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## Development of Spatial Memory Consolidation: A Comparison Between Children and Adults

Patrizia M. Maier<sup>1, 2</sup>, Iryna Schommartz<sup>3, 4</sup>, Deetje Iggena<sup>1, 2</sup>, Carsten Finke<sup>1, 2</sup>,

Christoph J. Ploner<sup>1</sup>, and Yee Lee Shing<sup>3, 4</sup>

<sup>1</sup> Department of Neurology, Charité—Universitätsmedizin Berlin

<sup>2</sup> Faculty of Philosophy, Berlin School of Mind and Brain, Humboldt-Universität zu Berlin

<sup>3</sup> Department of Psychology, Goethe-University Frankfurt

<sup>4</sup> Center for Individual Development and Adaptive Education of Children at Risk, Frankfurt am Main, Germany

Successful navigation to spatial locations relies on lasting memories from previous experiences. Spatial navigation undergoes profound maturational changes during childhood. It is unclear how well children can consolidate navigation-based spatial memories and if age-related variations in navigation during training predict spatial memory. The present study examined the immediate and long-delay (after a 2-week period) consolidation of navigation-based spatial memories in 6- to 8-year-old children (n = 33, 18 female/15 male,  $M_{\text{age}} = 7.61, SD_{\text{age}} = 0.71$ , 9- to 11-year-old children (n = 32, 13 female/19 male,  $M_{\text{age}} = 9.90, SD_{\text{age}} = 0.71$ ) 0.59), and 20- to 30-year-old adults (n = 31, 15 female/16 male,  $M_{age} = 23.71, SD_{age} = 2.87$ ). Our results showed that, with age, participants navigated more efficiently during training and formed better immediate spatial memories. Long-delay spatial memory retention after 2 weeks was comparable between children and adults, indicating robust consolidation even in children. Interestingly, while children successfully distinguished between perceptually detailed landmarks after 2 weeks, their abstract knowledge of spatial boundaries and cognitive map of landmark relations was poor. Developmental trajectories were similar for egocentric and allocentric spatial memory. Age-related variations in initial navigation were predictive of spatial memory, that is, children with a more mature initial navigation were more likely to find and remember spatial locations immediately and after a 2-week delay. Taken together, our results show an overall robust spatial memory consolidation in mid and late childhood that can be predicted by initial navigation behavior, coupled with nuanced age differences in the recall of spatial boundaries and cognitive maps.

#### **Public Significance Statement**

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The study suggests that, while children between 6 and 11 years have difficulties in encoding spatial information during navigation, their ability to retain this information over extended time periods can be as robust as in adults. Children with a more strategic and adultlike navigation during training were able to retain more spatial information later on; this link could be utilized in training studies to improve children's navigation competency and safety.

Keywords: child development, navigation, memory consolidation, allocentric, egocentric

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Elizabeth A. Gunderson served as action editor. Patrizia M. Maier b https://orcid.org/0000-0002-2958-3057 Iryna Schommartz b https://orcid.org/0000-0001-8655-9259 Deetje Iggena b https://orcid.org/0000-0001-8778-5127 Carsten Finke b https://orcid.org/0000-0002-7665-1171 Christoph J. Ploner b https://orcid.org/0000-0003-0983-4530 Yee Lee Shing b https://orcid.org/0000-0001-8922-7292

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Patrizia M. Maier played a lead role in conceptualization, data curation, formal analysis, software, visualization, and writing-original draft and an

Spatial navigation is a key cognitive skill that allows us to orient in space and find routes to destinations. During childhood, navigation undergoes maturational changes (Fernandez-Baizan et al., 2021; Newcombe, 2019; Pullano & Foti, 2022), which are closely linked to brain development (Gogtay et al., 2004; Mills et al., 2016; Murias et al., 2019; Pine et al., 2002). In familiar spatial environments, memory representations of previous experiences guide navigation (Eichenbaum & Cohen, 2014). It is conceivable that long-term storage or consolidation (Dudai et al., 2015) of navigation-based spatial memories may be less robust in children due to the ongoing brain development, especially in the medial temporal lobe (MTL) and prefrontal cortex (PFC; Gogtay et al., 2004; Murias et al., 2019). However, no study to date has investigated the robustness of navigation-based memory consolidation in developmental cohorts: We aim to address this knowledge gap in our study.

## Children May Have Less Robust Spatial Memory Consolidation Compared to Adults

In familiar environments, successful navigation does not just rely on navigational abilities but also on mnemonic and executive planning functions. During navigation, memories are created by associating objects within a spatial context to form events and arranging these events into temporal sequences, thereby creating episodes (Eichenbaum & Cohen, 2014). For example, we remember the park being north of the river and the necessity to cross the river to get from our home to the park. Spatial memories rely on medialtemporal brain structures, which typically reach maturation in mid or late childhood (Ghetti & Bunge, 2012; Shing et al., 2010). Additionally, prefrontal brain structures are highly relevant for navigation, in particular for strategic planning and executive control (Patai & Spiers, 2021) and the integration of prior knowledge and schemas into memory (Brod et al., 2013). For example, when a construction site blocks the familiar route across the bridge, planning and executive control are employed to device an alternative route. However, since prefrontal brain structures typically show a protracted maturation until adolescence or young adulthood (Gogtay et al., 2004; Murias et al., 2019; Pine et al., 2002), these executive planning functions may be less effective in childhood.

During memory consolidation, neural representations of spatial memories transform from hippocampus-dependency to integration into neocortical brain structures (Winocur & Moscovitch, 2011). Simultaneously, memory representations undergo qualitative changes, for example, from detailed to abstract (Winocur & Moscovitch, 2011). Spatial knowledge abstraction can occur on different levels that build upon each other: first, cognitive maps, which are representations of specific object-to-object relations;

second, gist, which refers to spatial core elements of a specific environment; and third, schemas, as an abstraction of core elements across multiple environments (Farzanfar et al., 2023). Spatial memories coexist on different levels (e.g., schema "town center" and cognitive map of a specific town center).

Preexisting knowledge and schemas facilitate consolidation in rodents (Tse et al., 2007) and adult humans (van Buuren et al., 2014; van Kesteren et al., 2018), resulting in improved learning of new spatial information, rapid hippocampus-independency, and increased prefrontal activation (Tse et al., 2007; van Buuren et al., 2014; van Kesteren et al., 2018). While schema formation is a longterm process that can take weeks to months (Alonso et al., 2021), gist extraction occurs more rapidly within hours to weeks (Alonso et al., 2021; Graves et al., 2020). Due to their limited life experience, children may have less knowledge and fewer schemas available to build upon. Moreover, developmental immaturity in MTL and PFC regions may compromise memory consolidation and knowledge abstractions in children (Østby et al., 2012). These postulations remain to be tested, as no study to date has investigated the consolidation of navigation-based spatial memories and spatial knowledge abstraction in children. Studies on nonnavigation-based spatial memory consolidation and semantic knowledge abstraction found less robust functioning in early or middle childhood (Ngo et al., 2021; Schommartz et al., 2023) and report distinct mechanisms behind successful abstraction in children compared to adults (Ngo et al., 2021).

## Children's Navigation Abilities Improve With Age, and This May Influence Consolidation

Consolidation is influenced by the initial learning experience during encoding. Thus, age differences in navigation are relevant for age differences in spatial memory consolidation. Rudimentary forms of navigation are already present in infants (Newcombe, 2019) and gradually improve from early (0-6 years) to middle childhood (6-12 years; Fernandez-Baizan et al., 2021; Pullano & Foti, 2022), with children approaching adultlike navigation by the age of 12 (Brucato et al., 2022; Nazareth et al., 2018). Children's navigation behavior becomes more efficient and strategic with increasing age. Namely, children make fewer pauses (Farran et al., 2022), navigate faster toward goal locations (Bullens et al., 2010; Burles et al., 2020; Murias et al., 2019), take more direct routes and shortcuts (Burles et al., 2020), and use better visual exploration strategies (Bullens et al., 2010). When children become more active navigators with age, this also predicts navigation success (Farran et al., 2022). Studies with adult navigators even provide evidence for a link between efficient navigation and improved spatial memory quality: Adults who took fewer pauses (Munion et al., 2019),

equal role in methodology, project administration, resources, and writingreview and editing. Iryna Schommartz played a lead role in conceptualization, investigation, and writing-original draft, a supporting role in visualization, and an equal role in formal analysis, methodology, project administration, resources, and writing-review and editing. Deetje Iggena played a supporting role in methodology, resources, and software and an equal role in conceptualization and writing-review and editing. Carsten Finke played a lead role in funding acquisition, a supporting role in conceptualization, resources, and writing-review and editing, and an equal

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Correspondence concerning this article should be addressed to Patrizia M. Maier, Department of Neurology, Charité—Universitätsmedizin Berlin, Augustenburger Platz 1, 13353 Berlin, Germany. Email: patrizia.maier@ charite.de

revisited fewer areas (Gagnon et al., 2018), and were biased toward more informative areas (Brunec et al., 2023) during spatial exploration formed more accurate spatial memories later on. It is unclear if developmental changes in children's navigation behavior also predict spatial memory and, specifically, how strongly the initial navigation pattern influences spatial memory retention after extended time delays.

