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Development of memory for spatial context: Hippocampal and cortical contributions

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ABSTRACT

The goal of the present study was to examine age-related differences in hippocampal and cortical contribution to episodic retrieval of spatial context in 3 age groups. Children ages 8–9 and 10–11 years old, and adults ages 18–25 (N=48) encoded black and white line drawings appearing either on the right side or the left side of a screen. Functional magnetic resonance imaging (*f*MRI) data were acquired while participants attempted to recall where each studied drawing had originally appeared. Correct recall of spatial source indicated successful episodic retrieval of spatial context. Activity in head and body of the hippocampus was associated with episodic retrieval in adults, but not in children. In children, individual differences in hippocampal activation for recognition predicted rates of correct spatial recall. Developmental differences were also found in regions in posterior parietal cortex, anterior prefrontal cortex, and insula. Overall, these results support the view that the development of episodic memory is supported by functional changes in the hippocampus as well as cortical regions.

1. Introduction

Research has consistently shown that episodic memory, the ability to recollect detailed information about previously experienced events, improves considerably during childhood (e.g., Brainerd, Holliday, & Reyna, 2004; Ghetti & Angelini, 2008; Schneider, Knopf, & Stefanek, 2002). More recently researchers have attempted to explain this improvement by characterizing the developmental trajectory of two sets of processes that are critical for episodic memory: binding and controlled processes (Ghetti & Lee, 2011; Ghetti, Lyons, & DeMaster, 2012; Shing, Werkle-Bergner, Li, & Lindenberger, 2008).

Binding processes involve the formation and subsequent retrieval of associations that integrate information about an event with information about the spatio-temporal contextual details associated with that event (Eichenbaum, Yonelinas, & Ranganath, 2007). In contrast, controlled processes involve those operations that guide encoding or monitoring of retrieval operations. In the adult neuroimaging literature there is evidence that successful episodic retrieval is dependent on binding operations supported by the hippocampus (Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011; Weis et al., 2004) in conjunction with controlled processes engaging both prefrontal cortex (e.g., Cansino et al., 2002; Dobbins et al., 2003; Hayes et al., 2011) and the parietal cortices (e.g., Dobbins, Foley, Schacter, & Wagner, 2002).

Motivated by age-related improvements evident in behavioral results, and what is known about the neural substrates that support binding and controlled processes in adults, developmental neuroimaging studies have explored the possibility that protracted development of brain regions critical for binding (e.g., hippocampus; DeMaster & Ghetti, 2013; Ghetti, DeMaster, Yonelinas, & Bunge, 2010; Güler & Thomas, 2013) and controlled processes (e.g., prefrontal and parietal cortices; Ofen, Chai, Schuil, Whitfield-Gabrieli, & Gabrieli, 2012) may be primary contributing factors to improvements in episodic memory in middle childhood.

These studies are reviewed in the next section. Here, we preview that the purpose of the present investigation is to examine the contribution of these regions to episodic memory retrieval in a task that is contingent on contextual retrieval of spatial information.

1.1. Neural changes underlying the development of episodic retrieval

Only a handful of neuroimaging studies have examined the development of the neural correlates supporting memory retrieval (DeMaster & Ghetti, 2013; Güler & Thomas, 2013; Ofen et al., 2012; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). To date, the results concerning the role of the hippocampus have been inconsistent.

Two studies have found age-related differences in the contribution of the hippocampus to episodic retrieval (DeMaster &

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Ghetti, 2013; Paz-Alonso et al., 2008). First, Paz-Alonso et al. (2008) found that hippocampal activation in 8-year-olds did not distinguish between studied items and non-studied lures; in contrast, stronger activation was observed for studied items compared to non-studied lures in 12-year-olds and adults. More recently, DeMaster and Ghetti (2013), showed a developmental dissociation along the longitudinal axis of the hippocampus in a task that required the retrieval of contextual details. Specifically, for 8- to 11-year-olds increased activation for correctly retrieved contextual details compared to incorrectly retrieved details were found in the tail of the hippocampus, but this pattern of activation was not reliable in more anterior regions. In contrast, the adult group showed activation patterns that were consistent with recollection of contextual details in the head of the hippocampus, but not in the tail. Overall, these results suggest that developmental differences in episodic retrieval may be mediated by the development of hippocampal function.

In contrast to results indicating age-related differences in hippocampal contribution to episodic recollection, Ofen et al. (2012) reported retrieval-related activation within the parahippocampal gyrus which did not change with age, and no statistically significant cluster in the hippocampus. It is likely that these mixed results are due to the nature of the tasks used rather than age invariance in hippocampal contribution to episodic retrieval. For example, Ofen et al. (2012) utilized a task requiring participants to distinguish between studied and novel outdoor scenes; thus the retrieval of the associations between items and their context, a signature of episodic recollection, was not necessary to respond accurately. In contrast, the task used in DeMaster and Ghetti (2013) required participants to retrieve the arbitrary association between encoded line drawings of everyday objects and the color of a border surrounding them.

