

SYMPOSIUM

Age Differences in Hippocampus-Cortex Connectivity during True and False Memory Retrieval

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Abstract

The present functional magnetic resonance imaging (fMRI) study investigated developmental differences in functional connectivity associated with true and false memory retrieval. A sample of 8- to 9-year-olds and adults ($N = 31$) was assessed with the Deese/Roediger-McDermott (DRM) paradigm, known to induce high levels of false recognition of lures that are semantically associated with studied items. The strength of semantic association among list items was manipulated. Relative to children, adults correctly recognized more studied items and falsely recognized more critical lures. High-association lists resulted in higher recognition of both studied items and critical lures. Functional connectivity analysis revealed that, overall, true recognition was supported by coupling within two hippocampal-temporal and fronto-parietal set of regions; in contrast, coupling among more distributed hippocampal-temporal-parietal-frontal regions was observed during false recognition. Critically, adults, compared to children, exhibited stronger hippocampal/parietal coupling and stronger hippocampal/dorsolateral prefrontal cortex (PFC) coupling for veridical recognition of high-associative strength items. In contrast, children, compared to adults, exhibited stronger hippocampus/ventrolateral PFC coupling and stronger bilateral middle-temporal gyrus/ventrolateral PFC coupling for high-associative strength critical lures. Our results underscored a role for the anterior hippocampus in true and false recognition, showing different functional patterns as a function of age and association strength. (*JINS*, 2013, 19, 1031–1041)

Keywords: Episodic memory, Recognition, Hippocampus, Middle-temporal gyrus, Prefrontal cortex, Functional connectivity

INTRODUCTION

Neuroimaging research holds much promise for elucidating the functioning principles of episodic memory, including neural signatures that might distinguish between true and false memories (Schacter, 1999). Over the past two decades, the DRM paradigm (Roediger & McDermott, 1995) has been used extensively in studies with children and adults (see Brainerd, Reyna, & Ceci, 2008, and Gallo, 2010, for reviews), as well as with clinical populations (e.g., Paz-Alonso, Ghetti, et al., 2013). One advantage of this paradigm is that it reliably induces robust false recognition by probing processes that are central to memory distortion (Zhu, Cheng, Loftus, Lin, & Dong, 2013) without relying on social pressure as other paradigms do (e.g., Loftus & Pickrell, 1995).

In the DRM paradigm, participants study several word lists (e.g., *bed, rest, tired, dream, wake, ...*), converging on a semantic theme captured in a word that is never studied (i.e., *sleep*; critical lure, CL); participants then perform an old/new recognition test that includes studied words (i.e., *bed*; targets), CLs (i.e., *sleep*), and other lures that are non-semantically associated with the studied materials (i.e., *flower*; unrelated lures, ULs). Adults are frequently as likely to falsely recognize CLs as they are to correctly recognize studied words (McDermott & Roediger, 1998). Age-related increases in both true and false recognition have been consistently reported in behavioral studies (e.g., Brainerd et al., 2008; Howe, Cicchetti, Toth, & Cerrito, 2004; but see Carneiro, Albuquerque, Fernandez, & Esteves, 2007; Ghetti, Qin, & Goodman, 2002), suggesting that access or activation of semantic associations becomes more automatic during middle childhood (e.g., Wimmer & Howe, 2009).

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Moreover, the DRM paradigm has been used in several neuroimaging studies to investigate the neural signatures of true and false memory (e.g., Atkins & Reuter-Lorenz, 2011; Cabeza, Rao, Wagner, Mayer, & Schacter, 2001). The fMRI research using this paradigm with children and adults has typically revealed activations in a left-lateralized set of regions, including lateral PFC, lateral temporal cortex, and parietal cortex (Cabeza et al., 2001; Konishi, Wheeler, Donaldson, & Buckner, 2000; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008; Slotnick & Schacter 2004). Neuroimaging research using this and other paradigms has also demonstrated that the medial temporal lobes (MTL) are involved in the recollection of semantic and sensory properties (e.g., Cabeza et al., 2001; Eichenbaum, Yonelinas, & Ranganath, 2007; Stark & Squire 2000). For example, Cabeza et al. (2001) reported functional differences between anterior and posterior hippocampus suggesting that the former supports the recovery of semantic information and the latter the recovery of specific perceptual features.

The anterior MTL, including hippocampus and perirhinal cortex has been considered a key component of the semantic system (Patterson, Nestor, & Rogers, 2007), because of its involvement in extracting systematic associations of features that define objects (Henson & Gagnepain, 2010). Unlike the posterior portions of the MTL typically involved in the processing of contextual features (Diana, Yonelinas, & Ranganath, 2007; Ranganath et al., 2004), the anterior MTL has been associated with familiarity (Henson & Gagnepain, 2010), including illusory familiarity to novel stimuli (Abe et al., 2008; see also Chadwick, Hassabis, Weiskopf, & Maguire, 2010).

Recent pediatric functional neuroimaging research has suggested differential involvement of anterior and posterior hippocampus in memory operations (DeMaster & Ghetti, 2013; Ghetti, DeMaster, Yonelinas, & Bunge, 2010; Maril et al., 2010; Paz-Alonso et al., 2008). The relevance of these findings is underscored by evidence of distinct trajectories of structural development of hippocampal subregions along its anterior–posterior axis (DeMaster, Pathman, Lee, & Ghetti, 2013; Gogtay et al., 2006).

