



Neural Organization of Episodic Memory and Navigation in Children and Adults

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Abstract

■ Episodic memory and spatial navigation are often viewed as interlinked, in part due to their shared reliance on medial-temporal lobe (MTL) structures. At the same time, there are important differences, for example, natural spatial navigation requires moving one's body through space while episodic memory does not. We investigated whether naturalistically encoded memories that were either episodic or additionally embedded in a navigational experience relied on overlapping or distinct neural networks. Children ages 8–13 years old and young adults viewed pictures of objects that they had previously encountered in real-world experiences, either on a tour of a new environment

or seated in a room, along with novel objects. Univariate fMRI analyses revealed tour-related activity in entorhinal (ERC) and perirhinal (PRC) cortices that differed between early adolescents and adults. Functional connectivity between ERC and PRC for episodic memory decreased with age. Exploratory findings suggested behavior-driven connectivity among the hippocampus, ERC, and lateral occipital cortex to support reconstruction of the spatial context. Naturalistic episodic and spatial contexts are processed in the MTL, but these regions may interact somewhat differently in episodic and navigational contexts, and in late childhood and early adolescence versus early adulthood. ■

INTRODUCTION

Navigating and building internal models of the world around us are essential for behavior, even in the age of Global Positioning System and smartphones. Over the years, various theories have been proffered regarding the computational and neural relationship between navigation and episodic memory (Ekstrom & Hill, 2023; Fan, Sokolowski, Rosenbaum, & Levine, 2023; Buzsáki & Moser, 2013); however, there are still diverging views about the neural overlap between these cognitive constructs, and little is known about the development of these systems in tandem.

Developmental behavioral studies suggest both congruence and incongruence between the two domains. In early childhood, children's episodic memory and place learning appear between 18 and 24 months (Newcombe, Balcomb, Ferrara, Hansen, & Koski, 2014; Newcombe, Huttenlocher, & Learmonth, 1999). Both cognitive constructs rely on the integration of multiple pieces of information to form a single cohesive representation, and both systems allow for flexible retrieval of information. Incongruences between domains appear later. For instance, 6-year-olds can perform as well as young adults on some relational binding tasks (Ngo, Lin, Newcombe, & Olson, 2019; Pathman, Larkina, Burch, & Bauer, 2013); however, 6-year-olds do not

navigate as well as adults. In fact, equivalent levels of performance on navigation are rarely reached before the age of 12 years (Brucato, Nazareth, & Newcombe, 2022; Nazareth, Weisberg, Margulis, & Newcombe, 2018). When 6- to 12-year-old children do have adult-like navigation performance, there is evidence that this occurs when there is robust learning and retention of key spatial information (Maier et al., 2024).

We recently tried to pull these constructs apart by asking whether there is evidence for a distinct factor structure in these domains. Using the participants described in this article, we found that behavioral metrics of spatial and episodic memory stemming from the same naturalistic encoding experience (the tour) overlapped to form two latent factors: spatiotemporal structure memory and perceptual/factual/locale memory (Nguyen, Olson, & Newcombe, 2025). When encoding of episodic and spatial information is concurrent, tasks that we typically use to separately measure episodic memory (e.g., free recall, cued recognition) and spatial knowledge (e.g., map building, route knowledge, pointing) did not load into distinct latent variables of "episodic" and "spatial." Therefore, inconsistencies in behavioral findings may stem from treating these constructs as individual entities. When we measure what happens in the real world, behavior overlaps considerably.

Neural findings also show substantial overlap in how navigation and episodic memory are coded. Studies

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investigating the neural substrates of navigation in adults have repeatedly shown the importance of medial-temporal lobe (MTL) regions, with relevant areas including the hippocampus (HC), parahippocampal cortex (PHC), entorhinal cortex (ERC), and retrosplenial complex (RSC; Tansan, Nguyen, & Newcombe, 2022; Epstein, Patai, Julian, & Spiers, 2017). The HC features prominently in the spatial navigation literature (Bartsch, Döhring, Rohr, Jansen, & Deuschl, 2011; Burgess, Maguire, & O'Keefe, 2002; O'Keefe & Nadel, 1978) as well as in the literature on episodic encoding, consolidation, and retrieval (Cowan, Schapiro, Dunsmoor, & Murty, 2021; Squire, Genzel, Wixted, & Morris, 2015; Squire, 2004). MTL regions form functional networks with cortical regions such as the pFC, portions of the parietal cortex, RSC, and the striatum to allow for long-term and stable memory representations (Cowan et al., 2021; Ekstrom & Ranganath, 2018; Epstein et al., 2017). Indeed, several studies have found functional connectivity between the HC and MTL regions for navigation, as well as object selective and scene-selective areas (Grande, Sauvage, Becke, Düzel, & Berron, 2022; Ma, Rolls, Huang, Cheng, & Feng, 2022; Boccia, Sulpizio, Nemmi, Guariglia, & Galati, 2017; Baldassano, Beck, & Fei-Fei, 2013). Furthermore, network models reproduce the computational flow of information between these regions (Chandra, Sharma, Chaudhuri, & Fiete, 2025; Brunec & Momennejad, 2022; Schapiro, Turk-Browne, Botvinick, & Norman, 2017).

The literature on the neural development of spatial navigation is small. There is some evidence that, during navigation, children's hippocampi are sensitive to landmarks at decision points (van Ekert, Wegman, & Janzen, 2015) and that they may need additional neural scaffolding compared with adults to resolve navigation decisions (Murias, Slone, Tariq, & Iaria, 2019). Regions supporting visual processing such as the parahippocampal place area and the RSC may have differing developmental timelines that can affect the concurrent development of behavioral navigation systems, but we lack the data to map out exact trajectories (Dilks, Kamps, & Persichetti, 2022).

There is more extensive research documenting the neural development of episodic memory. Using structural MRI, researchers have found that hippocampal volume correlates with differential development of pattern completion and pattern separation (Botdorf, Canada, & Riggins, 2022; Canada, Ngo, Newcombe, Geng, & Riggins, 2019; Daugherty, Flinn, & Ofen, 2017; Keresztes et al., 2017) and gains in episodic memory (Schlichting, Guarino, Schapiro, Turk-Browne, & Preston, 2017; DeMaster, Pathman, & Ghetti, 2013). Hippocampal functional connectivity relevant to episodic memory changes across development and reorganizes from early to later childhood (Riggins, Geng, Blankenship, & Redcay, 2016). Based on the existing literature, it seems plausible that the patterns of neural gains in episodic memory also could underlie improvements in spatial navigation in childhood. However, we currently do not have evidence

to show that the areas that influence episodic memory also support spatial cognition in the same way.

Current Study

In the current study, we aim to directly compare the development of episodic and navigational neural substrates stemming from real-world experiences. We tested 8- to 13-year-old children and young adults on two types of encoding manipulations. The first was a real-life naturalistic encoding experience of an environment (an entire floor of a large academic building) in which various objects were displayed (termed the "tour"). The second included only episodic representations of real objects while stationary (termed the "room"). After experiencing the tour and room conditions, individuals underwent an fMRI task where they viewed objects from the encoding experiences. We used a priori ROIs, including regions previously implicated in spatial navigation, episodic memory, and visual perception. ROIs included the HC, PHC, ERC, perirhinal cortex (PRC), inferior lateral occipital (LO), and RSC. Since these neural regions often work in tandem but also demonstrate dissociations in terms of their function in supporting these types of behaviors, we examined both univariate activation and functional connectivity of the ROIs. Importantly, participants viewed the encoded objects passively as cues for both types of events, demonstrating incidental memory retrieval. We examined age-related changes in univariate activations and functional connectivity to understand how children may differ (or not) from adults. Finally, we relate functional connectivity back to memory performance on the tour to grasp how memory strength guides neural organization.

METHODS

Participants

One hundred thirty (88 children ages 8–13 years and 42 adults ages 19–31 years) participants from the greater [location removed] area in three age groups (8–10 years, $n = 46$, $M = 9.36$ years, 22 girls; 11–13 years, $n = 42$, $M = 12.25$ years, 20 girls; and adults, $n = 42$, $M = 23.19$ years, 23 women) completed this study. The study protocol, recruitment, compensation, and consent/assent procedures were approved by the [location removed] Institutional Review Board. Consent was obtained from the adult participants and from parents/legal guardians, and assent was obtained from the children. All participants received monetary compensation at a rate of \$25/hr; parents were reimbursed for parking expenses, and children received an additional small toy prize. To recruit children, we used Facebook ads targeting parents, local flyers, and the [location removed] Infant and Child Lab database. To recruit adults, we used on-campus flyers and word of mouth.