## Children May Have Distinct Developmental Trajectories for Egocentric and Allocentric Navigation

Spatial navigation is based on two reference frames: In the egocentric frame, orientation is established based on one's own perceived position in space (inferred from visual, vestibular, and proprioceptive information), and routes are memorized as sequences of turns (Iglói et al., 2009). In the allocentric frame, navigation relies on the spatial relations between environmental features (Fernandez-Baizan et al., 2021). Studies found that egocentric abilities develop ontogenetically earlier than allocentric abilities (Broadbent et al., 2014; Bullens et al., 2010; Burles et al., 2020; Fernandez-Baizan et al., 2021; Newcombe, 2019). Children between 5 and 10 years preferentially used egocentric over allocentric information (Broadbent et al., 2014; Bullens et al., 2010; Burles et al., 2020) and performed more poorly in allocentric compared to egocentric tasks (Broadbent et al., 2014; Burles et al., 2020; Nardini et al., 2006). However, egocentric and allocentric performance also depends on task demands and spatial cue types. For example, children's allocentric deficits disappeared when an informative boundary cue was available and thus may be attributed to difficulties in using landmark cues but not allocentric navigation per se (Bécu et al., 2023). It is unclear how effectively children retain egocentric and allocentric information over extended time delays and how well they can abstract spatial knowledge during the consolidation process.

#### Hypotheses

In the present study, we examined the consolidation of navigation-based spatial memories in 6- to 11-year-old children and young adults over short delays (immediately after learning) and long delays (after a 2-week-period). We focused on children in mid

#### Table 1

Sample Characteristics by Age Group

to late childhood because spatial memory consolidation relies on the integrity of hippocampal-prefrontal networks, which undergo important maturational changes at this age. We predicted (a) a more pronounced advantage for egocentric over allocentric memory in younger participants, both immediately and after the 2-week delay, based on the finding that egocentric spatial abilities develop ontogenetically earlier; (b) age-related differences in immediate and long-delay spatial memory retention and in long-delay spatial knowledge abstraction because of the developmental immaturity in brain regions relevant for consolidation; and (c) that age variations in navigation behavior during training predict immediate and longdelay spatial memory retention, based on the established link between navigation efficiency and spatial memory in adults.

#### Method

#### **Transparency and Openness**

We report how we determined our sample size, all data exclusions (if any), all inclusion or exclusion criteria, whether inclusion or exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The study procedures and study analyses were not preregistered prior to the research being conducted. The digital study materials, the data that support the findings of this study, and the analysis code are openly available on the Open Science Framework at https://osf.io/ksfv8/(Maier et al., 2024).

### Sample

We recruited 104 participants, thirty-four 6- to 8-year-old children (6–8YO), thirty-four 9- to 11-year-old children (9–11YO), and 36 young adults (AD), in our study through word-of-mouth and online advertisement. All participants spoke German fluently, had normal or corrected-to-normal vision, reported to be in good health, and denied any history of a neuropsychiatric disorder. One 6–8YO child, two 9–11YO children, and five AD were excluded due to incomplete task execution, missing data, or technical issues during data acquisition. The final sample size consisted of thirty-three 6–8YO children (age range = 6.0-8.5), thirty-two 9–11YO children (age range = 9.0-11.0), and 31 AD (age range = 20.2-30.0; Table 1). Based on a previous study on (nonnavigation-based)

	6–8YO (	N = 33)	9–11YO	(N = 32)	AD (N	= 31)	Group effect
Variable	М	SD	М	SD	М	SD	р
Age	7.16	0.71	9.90	0.59	23.71	2.87	<.001 <sup>a</sup>
Sex (F/M)	18/15		13/19		15/16		.531 <sup>b</sup>
IQ score	108.26	19.69	106.52	10.74	103.94	7.97	.463 <sup>a</sup>
Self-reported average sleep hours	10.22	0.46	9.72	0.72	7.42	0.92	<.001 <sup>a</sup>
Self-reported average sleep quality	1.13	0.14	1.22	0.20	1.67	0.51	<.001 <sup>a</sup>
Socioeconomical status (income—family <sup>c</sup> )	5.80	1.08	5.27	1.34			.115 <sup>a,c</sup>

*Note.* Sleep quality is based on a 1–3 scale (1 = *very good*, 2 = *good*, 3 = *bad*); income is based on a 1–7 scale (1 = *less than* 15.000 $\notin$ , 2 = 15.000 $\notin$  to 25.000 $\notin$ , 3 = 25.000 $\notin$  to 35.000 $\notin$ , 4 = 35.000 $\notin$  to 45.000 $\notin$ , 5 = 45.000 $\notin$  to 75.000 $\notin$ , 6 = 75.000 $\notin$  to 100.000 $\notin$ , 7 = *more than* 100.000 $\notin$ ). 6–8YO = 6- to 8-year-old children; 9–11YO = 9- to 11-year-old children; AD = 20- to 30-year-old adults; F = female; M = male; IQ = intelligence quotient based Reynolds Intellectual Assessment Scales and Screening (Hagmann-von Arx & Grob, 2014).

<sup>a</sup> One-way analysis of variance.  ${}^{b}\chi^{2}$  test. <sup>c</sup> Comparison between child groups only.

spatial memory consolidation in children (Schommartz et al., 2023), we expected medium-sized effects. A priori power analysis using WebPower (Zhang & Yuan, 2018) was conducted with a medium effect size of 0.36, a significance level of a = 0.05, statistical power 1 - b = 0.8, and nonsphericity correlation coefficient of 1. The power analysis recommended a total sample size of at least N = 78 participants. We recruited more study participants to compensate for potential dropouts. Written informed consent was obtained from all participants or their legal guardians prior to participation. The study was approved by the ethics committee of Goethe-University Frankfurt and conducted in accordance with the Declaration of Helsinki.

## Task

## Virtual Maze Setup

We used a modified version of the *Starmaze* task (Figure 1A; Iggena et al., 2022; Iglói et al., 2009; Rondi-Reig et al., 2006). The virtual maze consisted of five symmetrically arranged peripheral alleys connected by five central alleys and was surrounded by five distant environmental landmarks. There were three fixed goal locations, one fixed original start location, and nine start locations for the allocentric probe trials. We created a rectangular arena for practicing the controller movements and a T-shaped maze for practicing the task instructions. The virtual environment and landmarks were custom-made in Blender (Version 2.79b, Blender Foundation). Additionally, we used four 3D objects (soccer ball, bike, chair, violin) from a validated database (Peeters, 2018).

The navigation task was implemented in Unity3D (Version 2018.2.14f, Unity Technologies); the trial structure and recording of movement trajectories were implemented using the Unity Experiment Framework (Brookes et al., 2020). The presentation order for goal and start locations were pseudorandomized. The 3D objects were randomly assigned to the goal locations. Participants navigated from a first-person perspective. The task was presented on a computer screen (15.6 in., resolution: 1920 ×1,080), and participants controlled their movement within the virtual environment with a joystick. For the postnavigational tasks, participants used a computer mouse.

#### **Experimental Procedure**

All participants completed a navigation task with training trials and egocentric and allocentric probe trials in two sessions. The first session ("learning") lasted 30–45 min and included a practice phase, followed by 24 training trials and 18 probe trials (nine egocentric and nine allocentric) in alternating order (Supplemental Table S1). The second session lasted 10–20 min, took place 2 weeks after the learning session, and included only probe trials (six egocentric and six allocentric). In the second session, participants also completed the postnavigational spatial knowledge tasks, and we asked them or their legal guardians about their sociodemographic information. We also collected self-reported information on sleep quality and quantity to ensure that participants had regular and age-appropriate sleep over the 2-week period (Table 1).

## Memory-Guided Navigation Task ("Starmaze")

The learning session began with a practice phase, where participants familiarized themselves with the joystick by navigating in a rectangular arena. We then asked participants to navigate to 10 sequentially appearing red balloons as quickly as possible. Then, participants familiarized themselves with the task instructions in a virtual T-maze for five trials. Afterward, participants performed the Starmaze task.

We informed participants that they were to find and remember the exact position of three goal locations marked by 3D objects. At the beginning of each trial, we presented an image of an objectlocation pair as a cue (Figure 1B). There was only one objectlocation pair tested per trial. During "training" trials, the 3D object was displayed at the goal location. Participants were asked to find the location as quickly as possible and collect the object. During "probe" trials, the 3D object was not visible. Participants were asked to go back to the remembered location and press a button. They did not receive any feedback on accuracy in probe trials. We explicitly told participants to pay attention to and memorize their paths as well as the surrounding environmental cues. In "egocentric probe" trials, the sky and distant landmark cues were removed. Participants started from the same start point as during training and had to navigate to the goal locations based on their memory of path sequences. During "allocentric probe" trials, the sky and distal landmark cues were visible. Participants started from a new start point within the maze and had to navigate to the goal locations based on their memory of landmark-to-goal-associations. We informed participants about changes (e.g., the removal of cues in egocentric probe trials) at the beginning of each trial. Trials were automatically terminated after 120 s. This time limit was chosen based on piloting. More details on the trial order can be found in Supplemental Table S1.

#### Postnavigational Spatial Knowledge Task

At the end of the second session, we asked participants to identify the correct maze boundary out of six options (Figure 1C). Then, we asked them to identify the correct five landmarks out of 15 options and the correct three goal objects out of eight options. Finally, we presented the correct boundary and the participant's choice of landmarks and goal objects and asked them to position them in a 2D map to test their knowledge of landmark relations.

## **Data Preprocessing**

### Navigation Data

We recorded the participant's position as *x*- and *y*-coordinates and *z*-rotations in a Cartesian coordinate system together with a timestamp. The data were downsampled to 20 Hz. We preprocessed the navigation data in MathWorks Matlab (Version 2021a). To capture distinct aspects of navigation-based spatial memory, we computed five variables. The first variable represents memory accuracy in probe trials, whereas the other four variables describe navigation behavior during training and probe trials.

