly (1) rapid encoding of contextual details of overlapping patterns, and (2) retention of these details over sleep-dependent delays. A wealth of evidence suggests that these functions are not apparent until 18–24 months, with behavioral discontinuities reflecting shifts in the neural structures subserving memory beginning approximately at this point in development. We discuss the implications of these observations for theories of memory and for identifying and measuring memory function in populations with typical and atypical hippocampal function.

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## 1. Introduction

Research examining the development of children's memory has often demonstrated that infants and young children show early competencies in memory function, remembering some items and associations across long term delays. For instance, 2-month-old infants can remember a specific mobile for as long as 2 weeks if encoding occurs across three 6-min sessions (Rovee-Collier, 1999), and 5–6 month olds remember a face they encode for 2 min up to 2 weeks later (Fagan, 1973). Such findings have been attributed to an early-maturing hippocampus (Rovee-Collier, 1997) or the functions this structure may first subserve in its developmental course (e.g., Richmond and Nelson, 2009). However, early competency is in contrast to children's delayed explicit verbal memory for everyday events, which slowly develops, emerging in an immature form after 24 months and undergoing continued refinement until 7 years (Peterson et al., 2011; Rubin, 2000) and beyond (Ghetti and Bunge, 2012; Ghetti et al., 2010). For instance, although some

young children can remember a small number of salient events they experience before 24 months, children retain more memories with greater detail after this age (Peterson et al., 2011), consistent with a demarcation between early- and late-developing memories. Prior to 18–24 months most children fail to form lasting, everyday memories they can consciously recollect (but see Bauer, 2015). This is often referred to as the a period of “childhood amnesia”. Consistent with such findings some have suggested that early and late developing memories may reflect development of separate memory systems, including an implicit and explicit system (Schacter and Moscovitch, 1984). Nadel and Zola-Morgan (1984) first attributed the lack of episodic detail in young children's memories to the late trajectory of hippocampal development, suggesting that it would not be until this structure was fully developed that children would be able to show robust episodic recall. Given rapidly emerging knowledge of the development of the hippocampus and the surrounding cortex, researchers have begun to theorize how disparate memory processes may map onto changes in these neural structures (Bachevalier, 2014; Lavenex and Banta Lavenex, 2013; Olson and Newcombe, 2014). Here we expand on recent findings in behavioral memory development and how these results may reflect the development of the medial temporal lobe (MTL) versus hippocampus.

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In adults, an established body of research supports the existence of distinct learning and memory systems in the brain, e.g., the basal ganglia reward system supporting procedural memory (Knowlton et al., 1996), and the MTL supporting episodic and semantic memory (Eichenbaum and Cohen, 2001; Nadel and Hardt, 2011; Tulving, 1972). There are also distinct roles for substructures within these systems. Within the MTL, for instance, perirhinal cortex [PRC] supports object recognition, parahippocampal cortex [PHC] supports scene recognition, and the hippocampus supports relational memory in its capacity to bind information from PRC and PHC (Eichenbaum and Cohen, 2001; Diana et al., 2007). The subfields of hippocampus (CA fields 1–4 and dentate gyrus) are also thought to serve specific functions. Work from animal and human neuroscience has shown that the neurons of CA3 are specialized to perform pattern completion, the dentate gyrus (DG) supports pattern separation, and CA1 has been linked to representation of space and temporal sequence over repeated exposures (Bakker et al., 2008; Gilbert et al., 2001; Nakashiba et al., 2008). The subfields of the hippocampus have different retention functions as does cortex. Memories supported by CA3 and DG neurons form rapidly in as little as one exposure in contrast to CA1, which requires repeated exposures for memory formation (Nakashiba et al., 2008). Memories are also thought to emerge gradually in networks of cortical neurons (McClelland et al., 1995) supported by architectures with shallow retention profiles that require extended or repeated exposure for long-term memory retention.

An important fact for memory development is that some of the MTL circuitry has a protracted period of development, with the functions of the PRC developing early, CA1 volumes developing substantially over the first two years, albeit at different rates based on layer input origination, and CA3 and the DG volumes developing the latest both in human and primate development (Bachevalier, 2014; Lavenex and Banta Lavenex, 2013). These varied developmental trajectories led these authors to propose that maturation of these substructures should reflect the emergence of different memory processes in development. A challenge for this proposal is how to reconcile this protracted view of development with recent reports of early memory function in tasks known to elicit hippocampal processing in adults, such as relational binding of a face to a scene (Richmond and Nelson, 2009; Richmond et al., 2004; Chong et al., 2015), memory for spatial relations between objects in a display (Richmond et al., 2015), remembering temporal relations between events in a scene (Barr et al., 1996; Bauer et al., 2003), relational inference (Rovee-Collier and Giles, 2010), demonstrations of context effects (Richmond et al., 2004; Edgin et al., 2014), and better retention after sleep than after a similar period of wakefulness (Friedrich et al., 2015; Seehagen et al., 2015).