All participants were screened by phone for their age, lack of psychological or developmental diagnoses, and

normal or corrected-to-normal vision and hearing. Neuroimaging screening included MRI contraindications such as metal on/inside the body, claustrophobia, and prior medical procedures that may cause discomfort. If eligible, participants were scheduled for two 2.5- to 3-hr sessions in the lab with no more than 7 days between the sessions. If participants expressed discomfort in the mock scanner on the first day or decided to not undergo the MRI, they were able to complete all the behavioral procedures on the first day. Fourteen participants completed the behavioral testing but were not scanned. fMRI exclusions included too much movement during the functional task ($n = 1$), not enough time points after source recognition exclusions ($n = 12$), or a combination of both ($n = 18$) across all age groups. Two participants were missing their source recognition data file, and one participant did not make enough correct choices on the source recognition. The final sample size for analysis was 82; twenty 8- to 10-year-olds ($M = 9.45$ years, $SD = .88$, 10 girls), twenty-five 11- to 13-year-olds ($M = 12.4$ years, $SD = .87$, 12 girls), and 37 adults ($M = 23.2$ years, $SD = 3.09$, 18 women). The analysis sample was 49% female, 13% Asian/Asian American, 17% Black, 54% White, 21% Hispanic, 7% more than one race, and 9% unreported race (Table 1).

The original sample size was an adequate sample to reach acceptable power for behavioral factor analyses (Nguyen et al., 2025). Another power analysis was not calculated for the fMRI data set; however, the authors used fMRI work in the current literature with children in

a similar age range to inform an acceptable sample size (Murias et al., 2019; van Ekert et al., 2015).

Encoding Experiences

Figure 1A shows an outline of the 2 days of testing. For full behavioral methodology details, please refer to Nguyen et al. (2025). Here, we summarize the methods used during encoding and behavioral testing from Day 1.

Tour Encoding

Participants were led on an 8-min in-person tour (Figure 1B) by an experimenter during which they encoded 16 real-life objects and learned the spatial layout of the objects in the tour space. The tour encoding had both spatial and episodic information embedded within the experience. For example, participants walked around and encountered each object while learning a fact about each object (e.g., giraffes hum to each other at night) and were tasked to remember the object locations. Participants were instructed to remember what the objects looked like, the facts the experimenter told them, and where the objects were located.

Room Encoding

The second encoding event was episodically rich but without encoding of spatial locations. Participants remained seated in the testing room while the experimenter

Table 1. Demographic Information for fMRI Analysis Sample Split by Age Groups

	8–10 YO	11–13 YO	Adults	All
<i>n</i>	20	25	37	82
Sex				
Female	10 (50%)	12 (48%)	18 (49%)	40 (49%)
Male	10 (50%)	13 (52%)	19 (51%)	42 (51%)
Race				
American Indian/Alaska Native	0	0	0	0
Asian/Asian American	2 (10%)	3 (12%)	6 (15%)	11 (13%)
Black	6 (30%)	3 (12%)	5 (14%)	14 (17%)
Native Hawaiian or Other Pacific Islander	0	0	0	0
White	9 (45%)	11 (44%)	24 (65%)	44 (54%)
More than one race	2 (10%)	3 (12%)	1 (3%)	6 (7%)
Other or not reported	1 (5%)	5 (20%)	1 (3%)	7 (9%)
Hispanic	4 (20%)	6 (24%)	7 (19%)	17 (21%)

Percentages were rounded to the nearest whole number. YO = years old.

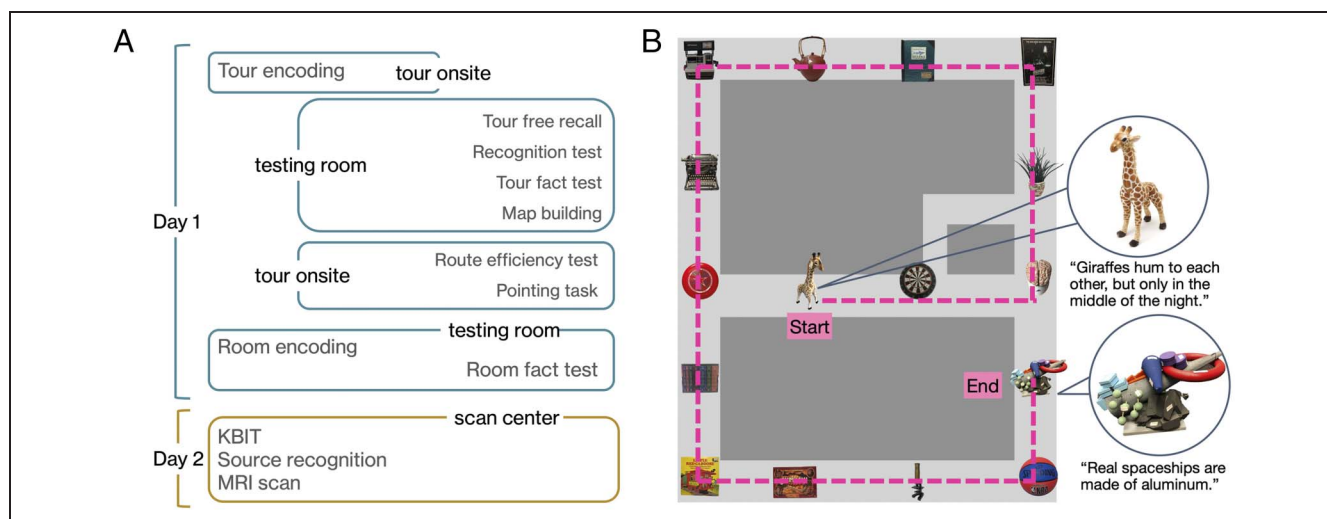


Figure 1. (A) Timeline of the 2-day testing sessions. (B) Schematic of the tour encoding environment with 16 object stimuli along the tour path (pink dotted line).

brought in the second set of objects (e.g., Set B) one by one. Again, the experimenter read from a script to identify the object, encouraged the participant to interact with the object, and relayed a fact about the object. Timing was closely matched to the tour encoding. None of the objects from Sets A and B were seen by the participant prior to the encoding experiences.

Encoding Object Sets

There were two object sets used in the tour and room encoding, A and B, which were counterbalanced across participants, such that half the participants saw Set A and half saw Set B during the tour and vice versa for the room. A third set (Set C) consisted of “new” objects presented for the first time during the source recognition task right before undergoing MRI scanning. Set C did not include any episodic or spatial encoding and did not function as novel stimuli inside the scanner due to a single exposure prior to the scan. Items within the sets were semantically matched, such that Items A1, B1, and C1 were different objects from the same category. See Nguyen et al. (2025) for full details.

Episodic Memory Tests

Tour Free Recall

Participants completed an audio-recorded free recall of the tour experience (Figure 2A). The interview questions were asked either by a second experimenter for the adults or a parent for the children. Participants were given 5 min to recall as much as they could. Audio recordings were transcribed using Otter.ai and then double-checked by a research assistant (J. E., G. A. O. C., L. N., A. M. Y.). The recall transcripts were scored by a reliable rater (J. E.) using the autobiographical interview method to extract a

count of internal (tour-related) and external event details (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002).

Tour Recognition

This test contained 40 four-alternative-forced-choice questions about perceptual details (16 questions), staged events (eight questions), and spatiotemporal details (16 questions) from the tour (Figure 2B) scored using a proportion correct (chance = .25). Spatiotemporal questions were presented last since these questions included pictures of the objects.

Fact Test

To ensure that participants learned the facts during both encoding experiences, they completed a two-alternative-forced-choice test (chance = .50) for each object set (Figure 2C). Both presented facts for each object were true, and participants had to choose the fact they learned during encoding. This task was administered after each encoding experience.

Tour Spatial Tests

Map Building

Participants were tasked to recreate the tour environment from a bird’s-eye view by placing pictures of the 16 objects onto a blank white screen (Figure 3A). The configuration of each participant’s map was compared with a correct map using bidimensional regression to get the R^2 (Friedman & Kohler, 2003). The R^2 is the variance of the correct map that is explained by the participant’s map, with scores closer to 1 indicating better mapping of object positions.

