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Neural specificity of scene representations is related to memory performance in childhood

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Abstract

Successful memory encoding is supported by medial temporal, retrosplenial, and occipital regions, which show developmental differences in recruitment from childhood to adulthood. However, little is known about the extent to which neural specificity in these brain regions, or the distinctiveness with which sensory information is represented, continues to develop during middle childhood and how it contributes to memory performance. The present study used multivariate pattern analysis to examine the distinctiveness of different scene representations in 169 children and 31 adults, and its relation to memory performance. Most children provided data over up to three measurement occasions between 8 and 15 years (267 total scans), allowing us to examine changes in memory and neural specificity over time. Memory performance was lower in children than in adults, and increased in children over time. Different scenes presented during memory encoding could be reliably decoded from parahippocampal, lateral occipital, and retrosplenial regions in children and adults. Neural specificity in children was similar to adults, and did not change reliably over time. Among children, higher neural specificity in scene-processing regions was associated with better memory concurrently. These results suggest that the distinctiveness with which incoming information is represented is important for memory performance in childhood, but other processes

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Competing Interests

None of the authors have any conflict of interest to declare.

operating on these representations support developmental improvements in memory performance over time.

Keywords

child development; fMRI; decoding; memory; scene; representation; parahippocampal; retrosplenial; occipital

The capacity to bind together different features of an episode, such as information about where, when, and what happened, plays a key role for the development of memory in childhood (e.g., Ghetti & Bunge, 2012; Lee, Wendelken, Bunge, & Ghetti, 2016; Ngo, Newcombe, & Olson, 2018). The hippocampus has long been recognized for supporting the binding of different features into a coherent mnemonic representation (e.g., Eichenbaum, 2017; Yonelinas, 2013). The hippocampus receives sensory input from occipital and parietal regions via neighboring cortical regions in the medial temporal lobe (e.g., Inhoff & Ranganath, 2017). The formation of distinguishable memories may thus depend on the precision with which incoming sensory information is represented in these brain regions. Accumulating evidence suggests that hippocampal and cortical activations associated with memory success continue to develop and contribute to developmental change in memory processes (e.g., Ghetti et al., 2010; Gomez & Edgin, 2016; Ofen et al., 2007; Sastre et al., 2016; Selmeczy et al., 2018). However, remarkably little is known about the extent to which neural specificity in the regions carrying sensory information, or the distinctiveness of their neural representations, additionally contributes to memory in childhood. The present study begins to fill this gap in the literature by examining how neural specificity of scene representations is associated with multiple measures of memory performance in child development.

A posterior brain network including the parahippocampal and retrosplenial cortex, along with the default mode network, supports scene construction and perception (e.g., Epstein & Kanwisher, 1998; Mullally & Maguire, 2011; Vann, Aggleton, & Maguire, 2009), and is involved in representing the relations between contextual features and individual events (e.g., Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath & Ritchey, 2012). Thus, the specificity with which information associated with different events is represented in these cortical regions may play a critical role for children's memory-guided behavior, especially when scenes or other contextual features are processed.

Behaviorally, strong age differences in memory are observed for scenes and other complex visual stimuli (e.g., Chai, Ofen, Jacobs, & Gabrieli, 2010; Mandler & Robinson, 1978), motivating the hypothesis that there may be developmental differences in the fidelity of memory representations, or the extent to which sensory and contextual representations carry precise enough information to capture subtle differences in complex events. The examination of neural specificity may provide new insights into the degree to which these age differences may reflect differences in the specific representation of incoming information. Alternatively, failure to find developmental differences in neural specificity – in the face of overall positive associations with memory accuracy – would suggest that

developmental improvements in memory ability are not driven by the distinctiveness of sensory representations.

Initial neuroimaging evidence has not provided a coherent picture about the role of neural specificity of incoming information for memory success in childhood. To date, multivariate approaches have not been used to understand memory development, and findings from univariate approaches are inconsistent. On the one hand, a few studies examining encoding-related activity for subsequently remembered relative to subsequently forgotten information have reported age differences in several cortical regions supporting sensory representations, including the parahippocampal gyrus (Ghetti et al., 2010), the fusiform gyrus (Güler & Thomas, 2013) or occipital areas (Maril et al., 2011). These results indirectly suggest that the representation of mnemonic information at the time of encoding may potentially vary with age in development. On the other hand, several studies have failed to find age differences in cortical regions supporting sensory representations during memory encoding (e.g., Menon, Boyett-Anderson, & Reiss, 20015; Ofen et al., 2007). With regard to scene processing, one study reported that 7- to 11-year-olds activated less voxels in parahippocampal regions than adults during scene viewing suggesting that maturation of the (left) parahippocampal place area may continue beyond this age range (Golarai et al., 2007). Another study found age-related increases in activation in parahippocampal cortex during encoding of more complex relative to less complex scenes (Chai et al., 2010), suggesting a link between information-specific processing during learning and subsequent scene memory in childhood.

