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The development of hippocampal-dependent memory functions: Theoretical comments on Jabès and Nelson review (2015)

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Abstract

Studies investigating the development of memory processes and their neural substrates have flourished over the last two decades. The review by Jabès and Nelson (2015) adds an important piece to our understanding of the maturation of different elements and circuits within the hippocampal system and their association with the progressive development of hippocampal-dependent memory processes in humans. In this accompanying commentary, we explore some additional connections between the nonhuman primate work and the human data, and take the opportunity to highlight some common and additional interpretations of the results. This commentary makes three points: (1) the recognition processes present in the first few days of life may be linked to the early maturation of the medial temporal cortical areas instead of, or in addition to, the early maturation of the subiculum; (2) recent findings on the differential protracted maturation of spatial relational memory processes in monkeys further support the notion proposed by Jabès and Nelson that this protracted development may reflect progressive maturation of the CA1 field of the hippocampus followed by further maturation of CA3/dentate gyrus; (3) finally, further considerations of the differential maturation of the longitudinal hippocampal axis and of the diencephalon are proposed as additional contributors to the refinement of episodic memory functions during development.

Keywords

incidental recognition; relational memory; medial temporal lobe; *Macaca mulatta*; longitudinal hippocampal axis; thalamus

There has been a great deal of progress in the last half century in our understanding of the neural substrates involved in memory processing in humans and animals. Through the course of examining patients with damage restricted to the medial temporal lobe region, such as H.M. (Corkin, Amaral, Gonzalez, Johnson, & Hyman, 1997; Scoville & Milner, 1957), as well as more recent animal models with rodents (Eichenbaum, 1992, 2003) and nonhuman primates (Alvarado & Bachevalier, 2008; Meunier & Bachevalier, 2010), memory processes have classically been divided into two major types: procedural and declarative memory (Squire, 1992; Tulving, 1972). Thus, human temporal lobe amnesia

severely and selectively disrupts declarative memory and leads in most patients to dense impairments in both recall and recognition tasks, while sparing procedural memory.

The accumulating evidence that these two memory systems do indeed exist elicited renewed interest to investigate their ontogenetic development. Thus, using behavioral tasks that are known to be selectively sensitive (or not) to hippocampal damage in adults, studies in rodents (Rudy et al., 1987; Green & Stanton, 1989), monkeys (Bachevalier & Mishkin, 1984; Mahut & Moss, 1986), and humans (Diamond, 1990; Overman et al., 1992) have suggested that the two memory systems are developmentally dissociable with the procedural memory system emerging earlier in ontogeny than the declarative memory system. In reviewing these earlier findings, Nelson (1995) concluded that the procedural memory system *preserved* in amnesic subjects with hippocampal lesions is present *early* in life and suggested an early maturation of brain structures mediating this function, namely the striatum and cerebellum. By contrast, the declarative memory system *impaired* in amnesic subjects develops *later* in infancy and appears to have memory processes emerging early in infancy that were labelled as “pre-explicit” memory (Nelson, 1995), whereas other “more sophisticated forms” of declarative memory became apparent later in childhood and early adolescence. At the time, the author proposed that this progressive postnatal maturation of declarative memory processes reflected the progressive development of the hippocampus and its connectional system with medial temporal lobe cortical areas as well as the prefrontal cortex. In light of critical observations on the anatomical and functional organization of the different components of the hippocampal system as well as of the flow of information coursing through this system during the last 20 years (Lavenex & Amaral, 2000), in the present review Jabès and Nelson (2015) reexamine recent results on the ontogeny of declarative memory processes and attempt to link the progressive maturation of these different processes to progressive maturation of distinct elements and circuits within the hippocampal system. Despite the inherent difficulty in correlating maturation of specific hippocampal circuits with emergence of specific memory processes, the authors demonstrate that the early emergence of incidental recognition memory processes (in the first days of life) appears to be associated with an early maturation of the subiculum, whereas other relational memory processes progressively emerge during the first decade of life in humans. Within these protracted relational memory processes, spatial and non-spatial relation memory becomes apparent within the 1–2 years of life and is linked with the progressive maturation during this period of the CA1 circuitry, followed by that of the CA3 and dentate gyrus circuits. Finally, episodic memory (the memory for specific events), which represents the latest emerging hippocampal-dependent function, may be linked to the continuous arrival of new granule cells within the dentate gyrus. This commentary makes three points: (1) the recognition processes present in the first few days of life may be linked to the early maturation of the medial temporal cortex instead of, or in addition to, the early maturation of the subiculum; (2) recent findings on the differential protracted maturation of spatial relational memory processes in monkeys further support the notion proposed by Jabès and Nelson that this protracted development may reflect progressive maturation of the CA1 field of the hippocampus followed by further maturation of CA3/dentate gyrus; (3) finally, further considerations of the differential maturation of the longitudinal hippocampal axis and of the

