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Comparative approaches to memory development

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Memories for events experienced during infancy and early childhood are rarely recollected later in life—a phenomenon termed infantile and childhood amnesia. The formation and retrieval of such episodic memories relies, in part, on the hippocampus. Characterizing the role of hippocampal development in offsetting infantile and childhood amnesia is key to understanding (i) why infantile and childhood amnesia occur and (ii) how episodic memory capacities develop in early ontogeny. Comparative research is necessary for this enterprise because many paradigms and techniques work better with humans or with non-human animals. The four papers in this symposium gather current work in developmental psychology, developmental cognitive neuroscience, and behavioral neuroscience that characterizes the complex and heterogenous developmental profile of behavioral gains in component processes underlying episodic memory capacity in humans and work on the mammalian hippocampus and how it accompanies development. By leveraging and triangulating multiple levels of analyses, we can gain insights that are unavailable using a siloed approach. This collection of work helps delineate clear future directions for a comparative approach in memory development.

Memory Development in Early Childhood

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Adaptive behavior in changing environments requires both the extraction of schematic knowledge that can be extrapolated to novel situations and the retention of episodic memories that detail the experiences of our pasts. Schematic knowledge relies on *generalization* by exploiting the commonalities across multiple episodes, whereas episodic memory relies on *pattern completion* that retrieve events holistically, and *pattern separation* that keeps individual events distinctive. The corpus of the memory development

literature is rich, but most studies have focused on only one process at a time, as opposed to examining a set of processes concurrently. Thus, litte is known about to the multivariate, compositional structure of memory development across childhood. We will present the findings from a literature review that aims at quantitatively characterizing memory development research over the past 50 years through the lens of memory processes, including (but not restricted to) generalization, pattern separation, and pattern completion. Though the various studies have used different theoretical frameworks, paradigms, and implied constructs, the contemporary constructs of pattern separation, pattern completion, and generalization have all been examined developmentally over the past 5 decades. However, the literature is uneven: The majority of studies has focused on within-event pattern completion, with much fewer studies targetting pattern separation or generalization. Crucially, very few studies have studied more than one process at a time. Hence, future investigations taking a multi-process approach are required for revealing the ontogenetic relation across component processes. We will discuss how the past half century of research can guide the next wave of future studies.

Investigating the Neurocognitive Development of Human Memory Using High-Resolution Magnetic Resonance Imaging

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The human hippocampus, a bilateral brain region in the medial temporal lobe is a key neural hub supporting human memory. Converging lines of animal, computational, and human research are deciphering the neural mechanisms implemented in the hippocampal circuitry supporting specific component processes of memory. Two such candidate neural computations performed by distinct hippocampal subfields are pattern completion, i.e., reinstating full representations based on partial neural input, and pattern separation, i.e., decreasing the overlap between similar neural inputs. Recent advances in high-resolution magnetic resonance imaging (hr-MRI) allow us to measure hippocampal structure and function at the level of its subfields and thus provide a proxy for pattern separation and pattern completion in vivo in

humans. To highlight the advantages of this approach, I will first present published cross-sectional data from two studies using structural hr-MRI and behavioral tasks in children aged 6-14 years suggesting that the developmental trajectory of hippocampal subfields is associated with a developmental shift from pattern completion to pattern separation. I will then contrast these findings with novel longitudinal hr-MRI and behavioral data from children aged 6-10 years suggesting a different picture of hippocampal subfield development. Departing from the discrepant cross-sectional and longitudinal results, I will highlight key challenges and potential future directions for neurocognitive investigations of memory development using hr-MRI.

The Development of Circuits Supporting the Brain's Representation of Space

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The entorhinal-hippocampal network contributes to the formation of episodic memories by creating an internal representation of the environment where experience unfolds [1]. Such internal representation, or cognitive map, is instantiated in the activity of several functionally-specific cell types whose activity is modulated by space. Among these cell types, we distinguish neurons that are active at one or more specific locations in the environment (place and grid cells), or next to borders (border cells), or when the animal faces specific directions (head-direction cells) [2]. In rodents, while the firing properties of head-direction and border cells are adult-like at the onset of spatial exploration, spatial tuning in grid and place cells emerges and is refined progressively during the first months of life [3,4]. This maturation process may depend on the establishment of specific connectivity motifs between the entorhinal cortex and the hippocampus. In fact, we previously showed that the functional maturation of such cell types is accompanied by the structural maturation of the entorhinal-hippocampal circuit, which is driven by an activity-dependent instructive signal that instructs the stepwise maturation of excitatory and inhibitory neurons at each stage of the network [5]. Here, we will discuss recent studies whose aim is to understand how the emergence of spatial tuning in the developing entorhinal-hippocampal network shapes learning and memory processes during early postnatal life. Furthermore, we propose that studying the functional ontogenesis of the brain's representation of space offers a unique opportunity to understand the contribution of individual cell types to hippocampal computations, and to dissect the contribution of such computations to learning and memory processes at multiple stages of an animal's life.

Memory Engrams Across Development

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Infantile amnesia, the developmental loss of memories formed in early childhood (prior to 2–4 years), is conserved across altricial mammals and can be studied in rodents. Although behavioral neuroscience studies have well established that mice display infantile amnesia, little is known about the basic neurobiology of the phenomenon. We aim to probe the question of how memories are stored in the brain throughout development, by integrating recently developed engram labelling technology with various rodent models of infantile amnesia. We will discuss our experimental studies of infant mice, where we use Pavlovian fear conditioning, object memory, and maze learning paradigms to study how infant mice learn, remember, and how infant formed memories are apparently lost in late infant development. We integrate behavioral studies with novel genetic methodologies for labelling the specific engram cells in the mouse brain that can be attributed to specific memories. Crucially, we can stimulate infant-formed engram cells in adult mice using optogenetic techniques, resulting in the retrieval of seemingly lost infant memories in adulthood. These developing studies demonstrate that memory engrams retain information following infantile amnesia, and that information contained through these cells can be accessed under the appropriate conditions. We will discuss our ongoing to work to understand the nature of infantile amnesia in rodents, investigating why the engrams are suppressed, how normal access can be restored, what the adaptive function of infantile amnesia is for mammals, and what infantile amnesia can tell us about learned information storage in general. This methodological framework will allow for the potential retrieval of seemingly lost-memories from early childhood, as well as a deeper understanding of how long-term memories are stored as an enduring and stable biological change.

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