Structural and functional differences between anterior and posterior hippocampus suggest a division of labor in memory processes which might depend, at least in part, on their connectivity with different cortical regions (Poppenk & Moscovitch, 2011). To further understand how differences in connectivity may be relevant for true and false memory, it is helpful to examine what regions have been previously associated with these phenomena. The only neurodevelopmental imaging study using the DRM paradigm (Paz-Alonso et al., 2008) found a developmental progression in the functional engagement of left anterior hippocampus, with 8-year-olds recruiting this region for correct identification of new ULs, 12-year-olds for true memories as well as for the correct rejection of ULs, and adults for distinguishing true from false memories. This study also found age-related differences in left-lateralized cortical regions found in prior DRM retrieval studies with adults [i.e., middle temporal gyrus

(MTG, BA21), posterior parietal cortex (PPC, BA7), ventrolateral PFC (BA47), and dorsolateral PFC (dlPFC, BA46)], which are thought to support recollection, semantic processing, and memory monitoring during true and false episodic retrieval (e.g., Cabeza et al., 2001; Kim & Cabeza, 2007; Okado & Stark, 2003; Slotnick & Schacter, 2004). Overall, this previous research provides us with a reasonable basis to guide the identification of relevant connectivity nodes for the present study.

The central goal of the present research is to expand our previous work by examining age-related differences in connectivity between anterior and posterior parts of the hippocampus and cortical regions during true and false recognition. In an analysis of functional connectivity during resting state, Kahn, Andrews-Hanna, Vincent, Snyder, and Buckner (2008) found that the anterior hippocampus was strongly correlated with regions in the lateral temporal cortex; in contrast, the more posterior parts of the hippocampus were correlated with lateral parietal cortex, posterior parahippocampal cortex, and regions along the posterior midline and ventral medial PFC. This posterior pathway is involved in recollection (Ranganath & Ritchey, 2012). These connectivity results concerning the hippocampal sub-regions map well onto the regions engaged in memory retrieval from fMRI studies reviewed earlier.

There is now a small set of studies documenting age-related and task-related differences in functional connectivity between MTL and PFC regions during memory encoding (Menon, Boyett-Anderson, & Reiss, 2005) and among MTL, PFC, and PPC during retrieval (Ofen, Chai, Schuil, Whitfield-Gabrieli, S., & Gabrieli, 2012; Paz-Alonso, Bunge, Anderson, & Ghetti, 2013). However, no study has examined developmental differences in functional connectivity during true and false memory. The main goal of the present research is to examine developmental differences in how hippocampal activity is coupled with activity in other cortical regions involved in true- and false-memory retrieval.

Based on the literature discussed thus far, we predicted that the anterior and posterior hippocampus may be differentially connected with various cortical regions supporting memory, and that the anterior hippocampus may be particularly involved in the DRM task because it might preferentially support processing of semantic relationships (Cabeza et al., 2001) in connection with other ventral regions, such as MTG (Dennis, Bowman, & Vandekar, 2012; Kahn et al., 2008). In contrast, consistent with recent research (Dennis et al., 2012), we expected false recognition to show be associated with a more distributed set of regions including frontal parietal, and posterior cingulate regions.

To help characterize age differences in connectivity in true and false memory retrieval, we manipulated list associative strength. This is relevant because false memories depend on associative activation in the DRM paradigm (e.g., Howe, 2005; Howe, Wimmer, & Blease, 2009), and children's domain-specific associative connections among related concepts (as well as the automaticity of the activation of these concepts) develop during middle childhood (Wimmer & Howe, 2009).

Therefore, we used high- and low-strength DRM lists based on association strength norms (Stadler, Roediger, & McDermott, 1999). The comparison of age groups in the processing of related concepts, differing in strength of semantic associations, allow for shedding new light onto whether developmental differences in behavioral performance in the DRM paradigm stem from differences in automaticity of access and activation of semantic concepts.

METHODS

Participants

Our sample consisted of 31 right-handed native English-speaking participants: fourteen 8- to 9-year-olds ($M = 9.07$ years; range = 8.03–9.82; 6 females) and 17 young adults ($M = 21.21$ years; range = 19.30–27.62; 9 females). Additionally, data from 10 participants were excluded from analysis due to excessive head motion (6 children and 1 adult whose head motion parameters exceeded 3 mm within at least one functional scan), technical difficulties during fMRI data acquisition (2 adults), or failure to understand the task (1 child who responded with the same button to most of the trials). Participants received either monetary compensation or course credit for their participation. Before participating, informed consent was obtained based on procedures approved by the UC Davis IRB. Children were prescreened with the Child Behavior Checklist (Achenbach, 1991). We note that none of the participants in the present study participated in our prior developmental DRM study (Paz-Alonso et al., 2008); however, we included 8- to 9-year-olds and adults here, corresponding to the youngest and oldest group tested in Paz-Alonso et al. (2008) to better relate the present results to our previous research.

Task and Procedure

Eighteen lists of 12 words each were adapted for use with children and adults from materials used previously in the DRM experimental paradigm (Roediger & McDermott, 1995). These lists were selected based on associative strength norms and their effectiveness in producing false recognition to CLs (Stadler et al., 1999). Half of the DRM lists were classified as having high-associative strength with false-recognition rates ranging from .71 to .84 ($M = .80 \pm .05$). The remaining nine lists were classified as having low-associative strength, with false-recognition rates ranging from .33 to .64 ($M = .55 \pm .11$). These high-associative *versus* low-associative DRM lists differed statistically in their effectiveness to produce false recognition, $t(17) = 11.93$; $p < .001$. Because of this associative strength manipulation, most of the lists used in the present study were different from those used in our previous developmental neuroimaging study (Paz-Alonso et al., 2008).