Taken together, results regarding age differences in neural activity associated with sensory processing during encoding are mixed. It should be noted, however, that previous studies vary considerably with respect to the age ranges examined and the specific tasks and stimuli used, thereby leaving open the question of whether differences in neural specificity are related to differences in memory ability beyond the context of a specific task.

Multivariate approaches may be particularly informative for examining neural specificity in childhood. Whereas univariate analyses provide information about activity in a voxel or averaged across a group of voxels, multivariate pattern analysis (MVPA, Haynes & Rees, 2006) can capture the patterns or configuration of activity across voxels (Chadwick, Bonnici, & Maguire, 2012, Coutanche & Thompson-Shill, 2013; Rissman & Wagner, 2012). It is therefore more sensitive to fine-grained activation patterns reflecting individual percepts or memory traces. Here, it can be expected that more distinct neural representations of incoming scene information will be associated with less overlapping patterns of neural activity (Li & Sikström, 2002). Given that greater overlap among representations should result in lower classification accuracy in MVPA, classification accuracy can be used as a measure of neural specificity (cf. Rissman & Wagner, 2012). In aging, neural specificity declines, such that distributed activity patterns evoked by different visual categories (e.g., faces, scenes, objects) are more similar in older than in younger adults (e.g., Carp, Park, Hebrank, Park, & Polk, 2011). Furthermore, lower category-level neural specificity has been associated with lower fluid reasoning and processing speed among older adults (Park, Carp, Hebrank, Park, & Polk, 2010), indicating that the distinctiveness of sensory information contributes to higher cognitive functions. The extent to which individual differences in

neural specificity are associated with children's memory, and cognitive abilities more broadly, is currently unknown.

Critically, recent studies have gone beyond classification of different categories (e.g., faces vs. scenes) to demonstrate that activity patterns can facilitate the classification of different exemplars of the same category (e.g., scene A vs. scene B), thereby allowing to capture the fidelity of memory representations at the item level (e.g., Favila, Chanales, & Kuhl, 2016; Xue, 2018). We adopted this approach to examine how the extent of differentiation among similar events (i.e., within the same general semantic category) is associated with memory performance during childhood. Three questions motivated the present research: (1) Are distributed activity patterns evoked by different scenes during memory encoding more similar in children (7–12 years) than in adults? (2) Is neural specificity related to individual differences in memory ability beyond a particular task? (3) Does neural specificity contribute to improved memory performance over time?

We investigated these questions in 169 children (7–12 years) and 31 adults (18–25 years) during encoding of scene-object pairings in the scanner. Children viewed one of three distinct scenes briefly before individual unique objects were superimposed on the scene. Children were instructed to remember the scene-object pair for a subsequent memory test. We trained and tested a MVPA classifier to distinguish patterns of multivoxel activity associated with each of the three scenes using a leave-one-run-out cross-validation. Age differences in neural specificity were examined in *a priori* regions of interest (ROIs) implicated in scene processing, including the lateral occipital cortex, parahippocampal cortex, retrosplenial cortex, and anterior hippocampus.

In line with previous findings in adults (cf. Diana, Yonelinas, & Ranganath, 2008; Rissman & Wagner, 2012), we predicted that the three scenes would be reliably decoded from areas associated with scene perception in both children and adults. However, we further predicted that classification accuracy for within-category exemplars would be higher for adults than children. Additionally, we predicted that children with better memory performance would exhibit greater neural specificity.

To examine the relation between neural specificity and memory beyond a specific task, we examined whether classification accuracy across scene-processing regions is associated with a latent factor of episodic memory that captured common variance in memory performance across three different tasks. We tested this hypothesis with structural equation modeling.

Finally, we sought to test the prediction that neural specificity at one timepoint would predict the growth of memory for individual children. To this end, we analyzed longitudinal data from two additional time points (time point 2 (T2) = 137 children, 8–14 years; time point 3 (T3) = 104 children, 9–15 years).

