

Introduction to the special issue on the ontogeny of hippocampal functions

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The views on hippocampal function and role in cognition evolved considerably during the last century. While at first the hippocampus was considered a conduit (Papez, 1995) and later a hub for emotional processing (MacLeans, 1949), the description of Henry Molaison's case (Scoville & Milner, 1957), and the recording of place cells by O'Keefe and Dostrovsky (1971), uncovered a role for the hippocampus in memory and spatial cognition, which soon came to be viewed as its primary functions and prompted the theory of the hippocampus as a cognitive map (O'Keefe & Nadel, 1978). To date, memory and spatial cognition are widely accepted as the predominant functions of the hippocampus, but paramount evidence exists also for the involvement of the hippocampus in emotion regulation, social behavior and sensorimotor integration (Bast & Feldon, 2003; Davidson et al., 2000; H. Leblanc & Ramirez, 2020; Maren et al., 2013). Current theories suggest that these seemingly disparate functions might be achieved through shared neural processes taking place within the hippocampus, and broadcasted globally to the rest of the brain by distributed networks connecting the hippocampus to multiple cortical and subcortical regions (Buzsaki & Moser, 2013; Eichenbaum, 2017). Across this wide diversity of cognitive domains, the key process engaging the hippocampus and relying on it is learning and memory.

The ability to learn from experience is arguably one of the most important functions of the brain and is critical for one's own survival, as it allows animals to compare current contingencies to previously encountered episodes, build expectations, and select appropriate behaviors based on predicted outcomes (Buzsaki & Moser, 2013; Tulving, 2002). This ability critically relies on the engagement of the hippocampus-dependent memory system, which promotes the

acquisition and consolidation of episodic memories (i.e., memories of autobiographical events that occurred in a specific spatial and temporal context; Eichenbaum et al., 2007; Scoville & Milner, 1957; Squire et al., 2004; Treves & Rolls, 1994; Tulving, 2002; Wood et al., 1999). Infancy and childhood are characterized by a high need for learning at a rapid pace. In fact, during this period, humans and animals acquire motor, social and communication skills, and build intrinsic representations of the world to which future experience might be compared (Buzsaki & Moser, 2013). Yet, the structural and functional maturation of the hippocampus, so important for these functions, extends past these windows. In altricial mammals, from rodents to humans, the number of neurons and synapses in the entorhinal-hippocampal network increases dramatically after birth, due to a protracted period of neurogenesis and synaptogenesis that does not reach adult-like levels until late childhood (Deguchi et al., 2011; Donato et al., 2017; Travaglia, Bisaz, Cruz, et al., 2016). Different areas of the circuit mature sequentially with distinct time courses. In the mouse, the medial entorhinal cortex, which processes information about the context of experience (Kitamura et al., 2015; Knierim et al., 2014), is already mature by the beginning of the third postnatal week (Donato et al., 2017; Ray & Brecht, 2016), while the lateral entorhinal cortex, which provides information about the content of experience and about episodic time (Deshmukh & Knierim, 2011; Tsao et al., 2013; Tsao et al., 2018), is largely immature until the end of the fourth (Donato et al., 2017). Prefrontal circuits take even longer to reach adult-like levels of maturity, as the establishment of new connections and synaptic remodeling processes associated with developmental plasticity extends into the sixth weeks of life in rodents (roughly

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corresponding to adolescence in humans (Chini & Hanganu-Opatz, 2021; Kolk & Rakic, 2022).

The fact that hippocampal circuits mature late during brain development compared to other cortical areas has fuelled the question of whether the infant hippocampus is engaged in learning and memory, spatial orientation, or emotional regulation. The long series of studies that set to answer this question revealed that these behaviors and their neurophysiological correlates emerge early in ontogeny and develop along a temporal gradient of increasing complexity. For example, in rodents the development of spatial cognition begins with homing toward the nest, which is followed sequentially by the emergence of cued, egocentric, and allocentric navigation (Wills et al., 2014). Similarly, simpler neural representations of space such as head direction cells emerge prior to place cells and are followed by grid cells (Langston et al., 2010; Wills et al., 2010). Network activity underlying both spatial and memory processing is sparse and uncoordinated in new born infants but develops into coordinated rhythms in the theta, gamma, and ripple bands during infancy and childhood (Lahtinen et al., 2002; M. O. Leblanc & Bland, 1979; Mohns & Blumberg, 2008).

Building on the observation that adults retain very few memories of events that happened during their infancy and childhood, at the beginning of the 20th century the expression “Infantile Amnesia” (IA) has been forged to describe the phenomenon by which most of us cannot remember what happened during the first years of our lives (Bauer, 2006; Freud, 1914; Miles, 1895). Since then, psychologists have put forward conflicting hypotheses about the nature, in infants, of the memories that in the adult rely on the hippocampus-dependent memory system for their encoding and retrieval, suggesting either that children are unable to encode memories of early-life events, or that these memories are repressed, or that they disappear rapidly once encoded. It was speculated that the accelerated forgetting of early-life memories was because children lack the cognitive tools necessary to interpret and organize their experience, like language, a sense of self, or a theory of mind (Harley & Reese, 1999). However, the discovery that infants of nonhuman species (i.e., rodents) also have rapid forgetting during their development has helped to address this conflict (Campbell & Campbell, 1962; Campbell & Spear, 1972), and indicated that biological mechanisms underlie evolutionarily conserved processes of memory development which go beyond an explanation entirely based on human premises (Alberini & Travaglia, 2017; Josselyn & Frankland, 2012). It was then proposed that IA was a manifestation of the immaturity of the hippocampus which resulted in an inability to produce long-lasting engrams during development (Akers et al., 2012; Travaglia, Bisaz, Sweet, et al., 2016), or that high levels of neurogenesis in the dentate gyrus would induce forgetting of newly generated memories (Akers et al., 2014).