#### Figure 1

Environment, Navigation Trial Types, and the Postnavigational Spatial Knowledge Task

#### (A) Environment



## (B) Navigation Trial Types



#### (C) Post-Navigational Spatial Knowledge Task



*Note.* (A) *Left to right:* Map and bird's eye view of the maze. (B) In training trials, participants searched for the 3D goal object, which was visible. In probe trials, participants navigated to the remembered goal location and pressed a button (no feedback). Egocentric probe trials began from the same start location as in training; no landmark information was presented. Allocentric probe trials began from new start locations; landmark information was presented. (C) *Left to right:* Participants were asked to select the correct maze boundary, the correct five landmarks, the correct goal objects (not shown), and to position the boundary and the participant's choice of objects in a cognitive map. See the online article for the color version of this figure.

 Memory score (%)—indicates how well participants remembered the goal locations based on the memory error (Euclidean distance) in probe trials (equation: Memory Error [virtual unit; vu] =  $\sqrt{(x_{\text{remembered}} - x_{\text{goal}})^2 + (y_{\text{remembered}} - y_{\text{goal}})^2)}$ . The memory score corresponds to the percentile rank of the memory error on a random error distribution (equation: Memory Score [%] = 1 – (proportion of random error scores <

memory error)) and ranges from 0 to 1, with 1 indicating perfect memory, and 0.5 corresponding to chance level (Bellmund et al., 2020; Iggena et al., 2023; see Supplemental Methods A).

- 2. *Latency* (s)—time to complete the trial in seconds (equation: Latency  $[s] = t_n t_1$ ).
- 3. *Excess path length* (vu)—indicates the directness of a participant's navigation (Bellmund et al., 2020) based on a comparison of the participant's path with the ideal path (equation: (Ideal)Path Length [vu] =  $\sum_{i=1}^{n} \sqrt{(x_i x_{i+1})^2 + (y_i y_{i+1})^2} \times 100$ ; Excess Path Length [vu] = path path<sub>ideal</sub>). Excess path length ranges from zero to infinity, with higher values denoting less direct paths.
- 4. *Excess distance to goal* (vu)—indicates if participants preferentially searched near or far from the goal location (similar to mean proximity; Iggena et al., 2022, 2023; Maei et al., 2009). Here, we computed the averaged distance between each coordinate point on the participant's path and the goal location (equation: (Ideal) Distance to Goal[vu] =  $\sum_{i=1}^{n} \sqrt{(x_i x_{goal})^2 + (y_i y_{goal})^2/n \times 100)}$ . We compared this value to an ideal reference value (averaged distance on ideal path with constant speed; equation: ExcessDistance to Goal [vu] = distance distance<sub>ideal</sub>). A positive value indicates that a participant searched further away from the goal location and more randomly, whereas a negative value indicates they searched close to the correct goal location.
- 5. *Initial rotation* (rad)—indicates the extent of visual landmark exploration during the initial orientation phase (Iggena et al., 2023; Santos-Pata & Verschure, 2018; Schmidt et al., 2013). Initial rotation is based on the change in *z*-rotation from the beginning of the trial on up until participants reach the first decision point (equation: Initial Rotation[rad] =  $\sum_{i=1}^{n_{initial}} |(z_i z_{i+1})|)$ . The value ranges from zero to infinity, with higher values denoting more visual landmark exploration for orientation (see Supplemental Methods A).

Trials were excluded from the analysis if the trial ended by timeout, if the trial ended after less than 3 s, or in case of no movement during the trial. In total, 50 trials out of 5,856 trials (0.85%) were excluded. Thirty trials were excluded in 6–8YO children, 16 trials in 9–11YO children, and four trials in AD. On average, less than one trial was excluded per person, in 6–8YO children, M = 0.91(SD = 1.33); in 9–11YO children, M = 0.50 (SD = 0.84); and in AD, M = 0.13 (SD = 0.34).

## Spatial Knowledge Data

*Boundary score* (%): Participants received 1 point for correctly identifying the maze boundary. *Landmark identity score* (%): Participants received 0.2 points for each of five correctly identified landmarks, resulting in a score from 0 to 1. *Landmark position score* (%): For evaluating the correctness of landmark positions, we used the Gardony Map Drawing Analyzer software (Gardony et al., 2016; Supplemental Methods A) and computed a composite score ranging

from 0 to 1, with larger values denoting higher landmark position accuracy.

#### Statistical Analysis

#### Standard Analysis With Linear Mixed Models

All statistical analyses were performed in R Studio (Version 4.2.1; R Core Team, 2021). Multitrial data was analyzed with linear mixed models (LMM) from the afex package (Singmann et al., 2022). For the analysis of navigation behavior in training trials, we included group (between-subjects factor: 6-8YO, 9-11YO, AD) and trial in block number (within-subjects factor from 1 to 8) as fixed effects and participant id as a random effect. For the analysis of the memory score in probe trials, we included group, condition (within-subjects factor: egocentric, allocentric), and session (withinsubjects factor: 1, 2) as fixed effects and participant id as a random effect. As model covariates, we included the participant's sex and a score for joystick control abilities (z-scored composite of time and excess path during practice to account for the individual's ability to use the joystick; Supplemental Methods B). We modeled all LMM with the maximal random effects structure (Barr, 2013; Matuschek et al., 2017; Supplemental Methods B). The models were estimated with restricted maximum likelihood. Degrees of freedom were computed using Satterthwaite's method as implemented in ImerTest (Kuznetsova et al., 2017). For all significant fixed effects, we computed post hoc contrasts with emmeans (Lenth, 2022), using Bonferroni corrections for multiple comparisons. To assess the effect size of fixed effects, we used the omega squared ( $\omega^2$ ) from effect size (Ben-Shachar et al., 2020).

For the analysis of single-trial data from the spatial knowledge tasks, we used the Fisher's exact test for binomial data and standard analyses of variance (ANOVA) from afex (Singmann et al., 2022). For all significant effects, we computed post hoc contrasts with emmeans (Lenth, 2022), using Bonferroni corrections for multiple comparisons. Plots were created with afex (Singmann et al., 2022) and ggplot2 (Wickham, 2016). The Results section of this article was written with the papaja package (Aust & Barth, 2022).

## Multivariate Correlation Analysis Using Partial Least Square Correlation

We applied multivariate partial least square correlation (PLSC; Keresztes et al., 2017; Krishnan et al., 2011; McIntosh & Lobaugh, 2004; Muehlroth et al., 2020) to investigate if age-related variations in navigation behavior predict spatial memory. PLSC is a powerful statistical technique that accounts for the intercorrelated nature of multiple indicators and is better suited than univariate approaches. First, we extracted a latent navigation profile that maximally shares common variance with age. We calculated the correlation matrix between (a) an *n*-vector with chronological age and (b) an  $n \times 4$ matrix with navigation indicators from training trials in the learning session (latency, excess path length, excess distance to goal, and initial rotation). We replaced missing values in chronological age (n = 2) with mean imputation and z-standardized all variables. The correlation matrix was decomposed into three components using singular value decomposition, based on which one latent variable (LV) was extracted in a least-square sense. The LV represents distinct profiles of navigation indicators that have the strongest relation to age, which yields a proxy for maturity in navigation. We ran 5,000 permutation tests to obtain a p value for the LVs. Next, we looked at the LV weights for each indicator, which represent the degree and direction (positive or negative association) to which they contribute to the LV. We identified the stability of LV weights by computing 5,000 bootstrap samples and obtained bootstrap ratios (BSR) by dividing each weight with the bootstrapped standard error. The BSRs are akin to z-scores; thus, values  $\pm 1.96$  correspond to  $\alpha$  < .05 and are considered significant. Second, we calculated a latent profile score (LPS) for each subject by multiplying the LV weights with the original data matrix. A higher LPS indicates that an individual expressed the age-related navigation profile more strongly. To test if age-related variations in the navigation LPS predict memory, we computed Pearson's correlations between the LPS and immediate and long-delay egocentric and allocentric memory. We used Fisher's r- to z-transformations and z-test statistics to determine significant differences in the magnitude of the correlations. All p values were Bonferroni-corrected for multiple comparisons.

#### Results

## Navigation Behavior and Immediate Spatial Memory During the Learning Session

#### Children Navigate Less Efficiently in Training Trials

We first computed LMM for latency, excess path length, excess distance to goal, and initial rotation in training trials and tested for changes across trials and age differences (see statistics in Table 2; Figure 2A; descriptive values in Supplemental Table S2). Latency decreased significantly across training trials (p < .001). In addition, there was a main effect of age group, showing that 6-8YO children required significantly more time to complete the training trials than 9–11YO children, t(90.67) = 2.97,  $p_{Bonferroni(3)} = .011$ , and AD, t(90.69) = 4.43,  $p_{\text{Bonferroni}(3)} = .001$ . Latency did not differ between 9–11YO children and AD, t(90.65) = 1.99,  $p_{Bonferroni(3)} = .149$  (ns). Similarly, participants had a significant decrease in excess path length across trials (p < .001). When comparing the age groups, we found that 6-8YO children had longer excess paths than 9-11YO children, t(90.60) = 3.47,  $p_{Bonferroni(3)} = .002$ , and AD, t(90.63) =5.44,  $p_{\text{Bonferroni}(3)} < .001$ , and 9–11YO children had longer excess paths than AD, t(90.56) = 2.64,  $p_{Bonferroni(3)} = .029$ . Participants also showed a significant decrease in excess distance to goal across trials (p < .001), meaning that they searched closer to the goal location after the first trial. Again, there was an age group difference, indicating that 6-8YO children searched further away from the goal location than 9–11YO children, t(90.86) = 3.18,  $p_{\text{Bonferroni}(3)} = .006$ , and AD, t(90.90) = 3.99,  $p_{\text{Bonferroni}(3)} < .001$ . Excess distance to goal did not differ between 9–11YO children and AD, t(90.82) = $1.25, p_{\text{Bonferroni}(3)} = .648$ . For initial rotation, there was a significant interaction between trial and age group (p = .045). Initial rotation decreased across trials in AD only, t(2182.04) = -2.81,  $p_{\text{Bonferroni}(3)}$ = .015, but stayed constant in children, 6–8YO: t(2182.08) = 0.94,  $p_{\text{Bonferroni}(3)} > .999; 9-11 \text{YO:} t(2181.93) = -0.11, p_{\text{Bonferroni}(3)} >$ .999. This indicates that adults, but not children, adjusted their visual exploration at the first decision point according to task demands. Sex did not affect navigation efficiency (all p > .213).