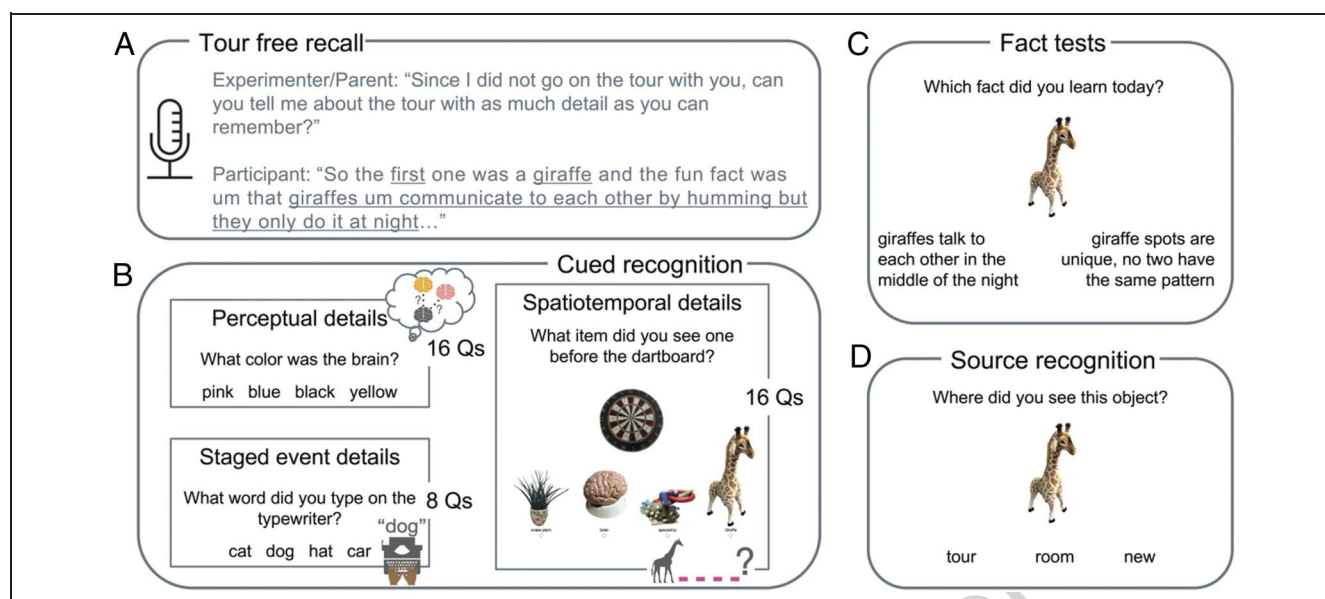


Figure 2. Episodic memory measures. (A) The autobiographical free recall procedure and scoring were modeled after Levine et al. (2002). The final score was the total number of tour-related details recalled. (B) The recognition test was administered on Qualtrics with three categories: perceptual details (16 questions), staged events (eight questions), and spatiotemporal details (16 questions). (C) Participants completed the fact test for the fact that they learned in the lab. (D) The source recognition test occurred right before the MRI scan on Day 2. For each object picture, participants chose if they saw the object on the tour, in the room, or if it was new to them that day (foils; chance = .33).

Route Efficiency

Back in the tour environment, participants started at one object and took the shortest path they remembered to 12 other objects on the tour, sequentially (e.g., basketball to giraffe, giraffe to plant, plant to teapot; Figure 3B). The experimenter recorded the number of objects passed along each route and then averaged across all 12 trials. The efficiency score was calculated by dividing the participant's average number of objects passed by the perfect score (e.g., 5.00/4.32). Efficiency scores closer to 1 were more efficient; scores were reversed such that higher values indicated better performance.

Pointing Task

Participants completed 10 trials of an onsite pointing task where they stood at one object and were told to face a specific direction (Figure 3C). While in this facing orientation, they were asked to think about the location of a target object in the tour and then indicate the direction of the target object using a 360° digital protractor (e.g., standing at the giraffe facing west, point to the record). Angular error (indicated angle – actual angle) was calculated for each trial and averaged; error was reversed such that higher values indicated better performance.

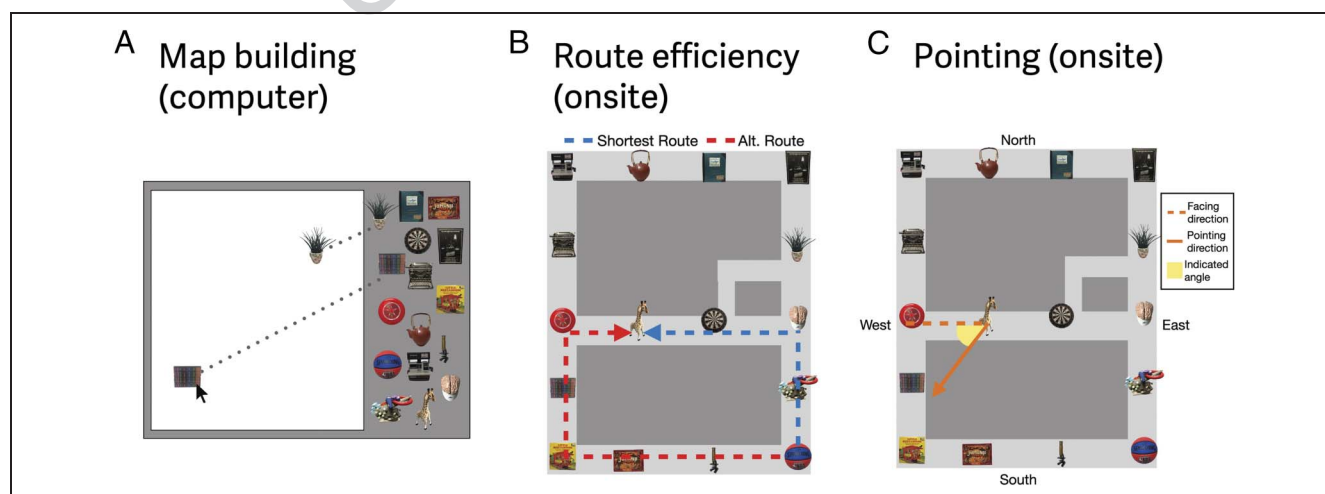
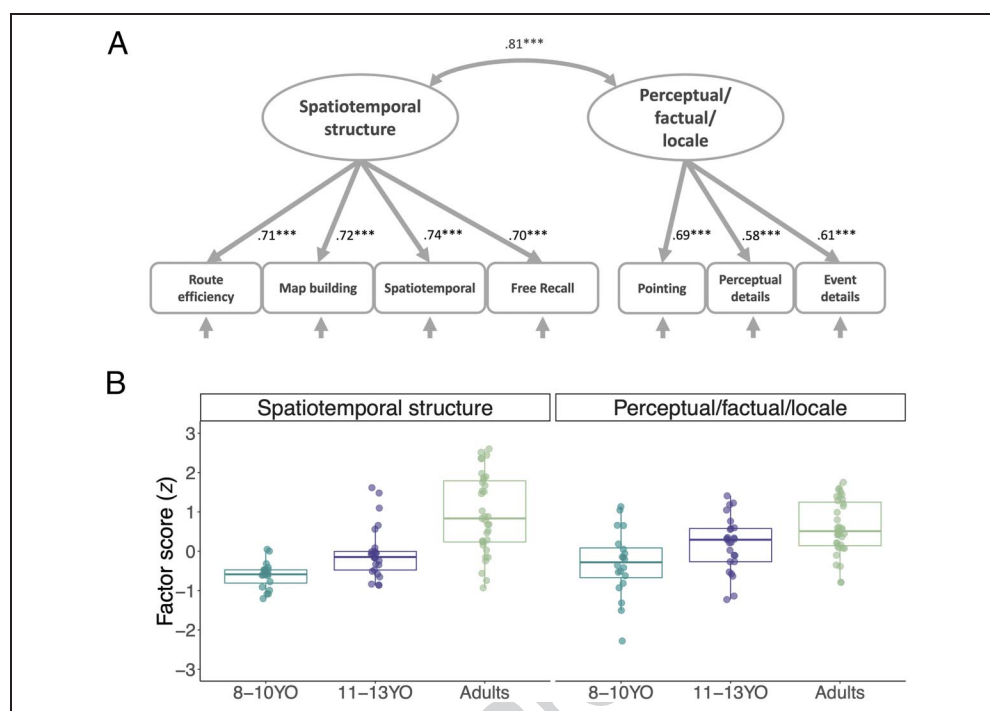


Figure 3. Schematic of the spatial memory tasks. (A) The map building task completed on a computer. (B) The route efficiency task and (C) the pointing task were completed in the real-life tour environment with experimenter guidance.

Figure 4. Measured memory variables from the tour contribute to two latent factors. (A) CFA of the seven variables grouped route efficiency, map building, spatiotemporal details, and free recall into one latent factor named “spatiotemporal structure” and pointing, perceptual details, and event details into another latent factor named “perceptual/factual/locale.” Full behavioral results are reported in Nguyen et al. (2025). (B) Factor scores for spatiotemporal structure ($r = .66, p < .001$) and perceptual/factual/locale ($r = .36, p = .001$) increased significantly with age. *** $p < .001$.



Generated Latent Memory Factor Scores

In a separate publication (Nguyen et al., 2025) with the same full 130-participant sample, we applied PCA and then confirmatory factor analysis (CFA) to the behavioral memory data to understand how these spatial and episodic memory metrics relate when measured from a common encoding experience, the tour. This PCA included the tour free recall and recognition (perceptual details, staged events, and spatiotemporal details), route efficiency,

map building, and pointing tasks. Based on PCA grouping, the CFA consisted of two latent factors (Figure 4A). The first factor included free recall, spatiotemporal details, route efficiency, and map building, which we termed “spatiotemporal structure” memory. The second factor included perceptual details, staged events, and pointing, which we named “perceptual/factual/locale” memory. From this, we generated latent memory factor scores for spatiotemporal structure and perceptual/factual/locale memory for each participant in this study (Table 2).