Researchers have long noted early and late stages of memory development (Carver and Bauer, 2001; Jabés and Nelson, 2015; Mullally and Maguire, 2014; Nelson, 1995; Piaget, 1973; Schacter and Moscovitch, 1984) placing the emergence of the “late” stage at about 9 months in human children. However, this proposal is inconsistent with evidence on brain development that exists in the literature that we also review (e.g., Bachevalier, 2014; Lavenex and Banta Lavenex, 2013). Our unique proposal is that 18–24 months of age reflects a major milestone in hippocampal development and its connections to cortex when circuitry among key hippocampal subfields and neocortical–hippocampal connections should be mature enough to support sleep neural replay. Before this time we propose that memory function is mostly supported by cortical structures characterized by an incremental learning profile with memories established through repeated exposure, inflexible representations and shallow retention profiles. In comparison, hippocampal memories are established rapidly in a couple exposures, objects and contexts are linked in memory but are also maintained separately, and retention profiles are robust, supported by neural replay during

sleep. Consistent with proposals by Bachevalier (2014), Lavenex and Banta Lavenex (2013) and Olson and Newcombe (2014), it is only after basic circuitry is established among the subfields of the hippocampus that we should see more advanced hallmarks of memory function associated with relational binding, spatial relations, temporal order, and the binding of items in scenes.

In the ensuing pages, we briefly review development of MTL anatomy. Next using examples from typical and atypical populations, we re-interpret several examples of early memory function in light of MTL development. We go on to propose unique behavioral signatures that should emerge with basic maturity of hippocampal circuitry as well as methods for investigating these signatures behaviorally with typical and atypical populations. Finally, we point to new issues and questions that arise from mapping memory development more closely to the development of different learning and memory structures.

We focus here on episodic memory development supporting retrieval of memories of specific learning events that are functionally and anatomically separate from memories supported by procedural habit systems, such as memories formed using conjugate mobile reinforcement which are nondeclarative in nature, likely engaging the basal ganglia and cerebellum (see Bauer, 2007; Jabés and Nelson, 2015; Nelson, 1995; Schacter and Moscovitch, 1984 for similar arguments).

## 2. Anatomical development of MTL

Encompassing the amygdala and hippocampus, the MTL is surrounded by perirhinal and parahippocampal cortices, with entorhinal cortex connecting hippocampal and cortical structures (see Fig. 1). Critically, regions of the MTL and subfields of the hippocampus and their connectivity develop at different rates (Bachevalier, 2014; Jabés and Nelson, 2015; Lavenex and Banta Lavenex, 2013). Some patterns of local neural firing in the MTL develop early in rat models, with hippocampal CA1 place cells, which fire in response to an organism’s position in the environment, emerging at postnatal day 16 (P16), and grid cells in entorhinal cortex developing at P20, substantially earlier than once thought (Wills et al., 2010). While glucose utilization and the number and density of synapses in most of the hippocampus are also adult-like by 6 months of age in humans (Seress and Ábrahám, 2008), the DG undergoes protracted development with rapid rates of neurogenesis at 8–16 months and achievement of adult like-morphology by 12–15 months (Bauer, 2007). Slow pruning of synapses to adult levels occurs after 4–5 years in DG (Bauer, 2007; Eckenhoff and Rakic, 1991). Myelination of hippocampus and its subfields also follows a protracted course (Arnold and Trojanowski, 1996), continuing to be modified into adolescence, with the DG showing the latest time frame to reach maturity (Ábrahám et al., 2010).

In adults, information converging on hippocampus from PRC and PHC via entorhinal cortex [ERC] takes two routes through the HIPPO, a short route through the monosynaptic circuit with bidirectional ERC  $\leftrightarrow$  CA1 connections and a longer route through the trisynaptic circuit (containing DG, CA3). While the short route is available in early infancy with CA1 mature by 2 years of age (Jabés and Nelson, 2015; Lavenex and Banta Lavenex, 2013), it is not until after 18–24 months that DG mossy fibers and CA3 Schaffer collaterals may acquire sufficient maturity for trisynaptic communication from DG and CA3 to the monosynaptic circuit of CA1 and between the hippocampus, parahippocampal gyrus containing PRC and PHC, and neocortex (Ábrahám et al., 2010; Eckenhoff and Rakic, 1991; Lavenex and Banta Lavenex, 2013), structures involved in the formation and retrieval of declarative memories (Nyberg et al., 1996).

A seminal study showed that the use of spatial context to guide search for objects emerged in a rudimentary fashion at 24 months

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