Taken together, participants from all age groups were able to significantly improve their navigation behavior across training

			Latency	/			Ex	cess path ]	length			Exc	ess distance	e to goal				Initial rotat	ion	
Fixed effect	F	$df^{s}$	$df_{\rm res}^s$	d	$\omega^2$	F	$df^{s}$	$df_{\rm res}^{\rm s}$	d	$\omega^2$	F	$df^{s}$	$df_{\rm res}^s$	d	$\omega^2$	F	$df^{s}$	$df_{\rm res}^{\rm s}$	d	$\omega^2$
Group	9.88	7	90.67	<.001	0.16	14.81	2	90.59	<.001	0.23	8.40	2	90.85	<.001	0.14	0.16	2	89.93	.851	-0.02
Trial in block	34.07	٢	2182.74	<.001	0.10	23.42	٢	2182.71	<.001	0.07	8.82	٢	2182.99	<.001	0.02	1.67	٢	2181.99	.112	0.00
Covariate sex	0.29	1	90.70	.593	-0.01	0.26	1	90.63	.611	-0.01	0.43	1	90.90	.514	-0.01	1.57	-	89.95	.213	0.01
Covariate motor score	14.08	1	90.71	<.001	0.12	5.73	1	90.65	.019	0.05	0.28	1	90.92	.599	-0.01	0.97	-	89.96	.328	0.00
Group × Trial in Block	1.12	14	2182.74	.338	0.00	1.46	14	2182.71	.118	0.00	0.20	14	2182.99	666.	-0.01	1.73	14	2181.99	.045	0.00
Random effect	SD					SD					SD					SD				
Participant ID Residual	4.28 10.24					12.84 41.07					1.25 4.63					0.28 0.65				

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*Note.* (A) *Left to right, top to bottom*: Better navigation with increasing age, that is, shorter latency, lower excess path length, lower excess distance to goal, and higher initial rotation in the first trial in older participants. Navigation differences were pronounced between 6–8YO children and both 9–11YO children and adults. Participants from all age groups improved their navigation across training trials. (B) Younger participants showed less immediate egocentric and allocentric spatial memory. Participants exhibited better spatial memory in the egocentric compared to the allocentric condition (main effect, not shown). There was a trend that this egocentric advantage was most pronounced in 9–11YO children (interaction effect, p = .047). YO = year-old; AD = adults; avg. distance = averaged distance. See the online article for the color version of this figure.

trials. Younger participants navigated less efficiently that is, slower, less direct, had a less focused search, and a lack of visual exploration during orientation. Navigation differences were pronounced between 6–8YO children in comparison to 9–11YO children and AD, but less evident when comparing 9–11YO children to AD.

## Children Have Less Immediate Egocentric and Allocentric Spatial Memory

Next, we analyzed participant's immediate egocentric and allocentric spatial memory in learning session probe trials. The LMM for memory score revealed significant main effects of age group (p < .001; see statistics in Table 3; Figure 2B; descriptive values in Supplemental Table S2) and condition (p = .029). Participants in all age groups reached above chance-level performance (tests against 0.5 all p < .001; see Supplemental Results A). The 6-8YO children had worse immediate spatial memory than 9–11YO children, t(93.56) = -3.81,  $p_{Bonferroni(3)} =$ .001, and AD, t(94.50) = -7.08,  $p_{\text{Bonferroni}(3)} < .001$ . The 9–11YO children had worse immediate spatial memory than AD, t(90.20) =-4.12,  $p_{\text{Bonferroni}(3)} < .001$ . Participants had better egocentric than allocentric memory. There was a trend for an interaction between condition and age group (p = .074), indicating that the egocentric advantage was pronounced in 9–11YO children, t(90.92) = 3.12,  $p_{\text{Bonferroni}(9)} = .022$ , but not 6-8YO children, t(92.91) = 0.01,  $p_{\text{Bonferroni(9)}} > .999$ , or AD, t(89.22) = 0.70,  $p_{\text{Bonferroni(9)}} > .999$ . Sex did not affect immediate spatial memory (p = .491). The LMM had a significantly better fit when including the random slope for condition,  $\chi^2(1) = 8.94$ , p = .003, indicating substantial interindividual variation in the condition response.

Taken together, immediate egocentric and allocentric spatial memory improved with increasing age. Participants exhibited better spatial memory in the egocentric compared to the allocentric condition. There was a trend that this egocentric advantage was most pronounced in 9–11YO children.

## Long-Delay Spatial Memory Retention and Spatial Knowledge After 2 Weeks

## Children Show an Equally Robust Navigation-Based Memory Consolidation as Adults

Next, we analyzed spatial memory consolidation. The LMM for memory score revealed main effects of age group (p < .001; see statistics in Table 4; Figure 3A; descriptive values in Supplemental Table S2), session (p < .001), and condition (p = .007). In parallel to our previous analysis, memory generally improved with increasing age, and we observed better memory in the egocentric than the allocentric condition. None of the interactions with condition were significant (all p > .224), meaning that the egocentric advantage was

#### Table 3

Fixed and Random Effects of Linear Mixed Models for Probe Trials in the Learning Session

		М	emory sc	ore	
Fixed effect	F	$df^s$	$df_{\rm res}^s$	р	$\omega^2$
Group	25.22	2	92.32	<.001	0.34
Condition	4.89	1	90.97	.029	0.04
Covariate sex	0.48	1	90.58	.491	-0.01
Covariate motor score	3.61	1	93.05	.060	0.03
Group × Condition	2.68	2	90.98	.074	0.03
Random effect	SD	r	р		
Participant ID (intercept)	0.08				
Condition (slope)	0.04		.003		
Participant ID × Condition		-0.63			
Residual	0.21				

#### Table 4

Fixed and Random Effects of Linear Mixed Models for Probe Trials Across Sessions

		Ν	Memory scor	e	
Fixed effect	F	$df^s$	$df_{\rm res}^s$	р	$\omega^2$
Group	26.70	2	98.59	<.001	0.34
Session	71.08	1	93.42	<.001	0.42
Condition	7.66	1	99.18	.007	0.06
Covariate sex	0.26	1	90.77	.609	-0.01
Covariate motor score	2.61	1	93.13	.110	0.02
Group × Session	1.62	2	93.43	.203	0.01
Group $\times$ Condition	1.52	2	99.19	.224	0.01
Session × Condition	0.04	1	2,550.68	.845	0.00
Group $\times$ Session $\times$ Condition	1.29	2	2,550.69	.276	0.00
Random effect	SD	r	р		
Participant ID (intercept)	0.10				
Session (slope)	0.07		<.001		
Condition (slope)	0.02		.037		
Participant ID × Session		-0.66			
Participant ID × Condition		-0.50			
Session × Condition		-0.22			
Residual	0.23				

consistent across age groups and sessions. Memory declined significantly over 2 weeks, but the interaction between age group and session was not significant (p = .203), indicating similar robustness of spatial memory retention across age groups. Sex did not affect spatial memory and consolidation (p = .609). The LMM had a significantly better fit when including the random slope for session,  $\chi^2(3) = 128.65$ , p < .001, indicating substantial interindividual variation in forgetting rates across the 2-week delay. Likewise, the model fit improved when including the random slope for condition,  $\chi^2(3) = 8.51$ , p = .037, indicating substantial interindividual variation in the condition response.

We ran a control analysis to further explore if encoding differences in immediate spatial memory (see last paragraph) account for the absence of age-related differences in spatial memory retention. Here, we restricted the analysis to object–location pairs that were well-learned in the first session (see Supplemental Results B; Table S3; Figure S1). We found a significant interaction between age group and session (p = .028), indicating a more robust spatial memory retention in AD compared to 6–8YO children (p = .012) and 9–11YO children (p < .001) for well-learned information. The 6–8YO and 9–11YO children did not differ (p > .999).

Taken together, children generally had a robust navigation-based memory consolidation similar to adults. In an exploratory analysis, we found tentative evidence that adults have a better spatial memory consolidation for initially well-learned information.

