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Development of the neural correlates of recollection

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Recollection of past events has been associated with the core recollection network comprising the posterior medial temporal lobe and parietal regions, as well as the medial prefrontal cortex (mPFC). The development of the brain basis for recollection is understudied. In a sample of adults ($n = 22$; 18–25 years) and children ($n = 23$; 9–13 years), the present study aimed to address this knowledge gap using a cued recall paradigm, known to elicit recollection experience. Successful recall was associated with activations in regions of the core recollection network and frontoparietal network. Adults exhibited greater successful recall activations compared with children in the precuneus and right angular gyrus. In contrast, similar levels of successful recall activations were observed in both age groups in the mPFC. Group differences were also seen in the hippocampus and lateral frontal regions. These findings suggest that the engagement of the mPFC in episodic retrieval may be relatively early maturing, whereas the contribution to episodic retrieval of more posterior regions such as the precuneus and angular gyrus undergoes more protracted maturation.

Key words: fMRI; children; core recollection network; memory retrieval; cued recall.

Memory recollection—the mental process that retrieves details of previous events—has been associated with a set of brain regions including the hippocampus, parahippocampal cortex, posterior cingulate cortex (PCC; Maddock et al. 2001; Natu et al. 2019), precuneus (Krause et al. 1999; Trimble and Cavanna 2008), lateral parietal cortex or angular gyrus (AG; Sestieri et al. 2011; Ben-Zvi et al. 2015; Rugg and King 2018), and the medial prefrontal cortex (mPFC; Kim 2010; Rugg and Vilberg 2013). These regions comprise what has been termed the "core recollection network" (CRN). Independent of the content of the memory, the CRN is engaged when a retrieval cue elicits recollection (Johnson and Rugg 2007; Hayama et al. 2012; Rugg and Vilberg 2013). Besides these regions, the frontoparietal control network regions such as the dorsolateral prefrontal cortex (PFC), superior parietal lobule, and intraparietal sulcus are often linked with retrieval success (Spaniol et al. 2009). Here, we asked how these regions develop from childhood to adulthood in support of recollection.

The mPFC, PCC, precuneus, and the angular gyrus are also major nodes of the well-established default-mode network (DMN; Raichle et al. 2001; Greicius et al. 2003). The DMN is a functional brain network typically deactivated during externally-oriented attention and activated during internally-oriented tasks. One such internally-oriented task that the brain is constantly engaged in is episodic memory retrieval. Several studies have demonstrated activation of a specific subnetwork within the DMN during episodic memory retrieval (Andrews-Hanna et al. 2010; Huijbers et al. 2013), especially when the retrieval involved a detailed recollection as opposed to general familiarity (Kim 2010).

Episodic retrieval can be differentiated from other processes in the DMN such as social cognitive processes (Buckner and DiNicola 2019; DiNicola and Buckner 2021). Furthermore, Sestieri et al. (2011) showed that parietal regions within the DMN directly supported memory retrieval, whereas non-DMN parietal regions were more involved in postretrieval processes such as memory-based decision-making.

Activation in the DMN typically shows a reversal in activation between successful episodic encoding and retrieval, whereas hippocampal and greater medial temporal lobe activity are increased in both phases (Vannini et al. 2011; Hayama et al. 2012). We previously examined the development of DMN activations during episodic memory encoding between ages 8 and 24 years and found that the posterior regions of the DMN including the PCC and angular gyrus were suppressed for successful subsequent memory in adults, but no reliable subsequent memory effects in the DMN were found in children (Chai et al. 2014; Tang et al. 2018), suggesting that episodic memory development is at least in part mediated by the functional maturation of the DMN during memory encoding. A small number of studies investigating the development of memory retrieval in the brain found age-related changes in activation in frontal and parietal regions that are mostly outside of the DMN. For example, an age-related increase in activation was found in the ventrolateral PFC and superior parietal lobule during successful retrieval when comparing correctly recognized old scenes (hits) and correctly identified new scenes (correct rejections; Ofen et al. 2012). Several other frontal and parietal control regions, including the anterior lateral PFC and

posterior parietal cortex (BA7) have also been reported to show age-related increases in activations during successful retrieval of words or objects (Paz-Alonso et al. 2008; DeMaster and Ghetti 2013).

These previous studies in episodic memory retrieval have relied on the recognition paradigm in which participants make old/new judgments for each item presented, which tends to activate frontoparietal regions that support pre- and postretrieval cognitive processes (O'Connor et al. 2010; Kim 2013). Paradigms that demand recollection (retrieval of subjective experience of remembering) invoke more consistent activations in the DMN (Kim 2016, 2020). The present study employed a cued recall paradigm which, compared with recognition experimental designs (Rugg et al. 1998), is more suited for investigating the engagement of the DMN in memory recollection across development. Magnetic resonance imaging (MRI) studies of cued recall in adults have revealed DMN and parahippocampal activations associated with successful retrieval, most consistently in more posterior DMN regions (Meltzer and Constable 2005; de Zubicaray et al. 2007; Habib and Nyberg 2008; Hayama et al. 2012). Behavioral studies of the development of cued recall suggest that accuracy increases from 7 to 11 years of age (Hall et al. 1979) and that recollection is more susceptible to interference in children versus adults (Ackerman and Rathburn 1984). Based on these previous findings and evidence that the DMN is less engaged during successful memory encoding in children compared to adults (Chai et al. 2014; Tang et al. 2018), we predicted that activations associated with successful cued recall in the core recollection network would be greater in adults compared to children.