During the study phase, participants studied the 18 word lists. Words within each list were presented in order of

decreasing associative strength. Participants were instructed to do their best to remember each word. Lists were presented auditorily at a rate of one word every 2500 ms, and the presentation order of the lists was randomized.

The time interval between the completion of the study phase and the beginning of the retrieval phase was 10 min. In preparation for the test phase, participants were instructed to respond “yes” if they remembered the word from the study session, or “no” if they did not. The recognition test included a total of 162 words: 54 studied items (Targets), 54 non-studied semantic associates (CLs), and 54 new unrelated items (ULs). Targets consisted of 3 studied items from each of the 18 lists (from serial position 1, 7 and 9) and CLs were the 1st, 4th, and 9th associate from each original DRM list, which were not presented during the study session. For example, from the original DRM list “*sleep, bed, rest, awake, tired, dream, wake, snooze, blanket, doze, slumber, snore...*”, the selected CLs to-be-presented only at retrieval were “*sleep*”, “*awake*”, and “*blanket*.” From the studied list of words “*bed, rest, tired, dream, wake, snooze, doze, slumber, snore...*”, the target items selected to-be-presented at retrieval were “*bed*”, “*doze*”, and “*snore*.” Finally, ULs were selected from non-semantically related words based on the MRC Psycholinguistic Database. These ULs matched the corresponding CLs from studied lists of high and low association strength in frequency, familiarity, concreteness, and age of acquisition norms.

The 162 trials were presented in two separate functional runs, with 16 randomized orders. First, participants viewed a drawing depicting an ear for 1500 ms, which signaled that a word was about to be presented auditorily. Next, the words “Yes” and “No” were projected on the screen for 2000 ms, instructing participants to respond by making left-handed key presses on a two-button fiber-optic box. Finally, a fixation cross-bar was displayed for 500 ms before the start of the next trial. Both encoding and retrieval phases were conducted while functional data were acquired; results from the encoding phase are not included in the present report.

fMRI Data Acquisition

Whole-brain fMRI data were acquired with a 3-Tesla Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the UC Davis Imaging Research Center using a standard whole-head coil. Functional images during retrieval were acquired in two separate runs using a gradient-echo echo-planar pulse sequence (interleaved acquisition, repetition time [TR] = 2000 ms; echo time [TE] = 25 ms; 35 axial slides; $2.75 \times 2.75 \times 3.4$ mm; no inter-slice gap; flip angle = 90° ; field of view = 220 mm; 185 volumes/run). High-resolution T1-weighted anatomical images were also collected. To limit head movement, the area between participants’ heads and the head coil was padded with foam. Snugly fitting headphones dampened background scanner noise and enabled auditory stimulus presentation and communication with experimenters.

Preprocessing of fMRI Data

Standard SPM5 (Wellcome Department of Cognitive Neurology, London) preprocessing routines and analysis methods were used. Images were corrected for differences in timing of slice acquisition, followed by rigid-body motion correction. Structural and functional volumes were spatially normalized to T1 and echo-planar imaging templates, respectively. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were resampled to $3 \times 3 \times 3 \text{ mm}^3$ voxels. Templates were based on the MNI305 stereotaxic space (Cocosco, Kollokian, Kwan, & Evans, 1997). These procedures have been validated with children ages 6 years and above (e.g., Burgund et al., 2002; Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003). After normalization, functional volumes were spatially smoothed with an 8-mm full width at half maximum isotropic Gaussian kernel.

fMRI Data Analysis

Statistical analyses were performed on individual participants' data using the general linear model (GLM). The fMRI time series data were modeled by a series of impulses convolved with a canonical hemodynamic response function (HRF). In addition to excluding participants whose head motion exceeded 3 mm in any parameter within at least one functional scan, we also included motion parameters for translation (i.e., x, y, z) and rotation (i.e., yaw, pitch, roll) as covariates of noninterest in the GLM. Although additional approaches to deal with age differences in motion have been proposed (Power, Barnes, Snyder, Schlaggar & Petersen, 2012; Van Dijk, Sabuncu, & Buckner, 2011), further research is still needed to determine how micro-movement artifacts should be examined (Power et al., 2012), thereby justifying our use of the standard approach.

Each trial was modeled as an event, time-locked to the onset of the cue period. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each condition were used in pairwise contrasts. Contrast images, computed on a participant-by-participant basis, were submitted to group analyses.

At the group level, whole-brain contrasts between conditions were computed by performing one-sample *t* tests on these images, treating participants as a random effect. Our standard statistical threshold for All > Null contrast was a False Discovery Rate (FDR) set to $q < .01$, with of at least 10-contiguous voxels extent threshold. All brain coordinates are reported in MNI atlas space (Cocosco et al., 1997). These contrasts provided the basis for identifying cortical regions to submit to functional connectivity analysis.