## Children Have Worse Boundary Knowledge and Cognitive Maps Than Adults After 2 Weeks

Furthermore, we analyzed the accuracy in the spatial knowledge tasks that were administered after 2 weeks (Figure 3B; descriptive values in Supplemental Table S2). We found significant age differences in the ability to identify the maze boundary (Fisher's exact (B) Spatial Knowledge Task



## Figure 3 Long-Delay Spatial Memory Retention and Spatial Knowledge After 2 Weeks

(A) Spatial Memory Retention

*Note.* (A) Memory declined significantly over 2 weeks. The amount of memory decline was comparable between children and adults. Across sessions and age groups, memory was significantly better in the egocentric than the allocentric condition and generally improved with increasing age. (B) *Left to right:* The probability to correctly identify the maze boundary increased across age groups. There was no age-related difference in landmark identification. Adults exhibited higher accuracy in positioning the landmark and goal objects in a cognitive map compared to both child groups. ego = egocentric; allo = allocentric; YO = year-old; AD = adults. See the online article for the color version of this figure.

test p < .001). The 6–8YO children performed worse than the 9–11YO children (p = .015) and AD (p < .001), and 9–11YO children performed worse than AD (p = .038). The performance of 6–8YO children did not differ from chance, t(30) = -0.61, p = .543, indicating that they chose randomly. In contrast, almost half of the 9–11YO children and almost all AD selected the correct option. There were no significant age differences in the ability to correctly identify landmark objects, F(2, 85) = 1.29, p = .280. Last, we did find significant age differences in the ability to correctly position the landmark and goal objects in a map, F(2, 85) = 9.74, p < .001. Here, AD performed better than 6–8YO children, t(85) = -3.78,  $p_{\text{Bonferroni}(3)} = .001$ , and 9–11YO children, t(85) = -3.94,  $p_{\text{Bonferroni}(3)} < .001$ , while there was no difference between both child groups, t(85) = 0.20,  $p_{\text{Bonferroni}(3)} > .999$ .

Taken together, both groups of children were as proficient as adults in identifying perceptually detailed landmarks. However, adults had superior boundary knowledge and cognitive maps at the end of the experiment.

## The Age-Related Multivariate Navigation Profile Predicts Spatial Memory

Finally, we tested if age-related variations in navigation behavior during training predict spatial memory. We applied PLSC and identified a single reliable LV (p < .001; Figure 4A) that maximally represented associations between age and a profile of navigation indicators from training trials in the learning session (r = .56, p < .001). We identified several stable components within the multivariate profile (BSR; values ±1.96 are significant  $\alpha < .05$ ), paralleling our previous results. Higher age was associated with shorter latency (BSR = -10.65), more direct navigation (excess path length; BSR = -13.31), and search near the goal (excess distance to goal; BSR = -4.74) but not visual exploration (initial rotation; BSR = -0.66). As a second step, we computed LPS for each participant. A more positive navigation LPS indicates that an individual expressed the age-related navigation profile more strongly (i.e., more adultlike). We then correlated the LPS with immediate and long-delay egocentric and allocentric memory scores (Table 5; Figure 4B). The navigation LPS correlated significantly with immediate egocentric (r = .82) and long-delay egocentric memory (r = .45), and the former was significantly higher than the latter,  $p_{\text{Bonferroni}(4)} < .001$ . The navigation LPS also correlated significantly with immediate allocentric (r = .55) and long-delay allocentric memory (r = .46). The correlation with immediate egocentric memory was significantly higher than with immediate allocentric memory  $p_{\text{Bonferroni}(4)} < .001$ .

Taken together, we found that participants with a more efficient, adultlike navigation profile during training had better spatial memory in egocentric and allocentric probe trials, both immediately and after a 2-week delay. There was a particularly strong association with immediate egocentric memory.

#### Discussion

We investigated developmental differences in the consolidation of navigation-based spatial memories by comparing navigation behavior and spatial memory in 6–8YO children, 9–11YO children, and AD, both during learning and after a 2-week delay. We tested three hypotheses. First, previous work indicated that egocentric spatial abilities develop before allocentric spatial abilities; thus, we predicted that younger participants have a more pronounced egocentric advantage, both immediately and after the 2-week delay. In contrast, we found a small- to medium-sized egocentric advantage that was present across age groups and sessions. Second, consolidation relies on hippocampal–prefrontal interactions, which are not fully developed in children; thus, we predicted age-related differences in immediate and long-delay spatial memory retention



#### Figure 4



*Note.* (A) We identified a single reliable LV (p < .001) that maximally represented associations between age and a profile of navigation indicators from training trials in the learning session. Stability of LV weights was assessed with bootstrap ratios (BSR; depicted as red line: values ±1.96 are significant  $\alpha < .05$ ). Higher age was associated with shorter latency, excess path length, and excess distance to goal during navigation in the initial training phase. (B) *Left*: Distribution of navigation LPS across age groups. *Right*: Significant correlations between navigation LPS and memory. Participants with a more adultlike navigation during training had better immediate and long-delay egocentric and allocentric spatial memory. allo = allocentric; ego = egocentric; s1 = Session 1; s2 = Session 2; YO = year-old. See the online article for the color version of this figure.

and spatial knowledge abstraction after the 2-week delay. We found a nuanced picture showing that immediate spatial memory improved with increasing age, while long-delay spatial memory retention was as robust in children as in adults. Additionally, children's spatial knowledge after 2 weeks was significantly worse compared to adults. Third, studies with adult navigators indicate a link between initial navigation and spatial memory. Based on this, we hypothesized that age differences in navigation behavior during training predict spatial memory retention, both immediately and after the 2-week delay. Our results supported this hypothesis. Participant's navigation behavior became more efficient (i.e., quicker, more direct, more focused) with increasing age, and this was predictive for spatial memory. In the following, the results are discussed in more detail.

## Similar Development of Egocentric and Allocentric Spatial Memory

Previous studies found that egocentric abilities develop before allocentric abilities (Broadbent et al., 2014; Bullens et al., 2010; Burles et al., 2020; Nardini et al., 2006). Thus, we expected a pronounced advantage for egocentric over allocentric spatial memory in the youngest cohort that gradually fades with increasing age. Contrary to our hypothesis, we found a small advantage for egocentric over allocentric memories that was present across age groups for both immediate and long-delay spatial memory. For immediate spatial memory, we additionally found a trend interaction with age, indicating that the egocentric advantage was most noticeable in 9–11YO children but less pronounced in 6–8YO children and AD.

Traditionally, allocentric representations have been associated with hippocampal function and egocentric representations with the striatum and posterior parietal cortex (Packard & McGaugh, 1996). However, recent imaging studies point toward overlapping networks for both representations (including the hippocampus, entorhinal, posterior parietal, and retrosplenial cortex; Ekstrom et al., 2017) and demonstrate similar benefits of and neural changes during sleep (Samanta et al., 2021). Egocentric navigation in the Starmaze requires the memorization of sequences of turns, which

Table	5
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Correlations B	Between	the .	LPS	and	Memory	Scor
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		Navigatio	n LPS			Comparisons	
Memory score in condition and session	r	95% CI	t	df	<i>p</i> <sub>Bonferroni(4)</sub>	Session 1 versus Session 2	Egocentric versus allocentric
Egocentric Session 1	.82	[.74, .88]	13.98	94	<.001		=.001
Egocentric Session 2	.45	[.28, .60]	4.93	94	<.001	<.001	>.999
Allocentric Session 1	.55	[.40, .68]	6.43	94	<.001		
Allocentric Session 2	.46	[.28, .60]	4.96	94	<.001	>.999	

*Note.* LPS = latent profile score; CI = confidence interval.

has episodic qualities (Eichenbaum & Cohen, 2014), and as such may also depend on the hippocampus. Indeed, a previous study found hippocampal activation in both egocentric and allocentric navigation in the Starmaze (Iglói et al., 2010). We postulate that egocentric and allocentric abilities may represent a continuum rather than distinct entities (Ekstrom et al., 2017) and share overlapping neural processing depending on task demands, leading to varying levels of performance differences across development. In line with this, Ruggiero et al. (2016) found that not just allocentric but egocentric spatial processing continues to mature beyond childhood.

The operationalization of "egocentric" representations varies considerably across studies (e.g., Ladyka-Wojcik & Barense, 2021), which may contribute to the mixed findings. A recent study found that children below 8 years have poorer egocentric memory when asked to navigate solely based on directional cues ("Go right, then left") rather than in combination with landmark cues ("Go left at the tree"; Lingwood et al., 2015). Since the egocentric condition in the Starmaze is purely directional, it may have precluded better egocentric memory in the youngest group. Performance in the allocentric task matched with developmental predictions. Allocentric memory was above chance already in 6-8YO children. This corresponds to prior work showing that children successfully use multiple (Negen et al., 2019) and distal landmarks (Broadbent et al., 2014; Bullens et al., 2010; Lehnung et al., 1998; Leplow et al., 2003) from 6 years on. Allocentric memory markedly improved in older children, potentially linked to the integration of spatial information sources, which was shown to emerge between 8 and 10 years (Nardini et al., 2008; Newcombe, 2019).

Taken together, we found similar developmental differences for immediate and long-delay egocentric and allocentric memories, in contrast to previous studies that postulate egocentric precedence in child development. Recent research suggests that egocentric and allocentric processing relies on overlapping brain networks and may not be as distinct as previously thought.

## Pronounced Age Differences in Immediate Spatial Memory and Nuanced Differences in Consolidation and Knowledge Abstraction

For immediate spatial memory in the learning session, we found age-related group differences (across conditions). Namely, 6–8YO children exhibited worse immediate spatial memory, having difficulties in finding the spatial locations despite above chance performance. The immediate spatial memory of 9–11YO children was significantly more accurate. Adults showed the highest immediate spatial memory compared to both child groups. The overall pattern replicates prior findings of a developmental milestone for spatial memory between 9 and 10 years (Broadbent et al., 2014; Bullens et al., 2010; Burles et al., 2020).

