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Current Opinion in Behavioral Sciences

Memory and the developing brain: are insights from cognitive neuroscience applicable to education?

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In this paper we present a succinct overview of the current knowledge about the neural correlates of memory development. Behavioral evidence strongly supports the view that developmental effects are specific to memory that is complex, and rich in contextual details. Neuroimaging evidence supports an emerging view that stability and change in memory functioning across age reflects the structural and functional maturation of the brain regions that support memory, particularly regions in the prefrontal cortex and the medial temporal lobe. Recent research efforts using functional neuroimaging have been directed to test hypotheses about the neural basis of age-related difference in memory capacities, prior knowledge, and effective use of strategies and metacognitive abilities. Additionally, we review recent evidence about how the development of the brain may set specific limits on, and present certain opportunities for, memory functioning. Finally, we discuss the challenges in applying insights from investigations into the neural basis of memory development to educational practices. We conclude that even though we have learned a great deal about the neural correlates of memory development, there are still several critical limitations in applying this knowledge to educational practices.

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Current Opinion in Behavioral Sciences 2016, **10**:81–88

This review comes from a themed issue on **Neuroscience of education**

Edited by **Dénes Szűcs**, **Fumiko Hoeft** and **John Gabrieli**

http://dx.doi.org/10.1016/j.cobeha.2016.05.010

Introduction

Designing effective pedagogical methods depends upon teachers' scientific understanding of students' cognitive capacities in acquiring, maintaining and retrieving information at different ages. These capacities are contingent upon the students' young brains, as the development of the brain may set the limits and provide opportunities for their manifestation. Advances in neuroimaging methods and their growing application in cognitive neuroscience research have generated excitement that knowledge gained through these methods will be meaningful for education and perhaps be able to inform and improve classroom practices. Indeed, identifying the neural correlates supporting memory development is an area of significant current research efforts, propelled by the desire to seek a mechanistic understanding of memory development and the hope to empower education by such understanding. Below we review recent studies that contribute to the identification of the neural correlates of memory development. We show how these efforts align with decades-long investigations into the elements that govern memory development, and we further discuss how brain development may impose endogenous constraints on the development of human memory. We end with consideration of the current challenges, and future potential, of applying the knowledge gained from investigations into the neural basis of memory development to inform educational practices.

The cognitive neuroscience of memory development

A growing body of research in cognitive neuroscience is devoted to characterizing the trends of memory development. In this section, we highlight some important trends first from a cognitive perspective and then from a brain-based perspective.

