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Developmental differences in hippocampal and cortical contributions to episodic retrieval

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ABSTRACT

Episodic memory, or the ability to form and retrieve conscious memories about specific past events, improves during childhood. Previous adult neuroimaging results indicate a central role of the hippocampus in episodic retrieval, but it is not clear whether the contribution of the hippocampus changes during development. Traditionally, developmental improvements in episodic retrieval have been thought to depend on strategic processes mediated by the prefrontal cortex (PFC), a region that is considered to have a protracted course of development relative to the hippocampus. The primary goal of the present study was to test the hypothesis that the development of episodic retrieval is also associated with changes in hippocampal function. Children ages 8- to 11-years-old and adults ages 18–25 ($N = 41$) encoded black and white line drawings surrounded by either a green or red border. Functional magnetic resonance imaging (fMRI) data were acquired while participants attempted to recall which colour was originally paired with each drawing. Correct recall of item-colour pairings indicated successful episodic retrieval. Activity in the anterior hippocampus, but not in the posterior hippocampus, was associated with episodic retrieval in adults, whereas activity in the posterior, but not in the anterior hippocampus, was associated with episodic retrieval in children. Developmental differences were also found in regions in anterior lateral PFC and posterior parietal cortex. Overall, these results support the view that the development of episodic memory is supported by functional changes in the hippocampus as well as in other critical cortical regions.

1. Introduction

The ability to recollect rich episodic memories develops substantially during middle and late childhood (Brainerd et al., 2004; Ghetti and Angelini, 2008; Schneider et al., 2002). The ability to remember the source of a memory is one of the most commonly used behavioural indicators of episodic memory (Johnson, 2006). Although it is possible to determine that an event was previously experienced without retaining any information about the source (i.e., the origin) of the memory, source information, such as where an event occurred, constitutes one of the most important features of episodic content.

Previous research documents age-related improvements in source memory during the childhood years, which are more robust than improvements in the ability to recognize the occurrence of an event without source information (e.g.,

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Lorsbach and Reimer, 2005; Cowan et al., 2006; for reviews see Ghetti et al., 2012; Raj and Bell, 2010). These robust improvements have been documented in working memory source tasks (Lorsbach and Reimer, 2005; Cowan et al., 2006) and task assessing memory over longer delays (Cycowicz et al., 2001; Ghetti et al., 2010). Since successful source memory is dependent on cognitive processes such as the ability to monitor the accuracy of retrieved information and the ability to initiate and guide strategic retrieval searches, including monitoring and attribution of source information (Roberts and Blades, 2000; Raj and Bell, 2010), age-related increases in prefrontally-mediated controlled mechanisms have been identified as forces driving improvement in source memory during the childhood years (Newcombe et al., 2007; Ofen et al., 2007). There is indeed ample evidence that a network of fronto-parietal regions supports the working memory and attentional processes engaged during memory retrieval (e.g., Badre and Wagner, 2007; Cabeza et al., 2008; Henson et al., 2005; Rugg et al., 2003). Several developmental ERP studies have contributed physiological evidence indicating age-related difference in prefrontal (PFC) contribution to strategic recollection and suggesting an association between protracted development of PFC and improvement in retrieval of source information during childhood (e.g., Czernochowski et al., 2005; Czernochowski et al., 2009; Sprondel et al., 2011).

An additional possibility is that changes in source memory also depend on changes in the process responsible for first forming and later re-enacting representations that bind together different features of an episode changes during childhood. This binding process has been ascribed to the hippocampus (e.g., Diana et al., 2007; Eichenbaum and Cohen, 2001). The possibility that change in the hippocampus contributes to episodic memory development during late childhood has been previously neglected due to the view that the hippocampus reaches maturity by early childhood (e.g., Seress et al., 2001).

However, there is now evidence of protracted change in hippocampal structure: a developmental decrease in volume of the anterior hippocampus and increase in the posterior hippocampus were found between 4 and 25 years of age (Gogtay et al., 2006). Furthermore, in Gogtay et al. (2006), these changes were more pronounced in the left compared to the right hippocampus. Finally, the few studies that have examined encoding-related activation have shown developmental differences in hippocampal function (Ghetti et al., 2010; Maril et al., 2010; but see Ofen et al., 2007). Particularly relevant for our current goals, Ghetti et al. (2010) showed an anterior region of the hippocampus, in which activity consistent with source encoding was observed in 14-year-olds and adults, but not in 8-year-olds and 10-year-olds: whereas these older participants recruited this hippocampal regions during trials for which source was subsequently recollected, younger participants were more likely to recruit the hippocampus for items subsequently recognized regardless of whether the source was remembered. Overall, these few studies lead to the prediction that changes in hippocampal function may contribute to the development of episodic retrieval.

To date, no study has examined developmental differences in hippocampal function during episodic retrieval. In contrast, the present research investigates age-related differences in hippocampal contribution to *retrieval* during a source memory task. Given the distinct developmental trajectories found in volumetric assessments of this structure along its longitudinal axis, we sought to examine whether age differences would be found with regard to function in the anterior versus posterior hippocampus.

In addition to examining age-related differences in hippocampal contribution to episodic retrieval, age-related differences in other regions were investigated. We expected to find developmental differences within the PFC and posterior parietal cortex (PPC) given their known roles in guiding controlled processes during retrieval (Badre and Wagner, 2007; Cabeza et al., 2008), and previous developmental work indicating that immature activation profiles in these regions are observed into adolescence in various aspects of working memory (e.g., Crone et al., 2006; Geier et al., 2009).

Consistent with these findings are those from the only published functional magnetic resonance imaging (fMRI) study examining development of item memory retrieval processes (Paz-Alonso et al., 2008). This study examined the neural correlates associated with the ability to discriminate between true and false memories. Children ages 8 and 12 years, and young adults studied lists of highly semantically associated words. Following a short delay, a recognition memory test was administered requiring words in the original lists to be discriminated from lures that were either semantically consistent words or inconsistent words (Roediger and McDermott, 1995). Results showed that activity in ventrolateral PFC (vl PFC; BA 47), left dorsolateral PFC (dl PFC, BA 9), and lateral anterior (aPFC; BA 10) exhibit increasingly differentiated patterns of activation with age. Adults showed a clear activation profile in these regions consistent with their purported functions in support of semantic retrieval cue, monitoring, and decision operations respectively (Paz-Alonso et al., 2008). In contrast, 8-year-olds exhibited an undifferentiated activation profile such that activation did not differ as a function of trial type, and 12-year-olds exhibited an intermediate pattern of activation between 8-year-olds and adults. In the same study, developmental differences were also found in PPC (BA 7), which responded in 12-year-olds and adults, but not in 8-year-olds to the perceived oldness of the items, regardless of their accuracy. Although the Paz-Alonso et al.'s study only required old/new decisions and thus does not provide any information about retrieval of additional specific episodic details, the results clearly underscore the importance of examining these regions to characterize the development of episodic retrieval (see also Ofen et al., 2007 and Ghetti et al., 2010; for evidence of developmental differences in PFC during episodic encoding).

To examine the neural correlates of the development of episodic retrieval, we conducted an fMRI study that included a group of children ages 8- to 11-year-olds and a group of young adults ranging in age from 18 to 25 years. A source memory task was utilized because it requires retrieval of an item and detail associations which is a fundamental operation to successful episodic retrieval. Furthermore, several neuroimaging studies with adults using source memory tasks show that retrieval of item and detail information strongly engages the hippocampus (Cansino et al., 2002; for a review see Diana et al., 2007). In this task participants encoded black and white drawings and the colour of the border surrounding the drawing outside of the