For long-delay spatial memory after 2 weeks, we expected an improved memory consolidation in adults compared to children because adults can rely on prior experience with spatial situations (Tse et al., 2007; van Buuren et al., 2014; van Kesteren et al., 2018) and mature brain systems (Gogtay et al., 2004; Mills et al., 2016; Pine et al., 2002). Our results showed a nuanced picture:

Navigation-based spatial memory declined significantly across the 2-week period, and there was a relatively high interindividual variation in the forgetting slopes but no systematic interaction with age. Thus, age differences in spatial memory after the 2-week delay were driven by age differences in encoding but not consolidation. In our experimental approach, we deliberately chose unrestricted encoding during the first session without a set learning criterion or extra trials for children to keep it naturalistic and avoid long experiment durations. However, this approach might have affected the extent to which we can capture age-related variability in memory consolidation. Indeed, a recent study on nonnavigation-based spatial memory consolidation, which ensured comparable encoding of children and adults during the first session, did find notably better 1-day and 2-week spatial memory retention in adults compared to 5- to 7-year-old children (Schommartz et al., 2023). To explore this option further, we ran an analysis using only trials with welllearned object-location pairs. Here, we found evidence for a more robust navigation-based consolidation in adults as evident by a significant interaction between age group and session. While memory retention of well-learned items did not differ between age groups in the learning session, there was less forgetting in adults than children after 2 weeks, showing a consolidation advantage for initially strong memories in adults.

After the 2-week delay, we also assessed the ability to abstract spatial knowledge. The 6-8YO children could not reliably identify the maze boundary, while half of the 9-11YO children and almost all the adults did. This replicates prior studies (Broadbent et al., 2014; Bullens et al., 2010). Both groups of children also performed more poorly compared to adults in positioning landmarks and goal objects in a cognitive map after 2 weeks. This task required a perspective shift and the integration of spatial cues. While previous studies show that the ability to integrate spatial cues emerges between 8 and 10 years (Nardini et al., 2008), our results imply that this ability continues to develop until adulthood. We did not find any age differences in landmark recognition, in line with studies showing that children successfully use distal landmarks from 6 years on (Broadbent et al., 2014; Bullens et al., 2010; Lehnung et al., 1998; Leplow et al., 2003). Thus, when assessing spatial knowledge, children were better in perceptual aspects, namely the landmark recognition that required distinguishing similar-looking lures, compared to aspects that required a certain level of abstraction, namely the spatial boundary and cognitive map. This corresponds to the observation that children rely more strongly on perceptual versus semantic processing (Brod et al., 2013) and suggests that the emergence of abstract spatial knowledge through consolidation occurs at later developmental stages compared to the mere stabilization of representations.

Taken together, we showed that children's immediate spatial memory gradually becomes more accurate from mid to late childhood. Our study is the first to investigate developmental differences in the consolidation of spatial memories. We found an equally robust consolidation of navigation-based spatial memories in 6- to 11-year-old children compared to adults; adults only had a consolidation advantage for well-learned information. On the other hand, 6- to 11-year-old children performed worse than adults at abstracting spatial knowledge after 2 weeks but successfully recognized and distinguished landmarks.

## Navigation Efficiency During Training Improves With Age and Predicts Immediate and Long-Delay Spatial Memory

Studies with adult navigators indicate that efficient navigation during initial exploration is predictive for spatial memory accuracy (Brunec et al., 2023; Gagnon et al., 2018; Munion et al., 2019). Thus, we hypothesized that developmental differences in initial navigation behavior predict spatial memory retention, both immediately and after the 2-week delay. This hypothesis was supported. First, we observed large age differences in navigation behavior during training. With increasing age, participants navigated more efficiently, even though all age groups were able to improve across trials. Children navigated more slowly and indirectly, their search was less focused on the goal area, and they did not show much visual exploration, compared to adults. There were pronounced age differences between 6-8YO children and older participants. The 9-11YO children were in an intermediate state: They navigated as quickly and focused as adults, even though they still required longer paths and did not adjust their visual exploration. This observation fits with the prediction that children approach adultlike navigation at 12 years (Brucato et al., 2022; Nazareth et al., 2018). Second, we showed that age differences in initial navigation behavior strongly predict spatial memory. Children who navigated more adultlike during training had higher chances of finding and remembering spatial locations in egocentric and allocentric probe trials, both immediately and after a 2-week delay. This complements a recent study showing that children with a more active navigation style successfully reached goals in shorter time (Farran et al., 2022). There was a particularly strong correlation with immediate egocentric memory, as egocentric navigation relies on the replication of learned path sequences and thus plausibly benefits from quick, direct, and confident navigation during training. The correlation with allocentric memory was less pronounced, indicating that successful allocentric navigation requires flexible deviations from navigation patterns used during training. Navigation behavior during training was more predictive for immediate compared to long-delay (egocentric) memory, but the correlations with long-delay memory were still high.

The age differences in initial navigation behavior were in line with previous studies showing that children require less time (Bullens et al., 2010; Burles et al., 2020; Murias et al., 2019) and take more direct routes (Burles et al., 2020) as they mature. We additionally found that children below 9 years old navigate more randomly, and children below 12 years old do not adaptively increase their visual exploration during the orientation phase. We also show for the first time that age differences in latency, path length, and goal-focused search patterns during training are relevant predictors for a child's ability to find spatial locations, both immediately and after a 2-week delay. This suggests a potential for targeted strategy training during sensitive periods in childhood to boost children's navigation competency and spatial memory, allowing them to remember routes and navigate safely. Relatedly, a recent large-scale study found that the topological environment during childhood critically determines navigational strengths and weaknesses in adulthood, thus shaping cognition for life (Coutrot et al., 2022). Thus, developing strong spatial cognition in childhood through targeted training may offer protective benefits across the lifespan and into old age.

The overall pattern shows that children between 6 and 11 years have difficulties with strategically planning, controlling, and executing navigation, which could be linked to the ongoing PFC development (Gogtay et al., 2004; Mills et al., 2016) and attenuated MTL-PFC connectivity in middle childhood (Ghetti & Bunge, 2012; Murias et al., 2019). Crucially, navigation efficiency correlated with spatial memory accuracy. In the developmental literature, lifespan changes in episodic memory are linked to both (a) associative binding in the MTL and (b) strategic control in the PFC (Shing et al., 2010). Because the MTL matures earlier than the PFC, episodic memory difficulties in middle childhood can be attributed to cognitive control in the PFC that is yet to develop, along with refinement of binding in the MTL (Ghetti & Bunge, 2012; Shing et al., 2010). Although we did not collect brainimaging data, we postulate a similar developmental mechanism for navigation-based spatial memory. More specifically, the lack of navigation efficiency in children indicates that strategic control operations are a crucial driver of navigation-based spatial memory formation and retention in children. The 6-8YO children had the lowest navigation efficiency and formed the least robust spatial memories. This could be due to a combination of less mature binding and control mechanisms in the corresponding neural structures (i.e., MTL and PFC). The 9-11YO children reached an intermediate level of navigation efficiency and spatial memory accuracy. At this age, children typically have mature hippocampal binding (except for microstructural changes; Ghetti & Bunge, 2012) but may exhibit less optimal strategic control compared to adults due to the ongoing maturation of PFC regions (Gogtay et al., 2004; Mills et al., 2016; Shing et al., 2010).

Taken together, our study is the first to show that children's navigation behavior becomes more efficient in mid to late childhood and that age variations in initial navigation are predictive for immediate spatial memory and can even have long-lasting effects on spatial memory consolidation.

#### Limitations

Several limitations are worth noting. Our navigation task was desktop-based and provided only visual information. The availability of multisensory information (e.g., proprioception) can facilitate navigation (e.g., Fernandez-Baizan et al., 2021; Iggena et al., 2023). Future studies should therefore investigate children's spatial memory consolidation under multisensory conditions, for example, by using real-life navigation or virtual reality paradigms. A second limitation of our study is that we did not collect brain-imaging data. Future studies should combine neuroimaging techniques with in-depth behavioral assessments to elucidate the relative contributions of the hippocampus and prefrontal cortex for children's remote spatial memory. Last, pronounced age differences in encoding may have concealed age differences in spatial memory consolidation in our study. Thus, future work should investigate age differences in consolidation by using an adaptive learning approach that better matches the initial performance of participants.

#### Conclusion

Our study provides novel evidence about the robustness of navigation-based spatial memory consolidation in mid to late childhood. Even though children had worse immediate spatial memory compared to adults, their spatial memory consolidation was as robust as in adults, indicating distinct age differences for encoding and consolidation. After 2 weeks, children performed worse than adults in spatial boundary and cognitive map tests, suggesting that the emergence of abstract spatial knowledge through consolidation is developmentally extended compared to the mere stabilization of representations. We also found similar age differences for egocentric memory (sequences of turns) and allocentric memory (environmental landmarks), in line with overlapping developmental trajectories for both representational modes. Last, navigation efficiency during training improved with increasing age and these age differences were linked to egocentric and allocentric memory retention, both immediately and after 2 weeks. Thus, children who expressed a more mature initial navigation had higher chances of finding and remembering locations after short and long delays. Lower navigation efficiency in children may be related to suboptimal strategic planning and control due to the ongoing PFC development and immature MTL-PFC connections. Future studies should investigate whether the link between navigation and memory represents a causal mechanism that could be utilized for training.