Materials and methods
Participants
Fifty-eight children ages 9–13 and young adults ages 18–25 participated in the study. After excluding participants who did not complete the study, had corrupted audio files from the recall trials, and those with excessive movement, the final sample consisted of 45 participants, including 23 children (mean age 11.26 ± 1.36 years; 57% female) and 22 adults (mean age 21.53 ± 1.95 years; 50% female). The ethnicity of the sample population was 57% white, 18% Asian, 7% black, and 18% mixed or other. Participants were recruited from the local community around Cambridge, MA, United States. Informed consent, written, or oral assent was obtained from all participants before participating. The IRB protocol was approved by the Massachusetts Institute of Technology Institutional Review Board. All participants were right-handed, had normal or corrected-to-normal vision, with no history of psychiatric or neurological disorder. All participants were tested on a standardized IQ test (KBIT). IQ scores did not differ between children and adults (child mean: 120.3 ± 9.49; adult mean: 120.1 ± 12.5, 3 values missing; $t(40) = 0.05$, $P = 0.964$).

Memory task
A total of 150 words pairs of were used. The words had an age-of-acquisition of 7 years of age or younger, and a mid-level range of familiarity and imageability ratings (Stadthagen-Gonzalez and Davis 2006). The words in each pairing were selected to have low relatedness and were matched on age-of-acquisition, familiarity, and imageability such that ratings on these measures did not differ between the first- and second-word lists ($ts(78) \geq 0.014$, $Ps \geq 0.123$). Participants were given a short practice session with

7 trials prior to the scanning session, and repeated if needed. In the scanner, participants were presented with 6 encoding-recall cycles in the scanner, illustrated in Fig. 1. Each cycle included 25 encoding and 25 recall trials.

In each encoding session, participants were presented 25 unrelated noun pairs. Participants were asked to try and remember the pairs and to indicate with one button press whether they thought they would be able to remember the word pair or press another button if they did not think they would be able to remember the word pair. Each word pair was presented on the screen for 4 s. Each encoding session lasted 2.5 min. Intertrial interval was jittered with fixations lasting 2, 4, or 6 s and ordered optimized for efficiency using optseq2 (https://surfer.nmr.mgh.harvard.edu). The recall session immediately followed each encoding session.

In each recall session, participants were cued to recall studied pairs with the word originally presented on the left serving as the cue word. Subjects were instructed to verbally recall the paired word that was presented on the right in the studied pair, or to say the word "pass" if they were unable to recall the word. Each cue word was presented on the screen for 4 s, followed by a 2-s fixation. Each recall session lasted 3.33 min. Recall responses were recorded in audio files and were later scored manually. A trial was classified as "Hit" if the correct target word was recalled, and "Miss" if the participant made an incorrect target response, "Pass" response, or failed to give a response. When the response on the audio file could not be decoded (unclear or volume too low), the trial was classified as "error." If the response was incorrect but the word named was related to the target word in meaning or sound, or was the target word from another pair, the trial was classified as "false memory."

Outside of the scanner, after completing the memory task, participants completed a questionnaire probing their spontaneous use of memory strategies and rated each on a scale of 1–5 for frequency of use (1 = never; 3 = sometimes; and 5 = always). Participants were probed on 3 shallow strategies ("Repeating the word pairs to myself"; "Studied the sounds of the words and related them to each other"; and "Studied the spelling of the words and related them to each other") and 3 deep strategies ("Making stories between the words"; "Relating the words to a personal event"; and "Making a picture of the words") intermixed.

Imaging procedure
MRI data were acquired on a 3T TrioTim Siemens scanner using a 32-channel head coil. T1-weighted whole brain anatomical images (MPRAGE sequence, 256×256 voxels, 1×1.3-mm in-plane resolution, 1.3-mm slice thickness) were acquired. Functional images were acquired with an interleaved EPI sequence in 32 transverse slices, covering the entire brain (repetition time = 2 s, echo time = 30 ms, flip angle = 90, $3 \times 3.1 \times 3.1$-mm voxels).

Data analysis
Preprocessing and functional magnetic resonance imaging analyses
Functional imaging data were analyzed using Nipype, a Python-based data processing framework that incorporates several neuroimaging data analysis packages (Gorgolewski et al. 2011). Standard functional image preprocessing (realignment, smoothing with 6-mm kernel, coregistration to structural images) and analysis were done using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/). Advanced Normalization Tools software (Avants et al. 2009) was used for warping functional data into MNI space. Data were inspected for artifacts and motion using custom software (http://www.nitrc.org/projects/artifact_detect/). First-level analysis was
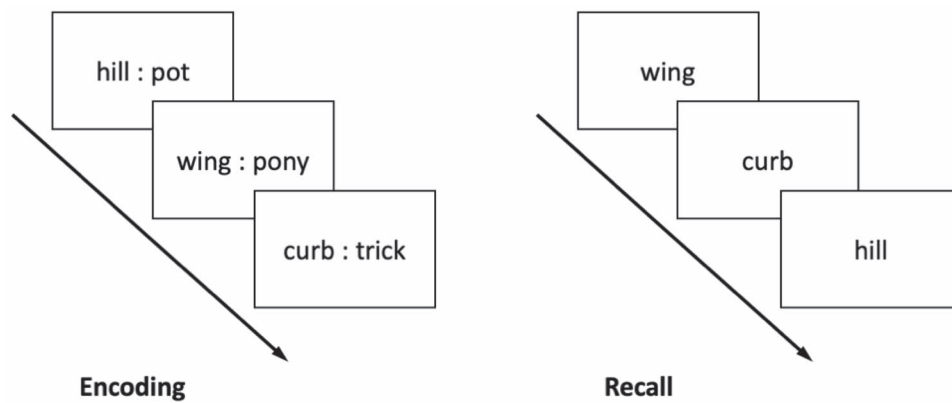
Fig. 1. Memory task stimuli including encoding and recall phases. In the encoding phase, each word pair was presented for 4 s. In the recall phase, the first word in each pair was presented for 4 s and subjects were instructed to verbally recall the second word or say "pass."