diencephalon are proposed as additional contributors to the refinement of episodic memory functions during development.

Early developing recognition memory processes

Recent longitudinal studies of recognition memory in monkeys have led to important information on our understanding of the role of the hippocampus in incidental memory processes measured by visual paired-comparison (VPC) task. This task measures the ability of subjects to look longer at novel stimuli occurring in their environment as compared to familiar ones (novelty preference). In monkeys (Bachevalier, Brickson, & Hagger, 1993; Gunderson & Sackett, 1984; Gunderson & Swartz, 1985, 1986), as in humans (Pascalis & de Schonen, 1994; Pascalis, de Haan, Nelson, & de Schonen, 1998; Pascalis & de Haan, 2003), novelty preference is present in the first days of life and becomes stronger with age when long delays are used (Pascalis & de Haan, 2003; Morgan & Hayne, 2011). In a recent longitudinal study following the developmental trajectory of recognition memory in monkeys from 1 to 18 months, Zeamer and colleagues (Zeamer, Heuer, & Bachevalier, 2010) demonstrated that novelty preference was present at the youngest age (1 month) across all delays (10s to 120s) and became more robust by 6 months of age. By 18 months of age, however, a delay-dependent effect emerged with novelty preference being more robust at the shortest delay of 10s (74 % of looking towards novel images) and weakening (65 %) at the longest delay of 120s. This delay-dependent effect is similar to that described in adult animals and its emergence between 6 and 18 months suggested critical changes during this period within the neural substrate supporting incidental recognition memory. To investigate whether the delay-dependent effect reflected functional shifts within the hippocampus, novelty preference was assessed at the same ages (1–18 months) in monkeys that had received selective bilateral neurotoxic hippocampal lesions (Neo-H) between 10–12 days of age (Zeamer et al., 2010). Preference for novelty in Neo-H monkeys was similar to that of controls and became stronger from 1 to 6 months of age, suggesting that structures other than the hippocampus could support this function in the first postnatal months. However, by 18 months of age, the decrease in novelty preference across all delays was steeper in Neo-H monkeys as compared to controls, with no group difference at the shortest delays but a significant decrease in novelty preference for the Neo-H monkeys at the longest delay of 120s. This pattern of impairment is strikingly similar to that reported in monkeys with adult-onset hippocampal lesions (Nemanic, Alvarado, & Bachevalier, 2004) and suggests that with maturation the animals with Neo-H lesions grow into a recognition memory deficit. Thus, both the emergence of delay-dependent recognition memory performance at 18 months of age in the control animals together with the recognition memory impairment observed after neonatal hippocampal lesions at that same age indicate that important maturational changes in the neural substrate supporting incidental recognition memory occurred after 6 months of age in monkeys. In their review, Jabès and Nelson (2015) interpreted the strong novelty preference at all delays in both the controls and Neo-H animals prior to 6 months of age as resulting from early maturation of the subiculum, an hippocampal field mostly spared in the animals with Neo-H lesions. However, when re-examining the extent of neonatal hippocampal lesions (Zeamer et al., 2010), it appears that two animals in the Neo-H group (Neo-H2 and Neo-H3; see Figs. 2–3) had extensive