#### References

- Alonso, A., Bokeria, L., van der Meij, J., Samanta, A., Eichler, R., Lotfi, A., Spooner, P., Navarro Lobato, I., & Genzel, L. (2021). The HexMaze: A previous knowledge task on map learning for mice. *eNeuro*, 8(4), 1–23. https://doi.org/10.1523/ENEURO.0554-20.2021
- Aust, F., & Barth, M. (2022). papaja: Prepare reproducible APA journal articles with R Markdown [R Package Version 0.1.1]. https://github.com/ crsh/papaja
- Barr, D. J. (2013). Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology*, 4, Article 328. https:// doi.org/10.3389/fpsyg.2013.00328
- Bécu, M., Sheynikhovich, D., Ramanoël, S., Tatur, G., Ozier-Lafontaine, A., Authié, C. N., Sahel, J.-A., & Arleo, A. (2023). Landmark-based spatial navigation across the human lifespan. *eLife*, *12*, Article e81318. https:// doi.org/10.7554/eLife.81318
- Bellmund, J. L. S., de Cothi, W., Ruiter, T. A., Nau, M., Barry, C., & Doeller, C. F. (2020). Deforming the metric of cognitive maps distorts memory. *Nature Human Behaviour*, 4(2), 177–188. https://doi.org/10.1038/s415 62-019-0767-3
- Ben-Shachar, M., Lüdecke, D., & Makowski, D. (2020). Effectsize: Estimation of effect size indices and standardized parameters. *Journal* of Open Source Software, 5(56), Article 2815. https://doi.org/10.21105/jo ss.02815
- Broadbent, H. J., Farran, E. K., & Tolmie, A. (2014). Egocentric and allocentric navigation strategies in Williams syndrome and typical development. *Developmental Science*, 17(6), 920–934. https://doi.org/ 10.1111/desc.12176
- Brod, G., Werkle-Bergner, M., & Shing, Y. L. (2013). The influence of prior knowledge on memory: A developmental cognitive neuroscience perspective. *Frontiers in Behavioral Neuroscience*, 7, Article 139. https:// doi.org/10.3389/fnbeh.2013.00139
- Brookes, J., Warburton, M., Alghadier, M., Mon-Williams, M., & Mushtaq, F. (2020). Studying human behavior with virtual reality: The Unity Experiment Framework. *Behavior Research Methods*, 52(2), 455–463. https://doi.org/10.3758/s13428-019-01242-0
- Brucato, M., Nazareth, A., & Newcombe, N. S. (2022). Longitudinal development of cognitive mapping from childhood to adolescence. *Journal of Experimental Child Psychology*, 219, Article 105412. https:// doi.org/10.1016/j.jecp.2022.105412

- Brunec, I. K., Nantais, M. M., Sutton, J. E., Epstein, R. A., & Newcombe, N. S. (2023). Exploration patterns shape cognitive map learning. *Cognition*, 233, Article 105360. https://doi.org/10.1016/j.cognition.2022 .105360
- Bullens, J., Iglói, K., Berthoz, A., Postma, A., & Rondi-Reig, L. (2010). Developmental time course of the acquisition of sequential egocentric and allocentric navigation strategies. *Journal of Experimental Child Psychology*, 107(3), 337–350. https://doi.org/10.1016/j.jecp.2010.05.010
- Burles, F., Liu, I., Hart, C., Murias, K., Graham, S. A., & Iaria, G. (2020). The emergence of cognitive maps for spatial navigation in 7- to 10-year-old children. *Child Development*, 91(3), e733–e744. https://doi.org/10.1111/ cdev.13285
- Coutrot, A., Manley, E., Goodroe, S., Gahnstrom, C., Filomena, G., Yesiltepe, D., Dalton, R. C., Wiener, J. M., Hölscher, C., Hornberger, M., & Spiers, H. J. (2022). Entropy of city street networks linked to future spatial navigation ability. *Nature*, 604, 104–110. https://doi.org/10.1038/ s41586-022-04486-7
- Dudai, Y., Karni, A., & Born, J. (2015). The consolidation and transformation of memory. *Neuron*, 88(1), 20–32. https://doi.org/10.1016/j.neuron.2015 .09.004
- Eichenbaum, H., & Cohen, N. J. (2014). Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron*, 83(4), 764–770. https://doi.org/10.1016/j.neuron.2014.07.032
- Ekstrom, A. D., Huffman, D. J., & Starrett, M. (2017). Interacting networks of brain regions underlie human spatial navigation: A review and novel synthesis of the literature. *Journal of Neurophysiology*, *118*(6), 3328– 3344. https://doi.org/10.1152/jn.00531.2017
- Farran, E. K., Blades, M., Hudson, K. D., Sockeel, P., & Courbois, Y. (2022). Spatial exploration strategies in childhood; exploration behaviours are predictive of navigation success. *Cognitive Development*, 61, Article 101153. https://doi.org/10.1016/j.cogdev.2022.101153
- Farzanfar, D., Spiers, H. J., Moscovitch, M., & Rosenbaum, R. S. (2023). From cognitive maps to spatial schemas. *Nature Reviews Neuroscience*, 24(2), 63–79. https://doi.org/10.1038/s41583-022-00655-9
- Fernandez-Baizan, C., Arias, J. L., & Mendez, M. (2021). Spatial orientation assessment in preschool children: Egocentric and allocentric frameworks. *Applied Neuropsychology: Child*, 10(2), 171–193. https://doi.org/10.1080/ 21622965.2019.1630278
- Gagnon, K. T., Thomas, B. J., Munion, A., Creem-Regehr, S. H., Cashdan, E. A., & Stefanucci, J. K. (2018). Not all those who wander are lost: Spatial exploration patterns and their relationship to gender and spatial memory. *Cognition*, 180, 108–117. https://doi.org/10.1016/j.cognition.2018.06.020
- Gardony, A. L., Taylor, H. A., & Brunyé, T. T. (2016). Gardony map drawing analyzer: Software for quantitative analysis of sketch maps. *Behavior Research Methods*, 48(1), 151–177. https://doi.org/10.3758/s13428-014-0556-x
- Ghetti, S., & Bunge, S. A. (2012). Neural changes underlying the development of episodic memory during middle childhood. *Developmental Cognitive Neuroscience*, 2(4), 381–395. https://doi.org/10.1016/j.dcn.2012.05.002
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., Nugent, T. F., III, Herman, D. H., Clasen, L. S., Toga, A. W., Rapoport, J. L., & Thompson, P. M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings* of the National Academy of Sciences of the United States of America, 101(21), 8174–8179. https://doi.org/10.1073/pnas.0402680101
- Graves, K. N., Antony, J. W., & Turk-Browne, N. B. (2020). Finding the pattern: On-line extraction of spatial structure during virtual navigation. *Psychological Science*, 31(9), 1183–1190. https://doi.org/10.1177/095679 7620948828
- Hagmann-von Arx, P., & Grob, A. (2014). RIAS. Reynolds Intellectual Assessment Scales and Screening. Deutschsprachige Adaptation der Reynolds Intellectual Assessment Scales (RIASTM) & des Reynolds Intellectual Screening Test (RISTTM) von Cecil R. Reynolds und Randy W. Kamphaus. Hans Huber.

- Iggena, D., Jeung, S., Maier, P. M., Ploner, C. J., Gramann, K., & Finke, C. (2023). Multisensory input modulates memory-guided spatial navigation in humans. *Communications Biology*, 6(1), Article 1167. https://doi.org/ 10.1038/s42003-023-05522-6
- Iggena, D., Maier, P. M., Häußler, S. M., Menk, M., Olze, H., Larkum, M. E., Finke, C., & Ploner, C. J. (2022). Post-encoding modulation of spatial memory consolidation by propofol. *Cortex*, 156, 1–12. https://doi.org/10 .1016/j.cortex.2022.08.004
- Iglói, K., Doeller, C. F., Berthoz, A., Rondi-Reig, L., & Burgess, N. (2010). Lateralized human hippocampal activity predicts navigation based on sequence or place memory. *Proceedings of the National Academy of Sciences of the United States of America*, 107(32), 14466–14471. https:// doi.org/10.1073/pnas.1004243107
- Iglói, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired as early as allocentric strategy: Parallel acquisition of these two navigation strategies. *Hippocampus*, 19(12), 1199–1211. https://doi.org/10.1002/hipo.20595
- Keresztes, A., Bender, A. R., Bodammer, N. C., Lindenberger, U., Shing, Y. L., & Werkle-Bergner, M. (2017). Hippocampal maturity promotes memory distinctiveness in childhood and adolescence. *Proceedings of the National Academy of Sciences of the United States of America*, 114(34), 9212–9217. https://doi.org/10.1073/pnas.1710654114
- Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial Least Squares (PLS) methods for neuroimaging: A tutorial and review. *NeuroImage*, 56(2), 455–475. https://doi.org/10.1016/j.neuroimage.2010 .07.034
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). ImerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. https://doi.org/10.18637/jss.v082.i13
- Ladyka-Wojcik, N., & Barense, M. D. (2021). Reframing spatial frames of reference: What can aging tell us about egocentric and allocentric navigation? Wiley Interdisciplinary Reviews: Cognitive Science, 12(3), Article e1549. https://doi.org/10.1002/wcs.1549
- Lehnung, M., Leplow, B., Friege, L., Herzog, A., Ferstl, R., & Mehdorn, M. (1998). Development of spatial memory and spatial orientation in preschoolers and primary school children. *British Journal of Psychology*, 89(3), 463–480. https://doi.org/10.1111/j.2044-8295.1998.tb02697.x
- Lenth, R. V. (2022). emmeans: Estimated marginal means, aka leastsquares means [R Package Version 1.8.1-1]. https://cran.r-project.org/pa ckage=emmeans
- Leplow, B., Lehnung, M., Pohl, J., Herzog, A., Ferstl, R., & Mehdorn, M. (2003). Navigational place learning in children and young adults as assessed with a standardized locomotor search task. *British Journal* of Psychology, 94(3), 299–317. https://doi.org/10.1348/000712603767 876244
- Lingwood, J., Blades, M., Farran, E. K., Courbois, Y., & Matthews, D. (2015). The development of wayfinding abilities in children: Learning routes with and without landmarks. *Journal of Environmental Psychology*, 41, 74–80. https://doi.org/10.1016/j.jenvp.2014.11.008
- Maei, H. R., Zaslavsky, K., Teixeira, C. M., & Frankland, P. W. (2009). What is the most sensitive measure of water maze probe test performance? *Frontiers in Integrative Neuroscience*, *3*, Article 4. https://doi.org/10 .3389/neuro.07.004.2009
- Maier, P. M., Schommartz, I., Iggena, D., Finke, C., Ploner, C. J., & Shing, Y. L. (2024, April 26). Development of spatial memory consolidation: A comparison between children and adults. https://doi.org/10.17605/OSF .IO/KSFV8
- Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing Type I error and power in linear mixed models. *Journal of Memory and Language*, 94, 305–315. https://doi.org/10.1016/j.jml.2017 .01.001
- McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: Applications and advances. *NeuroImage*, 23(Suppl. 1), S250–S263. https://doi.org/10.1016/j.neuroimage.2004.07.020