performed with a general linear model (GLM) with regressors for Hit and Miss trials during the recall phase. A regressor of no interest was included in the model for "false memory" and error trials. Error and false memory trials were lumped together due to the low number of these trial types (mean number of error trials for children: 3.77; adults: 4.64). Adults and children did not differ in their number of error/false memory trials ($t(43) = 0.502$, $P = 0.619$). Additional regressors accounted for head movement (3 translation and 3 rotation parameters) and outlier scans (images in which average intensity deviated > 3 standard deviations from the mean intensity in the session or in which movement exceeded 0.5 mm in translation or 0.01° in rotation from the previous image). Each outlier scan was represented by a single regressor in the GLM, with a 1 for the outlier time point and 0s elsewhere.

To compare brain activations associated with successful recall, we conducted second-level analyses to generate group-level activation maps contrasting hit > miss. Group-level maps were calculated using 1-sample *t*-tests for the child group and adult group. Furthermore, 2-sample *t*-tests were conducted to directly contrast adults > children and children > adults. Results were thresholded at $P < 0.001$ (voxel-level) and $P < 0.05$ cluster-level family-wise error corrected. DMN clusters resulting from these analyses were further investigated by extracting hit and miss activations independently and comparing them between adults and children using repeated measures ANOVAs (within-subjects: trial type, hit/miss; between-subjects: age group).

Region of interest exploratory analyses

In addition to whole-brain analysis described above, we examined activations during recall in additional CRN regions not identified in the 2-sample *t*-test of adults > children. These regions included the left angular gyrus, mPFC, and bilateral hippocampi and were created as 10-mm spheres around peak activations in a 1-sample *t*-test of all participants for hit > miss so as not to bias the location of the cluster to either group (left angular gyrus: −46, −62, 23, $t(44) = 7.43$; mPFC: −8, 39, −2, $t(44) = 10.09$; left hippocampus: −16, −27, −8, $t(44) = 5.78$; right hippocampus: 21, −17, −10, $t(44) = 4.64$).

Results
Recall accuracy

We compared recall performance between adults and children by comparing the mean percentage of hits in each age group. Adults recalled significantly more words (54.6% ± 22.5) than did children (29.6% ± 11.3, $t(43) = 4.75$, $P < 0.0001$, 2-tailed).

For the encoding task in which participants judged whether they would later recall the word pair, gamma correlations were calculated as an index of the accuracy of their prediction of memory outcome (Nelson 1984). No significant difference was found between children (mean gamma = 0.326 ± 0.237) and adults (mean gamma = 0.431 ± 0.323), ($t(43) = 1.25$, $P = 0.219$, 2-tailed), with relatively low judgment accuracy in both groups.

Memory strategy use

We compared the reported use of memory strategies between adults and children. For each of the 3 shallow strategies, there were no significant differences in frequency of use between the groups ($ts(31) \leq 1.12$, $Ps \geq 0.270$, 2-tailed). For each of the 3 deep strategies, adults reported more frequent use than children ($ts(31) \geq 2.74$, $Ps \leq 0.010$, 2-tailed).

Brain activations associated with successful recall

To examine memory activations for successful cued recall of words, we generated group-level activation maps contrasting hits > misses (Fig. 2; Table 1). In adults, there were significant cued-recall activations in the hippocampus, fusiform gyrus, regions in the CRN, including the precuneus and angular gyrus, and regions in the frontoparietal network, including the dorsolateral PFC and supramarginal gyrus (Fig. 2A). In children, there were significant cued-recall activations in CRN regions, including mPFC, left posterior parietal cortex (angular and supramarginal gyrus), PCC, and regions in the frontoparietal network including dorsolateral PFC, and the caudate (Fig. 2B).