Table 2. Descriptive Statistics for Behavioral Memory Factor Scores

	<i>n</i>	<i>Mean</i>	<i>Median</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Spatiotemporal structure						
8–10 YO	20	−0.61	−0.59	−0.33	−1.2	0.05
11–13 YO	25	−0.02	−0.15	0.66	−0.86	1.61
Adults	35	0.94	0.83	0.99	−0.93	2.6
Overall	80	0.25	−0.05	1	−1.2	2.6
Perceptual/factual/locale						
8–10 YO	20	−0.31	−0.28	0.84	−2.28	1.13
11–13 YO	25	0.18	0.29	0.69	−1.23	1.41
Adults	35	0.6	0.51	0.68	−0.79	1.75
Overall	80	0.24	0.26	0.8	−2.28	1.75

YO = years old.

Day 2 Tasks

KBIT-2 IQ

Participants completed the verbal, riddles, and matrix reasoning subtests to generate a general IQ score. Test stimuli were presented on a computer screen, and riddles were read aloud by an experimenter. Participants started each test at their designated age start and continued until they got four consecutive trials wrong or until the end of the test. The composite KBIT IQ score was age-standardized.

Source Recognition

Before the MRI scan, participants saw images of all 48 objects from Sets A, B, and C one by one on the screen and indicated with a keyboard button if the object was from the tour, room, or if it was new to them that day (i.e., Set C foils that they did not see in person on Day 1; Figure 2D). Exposure to the foils set was brief with each picture on the screen for as long as the participant needed to make a choice. Performance on this task was broken down by each individual item within each context and averaged across each context in Figure 5A. Only correct responses from this task were used to extract trials from the fMRI task for univariate and functional connectivity analyses. This ensured that the neural responses modeled were the most accurately remembered or identified as new to them on scan day. Because of high performance in source recognition, there were at least 11 out of 16 trials modeled for each context in the final sample, after also accounting for motion in the scanner (see MRI Analysis).

fMRI Task

This was an orthogonal task where images of the 48 objects were presented blocked by the source (tour, room, or foil) and the source order was counterbalanced across runs and participants (Figure 6A). During a run, each object was on the screen once for 3 sec, followed by a 3-sec fixation cross. During the fixation cross, participants pressed a button indicating the color of the cross (red or blue) for an alertness maintenance task. Participants completed four runs of the task, seeing each object once during each run (only two participants completed three runs due to fatigue or technical issues). Participants were instructed to observe the object images and to press a button to indicate the color of the fixation cross between each image trial.

MRI Acquisition

Data were acquired on a 3.0-T Siemens MAGNETOM Prisma scanner using a 64-channel head coil. Each functional scan was collected parallel to the genu-splenium axis of the corpus callosum in the sagittal plane, with 147 repetition times (TRs) at 2-mm thickness (TR = 2000 msec, echo time [TE] = 30 msec, flip angle = 77°, 86 × 86 matrix,

2.51 × 2.51 in-plane resolution, bottom-up interleaved acquisition). A T1-weighted 3-D MP-RAGE was acquired for image co-registration and for volumetric extraction (256 × 256 × 256 matrix; TR = 2400 msec, TE = 2.28 msec, inversion time = 1150 msec, flip angle 8°, with an isotropic voxel size of 0.9 × 0.9 × 0.9 mm³, and a bandwidth of 210 Hz/pixel). A T2 image was collected but not analyzed in this article.

Procedure

Figure 1A shows the timeline of the sessions. During the first session, participants completed the tour encoding, followed by questionnaires, episodic memory testing, and map building on a computer in the testing room. Then, they went back into the tour environment for two navigation tests (Pointing and Routes). After, they returned to the testing room to complete the room encoding and room fact test. On the second day, participants completed the KBIT-2, the source recognition test, and the MRI scanning. Parents completed the demographic and pubertal development forms on the second day. Computer tasks in Qualtrics or PsychoPy (Peirce et al., 2019) were completed on a 13-in. MacBook Air. Onsite tasks were completed in person in the tour environment.

MRI Analysis

fMRI Preprocessing

Results included in this article come from preprocessing performed using fMRIPrep 21.0.1 (Esteban et al., 2019; RRID:SCR_016216), which is based on Nipype 1.6.1 (Gorgolewski et al., 2011); RRID:SCR_002502). Digital Imaging and Communications in Medicine images were converted to Neuroimaging Informatics Technology Initiative format with Brain Imaging Data Structure nomenclature using dcm2niix (Gorgolewski et al., 2016). Each participant had at least one T1-weighted image and three out of four functional task runs. Preprocessed fMRI task runs and confound files were then used in subsequent analyses. Confounds included tissue segmentation of cerebrospinal fluid (CSF), white matter (WM), both mean signals, and motion outliers, namely, framewise displacement (FD) and DVARS. See Supplement A for full preprocessing pipeline.

Univariate Analysis

A priori ROIs were selected as the literature has implicated them in episodic memory, spatial navigation, and visual perception (Tansan et al., 2022; Epstein et al., 2017). See Table 3 for lateralized ROI Montreal Neurological Institute (MNI) coordinates. These included the HC, PHC, ERC, PRC, RSC, inferior LO, and primary visual cortex (V1). HC, PHC, ERC, LO, and V1 ROIs were from the Juelich atlas for the MNI 2-mm template. RSC and

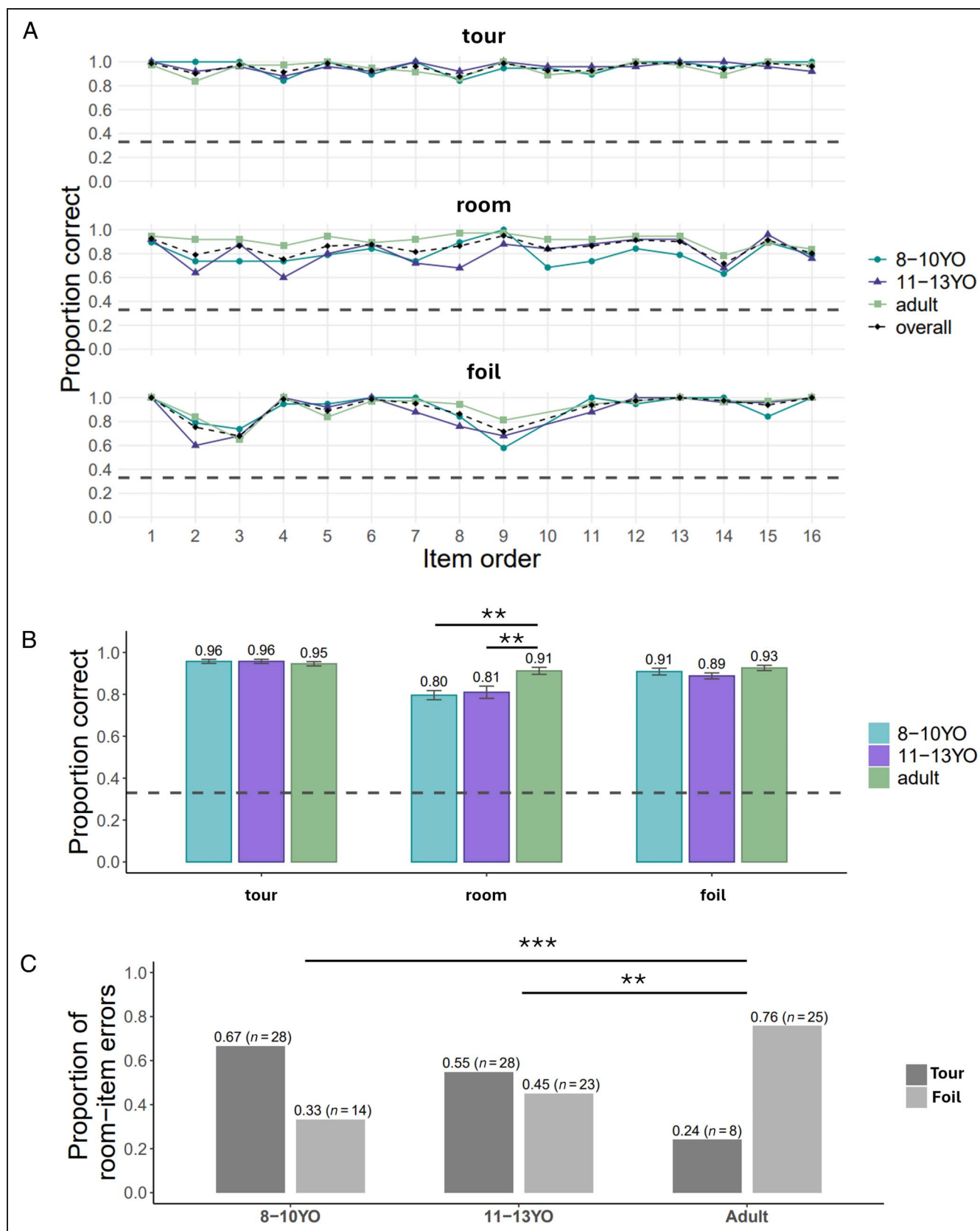


Figure 5. Source recognition performance. (A) Item-level recognition performance by age groups and context and an overall average. Item foil 10 was excluded for all participants due to task error. (B) Age group-level averaged performance by context from a mixed-effects ANOVA model indicating significantly lower performance within the room context between children and adults. $**p_{\text{adj}} < .01$. Bars indicate standard error; dashed lines indicate chance performance.