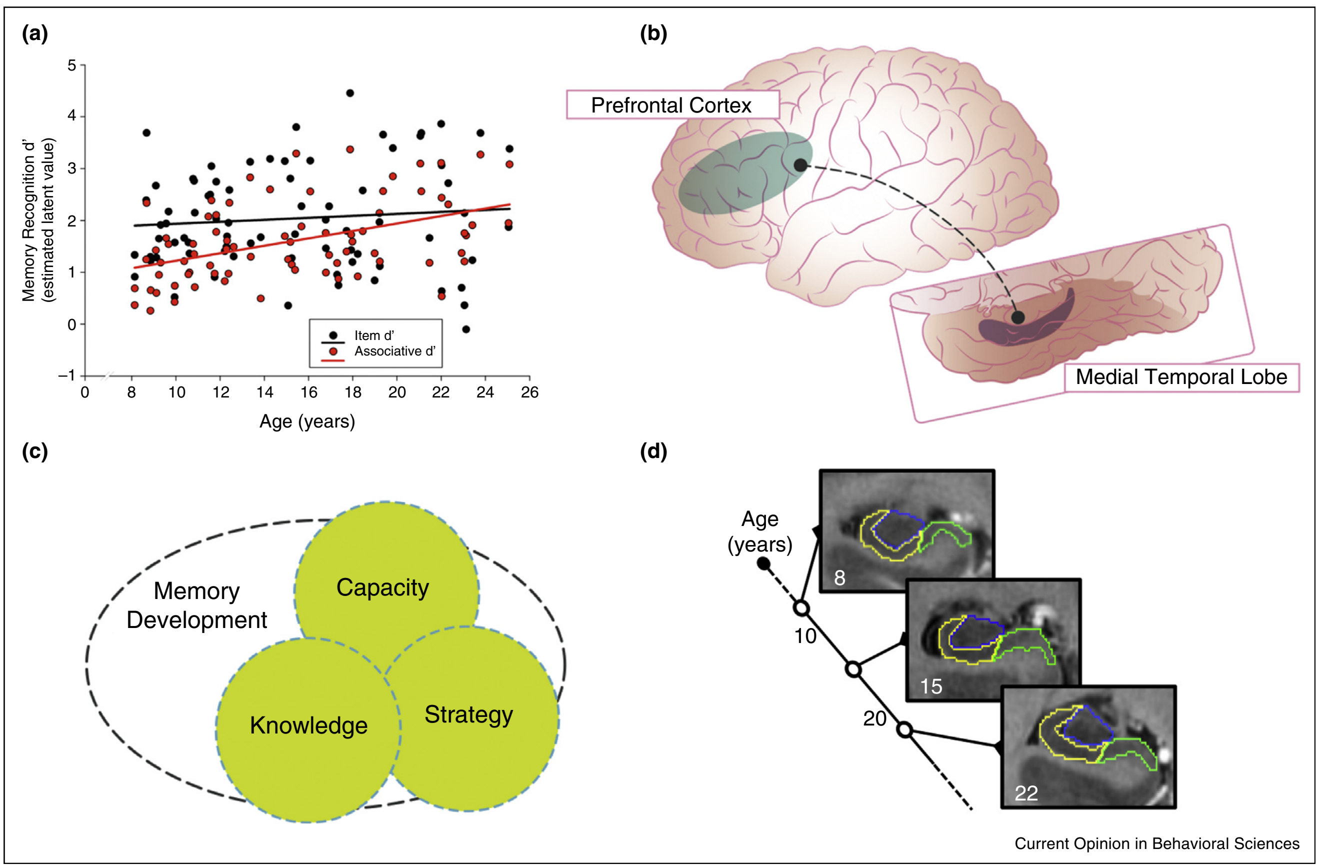
Cognitive perspective

Converging evidence suggests there exists little difference between children and adults when recognition is dependent primarily on the familiarity with studied materials; in contrast, there are large differences between children and adults for memories that depend on recollection of rich contextual details [1]. This notion has been further corroborated by recent studies using a wide range of experimental paradigms [2–6]. For example, Yim *et al.* [3] demonstrated that the ability to form memory with an increasingly complex relational context starts between the ages of 4 and 7 and continuously develops well into adulthood. The specific type of relational context may also determine the magnitude of developmental effects in the measured memory [4,6]. Finally, in a recent study Koenig *et al.* [5] used the process dissociation paradigm, to test developmental difference in familiarity and recollection processes. Participants studied a series of pictures with either one or two objects presented (e.g., two alligators, one glass) and tested for their recognition of the objects and for whether it was one or two objects that were presented during study. The combination of these testing conditions and an additional manipulation of the speed of response was used to show that although both familiarity and recollection processes are evident in children as young as 5 years, recollection is less robust in 5-year-olds compared to older children and adults. Overall, the recent behavioral evidence is consistent with the notion that age effects are found when the demanding aspects of memory are tested, and that children may rely more on a memory representations that retain less detailed information about the configuration and context in which the information was studied (see Figure 1a for an example).

Brain perspective

Developmental researchers in cognitive neuroscience aim to map the cognitive processes that constitute the developmental change in behavior to the brain. Among the multiple brain regions that support memory functioning, two key regions have been the focus of developmental studies: the prefrontal cortex (PFC) and the medial temporal lobe (MTL). A protracted structural development in the PFC is a consistent finding and is thought to underlie the well-documented increase in the recruitment of the PFC by children during memory encoding and retrieval [1,7–9]. In contrast, there are more modest changes in the MTL [10], and age effects in MTL

Figure 1



Toward a mechanistic understanding of memory development. **(a)** Behavioral evidence suggests that certain aspects of memory functioning are stable from middle childhood to adulthood, whereas others, which require detailed and flexible memory such as the ability to correctly recall specific associations, show protracted maturation. Memory sensitivity for item recognition (black) does not differ by age, whereas memory sensitivity for associative recognition (red) increases by age (adapted from [2]). **(b)** Memory development is linked to age difference in activation in key regions known to support memory, including the prefrontal cortex schematically shown on rendition of the lateral view of the brain and the medial temporal lobe shown on a partial rendition of a medial view of the brain. Additional evidence links memory development to age-related increase in the functional connectivity between these regions, represented by the line connecting the two regions. Original art by Julian Wong. **(c)** Decades-long answers to the question 'what is memory development the development of?' highlight the net effects of age differences in basic memory capacities, growth in the individual's knowledge base, and increase in the effective use of mnemonic strategies. **(d)** The development of the brain can be measured by comparing indices of regional volume. Because of the crucial role of the hippocampus in memory, recent advances in high-resolution structural imaging of the hippocampus and reliable methods of estimating regional hippocampal volumes constitute promising directions toward constructing a mechanistic understanding of how brain development supports the development of memory. Shown are example tracings of the hippocampal subfields on high resolution *in vivo* brain images obtained from a child, an adolescent, and a young adult.
Adapted from [38•].

activation that support memory formation or retrieval seem to depend on specific task or stimuli characteristics. For example, Chai *et al.* [11] observed an age-related activation increase during memory formation in the MTL scene-selective regions only when the to-be-remembered scenes are complex. Ghetti *et al.* [12] showed an age-related difference in MTL activation patterns during memory formation when the task involved detailed recollection. Similarly, for memory retrieval, some find no age-related differences in MTL activation profiles [1,9], whereas others find an age-related increase in MTL activation with certain tasks or stimuli [13,14]. Altogether, the recent evidence supports the view that age-related improvement in memory ability are linked to functional maturation of the PFC, differential recruitment of the MTL, and increased functional connectivity between these two key brain regions [15–17].