However, age-invariance has also been observed when arbitrary associations were tested. Güler and Thomas (2013) investigated age-differences in cortical contribution to retrieval found age invariance hippocampal recruitment. In this investigation, functional data were collected from children age 8–13-years during an encoding session and during a retrieval task requiring recall of paired associates. A region of the hippocampus was recruited for successful recall of pairs compared to forgotten pairs, but age-related differences in this region were not evident. It is possible that age differences in hippocampal contribution to this task would have been evident if Güler and Thomas (2013) had included an additional older group so that comparisons could be made between older adolescents or adults and children (Ghetti et al., 2010). Given this inconsistency, it is clear that more investigations are necessary to fully characterize developmental differences in hippocampal contribution to episodic memory. A central goal of the present study was to examine developmental differences in hippocampal function for a task requiring retrieval of items in association with their original spatial location across samples of children and adults.

In contrast to mixed results within the hippocampus, all studies to date have converged in showing developmental differences in the contribution prefrontal cortex (PFC) and posterior parietal cortex (PPC) to episodic retrieval. For example, Ofen et al. (2012) reported age-related increases in activation related to successful retrieval in regions of the PFC and superior parietal lobe and similar results were evident in Güler and Thomas (2013). Age-related differences in PFC were also found in Paz-Alonso et al.'s study (Paz-Alonso et al., 2008): different patterns of activation were found in 8-year-olds, 12-year-olds, and adults in the anterior, dorsolateral, and ventrolateral PFC, which suggested development of in the mechanisms underlying monitoring, decision processes, and assessment of semantic cues respectively. Finally, DeMaster and Ghetti (2013) reported age-related differences between a sample of 8- to 11-year-olds and adults in the anterior PFC and PPC in a task requiring participants to recollect a contextual feature associated with studied items. Although these studies were not designed to probe directly the various processes mediated by fronto-parietal mechanisms, they all converged in providing evidence of developmental change in cortical contributions to memory retrieval. One additional goal of the present study was to gather further evidence of developmental differences in cortical contribution to episodic retrieval.

2. The present study

The present study was aimed at further investigating developmental differences in hippocampal and cortical contribution to episodic retrieval of contextual features. To achieve this goal, we examined age differences in retrieval of associations between items and their spatial positions. By definition, episodic recollection requires the retrieval of an event along with its spatiotemporal context (Tulving, 2002; Wheeler, Stuss, & Tulving, 1997), and the neural substrates supporting retrieval of an item and its spatial location has been frequently examined in research with adults (e.g., Cansino et al., 2002; Hannula & Ranganath, 2008; Ross & Slotnick, 2008). Findings from these studies have implicated the network of regions typically involved in episodic retrieval, namely the medial temporal lobes, including the hippocampus, PFC and PPC regions (e.g., Dobbins et al., 2003; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; Kwok, Shallice, & Macaluso, 2012; Weis et al., 2004; Zhang & Ekstrom, 2012). For example, in Cansino et al. (2002), a study with a design similar to our own, items were encoded in one of four quadrants on a screen. During the retrieval phase, items were presented in the center of the screen and participants made a source judgment by selecting the quadrant in which the item was presented during the encoding phase. Neural activity in the hippocampal formation, medial and superior frontal gyri and lateral parietal cortex was associated with successful retrieval of correct spatial context. Given the consistent finding of hippocampal involvement, along with other MTL regions and those in the fronto-parietal network, we determined that a task requiring recollection of items in association with spatial information would prove sensitive to examine developmental differences in episodic retrieval.

We were particularly interested in further investigating age-related differences in hippocampal contribution to episodic retrieval along the longitudinal axis of the hippocampus. Specifically, consistent with our previous study (DeMaster & Ghetti, 2013), we expected reliably stronger recruitment of the hippocampal head for correct spatial context retrieval compared to incorrect spatial context in adults, but not in children. Predicting age-related differences in the hippocampal tail during this task is more difficult. On one hand, based on our previous study we should expect stronger recruitment of this sub-region in children compared to adults. On the other hand, however, the retrieval of spatial information frequently engages posterior hippocampal regions (Ekstrom et al., 2011; Ross & Slotnick, 2008) so a different pattern of results might be expected.

The present study sought not only to examine developmental differences between children and adults, but also between younger compared to older children. Comparing a child group to a group of young adults, DeMaster and Ghetti (2013) found age-related differences in hippocampal recruitment and recruitment of PFC and posterior parietal cortex in association with episodic retrieval. Middle to late childhood represents a period of rapid improvement in episodic memory (Ghetti & Angelini, 2008). Here, we investigated late childhood as a transitional period in episodic memory development. Thus, by isolating older children from