Recent evidence from rodent studies however has indicated that these interpretations are not correct or incomplete. In rodents, place cells can be observed during infancy (Langston et al., 2010; Wills et al., 2010), and are promptly able to support core computations linked to memory formation like pattern separation (Bjerknes et al., 2018; Muessig et al., 2016). Upon learning in infants, memory formation relies on mechanisms that are typical of critical periods

(Gao et al., 2018; Travaglia, Bisaz, Sweet, et al., 2016), and is accompanied by physical changes that persist in the adult brain (Bessieres et al., 2020; Guskjolen et al., 2018; Travaglia, Bisaz, Sweet, et al., 2016). Moreover, far from being lost, early-life memories can be reinstated in the adult through behavioral paradigms that re-expose the animal to individual elements of their original experience (Travaglia, Bisaz, Sweet, et al., 2016), or by the artificial stimulation of the engram neurons that were active during encoding (Bessieres et al., 2020; Guskjolen et al., 2018). In humans, months-old infants can remember experiences like playing with a specific mobile or seeing a specific face for up to 2 weeks ([Rovee-Collier & Cuevas, 2009] though whether these learning and memory skills are hippocampally mediated remains a point of debate), while toddlers exhibit episodic memory-related reactivation of hippocampal patterns during sleep when prompted to remember a previously learned song (Prabhakar et al., 2018) and also exhibit associative memory persistence (Saragosa-Harris et al., 2021).

This new evidence represents a paradigm shift in the way we think about the ontogenesis of the hippocampal function. Far from being incompetent to learn, the developing hippocampus participates in memory processes already during infancy, even though hippocampus-dependent memories produced at this time are qualitatively different from those produced in the adult, since they rely on distinct molecular pathways for their encoding and retrieval. Fundamental questions therefore remain to be answered: how does the infant hippocampus participate in navigational and memory processes when the maturation of its circuitry is far from complete? What molecular pathways support the formation of hippocampus-dependent memories during infancy? How does the interplay between brain states (e.g., active engagement and sleep) shape hippocampal involvement in memory processes during development? When and how does the hippocampal formation start interacting with other brain regions for the encoding of episodic memories? And lastly, how can distinct time-courses of hippocampal maturation across species inform us about the ontogeny of hippocampus-dependent function?

In this special issue, we will present a series of studies that focus on the molecular, cellular, network, and electrophysiological correlates of memory processes during early development, to advance our understanding of the ontogeny of hippocampus-dependent functions in rodents and humans.

This issue opens with a fascinating retrospective review by Lynn Nadel, on the pursuit of hippocampal development. Nadel takes us on a journey through milestone discoveries on the ontogeny of exploration, navigation, and contextual coding in normally and atypically-developing rodents and humans. Nadel pinpoints how the initial hypothesis, which predicted lack or deficiency of hippocampus-dependent behaviors in the immature organism, was revised by recent evidence to posit that the immature hippocampus can support classical functions albeit with different manifestations and mechanisms. Protracted developmental trajectories are evident in the hippocampus and its connected brain regions. The importance of these inter-areal connectivity to the maturation of behavior is less clear. Xia et al. investigate the emergence of spatial behavior and brain-wide activity

patterns in rat pups. This study shows that earlier than expected, postnatal day 16-old rats can already form persistent spatial representations and use these to regulate exploratory behavior. Interestingly, in the infant brain spatial novelty engages primarily the hippocampus, whereas the prefrontal cortex is activated by familiarity. Coordination of activity in cortico-hippocampal networks is critical for memory in adults. Geng et al. find that the same networks support memory encoding in young children, albeit with different attributes, reflecting immature functional and anatomical connectivity within the network. Beyond memory: Rio-Bermudez and Blumberg highlight sensorimotor integration as an important hippocampal function during development. They propose a compelling hypothesis that views active sleep, the predominant behavioral state on infants, as a unique window for activity dependent modulations of sensorimotor-hippocampal networks.

These studies echo the idea that hippocampal functions arise early in development to support the infant needs and critically shape adult behavior. Yet differences in molecular composition, activity, and connectivity patterns in the infant brain, necessitate a different set of plasticity mechanisms. Keith et al. suggest that recently discovered nonionotropic NMDAR-dependent plasticity, might be one. The authors review the literature and hypothesize that this form of plasticity could support latent memories in the infantile brain.

While the papers presented in this Special Issue highlight many findings that open a new prospective for the understanding of the ontogeny of hippocampal functions, they also advocate for a fundamental need to pursue a multidisciplinary approach to study the involvement of hippocampal circuits in cognitive processes early in life. Such an approach must aspire to the production of a comprehensive description of hippocampus development that spans the molecular, cellular, and network levels, and cuts across the evolutionary spectrum from rodents to human. Such effort is not only timely, but necessary, given the profound implications that understanding the neurotypical trajectory of hippocampal development has for understanding the pathological deviations that lead to severe neurodevelopmental disorders and their treatment.

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