Based on evidence from neuroimaging DRM studies with children and adults (e.g., Cabeza et al., 2001; Kim & Cabeza, 2007; Paz-Alonso et al., 2008), we conducted functional

connectivity analysis on regions-of-interest (ROIs) in left anterior hippocampus ($-25, -12, -18; 3728 \text{ mm}^3$), left posterior hippocampus ($-22, -38, 2; 1376 \text{ mm}^3$), left *pars triangularis/opercularis* ($-45, 18, 18; 10152 \text{ mm}^3$), left *pars orbitalis* ($-37, 27, -5; 344 \text{ mm}^3$), left dlPFC ($-43, 13, 39; 1304 \text{ mm}^3$), left MTG ($-58, -33, 4; 4208 \text{ mm}^3$), right MTG ($64, -34, 2; 912 \text{ mm}^3$), and left PPC ($-28, -56, 47; 2628 \text{ mm}^3$), with the MARSBAR toolbox for use with SPM (Brett, Anton, Valabretue, & Poline, 2002). All cortical ROIs consisted of active voxels identified from All > Null across all participants, FDR corrected $q < .01$ with a 10-voxel threshold extent within the specific MARSBAR anatomical ROI defined above (Supplementary Table 1). In contrast, hippocampal ROIs were not identified functionally from the All > Null contrast, but were anatomically defined. The absence of reliable hippocampal activations in this contrast is not surprising given the absence of an active baseline condition in the present research (Stark & Squire, 2001). Furthermore, our previous studies suggest that anatomically defined hippocampal ROIs may be more sensitive to age differences (e.g., DeMaster & Ghetti, 2013).

Functional connectivity analysis was conducted *via* the beta-series correlation method (Rissman, Gazzaley, & D'Esposito, 2004), implemented in SPM5 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition, and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. For each participant, we calculated the beta-series correlation between each ROI for each condition (high and low associative strength) across all types of responses (e.g., hits, false alarms) and for true and false recognition specifically. These indices were used for our analyses.

First, we sought to identify significant coupling strength between ROIs across all the main study conditions. To do so, beta-series correlation values (*r* values) were averaged across conditions and participants. Given our sample size ($N = 31$), *r*-values $\geq .36$ and $< .46$ corresponded to a *p*-value $\leq .05$, *r*-values $\geq .46$ and $< .57$ corresponded to a *p*-value $\leq .01$, and *r*-values $\geq .57$ corresponded to a *p*-value $\leq .001$; all of them two-tailed. Second, we sought to identify significant coupling strength between ROIs for true and false recognition and high and low association lists in children and adults; to do so, we averaged beta-correlations within each age group separately for each combination of factors (i.e., true-recognition/high-association; true-recognition/low-association, false-recognition/high-association; false-recognition/low-association).

Finally, we examined differential coupling strength between pairs of ROIs (i.e., nodes) during true and false recognition, as a function of Age and Associative Strength. To do so, *r* values for each pair of ROIs for each participant and condition were converted to Fisher's *Z* normally distributed values and submitted to *t* tests. Differential coupling strength was examined only for those pairs of nodes for which coupling strength was significant in at least one of the age groups for a given combination of factors

(e.g., false-recognition/high-association). All the reported significant differences in strength of coupling had a Δr value between an of .10 to .25.

RESULTS

Behavioral Results

Recognition memory

A 2 (Age: children vs. adults) \times 2 (Associative Strength: low vs. high) \times 3 (Response: targets, CLs, ULs) mixed analysis of variance revealed the significant main effect of Associative Strength, $F(1,29) = 8.15; p < .01; \eta_p^2 = .22$, such that across ages, the proportion of recognized items was higher for high-association lists ($M = 47.93 \pm 2.09$) compared to low-association lists ($M = 44.65 \pm 2.38$). Moreover, a significant main effect of Response was found, $F(2,58) = 196.18, p < .001, \eta_p^2 = .87$, which was qualified by a significant Age \times Response interaction, $F(2,58) = 3.25, p < .05, \eta_p^2 = .10$ (Figure 1).

Simple-effects analyses revealed that, compared to children, adults produced a higher proportion of hits, $F(1,29) = 6.05, p < .05, \eta_p^2 = .17$, and false alarms to CLs, $F(2,58) = 4.01, p = .05, \eta_p^2 = .12$. In contrast, both age groups falsely recognized ULs at comparable rates, $F < 1$. Thus, adults exhibited higher true recognition and false recognition of CLs than children. For response time results see Supplementary Materials.

fMRI Results

Our analytical approach for the fMRI data included whole-brain contrasts to identify cortical regions generally involved in the task and functional connectivity analyses to establish their functional relation with anatomically defined hippocampal regions. Whole-brain analysis for All > Null across all participants revealed activation in bilateral dIPFC

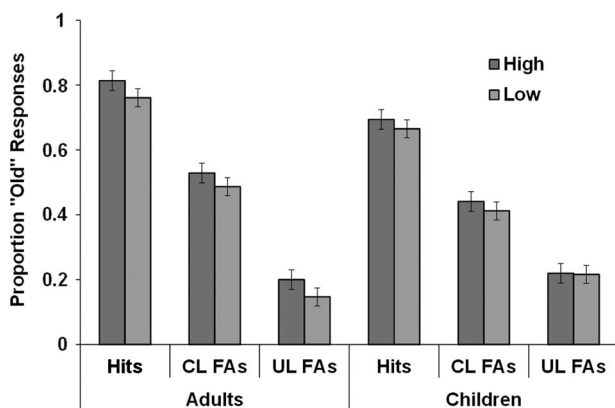


Fig. 1. Behavioral results. Mean proportion of recognition as a function of age, response type (Hits: CL FAs, or false alarms to critical lures; UL FAs, or false alarms to unrelated lures), and association strength.