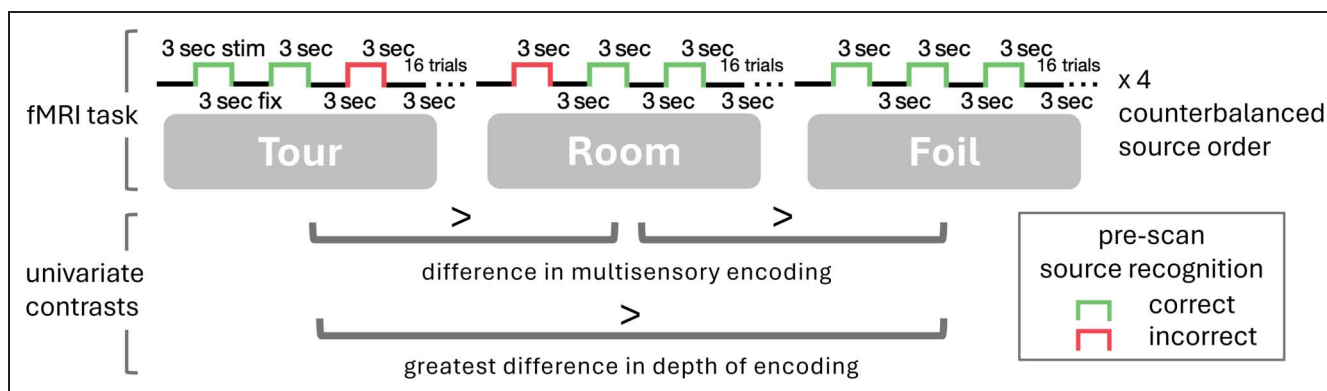


Figure 6. Schematic of fMRI task and univariate contrasts. The fMRI task was orthogonal viewing of the 48 object stimuli blocked by source of the object. Each stimulus was on the screen for 3 sec with a 3-sec fixation in between. During the fixation, participants pressed a button to indicate if the cross was red or blue to gauge wakefulness in the scanner. The general linear model for univariate contrasts included time points for correctly (green) and incorrectly (red) identified stimulus source from the prescan source recognition test. Contrasts included tour > room, tour > foil, and room > foil.

PRC were functionally derived ROIs from previous publications (RSC: Marchette, Vass, Ryan, & Epstein, 2015; PRC: Ritchey, Montchal, Yonelinas, & Ranganath, 2015) resampled to MNI 2-mm space. All ROI templates were thresholded to approximately 500 voxels to prevent bias due to volume differences between regions and then binarized as masks. Since the fMRI stimuli were images of objects, we used V1 as a control region, expecting to see activation for visual information in this lower-level visual region but not necessarily developmental changes. Preprocessed data were used in FEAT with grand-mean intensity normalization, filtering, and spatial smoothing carried out to isolate averaged BOLD signal activation in a blocked manner for each pairwise contrast (e.g., tour > room). All object trials were included in the general linear model; object trials were modeled as correctly or incorrectly identified from the prescan source recognition task (Figure 6B). This ensured that the signal detected was of the most accurate memory due to the delay between encoding and the scan. Each block was modeled with at least 11 out of 16 stimulus events contained within the source blocks (no more than 30% data loss due to source recognition errors and/or motion). Since there were so few incorrect trials, we did not have the power to include a correct > incorrect contrast within the context contrasts (Figure 6A). The model was convolved with a double-gamma hemodynamic response function and included temporal derivatives and motion outliers (FD, DVARs) not exceeding thresholds extracted from the preprocessing step (Schonberg et al., 2014; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012), as well as mean CSF and WM signal confounds. Correction for multiple comparisons was carried out at the whole-brain level (z threshold = 3.1) and within a priori ROIs at a cluster significance level of $p < .05$. Each run had a z -statistical image for each contrast. The subsequent z -statistic images were warped from native space to the MNI152 (2-mm) template brain using flirt.

The final contrasts included tour > room, which aimed to infer the spatial structure of the tour encoding experience not present in the room encoding; tour > foil, which encapsulated the entire naturalistic tour encoding (spatial and episodic combined); and room > foil, which only included the episodic encoding from the room experience (Figure 6B). The behavioral encoding process for each context was intentionally ordered to capture the ordinal differences between source contexts. We treated each contrast independently to test effects of each added behavioral construct while maintaining specificity. We did not predict a linear effect from one source context to the other; thus, bivariate contrast between sources was more fitting for our predictions.

Table 3. MNI Coordinates for ROIs

ROI	Hemisphere	X	Y	Z
HC	Left	-25.52	-21.58	-15.08
	Right	27.14	-20.13	-15.16
PHC	Left	-22.35	-32.12	-18.05
	Right	22.96	-30.19	-17.75
ERC	Left	-22.37	-8.82	-33.19
	Right	23.23	-5.15	-32.06
PRC	Left	-30.62	-8.65	-35.03
	Right	30.92	-10.97	-33.57
RSC	Left	-15.81	-59.68	9.39
	Right	16.91	-54.06	9.49
Inferior LO	Left	-49.14	-74.25	-1.77
	Right	50.94	-71.97	-2.14
V1	Left	-5.03	-87.29	3.55
	Right	13.74	-87.85	3.57
Heschl's gyrus	Bilateral	-43.05	-21.83	9.1

Functional Connectivity Analysis

The univariate analysis shows the underlying architecture related to naturalistic experiences, but only when each ROI is modeled individually. Since brain regions seldom work independently, we lose explanatory power when examining only univariate activation. Thus, we opted to run functional connectivity between ROIs (Zalesky, Fornito, & Bullmore, 2012) and across runs since each context only appears once per task run. In the functional connectivity analysis, the same ROIs were used with an additional Heschl's gyrus auditory cortex ROI from the Harvard-Oxford atlas as a connectivity control region, given that we do not expect to see any meaningful, significant connectivity with Heschl's gyrus due to the lack of audio stimuli. Using Nilearn (Abraham et al., 2014) in Python3, connectivity matrices of the signal were calculated for each participant's fMRI run. The ROI binary masks were loaded in using NiftiLabelsMasker. NiftiLabelsMasker.fit_transform was used to extract the time series for all participants from reprocessed fMRI runs with the same motion outliers, CSF, and WM confounds that were used in the univariate analysis. The time series data were then split into TRs corresponding to when each source block was presented, resulting in one file for tour and one file for room. Finally, correlation matrices were created from the time series data using ConnectivityMeasure with Fisher's z transformation. The final connectivity matrices for each source included each pairwise correlation of the signal between ROIs and an averaged network metric to gauge a more generalized MTL network. Along with connectivity metrics for the tour and room sources, a difference metric (tour – room) was calculated to isolate spatial-specific signals in functional connectivity. ANOVAs between the connectivity matrices for each run showed nonsignificant differences in strength; therefore, functional connectivity was averaged across the four runs for each participant. Time series data for each ROI and source were averaged across all runs and then tested for normality using the Shapiro–Wilk test, skewness, and kurtosis, passing all assumptions for parametric testing.

Statistical Analysis

All statistical analyses were completed in RStudio Version 4.2.3 (R Core Team, 2023), Python 3 (Rossum & Drake, 2012), and Jupyter Notebook (Kluyver et al., 2016). Data and analysis scripts are available at <https://osf.io/b9hvq/> (Nguyen, 2025); see Supplement B for a list of packages used.

Evaluation of the source recognition task included a mixed-effects ANOVA on individual accuracy with between-participants effect of age group and within-participant effect of source context and subsequent Tukey-adjusted pairwise comparisons and generalized eta-squared (η^2) effect sizes. In the univariate analysis, assumptions of normality, skew, and kurtosis were not met for some ROI contrast estimates; thus, nonparametric tests were

employed. The primary analysis looked at age group differences in activation with Kruskal–Wallis rank-sum tests and Wilcoxon pairwise comparisons with Benjamini–Hochberg correction. Secondary analysis was conducted as a sensitivity check with the univariate contrasts to include age group and number of correct source recognition trial as a covariate in robust regression models with model comparisons using robust Wald test. Functional connectivity metrics met assumptions for parametric testing; thus, ANOVAs with Tukey honestly significant difference post hoc tests were used in age group statistical analysis. Eta squared effect sizes are reported where appropriate.

Behavioral data analysis and results are presented in Nguyen et al. (2025). Here, we used the factor scores generated from the CFA from Nguyen et al. as latent metrics of spatiotemporal structure ($M = 0.25$, $SD = 1$) and perceptual/factual/locale ($M = 0.24$, $SD = .8$) memory from the real-world tour experience (Table 2). Scores for spatiotemporal structure ($r = .66$, $p < .001$) and perceptual/factual/locale ($r = .36$, $p = .001$) both increased with age (Figure 4B). Since the memory factor scores were tested only from the tour experience, we can only relate these scores to the functional connectivity for the tour – room subtraction as outcome variables. Two adult participants were excluded from this analysis due to missing behavioral data. To examine the relationship between functional network connectivity and memory strength, we ran general linear models using the spatiotemporal structure and the perceptual/factual/locale memory factor scores as predictors, along with control variables (age, sex, and IQ). Benjamini–Hochberg false discovery rate (FDR) correction was applied to linear models to correct for multiple comparisons. Linear model assumptions and multicollinearity (using the variance inflation factor [VIF]) were checked.