Methods

Participants

A total of 169 children were included in the present study at T1 ($M_{\text{age}} = 9.43$ years, $SD_{\text{age}} = 1.10$; $N_{\text{females}} = 86$). Of those, 99 children provided neuroimaging data for MVPA analysis ($M_{\text{age}} = 9.77$, $SD_{\text{age}} = 1.03$, $N_{\text{females}} = 56$). A total of 93 children provided both complete behavioral data and complete neuroimaging data. The remaining participants either contributed only behavioral data ($N = 45$), were excluded from neuroimaging analyses due to excessive motion ($N = 25$), or provided complete neuroimaging, but only partial behavioral data ($N = 6$). Additionally, 31 adults ($M_{\text{age}} = 19.18$ years, $SD_{\text{age}} = 1.34$, $N_{\text{females}} = 17$) were included at T1 for age difference analyses. A total of 137 children provided data at T2, which took place 0.7 to 3 years after the initial assessment (65 females, $M_{\text{age}} = 10.83$, $SD_{\text{age}} = 1.22$). Of those, 93 children provided neuroimaging data at T2 (49 females, $M_{\text{age}} = 10.83$, $SD_{\text{age}} = 1.08$). A total of 86 children provided both complete behavioral and neuroimaging data, while the remaining participants elected to contribute only behavioral data ($N = 28$), did not complete all three behavioral tasks ($N = 7$), or were excluded for excessive motion ($N = 16$). Finally, 104 children provided data at T3, which took place 0.7 to 2 years later (49 females, $M_{\text{age}} = 11.96$ years, $SD_{\text{age}} = 1.26$). Of those, 74 children provided neuroimaging data at T3 (30 females, $M_{\text{age}} = 12.00$ years, $SD_{\text{age}} = 1.22$), while the remaining participants elected to contribute only behavioral data ($N = 25$) or were excluded for excessive motion ($N = 5$). A total of $N = 65$ children provided complete behavioral and neuroimaging data, whereas $N = 11$ children provided full neuroimaging, but only partial behavioral data. The UC Davis Institutional Review Board approved the study. Informed consent was obtained from all participants and their parents.

Memory Tasks

Memory ability was assessed across a set of three tasks, including a scene-object task (fMRI), the WRAML picture subtest (behavioral), and a selective scene encoding task (behavioral). Successful performance in all these tasks required remembering scene information, but the tasks differed in the specific scenes used and the aspects of scene information that participants needed to focus on.

Scene-object task.—Participants performed three interleaved encoding and retrieval runs of a scene-object memory task. Each encoding run included 48 picture drawings of an object or an animal (cf. Cycowicz et al., 1997), presented on one of three possible background scenes: a farm, a park, or a city. Each trial began with presentation of one of the three scenes. After 1000 ms, an object or an animal was superimposed on the scene for 500 ms. Following, a visual prompt (“Does it belong?”) appeared above the scene-object pair, cueing participants to indicate whether they thought the drawing belonged to the corresponding scene. Participants were given up to 2000 ms for this decision. Trials were intermixed with a jittered fixation period (500 – 8000 ms).

Each retrieval run included the 48 drawings from the preceding encoding run, along with 16 novel drawings that had not been seen before. Participants were instructed to decide whether a drawing was previously studied (i.e., seen in the preceding encoding run) or new (i.e.,

never seen before). If participants recognized an object or an animal as previously studied, they were instructed to indicate the scene with which it had been studied – or, if they did not remember which scene it had been paired with, to select the “not sure” button.

Memory performance in this task was used as one of three indicators of episodic memory capacity. More specifically, performance was computed as hits (i.e., trials in which a scene was chosen for accurately recognized studied object) – false alarms (i.e., trials in which a scene was chosen for an inaccurately recognized novel object) (Snodgrass & Corwin, 1988). Note that the design of this task allows for the computation of additional indices of memory performance. However, we opted for computing recognition accuracy in this way to increase comparability to the remaining indicator tasks and because the decision about whether the object has been presented is not made separately and independently from choosing a scene, thereby allowing to capture how scenes are used in service of memory. Neuroimaging data from the encoding phase was used for MVPA analyses. Neuroimaging data from the retrieval phase were not included in the present analyses (see Sastre et al., 2016; Selmeczy et al., in press).

Wide Range Assessment of Memory and Learning (WRAML) picture subtest.

—Participants were shown 4 different scenes (a zoo, a classroom, a garage, and a living room) one at a time and could examine the scene for 10 seconds. Immediately after the 10 seconds, participants were presented with an altered version of the corresponding scene and were asked to identify elements of the scene that have been changed by placing a mark on each part of the picture that has been changed, moved, or added. Feedback was provided for the first scene.