Beyond the general trends: 'what is memory development the development of'?

The general trends reviewed above were drawn from observations of age-related differences in brain activation profiles in response to fairly simple memory tasks. In recent years, investigation of general trends has been making way for a more careful investigation of specific factors that may propel developmental changes. Below we review several current lines of investigation that intend to answer a decades-old question: 'what is memory development the development of?'[18,19] The answers available then and updated now with data from neuroimaging studies are very much alike: basic memory capacities, growth in knowledge base, and metacognitive skills in carrying out mnemonic strategies [20]. Below we highlight some recent progress and novel insights from applying a cognitive neuroscience approach to this 'old' question about the factors that contribute to the development of memory.

Basic memory capacities

The concept of capacity when applied to memory is typically considered as referring to working memory capacity. Working memory capacity is the limited amount of information that can be kept in mind for further processing over a short period of time [21]. Despite an apparent developmental increase in performance of working memory tasks, it is still debatable whether all aspects of working memory develop past early childhood [22]. Some propose that a basic storage component could be fixed after age 3–5, and that a processing component continues to develop. However, other empirical data seem to be in favor of a general age-related increase prevailing across modalities [23]. Using a cognitive neuroscience approach may shed new light on the question of whether the development of working memory reflects development in storage or in processing efficiency. Indeed, findings from neuroimaging studies with adult participants suggest that regions in the parietal cortex support the storage component [24], whereas regions in the PFC support the processing component and are involved in maintenance, updating and inhibition [25].

Another basic memory capacity is the ability to generate rich associations, that is, binding together disparate details and maintaining associative representations to allow successful retrieval of events [26]. There is some behavioral and brain-based evidence that an associative component in memory is fairly mature in children [27]. One exciting development in this line of investigation is the use of more sophisticated and realistic tasks to probe the naturalistic reliance on memory for daily functions. In one recent study, Picard *et al.* [6] used a naturalistic virtual environment to investigate three aspects of episodic memory — what, where, and when. They found that the ability to recall spatiotemporal context increases steadily from the age of 8 to young adulthood. Thus, developmental effects are likely different across different aspects such as what, when or where experiences occur [4,6]. Lee *et al.* [4] assessed the ability of children (ages 8–11) and adults to form associations between two items, between an item and a specific spatial location, or between an item and the time when it was presented. Overall, memory of the item-location association was high and relatively stable across age. In contrast, memory of the item-item and item-time associations improves from childhood to adulthood. An interesting notion proposed by Edgin *et al.* is that young children and individuals with Down syndrome, a population with MTL dysfunction, generate rigid associations of items embedded in context [28•]. In line with this notion, DeMaster *et al.* [29•] observed an increase in MTL activation during memory retrieval when comparing 8-year, 10-year olds, and adults. The increase in MTL activation was related to older participants' ability to correctly detect minor changes in the presentations of studied pairs during retrieval, such as a switch in the relative locations of the individual items between the presentations during study and test. Collectively, these new findings highlight that the basic memory capacity of forming, maintaining and retrieving detailed associations among studied material continues to improve with age, and that the maturation of the MTL likely plays a key role in these developmental effects.

Knowledge

Two important roles of prior knowledge for learning and memory — the assimilation of new information and accommodation to new environments — had been seminally recognized by Jean Piaget [30] in the early days of developmental psychology. At the dawn of cognitive revolution, George Miller documented another significant role of prior knowledge, that is, organizing information into chunks to effectively enhance immediate memory [31]. Individuals with more world knowledge are able to form more extensive associations among a long list of items to be remembered and thus reduce them into fewer independent units. Thus, prior knowledge can enhance chunking and lead to a vast increase in memory performance. Equipped with advanced neural imaging techniques and sophisticated analytical tools, recent work in cognitive neuroscience has rekindled the interest in understanding how such processes are carried out by the brain. In adults, evidence suggests that the integration of new information to form lasting schemas may be supported by an interplay between the anterior MTL and the medial PFC [32,33]. Influence of prior knowledge on learning and memory is likely of high importance for education in both theory and practice, and an avenue for future research. Studies of the effect of schooling and the gains in knowledge associated with schooling on the neural mechanisms of learning and memory will be of great interest to the field of education.