bilateral damage to the entire hippocampus, including the subiculum; yet, these two animals showed strong novelty preference at all delays prior to 6 months of age (see Table 3). Thus, we offered an alternative interpretation to the results and suggested that the normal novelty preference after neonatal hippocampal lesions in the first few months after birth could be supported by medial temporal cortical areas, such as the perirhinal and parahippocampal cortex, thought to be critical for familiarity judgments in adults (Brown & Aggleton, 2001; Buffalo, Ramus, Clark, Teng, Squire, & Zola, 1999; Murray, 2000; Nemanic et al., 2004; Yonelinas, 2002). This idea is supported by neurobehavioral experiments in adult monkeys as well as structural development of the medial temporal cortical areas in monkeys. First, although damage to the perirhinal cortex in adult monkeys impaired recognition memory as measured by VPC as did hippocampal lesions, the pattern of deficits varied according to the lesion site. That is, hippocampal lesions resulted in impairment only at delays longer than 60s, whereas perirhinal lesions altered recognition memory at all delays tested, except the shortest delays of 1s. Second, most of the neurogenesis in medial temporal cortical areas occurs prenatally with some morphological and neurochemical changes continuing in the first few months postnatally. Thus, at birth, the anatomical organization and chemical characteristics of the perirhinal and entorhinal cortex in the primate can be clearly identified and appear adult-like (Berger & Alvarez, 1994). Thus, if our interpretation is correct, one would predict that, unlike neonatal hippocampal lesions, damage to the perirhinal cortex in infancy might result in greater deleterious effects on incidental recognition memory processes, especially at the youngest ages. Our results are consistent with this prediction. Neonatal perirhinal lesions in monkeys altered novelty preference across all delays and at all ages tested (i.e. 1.5, 6 and 18 months) and this deficit became more profound as the animals matured (Zeamer & Bachevalier, 2014). Thus, the neurobiological evidence together with the present behavioral findings indicate the emergence of significant changes in functional interactions between the medial temporal cortical areas, such as the perirhinal cortex, and the hippocampus after 6 months of age. Similar changes in the functional organization of the medial temporal cortical areas and the hippocampus have recently been demonstrated in a functional neuroimaging studies in children and adolescents (Ghetti, DeMaster, Yonelinas, & Bunge, 2010). Thus, evidence suggests that incidental recognition memory processes appear to be more widely distributed in the immature brain but become more refined and committed to the hippocampal functioning as development progresses (Zeamer, Alvarado & Bachevalier, 2009; Webster, Ungerleider, & Bachevalier, 1995).

Maturation of relational memory processes

In their review, Jabès and Nelson (2015) showed that relational memory has a more protracted development than recognition memory. They suggest that more basic relational memory skills (i.e. memory for object-object relationships and object-location associations) appear by the end of the first year and second year in humans and might be associated with the maturation of the CA1 field and its connections. By contrast, more flexible relational memory skills emerge later (4–5 years in humans), corresponding to the maturation of the CA3 field and dentate gyrus. A similar protracted development of relational memory has recently been shown in monkeys as well (Blue, Richardson, & Bachevalier, 2013).