(BA9/46) and *pars opercularis, triangularis* and *orbitalis* (BA44/45/47), premotor cortex and frontal eye fields (BA6/8), bilateral anterior cingulate cortex (BA24/32), bilateral middle and superior temporal cortex (BA22/21), bilateral superior temporal pole (BA38), left parietal cortex (BA7/40), and subcortical regions including insula, putamen, and caudate (Supplementary Table 1 reports the results of this whole-brain contrast and other contrasts capturing the discrimination between true and false memories).

Functional Connectivity Supporting True and False Recognition

To better understand the functional dynamics among the regions involved in this task, we first sought to characterize the temporal coupling between brain regions across study conditions. To do so, we extracted pairwise correlations between ROIs for each participant and response condition (e.g., Hits, false alarms to CLs, correct rejections of CLs, correct rejections of ULs), and averaged them across participants, response, and list associative strength (Figure 2).

This analysis revealed that activity in the left anterior hippocampus was tightly coupled with activity in the posterior left hippocampus and with the left MTG. Left MTG was tightly coupled with regions within the left ventrolateral PFC (i.e., *pars orbitalis, pars triangularis/opercularis*)

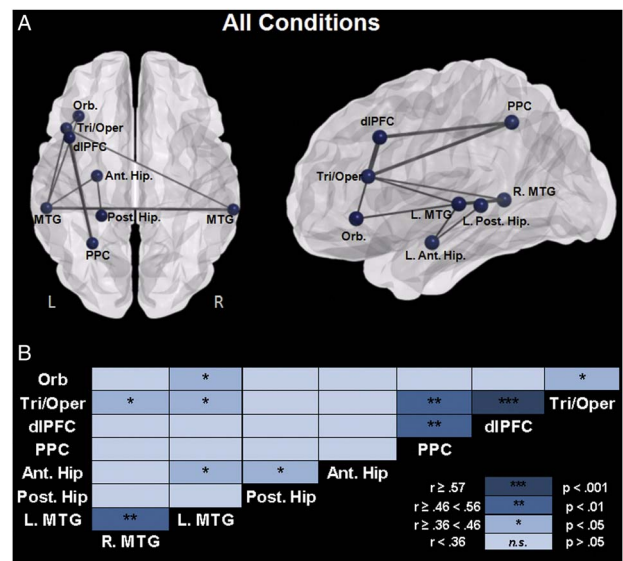


Fig. 2. Functional connectivity analyses for the main study conditions. (A) Axial and sagittal views show statistically significant pairwise correlations between regions of interest, including left anterior hippocampus (L. Ant. Hip.), left posterior hippocampus (L. Post. Hip.), left *pars triangularis/opercularis* (Tri/Oper), left *pars orbitalis* (Orb.), left dorsolateral prefrontal cortex (dIPFC), bilateral medial temporal lobe (MTL), and left posterior parietal cortex (PPC). (B) Correlation matrix showing the size of the correlations between pairs of nodes. Stronger pairwise correlations, averaged across participants and conditions, are shown in deeper blue. BrainNet Viewer was the network mapping tool used for this figure (Xia, Wang, & He, 2013).

and with the contralateral right MTG (all $ps < .05$). Right MTG also exhibited statistically significant coupling with the left *pars triangularis/opercularis* ($ps < .05$). Finally, we observed significant functional connectivity between left fronto-parietal nodes, including PPC, dlPFC and *pars triangularis/opercularis* ($ps < .01$).

True recognition

We then examined the temporal coupling between nodes involved in true recognition and tested for differences in these pairwise functional correlations as a function of age and list associative strength. During true recognition, significant functional connectivity among temporal regions was revealed such that the left anterior hippocampus, but not posterior hippocampus, was functionally coupled with the left MTG, which was connected with its contralateral counterpart ($ps < .05$; Figure 3A). Fronto-parietal regions were also tightly connected, including dlPFC, *pars triangularis/opercularis*, *pars orbitalis* and PPC nodes ($ps < .01$; Figure 3A). However, none of the nodes within the set of temporal regions and the set of fronto-parietal regions exhibited significant coupling with regions in the other set.

To investigate age differences in connectivity for high and low associative strength, average beta-series correlations for each age group at each level of associative strength were computed. Age differences in connectivity were apparent for high associative strength (Figure 3B), which was confirmed when we submitted Fisher's Z values to t tests.

Compared to children, adults exhibited stronger positive anterior hippocampus-dlPFC and anterior hippocampus-PPC coupling for true recognition of studied items from high-association lists ($p < .05$; Figure 3C). No age differences in coupling strength were observed for low-association lists. Similarly, no differences in coupling strength were observed between high- and low-association lists.

False recognition

Analysis of the functional connectivity during false recognition was conducted with the same methods as used for true recognition. The results, however, showed a more complex pattern with significant coupling strength observed across fronto-temporal-parietal regions (Figure 4A). More specifically, the left anterior hippocampus showed statistically significant temporal coupling with posterior hippocampus, left MTG, and left *pars orbitalis* ($ps < .05$). The left MTG was then also tightly coupled with all the PFC nodes ($ps < .05$). Finally, the left *pars triangularis/opercularis* exhibited significant functional connections with the remaining PFC nodes ($ps < .05$), and left PPC ($p < .01$).

To investigate age differences in connectivity for high and low associative strength, we again used the same methods used for the examination of true recognition. Results again showed that age differences were apparent for high-associative strength lists (Figure 4B), which was confirmed when we submitted Fisher's Z values to t tests.