Strategies and metamemory

As we have argued in the past [1], perhaps the most documented contribution to the development of memory is the increase in flexible use of deliberate mnemonic strategies such as rehearsal, elaboration and organization [34]. Here we refer to strategy as the cognitive operations over and above the processes that are natural consequences of carrying out the task, and are meant to achieve cognitive purposes that are potentially conscious and controllable. Strategy use begins before schooling and continues to mature through adulthood [20]. Neuroimaging and neuropsychological evidence strongly suggests that the PFC supports effortful execution of specific task demands and implementation of mnemonic strategies. Therefore, the PFC is likely a key player in the processes that govern mnemonic strategy use. Given what we reviewed above regarding contributions of the PFC to developmental effects in encoding and retrieval of rich associative memories, it is possible that an age-related increase in PFC activation reflects an age-related increase in flexible and effective utilization of mnemonic strategies. Strategy use can be influenced by metacognitive awareness of strategies (knowing that certain strategy exists or that a certain strategy is more or less effective than another) as well as by the individual's ability and motivation to execute the strategy. Teaching to use a strategy is an important and effective lever in improving children's cognitive performance [20]. The cognitive and neural mechanisms with which the utilization and effectiveness of children's strategy use manifest are still not well understood. Interestingly, in a recent study Brehmer *et al.* [35] demonstrated that when providing strategy training to groups of children and adults, the training-induced changes in the neural correlates of subsequent memory do not differ between the groups. Future investigation that includes longitudinal characterization of brain changes as a result of mastering flexible use of mnemonic strategies would help elucidate the role of strategy in memory development.

Brain development provides 'endogenous' constraints on the development of memory

The evidence reviewed above highlights functional MRI studies of the neural underpinnings of memory development and the factors that contribute to the development of memory. We show that age-related improvement in memory functioning often entails an increase in functional activation of the PFC, differential recruitment of the MTL and increase in the functional connectivity between regions in the PFC and the MTL. We reviewed factors that were suggested by decades-long behavioral research into the development of memory. In this short section, we highlight a complementary perspective for examining contributions of cognitive neuroscience to the understanding the development of memory — the development of the brain. We suggest considering brain development, assessed by measurements of brain structural and functional maturation, as providing 'endogenous' factors that influence the development of memory. This focus of investigation is complementary to investigations of specific hypotheses about the functional underpinnings of memory development, because it is in a way suggesting that brain provides limiting factors on the expression of certain behaviors. Mechanistic understanding of memory development will be facilitated by the identification of endogenous factors that modulate developmental changes in memory abilities. This notion is similar to the maturation view as described by Johnson [36], although we assert it as a complement to investigations focusing on developmental effects as reflecting mechanisms of functional network interactions [37]. Future investigations of brain–behavior associations may focus on identifying biological and environmental modifiers of brain development and investigate the effects of those modifiers on cognitive development. A few of the exciting lines of investigation into the endogenous factors that may promote developmental change are investigating the individual differences in regional hippocampal volumes [38•,39,40•,41,42], white matter organization and structural connectivity [43,44••], and the brain's resting-state functional connectivity, which was recently shown to be of relevance for memory development [45–47].

Implications for education

In a fundamental way, the study of learning unites education and cognitive neuroscience, with the latter revealing how the brain processes and stores the information one learns [48]. There is, however, a striking difference between the goals of the two disciplines. Cognitive neuroscientists aim to gain knowledge about how the brain supports learning and memory. For such knowledge to be applicable in educational settings, it should become a mean to improve pedagogical practices. Two main obstacles stand in the way for successful implementation. First, our understanding of the neuroscience of memory and the developmental effects within this domain remains, at this time, greatly limited. Second, even if our efforts lead to a complete understanding of the way the brain learns and remembers, there is no guarantee that such knowledge can be applied to and benefit classroom instruction. Below we expand on these two obstacles and highlight avenues for future efforts to mitigate their damning effects.

We begin with listing the major challenges for application of the growing knowledge about the neural basis of memory development to education. One is the lack of a strong theoretical background against which one can build a mechanistic framework of the neuroscience of memory development. Despite tremendous efforts, cognitive neuroscience researchers are still far from agreement about a descriptive brain-based model of memory systems. Moreover, there are frequent and interesting offerings of new conceptualizations that challenge long-standing models [49]. The other major challenge is a more practical one and pertains to the limited generalizability of findings obtained in the lab due to several methodological considerations. First, studies in cognitive neuroscience typically use lab-based experimental tasks that carefully assess specific cognitive domains. This practice is crucial for identifying neural correlates of cognition, yet it presents a problem for translating findings to a more complex environment such as the classroom. Second, studies typically use a small sample. This can be justified when testing hypotheses for which the investigators assume little individual differences, but it becomes a problem when one attempts to capture individual differences such as those carried by age or those related to classroom performance [50]. Third, there is relatively little effort to statistically model existing individual differences in developmental experiments. Because there are multiple sources of individual differences, conventional statistical approaches have limited power to tease apart the contribution of these sources and the possible interactions among them. One approach to address this issue is to use advanced statistical modeling such as structural equation modeling. Finally, and perhaps the most significant challenge is that currently the majority of our knowledge is based on results of cross-sectional studies. Future research should fully embrace longitudinal designs that are critical for drawing inferences about development. It is only with longitudinal data that one can estimate intra-individual change and the inter-individual difference in intra-individual change [50,51].