Following WRAML’s evaluation instructions, the raw number of correct responses was used as the main index of memory performance on this test in the analyses reported below. However, this index is based on correct identification of changed scene elements at test, without a penalty for incorrectly marked changes (i.e., indicating that a scene element has been changed when in fact it was the same). Control analyses were performed, in which we counted the number of incorrectly marked changes for each participant and used these to derive a memory score similar to the other tasks (i.e., correctly marked changes – incorrectly marked changes). Results were similar with both the raw number of correct responses and the difference between correct and incorrect responses.

Selective scene encoding task.—During encoding (cf. Fandakova et al., 2017), participants were presented with 24 blocks of 4 outdoor scenes each that were either assigned to an active encoding condition (16 blocks) or a passive encoding condition (8 blocks). Active blocks were designed to examine the modulation of attention; participants were instructed to attend to scenes presented on a green background, and to ignore (but still view) scenes presented on a red background. After each active block, participants were presented with a scene that was either one of the stimuli they had been asked to attend to (i.e., previously presented in green) or a novel scene, and were asked to indicate whether the item had been presented in the previous block. During passive blocks, participants were instructed to passively view scenes presented on a blue background. Following passive blocks, participants viewed an arrow and had to indicate the direction of the arrow. Each

scene was presented for 3 seconds, and the order of passive and active blocks was counterbalanced across participants.

Immediately after encoding, participants were given a self-paced recognition test involving stimuli from all 24 blocks. They viewed a scene and indicated whether they had seen it before, regardless of encoding condition (i.e., old scenes previously presented on a green, red, or blue background; 48 scenes) or novel (i.e., a new scene; 32 scenes). None of the test scenes had been used as probes during the encoding phase; thus, all the test scenes had been viewed only once before. As in the scene-object task, memory performance was computed as hits (i.e., studied scenes correctly recognized as “old”, irrespective of encoding condition) – false alarms (i.e., novel scenes incorrectly recognized as “old”).

fMRI Data Acquisition

Functional images were collected using a Siemens 3T Trio scanner with a 32-channel head coil and a gradient EPI sequence (TR = 2000 ms, TE = 23 ms, no interslice gap, FOV = 204 mm, 37 slices, voxel size = 3 × 3 × 3 mm). A T1-weighted MPRAGE was acquired for co-registration of the functional images (TR = 2500 ms, TE = 3.24 ms, FOV = 224 mm, voxel size = 0.7 × 0.7 × 0.7 mm).

Behavioral Data Analysis.

We conducted behavioral analyses in the structural equation modeling framework (McArdle, 2009). With three indicator measures of memory performance, we estimated a latent factor of memory ability. This approach allowed us to examine individual differences in memory ability without contamination by unique variability (i.e., measurement error) of the single memory tasks, while at the same time allowing for more flexibility in dealing with missing data (e.g., Kievit et al., 2017). The present indicator tasks were well suited for this type of analyses as demonstrated by their relatively high correlations among children (scene-object <-> selective encoding: children $r = .40$, $p < .001$, adults $r = .49$, $p = .005$; scene-object <-> WRAML picture: children $r = .25$, $p = .002$, adults $r = -.14$, $p = .46$; selective encoding <-> WRAML picture: children $r = .19$, $p = .02$, adults $r = .07$, $p = .72$).

Analyses were conducted using Onyx (von Oertzen et al., 2015). First, a latent memory factor was modeled separately for children and adults (see Supplementary Figure 1). Subsequently, we used multi-group models to compare the latent memory factor between children and adults. Based on previous research demonstrating superior memory in adults, we sought to confirm a higher factor mean in adults than in children. Parameters were tested by restricting the corresponding paths to zero or to equality across groups and comparing the model fit of the resulting nested models to the freely estimated models via the χ^2 statistic with degrees of freedom (DF) equal to the difference in the number of free parameters.

fMRI data analysis

Data were preprocessed using SPM8 (www.fil.ion.ucl.ac.uk/spm). Preprocessing steps included slice-time correction, realignment to the first volume using rigid body motion correction with sinc interpolation, co-registration to the MPRAGE, and smoothing with a 6-mm FWHM isotropic Gaussian kernel. These preprocessing steps have been shown to

minimally affect classification accuracy, while at the same time allowing for meaningful comparisons across subjects with variability in brain anatomy (Kamitani & Sawahata, 2010; de Beeck, 2010). Volumes with head motion > 1 mm or signal change > 2% were replaced with interpolated values using ArtRepair (<http://cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html>). If more than 25% of the volumes in one scan were replaced, the corresponding scan was excluded from further analyses. Participants with fewer than two valid functional scans were not included in analyses.

