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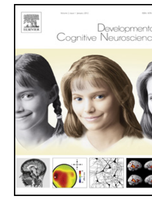

Age- and performance-related differences in hippocampal contributions to episodic retrieval

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ABSTRACT

The goal of the present study was to investigate whether hippocampal contribution to episodic memory retrieval varies as a function of age (8–9 versus 10–11 versus adults), performance levels (high versus low) and hippocampal sub-region (head, body, tail). We examined fMRI data collected during episodic retrieval from a large sample ($N = 126$). Participants judged whether a stimulus had been encoded previously, and, if so, which of three scenes it had been paired with (i.e., source judgment). For 8- to 9-years-olds as well as low-performing 10- to 11-year-olds, hippocampal activations did not reliably differentiate between trials on which item-scene associations were correctly recalled (correct source), incorrectly recalled (incorrect source), or trials on which the item was forgotten (miss trials). For high-performing 10–11-year olds and low-performing adults, selective hippocampal activation was observed for correct source relative to incorrect source and miss trials; this effect was observed across the entire hippocampus. For high-performing adults, hippocampal activation also distinguished between correct and incorrect source trialsl, but only in the hippocampal head, suggesting that good performance in adults is associated with more focal hippocampal recruitment. Thus, both age and performance are important factors for understanding the development of memory and hippocampal function.

1. Introduction

Episodic memory, or the ability to remember specific past events in the context in which they occurred, improves considerably during middle and late childhood (Brainerd et al., 2004; Ghetti and Angelini, 2008; Shing and Lindenberger, 2011). The hippocampus has been implicated in the encoding and integrating the contextual features of our experiences into bound representations and the retrieval of these representations (Diana et al., 2007; Eichenbaum et al., 2007). Thus, understanding developmental changes in hippocampal function in critical for understanding the development of episodic memory.

Although several studies have compared hippocampal function in children and adults in an attempt to explain age-related differences in episodic memory, these studies have yielded varying results. The majority of studies have found age-related differences in hippocampal activation profiles between children and adults (DeMaster and Ghetti, 2013; DeMaster et al., 2013; Ghetti et al., 2010; Paz-Alonso et al., 2008); however, the apparent nature of these developmental differences has not been consistent. For example, children have been found to show decreased memory-related hippocampal selectivity for episodic retrieval compared to adults across the entire hippocampus (DeMaster et al., 2013). However, in other studies developmental differences were restricted to the hippocampal head or tail (e.g., DeMaster and Ghetti, 2013; Paz-Alonso et al., 2008). Finally, other studies have failed to find age-related differences in hippocampal function altogether (Güler and Thomas, 2013; Ofen et al., 2012).

Part of this inconsistency may be due to the relatively small child sample sizes in previous studies.[1] It is critical to examine age-related differences with large enough sample sizes to differentiate among children of different ages, not just between children and adults, when investigating a developmental period in which behavioral change is robust. Middle childhood is one such period

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[1] Functional imaging studies (e.g., DeMaster and Ghetti, 2013; DeMaster et al., 2013; Ghetti et al., 2010; Güler and Thomas, 2013; Ofen et al., 2012; Paz-Alonso et al., 2008) that have directly attempted to characterize the relation between episodic memory and hippocampal activation, overall sample sizes (including all age groups) averaged to 58 participants, less than half the sample of the current study, ranging from 30 participants to 80 participants.

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of rapid change in memory performance. For example, several studies have shown consistent age-related improvements among children in this age range in assessments of episodic recollection (Ghetti and Angelini, 2008), source memory (Riggins, 2014) and recall (Schwenk et al., 2007). Developmental differences in hippocampal structure have similarly been reported during this period (DeMaster et al., 2014; Gogtay et al., 2006). Given these robust changes, studies that examine age differences among children are more likely to successfully characterize developmental processes than those which consider children as a single group. Results from one of the few studies of memory development in which children of multiple ages were examined separately (Ghetti et al., 2010) illustrate this possibility. In that study, there was evidence of non-linear change from middle childhood into adolescence, such that subsequent item-memory effects were observed in 8-year-olds, no subsequent memory effects were observed in 10- to 11 year-olds and subsequence source-memory effects were evident in 14-year-old and adults. This non-linear pattern underscores the importance of differentiating among children, and the risk of attenuating or misrepresenting age differences when children of different ages are examined together.