Translating knowledge to the classroom would entail making inferences from individual brain mechanisms that govern learning and memory to their operation in a complex, dynamic, social learning environment. Such an endeavor forces one to be bridging not only between disciplines but also between different levels of description and organization [52]. Admittedly, cases of a successful translation from cognitive neuroscience to education do exist. For example, knowledge of the neural basis of reading and math has enabled early detection of those who later struggle at school, as recent studies have identified a correlation between precursor abilities (e.g. phonological awareness, number sense) and future abilities [53]. Yet, even in those cases there is limited evidence that interventions actually work in the long run (Box 1).

One may still remain optimistic with the potential translational value of cognitive neuroscience research for education. First, with a larger arsenal of experimental tools, researchers may be able to model the neural basis of more complex and ecologically valid aspects of human memory such as self-directed learning, multimedia learning and collaborative learning in which content is embedded in a realistic context [54,55]. Second, advances in analytic techniques with big data sets may also provide opportunities for the translation of research into the classroom. Nowadays, cognitive neuroscience researchers are striving to take advantage of 'big data' to accommodate the highly complex environments they encounter in testing their research hypotheses.

Both theoretical and empirical work is needed to begin bridging between investigations of the cognitive neuroscience of memory development and education. A good starting point would be to increase the cross talk between the two disciplines. If the questions asked by educators and parents become the initiating forces of cognitive neuroscience research programs, these programs would

Box 1 Can findings from the developmental neuroscience laboratory directly transfer to educational settings?

Findings in developmental neuroscience have led to a number of consensuses. It is generally accepted that brain development maintains a very rapid rate during the first couple years of life and thereafter subsides to a much lower rate, the human brain can be modified and shaped by experience through life, and the plasticity of the brain dramatically declines when it passes certain periods. However, disagreement exists when it comes to the implication of these findings on education. Some researchers and many policy makers consider such findings as evidence for early childhood intervention which may put young children on a positive developmental trajectory early on and maximize the return of educational investment in terms of both intellectual and financial outcomes for either individuals or the public. In contrast, other researchers argue against the direct generalization of findings in the developmental neuroscience laboratory to classroom applications, citing methodological boundaries such as small sample size and sample selectivity as well as social constraints with empirical studies in basic research [58]. Early childhood intervention programs offer a revealing example for the controversial views about bridging neuroscience and education. Some intervention programs have been shown to produce a short-term effect on school readiness and a long-term effect in reducing crime and improving earnings, whereas the largest U.S. preschool program, Head Start, suffers from a fade-out effect of losing the short-term learning gains in the first grade and a negative effect of emotional harm that persists into the later grades [59,60]. In the relative infancy of cognitive neuroscience, attempts to transfer findings from the developmental neuroscience laboratory directly to educational settings are not always fruitful and not without risk.

Box 2 Open questions

1. *How does communication between the MTL and PFC support memory development*? So far, not much is known about the nature of the interaction between these regions and the dynamic role of such interaction, especially the timing of neuronal events that coordinate the interaction, in contributing to developmental effects. With the technique of functional MRI alone, researchers are limited in their ability to answer the question. Further methodological advances are needed to explore the nature of information flow between the MTL and PFC that support memory development.
2. *How does the structural maturation of the PFC and the MTL contribute to memory development?* More research and advancement in technology may enable reliable measurements of change in the volume or shape of these structures. With such measures we may be able to develop a deeper understanding of how individual differences in brain structures and individual differences in the change in those brain structures relate to individual change in memory abilities.
3. *Are there unique periods for memory development that correspond to unique periods in brain development?* Certainly there are robust changes in early childhood, but some researchers suggest that during adolescence there may be additional changes unique to this developmental stage.
4. *What about the cohort effects?* No doubt that children today grow up in a different world than even a decade or two ago. How can studies enhance interpretations of changes across age as reflecting 'true' development rather than the role of technology in the life of children growing up in today's world?

Many other similar factors that may modify brain and cognition remain to be investigated, such as environmental factors, life-style factors (e.g. exercise and sleep), the role of instruction versus unsupervised play, and individual differences in motivation and personality. All these factors are important avenues for future investigation, as building a solid understanding of their contribution will definitely help bridge the gap between our understanding of the neural basis of memory development and the implication of such knowledge in education.

likely be able to provide insights relevant for the classroom. The effects and value of testing seem to be an example of one such question on the minds of educators and parents for which cognitive neuroscience approach may provide useful insights. Recent studies begin to map the mechanisms by which testing rather than simply re-studying information improves the long term retention of the information [56,57].