In this study, the same control monkeys and monkeys with Neo-H lesions reported above were also given a modified version of the VPC task to measure spatial-relational memory. A VPC-Spatial-Location task tested memory for object-locations that could be solved using an egocentric spatial frame of reference and a VPC-Object-In-Place task taxed memory for spatial relations using an allocentric reference frame. All animals were tested in both tasks as infants (8 months), juveniles (18 months), and adults (5–6 years). The data from control animals demonstrated that spatial memory has a protracted development as has been shown already in humans (Ribordy, Jabès, Banta Lavenex, & Lavenex, 2012), and that memory for spatial locations emerged earlier in the juvenile period, while memory for object/place association occurred later. Although the exact ages at which both types of memory becomes available are still unknown, it is likely that memory for a familiar object in a new location may be present by the end of the first year in monkeys (Lavenex & Banta Lavenex, 2006). Yet, development of memory for object/place associations occurred later in early adolescence. This developmental patterns of spatial relational memory support the notion developed by Jabès and Nelson (2015), and following their suggestion may reflect a progressive development first of the CA1 field of the hippocampus followed by maturation the CA3 and dentate gyrus later on. Interestingly, significant increases in CA3/DG volumes were recently demonstrated in humans from childhood to early adolescence and these volumetric changes were positively correlated with memory performance (Lee, Ekstrom, & Ghetti, 2014). In light of these findings, it was not surprising to find that neonatal damage of the hippocampus did impact performance on both tasks and more importantly this impairment occurred at an age when these types of memory first emerged in the control monkeys, i.e. at 18 months for the VPC-object-location and adults for the VPC-object-in-place (Blue et al., 2013). The effects of Neo-H lesions parallel those reported in recent studies of spatial memory performance in developmental amnesic cases with perinatal hippocampal damage who demonstrate as adolescents normal performance on task measuring visuo-spatial memory that could be solved using an egocentric frame of reference (Gadian et al., 2000), but profound memory deficits for scenes and topographical information using an allocentric frame of reference (Bird, Vargha-Khadem, & Burgess, 2008; King, Trinkler, Hartley, Vargha-Khadem, & Burgess, 2004; Spiers et al., 2001).

Other considerations

In conclusion, the Jabès and Nelson review bridges what we know from memory development in humans with basic research with laboratory animals as well as more recent information using cutting-edge imaging techniques in children and adolescents. Clearly, the review goes a long way toward demonstrating how the emergence of memory skills from birth to 4–5 years reflects some critical structural changes within the hippocampal circuits. As noted by the authors, the field of memory development and its neural basis remains in its infancy and underscores the need to further investigate the link between the occurrences of memory processes with maturation of specific brain circuits. To the accounts provided by the authors, here are a few other accounts that will need to be considered.

The first is the increase in white matter processes, which in addition to the maturation of cellular fields of the hippocampus, is likely to strengthen memory performance across early ages. In addition, strengthening of connections and white matter increases in fiber tracts

connecting the medial temporal lobe to prefrontal regions may also improve memory performance at later developmental ages (Wendelken, Lee, Pospisil, Sastre, Ross, Bunge, & Ghetti, 2014).

The second is a consideration of the functional development of the hippocampus in its anterior-posterior longitudinal axis. Both earlier studies in rodents (see for review Moser & Moser, 1998) and monkeys (Jackson, 1984; Colombo, Fernandez, Nakamura, & Gross, 1998) as well as more recent functional neuroimaging studies in humans (see for review Small, 2002; Nadel, Hosccheidt, & Ryan, 2013) demonstrate a functional differentiation along the longitudinal axis of the hippocampus, with the posterior (dorsal in rodents) hippocampus being crucial for precise spatial behavior, and the anterior (ventral in rodents) hippocampus being crucial for context coding. A recent structural neuroimaging study in children and adolescents (DeMaster, Pathman, Lee, & Ghetti, 2013) showed that adults with a smaller right anterior hippocampal volume and larger right hippocampal body obtained better episodic memory scores. This relationship between head and body of the hippocampus and episodic memory performance was not found in children. Thus, age-related changes in the longitudinal axis of the hippocampus may represent another contributor to improvement in episodic recollection.

Finally, in addition to the participation of the prefrontal cortex in the development of hippocampal-dependent memory processes, one will need to consider that of the diencephalon. Diencephalic structures, such as the medial thalamus and mammillary bodies play a critical role in recognition memory processes and episodic memory, as long known from human Korsakoff patients (whose alcoholism-induced damage to this brain region yields to global amnesia; Squire, 1982; Squire, Amaral, & Press, 1990) and from numerous lesion studies in animals (Aggleton & Mishkin, 1983; Aggleton & Brown, 1999; Vann & Aggleton, 2004). Yet, knowledge of the development of this brain area is at the present time unavailable. Thus, it is now in the hands of behavioral neuroscientists of the next generation to continue refining our knowledge on the specific neural bases of episodic memory development.

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