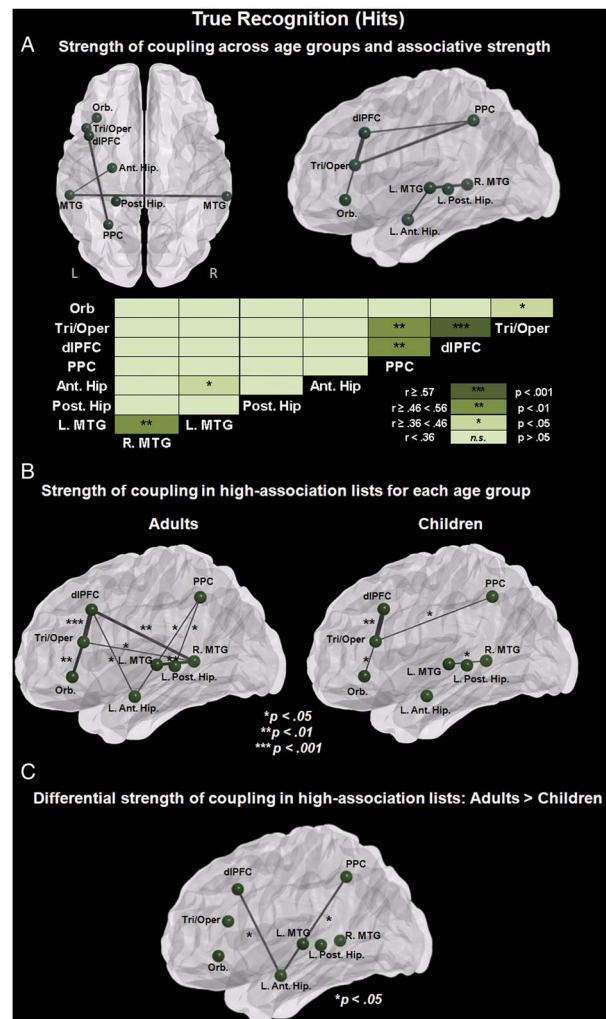


Fig. 3. Functional connectivity analyses for true recognition (Hits). (A) Axial and sagittal views show statistically significant pairwise correlations between regions of interest (ROIs), including left anterior hippocampus (L. Ant. Hip.), left posterior hippocampus (L. Post. Hip.), left *pars triangularis/opercularis* (Tri/Oper), left *pars orbitalis* (Orb.), left dorsolateral prefrontal cortex (dlPFC), bilateral middle temporal gyrus (MTG), and left posterior parietal cortex (PPC). The correlation matrix shows the size of the correlations between pairs of nodes. Stronger pairwise correlations during hit responses, averaged across participants, are shown in deeper green. (B) Sagittal views show statistically significant pairwise correlations between ROIs in adults and children for hit responses to items from lists of high associative strength. (C) A sagittal view shows increased strength of coupling for adults compared to children for hit responses to items from lists of high associative strength. BrainNet Viewer was the network mapping tool used for this figure (Xia et al., 2013).

Children exhibited significantly stronger positive hippocampal-*pars orbitalis*, and bilateral MTG-*pars triangularis/opercularis* coupling relative to adults for CLs from high association lists ($ps < .05$; Figure 4C). In contrast, no age differences were observed for false recognition of CLs in low-association lists. Finally, no differences were observed between high- and low-association lists.