Can there be a solid bridge between neuroscience of memory development and education? The jury is still out. There is certainly great interest in such endeavor coming both from academics and the private sector. Based on the evidence we review here, we argue that more research is needed in charting the terrain of memory development in the brain (Box 2). Better understanding of the terrain is necessary before lasting and useful bridges can be set.

Conflict of interest statement

Nothing declared.

Acknowledgements

We would like to acknowledge the support of the Institute of Gerontology and the Office of the Vice President of Research, Wayne State University. We also thank Daniel Schoff for help with the preparation of the manuscript, Julian Wong for the illustrations in Figure 1, and Ryan Liddane and Lingfei Tang for help in editing the text.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Ofen N: **The development of neural correlates for memory formation**. *Neurosci Biobehav Rev* 2012, **36**:1708-1717.
2. Daugherty AM, Ofen N: **That's a good one! Belief in efficacy of mnemonic strategies contributes to age-related increase in associative memory**. *J Exp Child Psychol* 2015, **136**:17-29.
3. Yim H, Dennis SJ, Sloutsky VM: **The development of episodic memory: items, contexts, and relations**. *Psychol Sci* 2013, **24**:2163-2172.
4. Lee JK, Wendelken C, Bunge SA, Ghetti S: **A time and place for everything: developmental differences in the building blocks of episodic memory**. *Child Dev* 2015.
5. Koenig L, Wimmer MC, Hollins TJ: **Process dissociation of familiarity and recollection in children: response deadline affects recollection but not familiarity**. *J Exp Child Psychol* 2015, **131**:120-134.
6. Picard L, Abram M, Orriols E, Piolino P: **Virtual reality as an ecologically valid tool for assessing multifaceted episodic memory in children and adolescents**. *Int J Beh Dev* 2015.
7. DeMaster DM, Ghetti S: **Developmental differences in hippocampal and cortical contributions to episodic retrieval**. *Cortex* 2013, **49**:1482-1493.
8. Ofen N, Kao YC, Sokol-Hessner P, Kim H, Whitfield-Gabrieli S, Gabrieli JD: **Development of the declarative memory system in the human brain**. *Nat Neurosci* 2007, **10**:1198-1205.
9. Guler OE, Thomas KM: **Developmental differences in the neural correlates of relational encoding and recall in children: an event-related fMRI study**. *Dev Cogn Neurosci* 2013, **3**:106-116.
10. Gogtay N, Nugent TF 3rd, Herman DH, Ordonez A, Greenstein D, Hayashi KM, Clasen L, Toga AW, Giedd JN, Rapoport JL, Thompson PM: **Dynamic mapping of normal human hippocampal development**. *Hippocampus* 2006, **16**:664-672.
11. Chai XJ, Ofen N, Jacobs LF, Gabrieli JD: **Scene complexity: influence on perception, memory, and development in the medial temporal lobe**. *Front Hum Neurosci* 2010, **4**:21.
12. Ghetti S, DeMaster DM, Yonelinas AP, Bunge SA: **Developmental differences in medial temporal lobe function during memory encoding**. *J Neurosci* 2010, **30**:9548-9556.
13. DeMaster DM, Pathman T, Ghetti S: **Development of memory for spatial context: hippocampal and cortical contributions**. *Neuropsychologia* 2013, **51**:2415-2426.
14. Paz-Alonso PM, Ghetti S, Donohue SE, Goodman GS, Bunge SA: **Neurodevelopmental correlates of true and false recognition**. *Cereb Cortex* 2008, **18**:2208-2216.
15. Ofen N, Chai XJ, Schuil KD, Whitfield-Gabrieli S, Gabrieli JD: **The development of brain systems associated with successful memory retrieval of scenes**. *J Neurosci* 2012, **32**:10012-10020.
16. Qin S, Cho S, Chen T, Rosenberg-Lee M, Geary DC, Menon V: **Hippocampal–neocortical functional reorganization underlies children's cognitive development**. *Nat Neurosci* 2014, **17**:1263-1269.
17. Paz-Alonso PM, Gallego P, Ghetti S: **Age differences in hippocampus-cortex connectivity during true and false memory retrieval**. *J Int Neuropsychol Soc* 2013:1-11.

18. Flavell JH: **First discussant's comments: what is memory development the development of?** *Hum Dev* 1971, **14**:272-278.

19. Schneider W, Ornstein PA: **The development of children's memory**. *Child Dev Perspect* 2015, **9**:190-195.

20. Schneider W, Pressley M: *Memory Development Between Two and Twenty*. Lawrence Erlbaum Associates; 1997.

21. Cowan N: **The magical number 4 in short-term memory: a reconsideration of mental storage capacity**. *Behav Brain Sci* 2001, **24**:87-114 discussion 114–185.