Two-sample *t*-tests were conducted to directly contrast between the activations associated with successful recall in adults compared with children (Fig. 3A; Table 2). Of note, within the CRN regions that are the focus of this study, adults showed significantly higher activation than children in the right angular gyrus and right precuneus, but not in mPFC regions. Adults also had greater successful recall activation in the right insula, right fusiform, and lingual gyri. There were 2 regions showing greater hit > miss contrast in children compared with adults identified in the left middle frontal gyrus and left triangularis. We repeated the 2-sample *t*-test with performance accuracy as a covariate, resulting in a highly similar activation map with the right angular and precuneus clusters persisting at the same threshold.
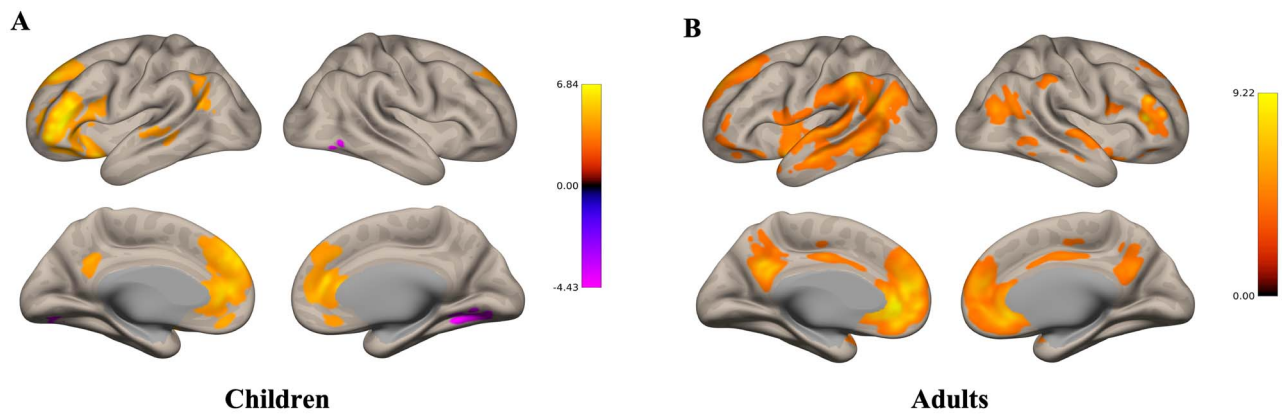
Fig. 2. Group-level activations associated with successful recall hits > misses in adults A) and in children B).

Table 1. Clusters showing significant activations for adults and children for the hit > miss contrast.

	Cluster peak	BA	x	y	z	T	k
Adults							
R	mPFC	10/32	2	33	−9	10.46	174,049
	Inferior frontal gyrus	46	49	38	9	10.19	
L	Supramarginal/angular gyrus	40/39	−62	−2	−19	8.10	
L	Precuneus	31/7	−6	−57	29	7.68	12,032
R	Angular gyrus	39	52	−69	26	6.16	7,798
R	Superior temporal gyrus	21	65	4	−5	6.03	3,701
R	Fusiform gyrus	37/21	67	−49	−12	5.51	2,516
R	Supramarginal gyrus	40	66	−27	44	5.46	1,299
L	Middle cingulum	24	−3	−11	40	5.32	4,771
R	Cerebellum		31	−41	−46	5.08	1,005
R	Hippocampus		18	−23	−12	4.77	701
R	Putamen		30	−13	6	4.17	771
Children							
L	mPFC/inferior frontal gyrus	10/32/46	−7	49	36	7.91	96,561
L	Supramarginal/angular gyrus	40/39/31	−34	−58	26	7.24	9,441
	PCC		−17	−52	33	5.41	
R	Caudate		12	11	−1	5.08	1,846
L	Middle temporal gyrus	22/21	−53	−39	−7	5.06	3,364

Coordinates are in Montreal Neurological Institute space. BA, Brodmann area; k, cluster size (number of voxels); L, left; R, right; mPFC, medial prefrontal cortex; and PCC, posterior cingulate cortex.
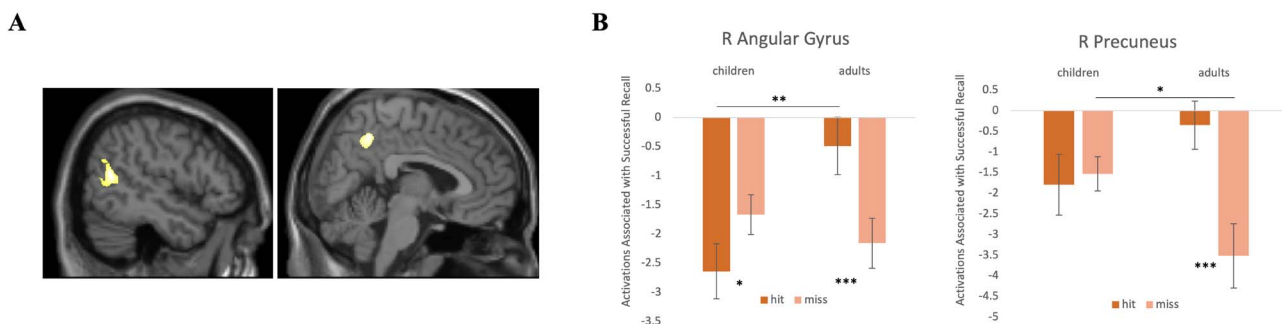

Fig. 3. A) Adults > children activation maps contrasting hits > misses. B) Activation values for children and adults extracted from the right angular gyrus cluster (peak: 49, −65, and 26) and the right precuneus cluster (peak: 5, −50, and 46) for hit and miss trials. Error bars show standard error of the mean. *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

Post hoc CRN cluster analyses

To further investigate age differences in activation of the right angular gyrus and right precuneus for hit and miss trials, we extracted activations for each participant for each of the aforementioned clusters from Fig. 3A (angular gyrus peak: 49, −65, 26; precuneus peak: 5, −50, 46) for hit and miss trials separately (Fig. 3B). A repeated measures analysis of variance (ANOVA)

with trial type (hit or miss) as a within-subjects factor and age group as a between-subjects factor for data from each cluster demonstrated the significant trial type by age interaction (right angular gyrus: $F(1,43) = 18.28$, $P < 0.001$; precuneus: $F(1,43) = 13.86$, $P < 0.001$). Simple main effects revealed a significant effect of trial type (hit > miss) in the adult group ($F(1) = 16.49$, $P < 0.001$) and a weak trial type effect in the child group ($F(1) = 4.50$, $P = 0.045$) for

Table 2. Clusters showing significant group difference for hit > miss contrast.