RESULTS

Source Recognition Performance across Age and Contexts

Performance range on source recognition was high across age and context, although there were some minor differences. A mixed-effects ANOVA showed a significant interaction of age group and context, $F(3.26, 127.16) = 6.38$, $p < .001$, $\eta^2 = .08$ (Figure 5B). Children in both age groups performed significantly worse than the adults in the room context (8–10 years old: $\text{diff} = -0.12$, $SE = .03$, $p_{\text{adj}} = .002$; 11–13 years old: $\text{diff} = -0.10$, $SE = 0.03$, $p_{\text{adj}} = .003$), with performance on the room items significantly lower than the tour and foil items ($p_{\text{adj}} < .05$; see Supplement C for full model results).

Age Group Activation Differences in Spatial and Object-sensitive Regions

Neural contrast estimates (beta values) were extracted for HC, ERC, PHC, PRC, RSC, LO, and V1 (univariate control)

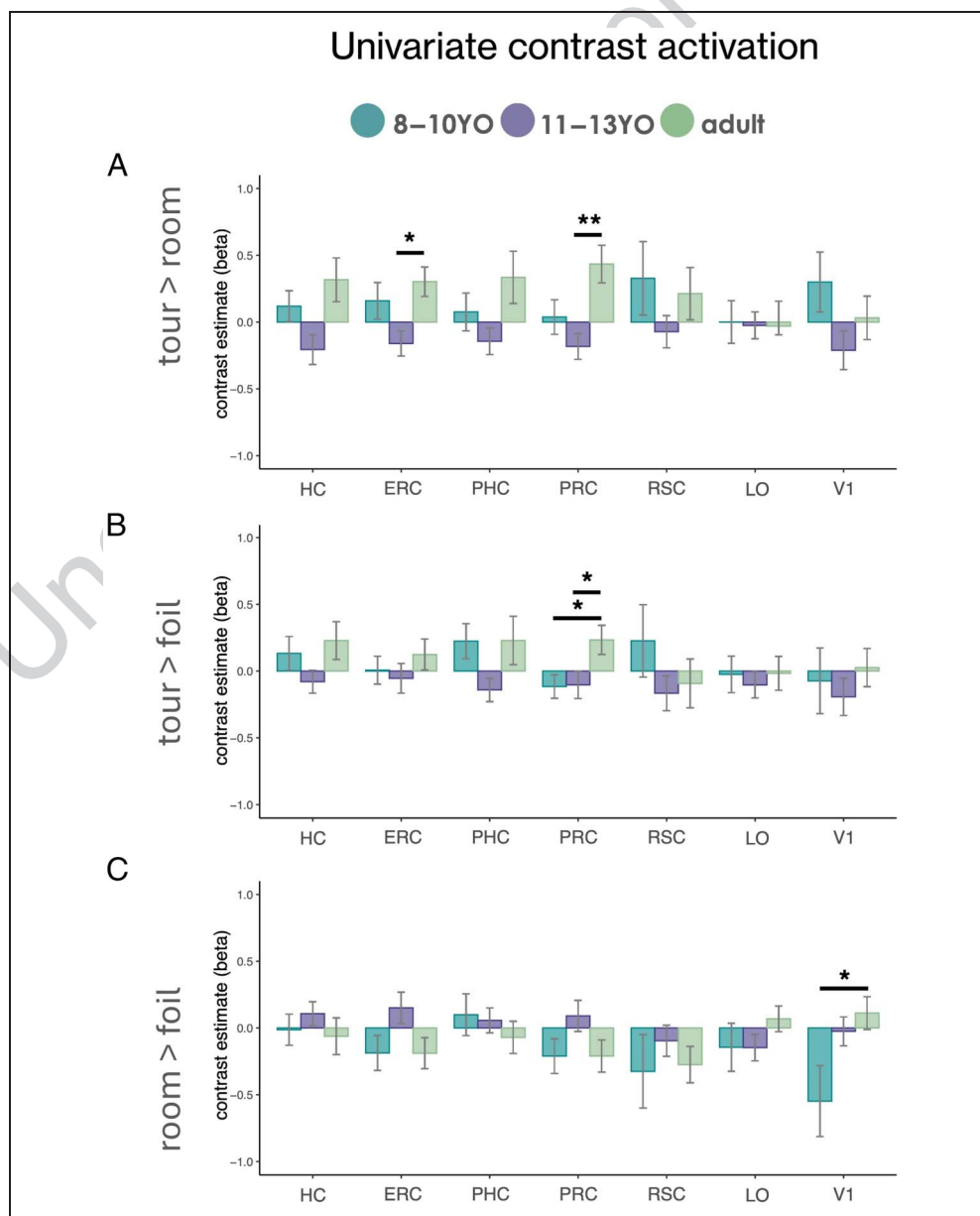
for the three contrasts of interest: tour > room, tour > foil, room > foil (Figure 6B). The contrast data showed nonnormal distribution, skewness, and some kurtotic patterns; thus, nonparametric tests were used (Supplement D). Each ROI contrast estimate in all age groups was not significantly above 0 ($p_s > .05$); thus, our primary focus is on age group comparisons rather than response patterns for any individual age group (Supplement E).

As shown in Figure 7A, adults had greater activation in the ERC (diff = 0.436, $p = .03$, $\eta^2 = .062$) and PRC (diff = 0.59, $p = .007$, $\eta^2 = .09$) than the 11- to 13-year-olds for items encoded during navigation rather than a static spatial context. As shown in Figure 7B, adults had greater PRC ($\eta^2 = .092$) activation than either the 8- to 10-year-olds (diff = 0.344, $p = .02$) and the 11- to 13-year-olds (diff = 0.357, $p = .02$) for items encoded during navigation than items recently encountered. Adults showed greater

activation in V1 than children 8–10 years old for items encountered in a static spatial situation than items recently encountered (diff = 0.665, $p = .03$, $\eta^2 = .079$; Figure 7C). However, adult activation was not significantly different from 0, and we do not discuss this puzzling difference further.

As a secondary sensitivity analysis, we fit robust regression models to examine whether age group effects persisted after adjusting for source recognition performance using the number of correct trials. Models including correct trials did not generally improve model fit relative to age group alone, with the exception of tour > room in the PRC, $\chi^2(1) = 7.96$, $p = .005$, $\Delta R^2 = .056$ (Supplement F), where the main effect of age group did not remain. For all other comparisons, the primary age group findings are largely robust to adjustment for recognition performance. The lack of global effect of accuracy

Figure 7. Univariate contrast activation within ROIs and functional connectivity between ROIs. Nonparametric Kruskal–Wallis tests were run for each comparison. (A) Adults had greater activation in the ERC (diff = 0.436, $p = .03$) and PRC (diff = 0.59, $p = .007$) compared with the older children with the tour > room contrast. (B) Adults had greater activation in the PRC compared with both younger (diff = 0.344, $p = .02$) and older children (diff = 0.357, $p = .02$) with the tour > foil contrast. (C) Young children had lower activation in V1 compared with adults (diff = 0.665, $p = .03$) with the room > foil contrast. * $p < .05$, ** $p < .01$. Bars indicate standard error.



may be a result of using high performance on source recognition as an inclusion criterion. See Supplements F, G, and H for full results for each contrast.

In summary, adults had greater activation for the tour items (spatial structure and overall experience) in areas sensitive to allocentric coding of environmental cues (ERC) and familiar objects (PRC), although additional sensitivity results may not support a robust effect in the PRC. Surprisingly, there were no reliable differences in hippocampal activation but rather regions that feed into the HC.