22. Cowan N, Ricker TJ, Clark KM, Hinrichs GA, Glass BA: **Knowledge cannot explain the developmental growth of working memory capacity**. *Dev Sci* 2015, **18**:132-145.

23. Gathercole SE: **The development of memory**. *J Child Psychol Psychiatry* 1998, **39**:3-27.

24. Todd JJ, Marois R: **Capacity limit of visual short-term memory in human posterior parietal cortex**. *Nature* 2004, **428**:751-754.

25. Badre D, D'Esposito M: **Functional magnetic resonance imaging evidence for a hierarchical organization of the prefrontal cortex**. *J Cogn Neurosci* 2007, **19**:2082-2099.

26. Schlichting ML, Mumford JA, Preston AR: **Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex**. *Nat Commun* 2015, **6**:8151.

27. Shing YL, Werkle-Bergner M, Brehmer Y, Muller V, Li SC, Lindenberger U: **Episodic memory across the lifespan: the contributions of associative and strategic components**. *Neurosci Biobehav Rev* 2010, **34**:1080-1091.

28. Edgin JO, Spano G, Kawa K, Nadel L: **Remembering things without context: development matters**. *Child Dev* 2014, **85**:1491-1502.
•
Edgin *et al.* tested the development of context effects in associative memory. Participants studied objects embedded in scenes and were later tested for their recognition of objects that were either shown embedded in the same scene or removed from the scene. The authors found evidence that young children were able to demonstrate context effects; however, their representation of studied associations did not seem to be flexible. Older participants demonstrated a more flexible representation of the context in which objects were presented. These findings are interesting in that they suggest nonlinearity in the development of associative memory. Moreover, by testing individuals with Down syndrome, the researchers suggest that these effects relate to the development of the hippocampus.

29. DeMaster DM, Coughlin C, Ghetti S: **Retrieval flexibility and reinstatement in the developing hippocampus**. *Hippocampus* 2015.
•
This fMRI study used an associative recognition task to test whether age-related differences in hippocampal activation are associated with individual differences in retrieval of contextual details. Participants were required to recognize pairs of pictures that were either in the same location as during encoding or in a flipped location. Compared to children, adults recruited the hippocampus more strongly when accurately retrieving pairs that were originally presented in the flipped location. This age difference was localized along the long axis of the hippocampus.

30. Piaget J: *The Child's Conception of the World*. New York: Harcourt Brace; 1929.

31. Miller GA: **The magical number seven, plus or minus two: some limits on our capacity for processing information**. *Psychol Rev* 1956, **63**:81-97.

32. Brod G, Lindenberger U, Werkle-Bergner M, Shing YL: **Differences in the neural signature of remembering schema-congruent and schema-incongruent events**. *Neuroimage* 2015, **117**:358-366.

33. Schlichting ML, Preston AR: **Memory integration: neural mechanisms and implications for behavior**. *Curr Opin Behav Sci* 2015, **1**:1-8.

34. Bjorklund DF, Dukes C, Brown DR: **The development of memory strategies**. In *The Development of Memory in Infancy and Childhood.* Edited by Courage , Cowan . NY: Psychology Press; 2009.

35. Brehmer Y, Shing YL, Heekeren HR, Lindenberger U, Backman L: **Training-induced changes in subsequent-memory effects: no major differences among children, younger adults, and older adults**. *Neuroimage* 2016, **131**:214-225.

36. Johnson MH: **Interactive specialization: a domain-general framework for human functional brain development?** *Dev Cogn Neurosci* 2011, **1**:7-21.

37. Byrge L, Sporns O, Smith LB: **Developmental process emerges from extended brain–body–behavior networks**. *Trends Cogn Sci* 2014, **18**:395-403.

38. Daugherty AM, Bender AR, Raz N, Ofen N: **Age differences in hippocampal subfield volumes from childhood to late adulthood**. *Hippocampus* 2016, **26**:220-228.
•
The researchers used manual demarcation to assess age differences in the volume of the hippocampus subfields across the lifespan in participants ages 8–82 years. The hippocampus subfields are postulated to have unique functional specializations, yet the role of hippocampal maturation in memory changes both in development (see [49–51]) and later life is not clear. In this first investigation using manual demarcation to assess hippocampal subfield volumes across the lifespan, the authors identified both linear and nonlinear age differences in volumes of the hippocampal subfields.

39. DeMaster DM, Pathman T, Lee JK, Ghetti S: **Structural development of the hippocampus and episodic memory: developmental differences along the anterior/posterior axis**. *Cereb Cortex* 2014, **24**:3036-3045.