	Cluster peak	BA	x	y	z	T	k
Adults > children							
R	Angular gyrus	39/22	51	−58	13	4.25	1,597
R	Precuneus/PCC	7/31	5	−50	46	4.01	801
R	Fusiform gyrus	19/37	24	−56	−12	4.39	2,706
R	Insula	13/44	39	−3	14	4.55	4,081
R	Cuneus	17	14	−94	2	3.70	597
L	Posterior cerebellum		−55	−65	−38	5.00	9,675
Children > adults							
L	Inferior frontal gyrus	11/47	−28	33	10	5.20	4,663
L	Middle frontal gyrus	46/9	−52	31	29	4.43	609

Coordinates are in Montreal Neurological Institute space. BA, Brodmann area; k, cluster size (number of voxels); L, left; R, right; PCC, posterior cingulate cortex.
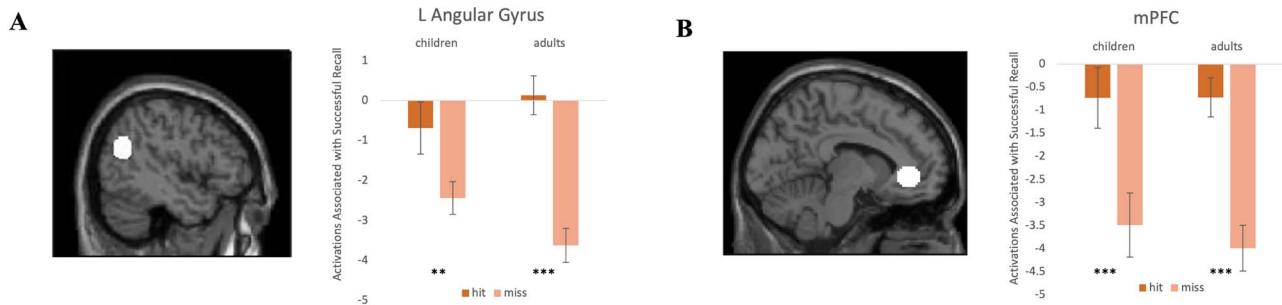

Fig. 4. Activation values for children and adults extracted from each cluster for hit and miss trials for the left lateral parietal cortex (peak: −46, −62, 23; A) and the mPFC (peak: −8, 39, −2; B). Error bars show standard error of the mean. **$P < 0.01$ and ***$P < 0.001$.

the right angular gyrus. In the precuneus, there was a significant effect of trial type in the adult group ($F(1) = 21.68$, $P < 0.001$), but not in the child group ($F(1) = 0.177$, $P = 0.678$). We repeated each ANOVA with the number of hits as a factor and found the same trial type by age interaction in both clusters (right angular gyrus: $F(1,43) = 8.90$, $P = 0.005$; precuneus: $F(1,43) = 8.68$, $P = 0.005$).

Exploratory CRN ROI analysis

We conducted exploratory analyses in additional CRN regions that showed significant hit > miss activations but no group difference including the left angular gyrus, mPFC, and bilateral hippocampi. Region of interests (ROIs) were created as 10-mm spheres based on coordinates from the 1-sample *t*-test for all participants for the left angular gyrus (peak: −46, −62, 23; Fig. 4A.) and the mPFC (peak: −8, 39, −2; Fig. 4B.). For the left angular ROI, a repeated measures ANOVA with trial type (hit or miss) as a within-subjects factor and age group as a between-subjects factor revealed a significant interaction of trial type and age ($F(1, 43) = 6.33$, $P = 0.016$), indicating that adults had higher activations associated with successful recall compared to children. Simple main effects revealed significant effects of trial type for both adults and children ($Fs(1) \geq 10.23$, $Ps \leq 0.004$), with higher activations for hits compared with misses. For the mPFC, there was no interaction or main age effects, but significant main effects of trial type for both adults and children were found ($Fs(1) \geq 26.25$, $Ps < 0.001$).

Due to the lack of developmental effects found in the mPFC, we investigated the possibility of mPFC as a compensatory region in children with high memory accuracy. To do so, we median-split the original child group based on recall accuracy, resulting in 2 groups of $n = 11$ and one remaining participant falling on the median, and compared high-performing children to low-performing children and to adults. No differences in mPFC

activation during hits, misses, or hits minus misses were found between high-performing children and either low-performing children or adults (ts ≤ 1.19, Ps ≥ 0.244).