Age Group Decreases in Functional Connectivity for Episodically Encoded Objects

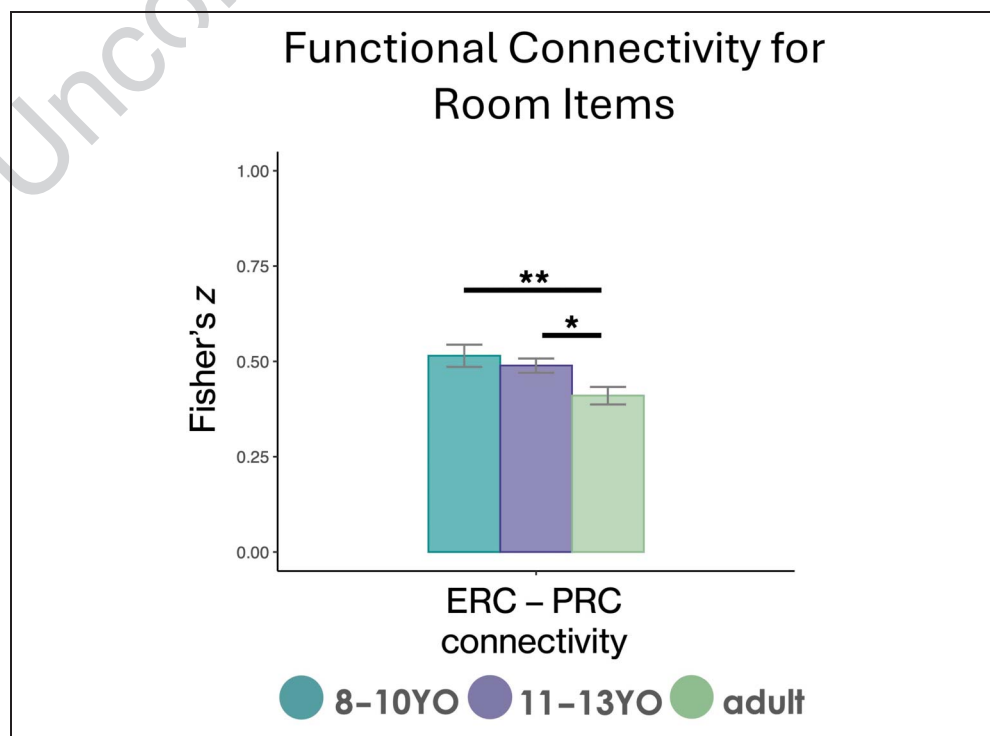
We captured implicit memory of the tour and room in overall ROI activation, but that does not reveal how these regions function relative to one another and if these connections support naturalistically encoded information. Considering regions in the MTL and related cortical areas often work in concert, we queried if functional connectivity between these regions varies across age, too. ROI time series for each participant's functional run satisfied assumptions of normality, skew, and kurtosis; hence, parametric tests were used (Supplement I). Analyses were run for each pairwise connection (e.g., HC and ERC) and the averaged network metric for tour, room, and a subtraction of tour – room (Supplement J). All connectivity metrics were significantly above 0 ($p < .05$) except for connectivity with the control region, Heschl's gyrus. Functional connectivity between ERC and PRC for the room source (Figure 8; $\eta^2 = .12$) was lower in the adults compared with

the 8- to 10-year-olds (diff = 0.10, $p = .01$) and 11- to 13-year-olds (diff = 0.08, $p = .047$). The same statistical tests revealed no significant age group differences in functional connectivity for the tour source and tour – room after accounting for multiple comparisons (Supplement J). When the main mode of encoding was episodically rich without a spatial layout, communication between ERC and PRC was enhanced for the room memory, especially for children.

Memory May Predict Functional Connectivity Specificity for Spatially Encoded Information

Lastly, we aimed to see if memory for the tour experience would relate to neural responses for this information after encoding. More specifically, we examined if memory strength reflects functional connectivity between key regions that we know can support tour-specific memory. Relating memory to functional connectivity for the tour – room subtraction, that is, isolating the spatial component of the tour (see Figure 9 and Table 4), we found a main effect of spatiotemporal structure memory predicting connectivity between the HC and ERC ($\beta = .30$, $p = .046$, $SE = 0.15$, $\eta^2_{\text{partial}} = .04$) and ERC and LO ($\beta = .30$, $p = .049$, $SE = 0.15$, $\eta^2_{\text{partial}} = .04$); however, these effects do not pass FDR correction. Both models passed assumptions of skewness, kurtosis, homoscedasticity, and link function with 4 degrees of freedom and p s $> .05$ and had low multicollinearity (VIFs < 2). We also tested for an age by spatiotemporal structure memory interaction, but this yielded nonsignificant results. Other pairwise tour – room connections and the average network metric

Figure 8. Functional connectivity age-related changes for room items. Age group differences in functional connectivity were seen only for episodically encoded room objects. Children 8–10 years old (diff = 0.10, $p = .01$) and 11–13 years old (diff = 0.08, $p = .047$) had greater connectivity than adults between the ERC and PRC. * $p < .05$, ** $p < .01$. Bars indicate standard error.



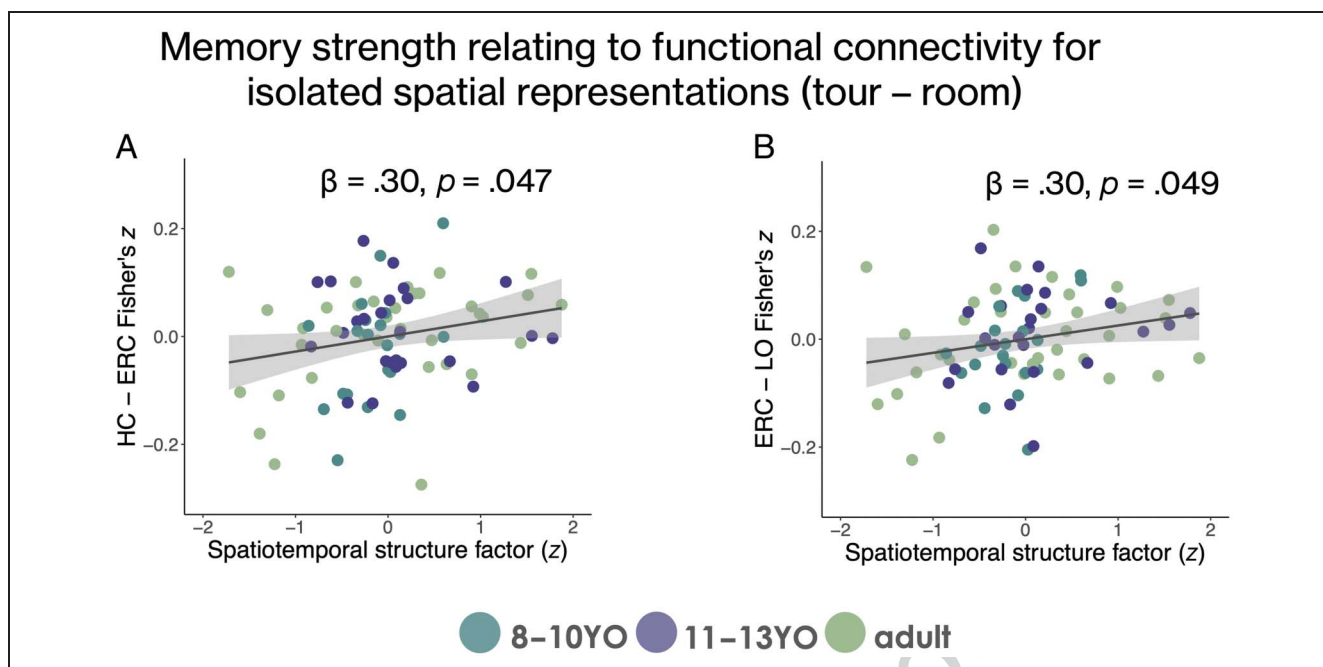


Figure 9. Linear relationship between memory strength and functional connectivity. Better spatiotemporal structure factor scores were related to greater functional connectivity between the (A) HC and ERC and (B) ERC and LO that was related to the spatial component of the tour. These models control for age, sex, and KBIT IQ. Note that this result does not survive FDR correction.

Table 4. Linear Models of Tour Memory Predicting Functional Connectivity

	HC-ERC	ERC-LO
Spatiotemporal structure (z)	0.299 (0.010, 0.588) $p = .047^*$	0.296 (0.007, 0.584) $p = .049^*$
Age	-0.023 (-0.067, 0.022) $p = .323$	-0.026 (-0.071, 0.018) $p = .253$
Sex	-0.020 (-0.457, 0.417) $p = .929$	0.253 (-0.183, 0.689) $p = .260$
KBIT IQ (z)	-0.130 (-0.351, 0.090) $p = .251$	-0.099 (-0.318, 0.121) $p = .383$
Constant	0.383 (-0.407, 1.170) $p = .345$	0.300 (-0.488, 1.090) $p = .458$
Observations	80	80
R^2	0.07	0.075
Adjusted R^2	0.021	0.025
Residual SE ($df = 75$)	0.99	0.085
F statistic ($df = 4; 75$)	1.41	1.51

Measured connectivity was from the tour – room subtraction, isolating the spatial component of the tour experience. Shaded cells indicate significant results; however, the main effect of spatiotemporal structure memory does not pass FDR correction for multiple comparisons. All models are presented in Supplement K. 95% Confidence intervals are in parentheses. Two adults were excluded due to missing behavioral data.

* $p < .05$.

models were nonsignificant with memory as a predictor (Supplements K and L). It is possible that good spatiotemporal structure memory predicts functional connectivity between the HC and ERC and the ERC and LO, regardless of age, but these effects were not robust.

DISCUSSION

In everyday life, we navigate through our surroundings, forming episodic memories and spatial maps as we go. This study used real-world encoding punctuated by small events to study spatial cognition and episodic memory simultaneously. Additionally, we examined how the MTL supports memory for these learned events to then relate to developmental changes and behavioral performance. We tested 8- to 13-year-olds at an age when refinement of these two skills occurs and compared them with young adults. Our findings show how neural systems in the MTL that support both spatial and episodic memory vary across development.