40. Riggins T, Blankenship SL, Mulligan E, Rice K, Redcay E: **Developmental differences in relations between episodic memory and hippocampal subregion volume during early childhood**. *Child Dev* 2015, **86**:1710-1718.
•
Using a source memory paradigm, Riggins and colleagues studied associations between episodic memory and volumes of the anterior (head), middle (body) and posterior (tail) portions of the hippocampus in early childhood. They show a positive association between episodic memory and volumes of the anterior portion of the hippocampus in 6 but not in 4-year-old children. These are initial findings showing that regional hippocampal volumes may be differentially related to individual differences in memory in childhood. Longitudinal evidence should corroborate these interesting findings.

41. Lavenex P, Banta Lavenex P: **Building hippocampal circuits to learn and remember: insights into the development of human memory**. *Behav Brain Res* 2013, **254**:8-21.

42. Lee JK, Ekstrom AD, Ghetti S: **Volume of hippocampal subfields and episodic memory in childhood and adolescence**. *Neuroimage* 2014, **94**:162-171.

43. Olson IR, Von Der Heide RJ, Alm KH, Vyas G: **Development of the uncinate fasciculus: implications for theory and developmental disorders**. *Dev Cogn Neurosci* 2015, **14**:50-61.

44. Wendelken C, Lee JK, Pospisil J, Sastre M 3rd, Ross JM, Bunge SA, Ghetti S: **White matter tracts connected to the medial temporal lobe support the development of mnemonic control**. *Cereb Cortex* 2015, **25**:2574-2583.
••
In this study, the authors tested the relation between the structural integrity of selected white matter tracts and an experimental measure of memory enhancement by using mnemonic control. They show that across age groups there was a positive relation between the integrity of uncinate fasciculus and mnemonic enhancement. In adults, but not in children, there was a relation between mnemonic enhancement and indices of ventral cingulum bundle and ventral fornix/fimbria. These findings link the maturation of brain structural connectivity to episodic memory. It thus provides an excellent example about how brain development supports cognitive development.

45. Chai XJ, Ofen N, Gabrieli JD, Whitfield-Gabrieli S: **Selective development of anticorrelated networks in the intrinsic functional organization of the human brain**. *J Cogn Neurosci* 2014, **26**:501-513.

46. Chai XJ, Ofen N, Gabrieli JD, Whitfield-Gabrieli S: **Development of deactivation of the default-mode network during episodic memory formation**. *Neuroimage* 2014, **84**:932-938.

47. Riggins T, Geng F, Blankenship SL, Redcay E: **Hippocampal functional connectivity and episodic memory in early childhood**. *Dev Cogn Neurosci* 2016, **19**:58-69.

48. Goswami U: **Neuroscience and education: from research to practice?** *Nat Rev Neurosci* 2006, **7**:406-413.

49. Cabeza R, Moscovitch M: **Memory systems, processing modes, and components: functional neuroimaging evidence**. *Perspect Psychol Sci* 2013, **8**:49-55.

50. Lindenberger U, von Oertzen T, Ghisletta P, Hertzog C: **Cross-sectional age variance extraction: what's change got to do with it?** *Psychol Aging* 2011, **26**:34-47.

51. Maxwell SE, Cole DA: **Bias in cross-sectional analyses of longitudinal mediation**. *Psychol Methods* 2007, **12**:23-44.

52. Dudai Y, Morris RG: **Memorable trends**. *Neuron* 2013, **80**:742-750.

53. Gabrieli JD: **Dyslexia: a new synergy between education and cognitive neuroscience**. *Science* 2009, **325**:280-283.

54. Kirschner PA: **Cognitive load theory: implications of cognitive load theory on the design of learning**. *Learn Instruct* 2002, **12**:1-10.

55. Mayer RE, Heiser J, Lonn S: **Cognitive constraints on multimedia learning: when presenting more material results in less understanding**. *J Educ Psychol* 2001, **93**:187-198.

56. Nelson SM, Arnold KM, Gilmore AW, McDermott KB: **Neural signatures of test-potentiated learning in parietal cortex**. *J Neurosci* 2013, **33**:11754-11762.

57. McDermott KB, Agarwal PK, D'Antonio L, Roediger HL 3rd, McDaniel MA: **Both multiple-choice and short-answer quizzes enhance later exam performance in middle and high school classes**. *J Exp Psychol Appl* 2014, **20**:3-21.

58. Sander MC, Werkle-Bergner M, Gerjets P, Shing YL, Lindenberger U: **The two-component model of memory development, and its potential implications for educational settings**. *Dev Cogn Neurosci* 2012, **2(Suppl. 1)**:S67-S77.

59. Magnuson KA, Ruhm C, Waldfogel J: **Does prekindergarten improve school preparation and performance?** *Econ Educ Rev* 2007, **26**:33-51.

60. Barnett WS: **Effectiveness of early educational intervention**. *Science* 2011, **333**:975-978.