Hippocampal ROIs were defined as 10-mm spheres around the peak voxel identified in the 1-sample *t*-test group-level cued-recall (hits > misses) activation maps (left: −16, −27, −8, $t(44) = 5.78$; right: 21, −17, −10, $t(44) = 4.64$), as seen in Fig. 5A. Contrast values were extracted for each ROI for hits and misses for each participant and compared between the age groups. In the left hippocampus, there were no significant interactions, but significant main effects were found for trial type ($F(1, 43) = 14.92$, $P < 0.001$) and age ($F(1, 43) = 6.84$, $P = 0.012$). A simple main effect of trial type existed for adults ($F(1) = 11.55$, $P = 0.003$), as well as a significant simple main effect of age for hits ($F(1) = 6.36$, $P = 0.015$), as demonstrated in Fig. 5B. In the right hippocampus, there was no significant interaction, but a significant main effect of trial type was found ($F(1, 42) = 9.05$, $P = 0.004$), with a simple main effect of trial type for adults ($F(1) = 8.99$, $P = 0.007$).

Discussion

We investigated developmental differences in the neural correlates of episodic retrieval using cued recall of word paired associations. Successful recall was associated with activations in default mode network regions including the mPFC, bilateral angular gyrus, PCC/precuneus, the hippocampus, and regions in frontoparietal network. As hypothesized, we observed a greater engagement of CRN regions in adults than in children, specifically in the posterior regions of the CRN. Adults exhibited greater successful recall activations compared with children in the precuneus and angular gyrus. In contrast, successful recall activation in the mPFC was observed in both adults and children. Developmental increases were also seen in fusiform gyrus and
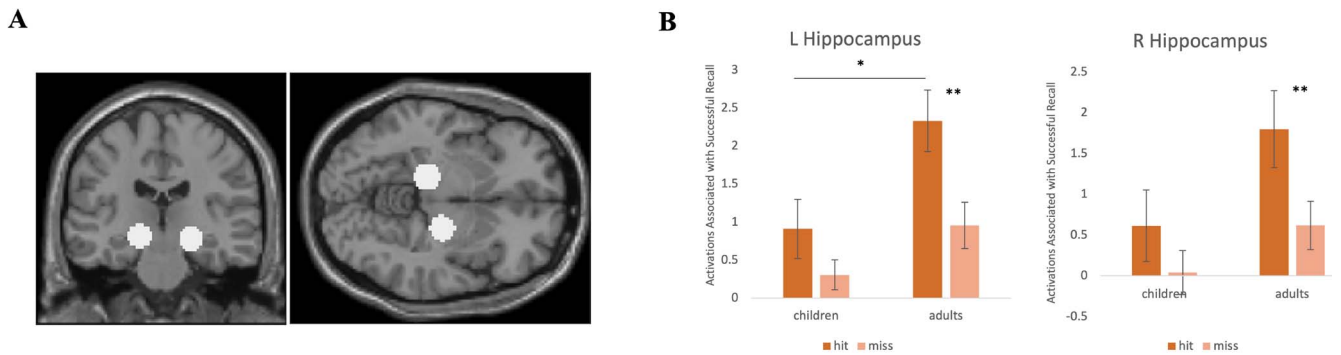
A

B

Fig. 5. A) Hippocampal ROIs (left: −16, −27, −8, right: 21, −17, −10). B) Activation values for children and adults in the left and right hippocampus for hit and miss trials. Error bars show standard error of the mean. *P < 0.05 and **P < 0.01.

hippocampus activation, along with developmental decreases in dorsal lateral prefrontal activation. This is the first study to our knowledge that demonstrated developmental differences in DMN and CRN activations during cued recall, a paradigm that elicits greater recollection experience compared with the typically used recognition memory paradigm. Our findings add to the growing body of work investigating the neural correlates of episodic memory retrieval by placing focus on DMN contributions to developmental gains in memory that were previously linked to frontoparietal and hippocampal regions during recognition memory retrieval (Paz-Alonso et al. 2008; Ofen et al. 2012; DeMaster and Ghetti 2013).

In agreement with previous research on episodic memory retrieval, successful recall of cued words was associated with activation in the CRN, which overlaps with the DMN (Hayama et al. 2012; Rugg and Vilberg 2013). The activation patterns associated with successful recall in our study aligned well with previous memory retrieval studies that elicited more subjective recollection experience, which consistently activated the DMN (see Kim 2020 for a review). A developmental difference was seen in posterior, but not anterior, regions of the DMN, in the precuneus and right angular gyrus. This manifested as greater activation for successful hit trials versus miss trials in adults but not children, a pattern consistent with previous cued recall studies (Hayama et al. 2012). These developmental findings in the posterior regions of the DMN are complementary to developmental findings reported in episodic memory encoding in which DMN deactivations in mPFC, bilateral lateral parietal cortex, and PCC were associated with successful memory formation in adults but not in children (Chai et al. 2014). Tang et al. (2018) also reported an age-related increase in subsequent memory deactivations in the superior prefrontal and mPFC. These developmental differences in DMN deactivations during successful encoding may be related to the less optimal allocation of neural resources to support the external attention needed for memory encoding. Together, these studies suggest that DMN, or more specifically CRN, regions are less engaged in supporting episodic memory for both the encoding and retrieval phase in children compared to adults, but that the developmental trajectories for each process differ in the specific regions showing developmental effects. These findings suggest that at least part of the posterior DMN, namely the precuneus and right angular gyrus, show a similar functional developmental trajectory in both encoding and recall.