Age is not the sole source of potential variation in hippocampal activation. Individual differences in task performance may also yield differences in activation. For example, there is evidence from previous research that differences in activation profiles may be more strongly associated with individual differences in performance than with age (Paz-Alonso et al., 2013). In this study examining the neural substrates of memory suppression, some participants were able to suppress memory retrieval and some participants were not within each age group, despite overall better performance in 10–12 year old children compared to 8–9 year old children. Individual differences in performance were more strongly predictive of differences in neural activation than were age differences. Notably, these performance-related activation differences were examined in regions associated with cognitive control, and not within the hippocampus. Thus, the extent to which age and performance differences affect hippocampal activation remains a key question for investigation. A large sample allows for the examination of potential relations between hippocampal activations during retrieval and task performance, which together may paint a more coherent picture how hippocampally-mediated binding processes contribute to the development of episodic memory.

In addition to examining age- and performance-related differences in hippocampal activation, we aimed to further investigate whether this activation would differ as a function of position along the hippocampal axis. The discussion about whether there are differences in function along the longitudinal axis of the hippocampus has gained momentum in recent years (Poppenk and Moscovitch, 2011; Poppenk et al., 2013) and, although there is no consensus about the exact meaning of these differences, initial evidence from developmental dissociations has bolstered the claim in favor of functional distinctions. This initial evidence has come both from structural and functional developmental studies. Functional differences have been reported with children failing to recruit the hippocampal head to the same extent as adults (DeMaster and Ghetti, 2013; Paz-Alonso et al., 2008), and with children, but not adults, engaging the hippocampal tail (DeMaster and Ghetti, 2013). In these studies, children ages 8–11 years were examined as one group, reducing the possibility of fully appreciating development during this period. Furthermore, in other studies, age differences in hippocampal activation extended throughout the entire structure (DeMaster et al., 2013), possibly suggesting that functional distinctions along the longitudinal axis are subtle and may depend on specific aspects of the task. The present study offers the opportunity to examine these regional differences while accounting for both age- and task-related performance.

Consistent with this functional evidence, a study of hippocampal structure has shown that in children, source retrieval was positively associated with volume in the hippocampal tail, whereas in adults it was associated with volumes of more anterior regions (i.e., negatively with the hippocampal head and positively with the hippocampal body; DeMaster et al., 2014). Interestingly, the direction of the volume–behavior associations in adults reflected the direction of development differences: indeed, adults compared to children had a smaller hippocampal head, and adults with smaller hippocampal heads exhibited better source retrieval. Thus, there is strong evidence from anatomical as well as functional investigations for developmental differences along the longitudinal axis of the hippocampus, and consideration of these differences may be critical for understanding hippocampal contributions to improvements in episodic retrieval during childhood.

2. The present study

The present study was aimed at examining age- and performance-related differences in hippocampal function during episodic retrieval. In addition, we were interested in investigating whether these differences varied as a function of location along the longitudinal axis of the hippocampus. To achieve these goals, we assessed a sample of 8- to 11-year-olds and young adults with a source memory task that required participants to remember which of three scenes was initially paired with individual objects. The task was designed to: (1) reflect the basic structure of source memory tasks used in prior studies (Ghetti et al., 2010); (2) be appropriate for a wide age range; and (3) incorporate meaningful item-context pairings. In particular, contextual information in this task (i.e., the scenes) is visually and semantically richer than contextual information used in previous studies such as position (DeMaster et al., 2013), colored borders (DeMaster and Ghetti, 2013), or another paired item (Güler and Thomas, 2013).

We predicted that, compared with adults, children would not show as strong hippocampal selectivity for correct source trials compared to incorrect source trials and forgotten trials. Furthermore, we predicted differences in hippocampal activation profiles among children of different ages, given the consistent age-related behavioral differences (Ghetti and Angelini, 2008; Ghetti et al., 2010) and some initial evidence of differences in hippocampal activation observed during this period (DeMaster et al., 2013; Ghetti et al., 2010; Paz-Alonso et al., 2008). For example, in a study examining encoding-related activity (Ghetti et al., 2010), 8-year-olds recruited the hippocampus successfully, but this activation did not differ as a function of subsequent source accuracy (i.e., whether the item was subsequently remembered with the correct or incorrect source). By contrast, 10- to 11 year-olds showed a tendency for increased activation for subsequently correct source, but this difference was not as strong as in adults.

Recent work has highlighted the importance of matching participants for behavioral performance when analyzing functional results (Ghetti et al., 2010; Güler and Thomas, 2013). Given the high cognitive demand of the tasks and these previous findings, we predicted large individual differences in episodic memory among both children and adults. Thus, we sought to further characterize age-related differences in hippocampal contribution to episodic retrieval by contrasting task-related activations of higher and lower performing individuals within each age group.

Finally, we hypothesized that activation patterns and age-related differences would vary as a function of location along the longitudinal axis of the hippocampus (DeMaster and Ghetti, 2013; DeMaster et al., 2014; Gogtay et al., 2006; Poppenk et al., 2013). Based on this prior work, we predicted that adults would recruit more anterior regions during episodic retrieval compared