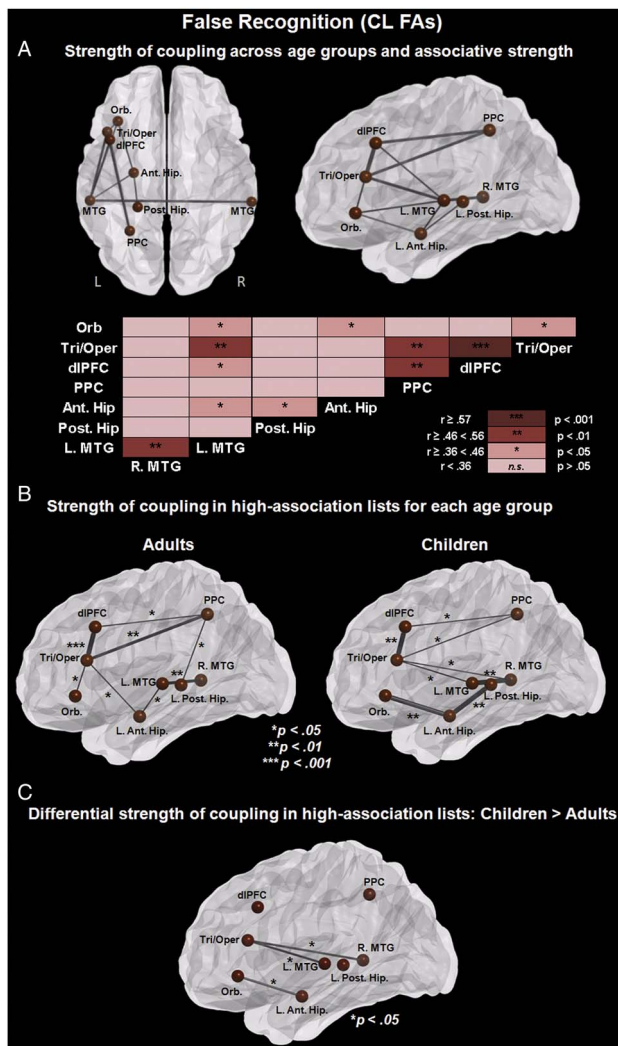


Fig. 4. Functional connectivity analyses for false recognition (critical lure false alarms, CL FAs). (A) Axial and sagittal views show statistically significant pairwise correlations between regions of interest (ROIs), including left anterior hippocampus (L. Ant. Hip.), left posterior hippocampus (L. Post. Hip.), left *pars triangularis/opercularis* (Tri/Oper), left *pars orbitalis* (Orb.), left dorsolateral prefrontal cortex (dlPFC), bilateral middle temporal gyrus (MTG), and left posterior parietal cortex (PPC). The correlation matrix shows the size of the correlations between pairs of nodes. Stronger pairwise correlations for false alarms to CLs, averaged across participants, are shown in deeper red. (B) Sagittal views show statistically significant correlations between pairs of ROIs in adults and children for false alarms to items from list of high-associative strength. (C) A sagittal view shows increased strength of coupling for children compared to adults for false recognition of CLs from lists of high associative strength. BrainNet Viewer was the network mapping tool used for this figure (Xia et al., 2013).

Although the present study was not aimed at examining whether individual differences in coupling strength predicted performance, an exploratory analysis revealed that overall false recognition of CLs was negatively associated with anterior hippocampus-*pars orbitalis* connectivity across participants, $r(29) = -.43, p < .05$; this correlation persisted

even when participants' age was partialled out, $r(28) = -.41, p = .05$. No other significant correlations between behavioral performance and connectivity were found.

DISCUSSION

The goal of the present study was to investigate age-related and semantic strength-related differences in functional connectivity between the hippocampus and cortical regions involved in true and false recognition. Informed by our previous study (Paz-Alonso et al., 2008) and other neuroimaging studies using the DRM paradigm with adults (e.g., Cabeza et al., 2001; Kim & Cabeza, 2007), we focused on a left-lateralized set of regions including anterior and posterior hippocampus, lateral temporal cortex, parietal cortex, and lateral PFC. Furthermore, we included right MTG because prior neurodevelopmental evidence suggests that children recruit this region to access semantic representations to support their not yet fully developed semantic system (e.g., Blumenfeld, Booth, & Burman, 2006; Chou et al., 2006). These cortical regions emerged from our initial unbiased whole-brain contrast analysis fully consistent with previous evidence concerning episodic retrieval (e.g., Cabeza et al., 2001; Dennis, Kim, & Cabeza, 2008; Okado & Stark, 2003; Paz-Alonso et al., 2008).

Previous neurodevelopmental studies have reported functional connectivity analyses between hippocampal regions and frontal, parietal and lateral temporal cortices during memory retrieval in general (e.g., Ofen et al., 2012; Paz-Alonso, Bunge, et al., 2013), and during true and false memories in particular (Dennis et al., 2012). However, no prior study has examined differences in functional connectivity as a function of age and semantic association strength.

True recognition was associated with coupling among ventral regions including hippocampus and temporal cortices consistent with previous research (Dennis et al., 2012), as well as coupling among a more dorsal fronto-parietal set of regions. These sets of regions appeared to be segregated: nodes within hippocampal-temporal and fronto-parietal sets were tightly coupled, but none of the nodes within each of these two sets exhibited significant coupling with nodes in the other set. In contrast, false recognition was associated with a more distributed hippocampal-temporal-parietal-frontal set of regions.

The apparent segregation evident in true recognition might suggest that accurate item retrieval emerges from processes that might be more readily dissociable than those involved in false recognition (e.g., tighter coupling of hippocampus and regions in the MTG might support retrieval of item-specific semantic features; tighter fronto-parietal coupling might support retrieval monitoring or post-retrieval decision processes; e.g., Dobbins, Simons, & Schacter, 2004; Shannon & Buckner, 2004). However, we note that this apparent segregation is no longer evident when the analysis was restricted to high-association lists and when age differences were examined. These findings are discussed next.

Differential Coupling Strength during True and False Recognition as a Function of Age and Association Strength

A direct examination of age differences associated with true recognition showed that adults, compared to children, exhibited stronger hippocampus-PPC and hippocampus-dIPFC connectivity in high association lists. Left PPC activation has been associated with successful episodic retrieval (Cabeza et al., 2001; Shannon & Buckner, 2004; Slotnick & Schacter, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005), and amount of retrieved information (e.g., Cabeza, 2008; Donaldson, Wheeler, & Petersen, 2010; Konishi et al., 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000). Furthermore, dIPFC might support subsequent post-retrieval decision processes associated with further attempts to recollect studied items (e.g., Dobbins et al., 2004; Nolde, Johnson, & D'Esposito, 1998). Finally, there is evidence for age-related differences in activation in left PPC and dIPFC from middle childhood to adulthood during memory retrieval of DRM items (Paz-Alonso et al., 2008).

Thus, age differences in connectivity might reflect stronger engagement in retrieval searches in adults to support accurate post-retrieval decision processes. Given that adults are more likely to fall prey to false memories with the DRM paradigm, it is conceivable that greater retrieval resources may be necessary to identify true memories. However, these differences might also reflect more frequent recollective experiences in adults compared to children (Ghetti & Angelini, 2008); for example, stronger connectivity between hippocampus and PPC in adults, compared to children, may be suggestive of the stronger capture of attention for vivid memories characteristic of recollection (e.g., Cabeza, Ciaramelli, Olson, & Moscovith, 2008). Additionally, retrieval of qualitative details has been found to increase with age during childhood for true recognition in the DRM paradigm (Del Prete, Mirandola, Cornoldi, & Ghetti, in press) and in general (Ghetti & Angelini, 2008). Our functional connectivity results are fully consistent with these possibilities, and with prior evidence showing age-related increases in hippocampal-PPC and hippocampal-dIPFC functional connectivity during memory retrieval (e.g., Paz-Alonso, Bunge et al., 2013). These different, but not mutually exclusive interpretations of age differences in connectivity cannot be disambiguated in the present research.