A substantial body of research investigating the involvement of the precuneus in episodic memory has found that activation in the precuneus is highly correlated with the imageability of an integrated event in memory (Ritchey and Cooper 2020), a

measure of how easily one can invoke a mental image of an event, word, item, etc. in memory. The precuneus plays a key role in the mental image of episodic memories (Buckner et al. 1995; Fletcher et al. 1996; Halsband et al. 1998; Henson et al. 1999; review by Trimble and Cavanna 2008), so much so that Fletcher et al. (1995) labeled the precuneus as the "mind's eye." This is supported by research showing precuneus activation associated with the amount of detail reported in vivid autobiographical memories (Sreekumar et al. 2018) and increased source memory, the number of context-details recalled (Lundstrom et al. 2003). In addition to its contributions to imageability, the precuneus seems to show more general sensitivity to the success of episodic memory retrieval. A study of cued recall of both imaginable and abstract word pairs administered both visually and auditorily to adults resulted in activation of the precuneus in all conditions, demonstrating that it is not only sensitive to the level of imageability, but to multimodal retrieval success in general (Krause et al. 1999). These findings have been demonstrated in additional imaging studies such as Schmidt et al. (2002) and Platel et al. (2003). Our findings suggest that children have less engagement of the precuneus during cued recall compared with adults. Taken together with previous literature, this may suggest that children have diminished imageability or general sensitivity to correct versus incorrect episodic recollections, therefore leading to their poorer recall accuracy compared with adults. Furthermore, adults may have been more likely to spontaneously access these mental images supporting their recall, whereas children may not have done so. If specific instructions were given during the encoding trials (e.g. try to create an image linking the 2 words), it is possible that the differences in performance and brain activation between adults and children may have been reduced.

Complementary to the apparent role of the precuneus in the imageability of episodic memories, the lateral parietal cortex shows demonstrated involvement in the level of recollection detail (Spaniol et al. 2009; Cabeza et al. 2012; Thakral et al. 2017, 2020), source memory accuracy (Duarte et al. 2011), and representation of retrieved episodic multimodal and multi-domain information (Rugg and King 2018). It has been proposed that the precuneus and the AG work in tandem to support the imageability of integrated episodic events in memory (Ritchey and Cooper 2020). Specific to cued recall, the AG has been shown to be involved in the bottom-up detection of relevant stimuli or cues (Cabeza et al. 2008; Ciaramelli et al. 2008, 2010; Cabeza et al. 2012). In addition, in a study of cued recall following paired associate learning, stroke patients with parietal damage had impaired memory for cued pair words and pictures (Ben-Zvi et al. 2015), suggesting that a functioning parietal cortex is necessary for cued

recollection. In our data, children's engagement of the AG does not show adult-level function, complementing the aforementioned study showing impaired cued recall. The mechanism may be similar to that of the precuneus in that less engagement of the AG results in poorer mental imageability of the word pair associates and therefore poorer recall accuracy in children versus adults.

Adults reported more frequent use of deep learning strategies compared to children including making stories between words, relating words to personal events, and making a picture of the words. In particular, the precuneus and AG may have mediated these strategies by supporting the creation of mental images, as described previously. Furthermore, activation in the left angular gyrus likely contributed to the former strategy through its well-studied role in semantic processing (Binder et al. 2009), needed for both the processing of word meaning and the generation of novel stories through the retrieval and integration of concepts (Binder et al. 2009; Price et al. 2015). It is also worth noting that participants in this study were recruited in the surrounding area of a large university where the study was held, and it is likely that many young adult participants were students at the university who are highly practiced in memorizing information. This factor may have contributed to the increased spontaneous strategy use and, in turn, higher recall in the adult versus child group. The hippocampus also holds a key position in the CRN and is often included in, or at least interacts greatly with, the DMN. Unlike other episodic memory studies with no developmental effects in the hippocampus (Ofen et al. 2007, 2012; Tang et al. 2018), our results show a developmental difference such that adults demonstrated greater activations in bilateral hippocampus for hits versus misses, whereas children showed no such difference. This suggests that the developmental trajectory of the hippocampus in episodic memory may differ depending on the phase of memory and task demands. The literature suggests that the hippocampus's role in episodic memory involves binding and later reactivating the contextual framework of event features stored in the cortex (Ranganath and Ritchey 2012; Ritchey et al. 2015; Reagh and Ranganath 2018). A study by DeMaster and Ghetti (2013) investigated the role of the hippocampus during the retrieval of object-spatial location association in children and adults and demonstrated successful retrieval-related activation of the hippocampus in adults but not in children. Further support for the important role of hippocampus in developmental gains in memory comes from a series of studies linking structural variation in hippocampal volume with age related differences in memory (DeMaster et al. 2014; Daugherty et al. 2017; Keresztes et al. 2017). For example, a study by Daugherty et al. (2017) demonstrated that age-related differences in hippocampal subfield volumes were associated with an age-related increase in paired associate memory, but not item memory. Therefore, there may have existed differences in the engagement of hippocampal subregions in children and adults during episodic memory processes.