First, univariate activation in the ERC and PRC was sensitive to spatial information but variably across the three age groups. Adults had greater differential activation for items that were encoded in the structured tour from those seen in less structured room and foil contexts compared with children, who may start to differentiate the contextual conditions of the items across encoding experiences around early adolescence. Importantly, these age effects were largely robust to adjustment for source recognition performance in the ERC, suggesting that they were not explained solely by age-related differences in behavioral performance. However, the tour > room contrast cannot determine whether these activation differences specifically reflect retrieval of spatial information. Greater ERC and PRC activation for tour-encoded items indicates sensitivity to differences in the contexts in which the items were originally experienced. This effect may reflect memory of the structured spatial context, the richer multisensory and embodied features of the tour experience, or a combination of these contextual properties.

Nevertheless, the developmental differences observed in the ERC are consistent with the possibility that sensitivity to information associated with structured spatial experiences continues to mature through adolescence. In adults, the lateral ERC and PRC are preferentially engaged by object identity interference, and medial ERC and PHC by spatial interference (Reagh & Yassa, 2014). Furthermore, the adult ERC can exhibit grid-like response to navigational tasks after repeated training (Horner, Bisby, Zotow, Bush, & Burgess, 2016; Doeller, Barry, & Burgess, 2010). However, we do not know how the ERC functionally matures in humans. There is evidence of ERC thickening throughout the first 20 years of life (Hasan et al., 2016), but no significant change in overall volume from ages 4–30 years (Keresztes et al., 2017). Our findings provide initial evidence that ERC sensitivity to differences between items encoded within a structured tour and those encoded in

less structured contexts develops relatively late. Most adult studies use active navigation paradigms in the scanner to isolate grid-like signals, and here we show that ERC sensitivity is associated with a previously experienced, spatially structured context, possibly due to the consolidation of information in this region (Takehara-Nishiuchi, 2014).

Activation in the PRC was expected as it is implicated in item/object representation and familiarity (Haskins, Yonelinas, Quamme, & Ranganath, 2008; Davachi, Mitchell, & Wagner, 2003; Cansino, Maquet, Dolan, & Rugg, 2002), discrimination (Eichenbaum, Yonelinas, & Ranganath, 2007; Buckley, 2005), and differentiating semantically similar concepts (Wright, Randall, Clarke, & Tyler, 2015). On the other hand, we know very little about the development of PRC. One study used movie clips to understand children's contextual representations compared with adults. Children 4–10 years old showed no difference in similarity for movie clips from the same context and different contexts, contrary to adults who differentiated clips by context (Benear et al., 2022). We show that activity in the PRC to naturalistically encoded object stimuli is not yet adult-like in early adolescence, although not a strong robust effect overall. This nuanced age effect may be more pronounced throughout adolescence, but without the full age range, we do not have the full picture of the developmental trajectory.

Despite condition-related differences in univariate activation, we do not find significant functional connectivity for the tour-encoded objects. Instead, ERC–PRC functional connectivity decreased across age specifically during viewing of room-encoded objects. Because the room condition involved objects encountered within a common but less spatially structured setting, stronger ERC–PRC coupling in younger children may reflect greater reliance on coordinated processing of object information and its associated local context. The absence of a comparable effect in the tour condition suggests that this developmental pattern does not reflect episodic memory broadly but may be particularly relevant when memory is cued for objects from contexts that provide fewer spatial or navigational cues or are overall less salient. Since HC-related functional connectivity is associated with episodic memory in 6-year-olds but not 4-year-olds (Riggins et al., 2016), we may be capturing further development of cortical regions that input into the HC to support memory. This implies that children may need more scaffolding and support between these areas, even at an age where episodic memory behavior is relatively advanced (Newcombe, Benear, Ngo, & Olson, 2024).

Finally, we related memory behavior to functional connectivity. Although exploratory, the ERC may be central to the representations tested. However, we were unable to see robust effects with correction (see Limitations). It is plausible that connectivity between the HC, a hub for memory encoding and retrieval, and the ERC imposes a previously experienced spatial structure onto the objects stemming from the tour. There is ample evidence in adults

that memory retrieval depends on the interactions of the HC with its neighboring structures such as the ERC (Robin & Moscovitch, 2017; Takehara-Nishiuchi, 2014; Insel & Takehara-Nishiuchi, 2013). Additionally, information may flow between the ERC and LO to apply context to objects. The LO is sensitive to object recognition (Grill-Spector, Kourtzi, & Kanwisher, 2001), as well as functionally important for relating memories that overlap in context (Ezzyat & Davachi, 2014). We speculate that the HC helped process previously learned information about the tour, the ERC embedded the objects into a spatial structure, and the LO bound the objects into their overlapping source context to support a mental reconstruction of the tour events. Existing models of memory suggest that this idea is a plausible hypothesis (Robin & Moscovitch, 2017; Schapiro et al., 2017; Ritchey, Libby, & Ranganath, 2015; Buzsáki & Moser, 2013). These connections may be strengthened when participants have good immediate memory for the tour experiences even while hippocampal inputs (e.g., ERC and PRC) are still developing. When children learn spatial information as efficiently as adults, they can have adult-like behavioral consolidation (Maier et al., 2024), and we theorize that this could be the case neurally.

Because of the real-world design of the study and limitations with testing children, we prioritized salience of encoding to ensure that children were able to learn and remember the tour and room experiences with high accuracy, given the delay between encoding and the scanning session. Indeed, children had high performance across all three source contexts, albeit with some differences when compared with adults and across contexts. We did not have enough incorrect recognition trials to compare remembered versus not remembered items, which may yield more robust effects on group-level activation, especially for the room versus foil contrast. However, we believe that what was captured is as related to the fidelity of the naturalistic experiences as possible.

Limitations and Future Directions

The encoding design incorporated an isolated episodic experience (the room), but not an isolated spatial experience (navigation sans episodic information). Including such behavioral contrasts is useful, so a redesign of this paradigm could involve three encoding experiences stratified by levels of overlap between cognitive constructs: navigation, episodic, and combined navigation and episodic.

The blocked design of the fMRI task was intended for univariate analysis; therefore, the multivariate investigation not passing FDR corrections may be attributed to a suboptimal task design that did not allow for robust measurement of functional connectivity. To properly answer the multivariate questions, an event-related task with shorter source stimulus presentation and more item-level trials should be used or shorter blocks of source stimuli (Mur, Bandettini, & Kriegeskorte, 2009; Kriegeskorte,

Mur, & Bandettini, 2008). We also suggest that a pre-post fMRI design could better capture the effects of encoding and/or consolidation. It is intriguing that our findings show implicit structuring of objects based on encoding source, but asking participants to think about where they saw the objects or incorporating source recognition into the fMRI task could elicit a stronger and more reliable signal. Another method could probe active retrieval during the fMRI task. Although this part of the investigation was exploratory, we encourage future work to focus on more salient and naturalistic encoding of spatial information to better represent how children and early adolescents may code these representations in the brain.

We were unable to fully track the later maturing functional activation of the ERC and PRC due to a gap in our age range from 14 to 18 years. Future research should extend from our findings and track the development of the functional signal to coincide with current knowledge of the structural maturation of the ERC (Šimić et al., 2022; Hasan et al., 2016; Insausti, Tuñón, Sobreviela, Insausti, & Gonzalo, 1995) and PRC and expand to cortical regions outside the MTL to capture more robust developmental patterns in episodic retrieval.

Conclusion

This study aimed to clarify questions about where and how the brain supports two cognitive constructs crucial to our everyday function—spatial navigation and episodic memory. We found common MTL regions across age. However, adults used the ERC and PRC more for differentiating tour-related retrieval, while children seemed to require stronger communication between these two regions to support episodic retrieval. These effects coincided with behavioral gains in both navigation and episodic memory. Exploratory investigation hinted at an age-invariant effect of memory strength on subsequent functional connectivity for spatial information, opening a future avenue of inquiry.

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Data Availability Statement

The de-identified raw MRI data are available upon request; please contact the RISC lab at riscab@temple.edu. The data set and analysis scripts are available at Center for

Open Science (OSF) at <https://osf.io/b9hvf/>. Supplemental materials can be accessed on this article's homepage: <https://doi.org/10.1162/JOCN.a.2688>.

Author Contributions

Kim V. Nguyen: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Lena J. Skalaban: Formal analysis; Writing—Review & editing. Büşra Tanriverdi: Formal analysis; Writing—Review & editing. John J. Erardi: Data curation; Formal analysis; Investigation; Writing—Review & editing. Giovanna Arantes de Oliveira Campos: Data curation; Formal analysis; Investigation; Writing—Review & editing. Vishnu P. Murty: Formal analysis; Methodology; Writing—Review & editing. Ingrid R. Olson: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing—Review & editing. Nora S. Newcombe: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing—Review & editing.

Declaration of Artificial Intelligence (AI) and AI-assisted Technologies

The authors declare that AI was not used for any aspect of the research described here, nor in article preparation.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this paper report its proportions of citations by gender category to be: $M/M = .424$; $W/M = .254$; $M/W = .085$; $W/W = .237$.

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