- Mills, K. L., Goddings, A.-L., Herting, M. M., Meuwese, R., Blakemore, S.-J., Crone, E. A., Dahl, R. E., Güroğlu, B., Raznahan, A., Sowell, E. R., & Tamnes, C. K. (2016). Structural brain development between childhood and adulthood: Convergence across four longitudinal samples. *Neuro-Image*, 141, 273–281. https://doi.org/10.1016/j.neuroimage.2016.07.044
- Muehlroth, B. E., Sander, M. C., Fandakova, Y., Grandy, T. H., Rasch, B., Lee Shing, Y., & Werkle-Bergner, M. (2020). Memory quality modulates the effect of aging on memory consolidation during sleep: Reduced maintenance but intact gain. *NeuroImage*, 209, Article 116490. https:// doi.org/10.1016/j.neuroimage.2019.116490
- Munion, A. K., Stefanucci, J. K., Rovira, E., Squire, P., & Hendricks, M. (2019). Gender differences in spatial navigation: Characterizing wayfinding behaviors. *Psychonomic Bulletin & Review*, 26(6), 1933–1940. https:// doi.org/10.3758/s13423-019-01659-w
- Murias, K., Slone, E., Tariq, S., & Iaria, G. (2019). Development of spatial orientation skills: An fMRI study. *Brain Imaging and Behavior*, 13(6), 1590–1601. https://doi.org/10.1007/s11682-018-0028-5
- Nardini, M., Burgess, N., Breckenridge, K., & Atkinson, J. (2006). Differential developmental trajectories for egocentric, environmental and intrinsic frames of reference in spatial memory. *Cognition*, 101(1), 153–172. https:// doi.org/10.1016/j.cognition.2005.09.005
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, 18(9), 689–693. https://doi.org/10.1016/j.cub.2008.04.021
- Nazareth, A., Weisberg, S. M., Margulis, K., & Newcombe, N. S. (2018). Charting the development of cognitive mapping. *Journal of Experimental Child Psychology*, 170, 86–106. https://doi.org/10.1016/j.jecp.2018.01.009
- Negen, J., Bou Ali, L., Chere, B., Roome, H. E., Park, Y., & Nardini, M. (2019). Coding locations relative to one or many landmarks in childhood. *PLOS Computational Biology*, 15(10), Article e1007380. https://doi.org/ 10.1371/journal.pcbi.1007380
- Newcombe, N. S. (2019). Navigation and the developing brain. *The Journal of Experimental Biology*, 222(Suppl. 1), 1–11. https://doi.org/10.1242/jeb .186460
- Ngo, C. T., Benear, S. L., Popal, H., Olson, I. R., & Newcombe, N. S. (2021). Contingency of semantic generalization on episodic specificity varies across development. *Current Biology*, 31(12), 2690–2697.e5. https://doi.org/10 .1016/j.cub.2021.03.088
- Østby, Y., Tamnes, C. K., Fjell, A. M., & Walhovd, K. B. (2012). Dissociating memory processes in the developing brain: The role of hippocampal volume and cortical thickness in recall after minutes versus days. *Cerebral Cortex*, 22(2), 381–390. https://doi.org/10.1093/cercor/ bhr116
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory*, 65(1), 65–72. https://doi.org/10.1006/nlme.1996.0007
- Patai, E. Z., & Spiers, H. J. (2021). The versatile wayfinder: Prefrontal contributions to spatial navigation. *Trends in Cognitive Sciences*, 25(6), 520–533. https://doi.org/10.1016/j.tics.2021.02.010
- Peeters, D. (2018). A standardized set of 3-D objects for virtual reality research and applications. *Behavior Research Methods*, 50(3), 1047– 1054. https://doi.org/10.3758/s13428-017-0925-3
- Pine, D. S., Grun, J., Maguire, E. A., Burgess, N., Zarahn, E., Koda, V., Fyer, A., Szeszko, P. R., & Bilder, R. M. (2002). Neurodevelopmental aspects of spatial navigation: A virtual reality fMRI study. *NeuroImage*, 15(2), 396–406. https://doi.org/10.1006/nimg.2001.0988
- Pullano, L., & Foti, F. (2022). The development of human navigation in middle childhood: A narrative review through methods, terminology, and fundamental stages. *Brain Sciences*, 12(8), Article 1097. https://doi.org/10 .3390/brainsci12081097
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-proje ct.org/

- Rondi-Reig, L., Petit, G. H., Tobin, C., Tonegawa, S., Mariani, J., & Berthoz, A. (2006). Impaired sequential egocentric and allocentric memories in forebrain-specific-NMDA receptor knock-out mice during a new task dissociating strategies of navigation. *The Journal of Neuroscience*, 26(15), 4071–4081. https://doi.org/10.1523/JNEUROSCI.3408-05.2006
- Ruggiero, G., D'Errico, O., & Iachini, T. (2016). Development of egocentric and allocentric spatial representations from childhood to elderly age. *Psychological Research*, 80(2), 259–272. https://doi.org/10.1007/s00426-015-0658-9
- Samanta, A., van Rongen, L. S., Rossato, J. I., Jacobse, J., Schoenfeld, R., & Genzel, L. (2021). Sleep leads to brain-wide neural changes independent of allocentric and egocentric spatial training in humans and rats. *Cerebral Cortex*, 31(11), 4970–4985. https://doi.org/10.1093/cercor/bhab135
- Santos-Pata, D., & Verschure, P. F. M. J. (2018). Human vicarious trial and error is predictive of spatial navigation performance. *Frontiers in Behavioral Neuroscience*, 12, Article 237. https://doi.org/10.3389/fnbeh .2018.00237
- Schmidt, B., Papale, A., Redish, A. D., & Markus, E. J. (2013). Conflict between place and response navigation strategies: Effects on vicarious trial and error (VTE) behaviors. *Learning & Memory*, 20(3), 130–138. https:// doi.org/10.1101/lm.028753.112
- Schommartz, I., Lembcke, P. F., Pupillo, F., Schuetz, H., de Chamorro, N. W., Bauer, M., Kaindl, A. M., Buss, C., & Shing, Y. L. (2023). Distinct multivariate structural brain profiles are related to variations in short- and long-delay memory consolidation across children and young adults. *Developmental Cognitive Neuroscience*, 59, Article 101192. https:// doi.org/10.1016/j.dcn.2022.101192
- Shing, Y. L., Werkle-Bergner, M., Brehmer, Y., Müller, V., Li, S. C., & Lindenberger, U. (2010). Episodic memory across the lifespan: The contributions of associative and strategic components. *Neuroscience and*

*Biobehavioral Reviews*, 34(7), 1080–1091. https://doi.org/10.1016/j.neu biorev.2009.11.002

- Singmann, H., Bolker, B., Westfall, J., Aust, F., & Ben-Shachar, M. S. (2022). afex: Analysis of factorial experiments [R Package Version 1.1-1]. https://CRAN.R-project.org/package=afex
- Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., Witter, M. P., & Morris, R. G. M. (2007). Schemas and memory consolidation. *Science*, *316*(5821), 76–82. https://doi.org/10.1126/science .1135935
- van Buuren, M., Kroes, M. C. W., Wagner, I. C., Genzel, L., Morris, R. G. M., & Fernández, G. (2014). Initial investigation of the effects of an experimentally learned schema on spatial associative memory in humans. *The Journal of Neuroscience*, 34(50), 16662–16670. https://doi.org/10 .1523/JNEUROSCI.2365-14.2014
- van Kesteren, M. T. R., Brown, T. I., & Wagner, A. D. (2018). Learned spatial schemas and prospective hippocampal activity support navigation after one-shot learning. *Frontiers in Human Neuroscience*, 12, Article 486. https://doi.org/10.3389/fnhum.2018.00486
- Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer. https://doi.org/10.1007/978-3-319-24277-4
- Winocur, G., & Moscovitch, M. (2011). Memory transformation and systems consolidation. *Journal of the International Neuropsychological Society*, 17(5), 766–780. https://doi.org/10.1017/S1355617711000683
- Zhang, Z., & Yuan, K.-H. (2018). Practical statistical power analysis using Webpower and R. ISDSA Press. https://doi.org/10.35566/power

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