In contrast to the developmental effect seen in posterior CRN regions, we saw similar activation for successful retrieval in the mPFC for both adults and children such that hits were associated with greater activation compared to misses. Unlike the more posterior regions, these data suggest that the more anterior CRN may already be mature by the age of 9 to 13 years. This finding is complementary to previous research such as Güler and Thomas (2013) who used a cued recall paradigm involving image pairs and demonstrated developmental differences between 8- to 9-year-olds and 12- to 13-year-olds in lateral and mPFC regions. Taken together with our findings, we suggest that the functional development of the mPFC in cued recall takes place during this late-childhood period. The mPFC is hypothesized to play a role in self-processing, contextual and schema integration, and memory updating within the core recollection network (Rugg and Vilberg 2013; Kurczek et al. 2015; Schlichting and Preston 2016; Ritchey and Cooper 2020). The ventral mPFC in particular has been proposed to process schema or coarse details for the "gist" representation of memory during retrieval (Sekeres et al. 2018). It is possible that the relatively early maturation of the mPFC mediates the retrieval of coarse or gist representation of the information in children, which is consistent with the early development of memory that lacks rich contextual and perceptual details (Ghetti et al. 2002; Brainerd et al. 2004; Ghetti and Angelini 2008; Czernochowski et al. 2009). Children in our study may have relied more on coarse representations during recall, engaging the mPFC to do so. This is supported by the fact that children reported less deep encoding strategy use, potentially signaling less vivid traces. Furthermore, it has been proposed that the role of the mPFC in episodic memory is processing of self-relevancy, or integration with the self and other schemas (Andrews-Hanna et al. 2014; Ritchey and Cooper 2020) and that referencing the self during memory encoding facilitates later recall in both adults and children (Rogers et al. 1977; Cunningham et al. 2013, 2014; Sweatman et al. 2022). These results suggest that the interplay between the self-concept and episodic retrieval through the mPFC may already be further developed in children compared to more posterior core recollection regions.

Along with its role in the CRN, the mPFC activation observed in both groups may be partially attributable to performance monitoring, a set of cognitive processes supported by the mPFC in both adults and children (Ridderinkhof et al. 2004; Fitzgerald et al. 2010). Employing a judgment of learning as our encoding task likely promoted performance monitoring during encoding that may have had a role in supporting successful cued recall. However, although activation of the mPFC in performance monitoring shows a developmental increase from ages 8 to 18 years (Fitzgerald et al. 2010), in the cued recall task we employed we did not identify a difference in mPFC activations between the groups. It is possible that the way by which mPFC supports cued recall is masking developmental effects otherwise implicated for mPFC involvement in performance monitoring. Alternatively, it is possible that the demand for performance monitoring during encoding led children to recruit the mPFC to the same extent as that of adults. Another potential explanation for the lack of developmental effects seen in the mPFC is that of compensatory activation, with high-performing children engaging the mPFC more highly to support their recall. We were unable to find evidence to support this argument, with no significant differences in mPFC activation between high-performing children and either low-performing children or adults. However, this lack of effect may be due to the low sample size after splitting the child group in 2. The possibility of compensatory mPFC activation for recall in children warrants further investigation.

In addition to posterior DMN and CRN, developmental increases in hit versus miss contrasts were also seen in the posterior cerebellum and insula. Cerebellar activity has been repeatedly reported in episodic retrieval (Desgranges et al. 1998; Nyberg 1998; Wiggs et al. 1998; Fliessbach et al. 2007). In addition, memory tasks involving paired-associates evoke greater cerebellar activity than visual word recognition (Cabeza et al. 1997). Studies of cerebellar activation during different memory tasks suggest that the cerebellum is associated with executive functions necessary for explicit memory tasks and that impairments in cerebellar function partially impair memory recall via

executive impairment (Appollonio et al. 1993). Developmental changes in cerebellar activation during recall have been reported in late childhood (Güler and Thomas 2013) and, when taken together with our findings, suggest a protracted development of the cerebellum in episodic retrieval from as early as 8 years old to 18 years old and above. The insular cortex has been proposed to be involved in metacognitive processes of recall, monitoring recall accuracy and uncertainty and developing from late childhood to adulthood, consistent with our findings (Fandakova et al. 2017). The insula is also a key region in the ventral network for salience processing in episodic memory (Kim 2010), and children appear to show less functional segregation between the ventral attention and salience networks compared to adults (Farrant and Uddin 2015), suggesting that the insula's role in salience processing develops into early adulthood, as reflected in our data.

In contrast, children had greater activations associated with successful recall in the lateral frontal cortex, specifically the left inferior frontal gyrus (IFG) known for its involvement in language processing and word retrieval (Hirshorn and Thompson-Schill 2006). Interestingly, this region has been shown to be activated for misses > hits in adults during cued recall (Rugg et al. 1998; Hayama et al. 2012; Okada et al. 2012). The activation of the left IFG during unsuccessful cued recall may be associated with the selection of additional candidate completions of word stems that failed to elicit successful recall (Rugg et al. 1998; Hayama et al. 2012). This left IFG region is also involved in seeking candidate word pairs, including incorrect words that interfere with successful word selection (Henson et al. 2002). Greater activations in this region in children found in our study might reflect greater task demand and greater difficulty to retrieve the correct word pairings in this age group.

Together, our findings demonstrated a dissociation in development of CRN regions in episodic memory retrieval as measured by cued recall. Specifically, we showed that the engagement of the mPFC may already be mature by age 9- to 13-year old, whereas more posterior regions such as the angular gyrus, precuneus, and hippocampus are still maturing compared with young adults in support of successful memory recollection. The delayed maturation of these regions and the frontoparietal control regions may manifest in behavior via reduced imageability, binding of contextual details, executive function, and metacognitive processes.

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Data availability

The dataset used for this study will be made available on the Open Science Framework after all analyses have been completed.

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