Age-related differences in functional connectivity also emerged for false recognition of high-associative strength items. In children, compared to adults, activity of the anterior hippocampus was more tightly coupled with activity in *pars orbitalis*, which is involved in the controlled retrieval of stored conceptual representations (e.g., Badre & Wagner, 2007); moreover, activity in MTG was more strongly connected with activity in *pars triangularis/opercularis*, which are engaged in control processes surrounding the selection of activated representations. Therefore, false recognition of CLs in children seemed to emerge from tighter coupling among regions supporting semantic representation, access,

and elaboration of items relative to adults (e.g., Chou et al., 2006; Kim & Cabeza, 2007; Prince, Daselaar, & Cabeza, 2005; Wagner, Desmond, Domb, Glover, & Gabrieli, 1997). Consistent with this interpretation is the negative correlation across participants between false recognition and hippocampal-*pars orbitalis* connectivity: just as children, as a group, generally succumbed less to the DRM memory illusion and showed tighter hippocampus-*pars orbitalis* coupling, individuals who are generally less prone to the illusion exhibit tighter coupling among these nodes. Furthermore, *pars orbitalis* and MTG exhibited age-related differences in activation profiles (Paz-Alonso et al., 2008), likely due to increasing automatic access to semantic representations with age (Blumenfeld et al., 2006; Paz-Alonso et al., 2008).

Overall, developmental differences in hippocampal-cortical connectivity were evident for high-associative strength items. For veridical memory, adults exhibited stronger connectivity than children, suggesting stronger involvement of controlled processes and/or stronger recollective experiences in adults. For false memories, children exhibited stronger connectivity than adults, suggesting that access to and elaboration of semantic representations may be less automatic in children.

Role of Anterior Hippocampus in True and False Recognition

Connectivity between hippocampus and cortical regions was evident in both true and false recognition. However, whereas anterior hippocampus was functionally connected with other regions of the temporal, parietal, and prefrontal cortex, the posterior hippocampus was not. Its sole statistically significant coupling was observed with anterior hippocampus. The role of anterior hippocampus in veridical and illusory retrieval of semantically related information is consistent with our hypothesis. Our hypothesis is based on evidence that the anterior hippocampus is involved in episodic retrieval of semantic information (e.g., Abe et al., 2008; Cabeza et al., 2001; Chadwick et al., 2010; Paz-Alonso et al., 2008; Prince et al., 2005) and is functionally connected to temporal regions storing semantic representations (e.g., Kahn et al., 2008). These findings are in turn consistent with models proposing that the anterior hippocampus is a key component of an anterior network of regions that support semantic processing, because it can extract and form representations of systematic combinations of item features that co-occur repeatedly and is involved in various cognitive operations including episodic memory (e.g., Ranganath & Ritchey, 2012).

Future studies should relate the differences in functional connectivity reported here to underlying structural development. The anterior hippocampus has been shown to undergo volumetric changes during childhood (DeMaster et al., 2013; Gogtay et al., 2006), which might influence network connectivity. Furthermore, white matter tracts connecting the anterior hippocampus with PFC achieve stronger integrity during childhood (Lebel & Beaulieu, 2011). All of these changes may influence functional connectivity.

Future studies should also characterize individual differences in addition to developmental differences. The preliminary evidence of associations between individual differences in connectivity and individual differences in false recognition, which was the only moderate-size association we found between connectivity and performance, suggests that future studies should be powered to examine individual variation more thoroughly.

CAVEATS AND CONCLUSIONS

Before we conclude, we note several caveats in the present study. First, age differences in connectivity were observed with high-association lists. It is not clear why low-association lists did not yield consistent age differences in connectivity. Second, we elected to focus on functional connectivity among left-lateralized regions (except for right MTG). Although this approach is justifiable as discussed earlier, a more holistic approach that includes regions across the entire brain might yield additional or relatively different results. Third, we identified cortical regions to conduct connectivity analyses from all participants and across all conditions; although this approach is unbiased, it selected, by definition, regions that are involved in both true and false recognition in both children and adults, thereby potentially overlooking the contribution of regions uniquely involved in true or false recognition, or regions uniquely recruited by either children or adults. These problems do not apply to hippocampal regions, as they were identified anatomically, but the use of the hippocampal anatomical templates provided by the Automated Anatomic Labeling (AAL) atlas may reduce precision. Fourth, age differences in motion may have affected the current results despite the rigorous measures we used to limit this problem. The fact that adults exhibited stronger hippocampal–cortical connectivity for true recognition, but weaker for false recognition, makes it less likely that movement is a central source of contamination in the present study; if that were the case, adults should have exhibited overall stronger coupling than children between the nodes examined here (Power et al., 2012).

Despite these limitations, age-related differences in connectivity in the present study suggest that hippocampal activity might be more or less temporally coupled with cortical regions depending on memory veridicality and strength of semantic associations. These variables may have implications for understanding not only how children discriminate true from false memories, but also for how they extract and retain meaning from such common sources of information such as texts and stories.

Supplementary material

To view supplementary material for this article, please visit <https://dx.doi.org/10.1017/S1355617713001069>

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