MVPA analyses were performed in the following steps. First, we independently defined ROIs for this analysis. To this end, we performed a Neurosynth search (search term “scenes”, June 2016; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) and identified brain regions involved in scene processing across the 178 recovered studies (reverse inference, $p < .01$, FDR-corrected). From this mask, we isolated clusters including more than 100 voxels (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Cluster>). These regions included the bilateral lateral occipital cortex (Lat Occip), bilateral posterior parahippocampal cortex, extending into the lingual gyrus and the fusiform gyrus (PHG), bilateral retrosplenial cortex (RSC), and the bilateral anterior hippocampus (Ant HC). Two additional clusters in the right inferior occipital cortex and the middle temporal gyrus were not included in the present analyses, which were restricted to theoretically motivated ROIs involved in scene processing. To ensure the anatomical specificity of each ROIs, the Neurosynth activation map was masked with a bilateral anatomical mask of each of these regions from the AAL atlas, resulting in a total of four bilateral ROIs used in subsequent analyses. Given that the posterior hippocampus has been implicated in scene processing (Ranganath & Ritchey, 2012), in additional control analyses we examined bilateral anatomical ROIs of the hippocampal body and tail based on the AAL atlas.

Second, we identified the most active voxels for each individual participant in each ROI. More specifically, we used the general linear framework to estimate the contrast trial > baseline at encoding in each individual participant. We modeled encoding-related activity with trial as a main regressor of interest and six estimated motion parameters as regressors of no interest. The resulting individual whole-brain maps were masked with each ROI to extract the 50 or 100 most active voxels within the corresponding ROI within each individual participant. We selected these two different voxel sizes to ensure that the number of included voxels did not affect the reported results. All analyses were corrected for multiple comparisons using an FDR correction.

Third, we used the TDT toolbox (Hebart, Görgen, & Haynes, 2015) to perform MVPA analysis. MVPA analyses were performed in native space. A $L2$ -norm regularized support vector machines classifier (Hebart et al., 2015) was trained to classify the currently presented scene at encoding using a leave-one-run-out cross-validation. Parameter estimates for single trials were derived based on a stick function to model the onset of the trial. Note that since analyses were performed on the encoding data of the scene-object paradigm, the data in each run are balanced. We tested whether classification accuracy in the ROIs differed from chance (33.3%, given a choice among three scenes) and between age groups.

Finally, we related classification accuracy to the latent memory factor to examine the extent to which neural specificity of distributed activation patterns in scene-processing brain regions was positively associated with memory ability in children. As we did not have specific hypotheses about differences among areas involved in scene processing, we formed a composite score representing average classification accuracy across ROIs with above-chance accuracy, and related it to the latent memory factor.

Longitudinal analyses including T2 and T3 were performed following the same procedures as at the initial assessment, with the 50 and 100 most active voxels being determined separately for each time point. Thus, we used the same identical Neurosynth-based ROIs at each time point, but we performed the trial > baseline contrast separately at each time point, and selected the most active voxels within the corresponding ROI separately at each time point. This approach ensures that conclusions are based on the most active group of voxels within an individual at any given point in time within established ROIs.

To assess relations of change over time between classification accuracy and memory ability, we fit continuous time structural equation models using the ctsem software (Driver, Oud, & Voelkle, 2017). Here again we used composite scores for the neural specificity factor. This factor was conceptualized in terms of classification accuracy across all scene-processing regions with above-chance classification accuracy, and thus with only a single measurement error term. The models were structured as is typical for latent change and continuous time models, with initial intercepts and slopes for each factor, while at the same time accounting for individual differences in age and time intervals between measurement occasions. Because of the limited number of time points and the research focus on relations between overall change, the model we focused on did not incorporate shorter-term fluctuations from time point to time point. We did, however, repeat the analysis using an expanded model including stochastic change terms and cross-effects to check the consistency of inferences between the simpler and expanded model. While point estimates differed somewhat, results were similar across both models. Thus, we report the simpler model for both ease of understanding, and because of its lower AIC value (Akaike, 1973), indicating it is more likely to be an appropriate model. We performed control analyses including mean age (standardized) as a time-invariant predictor in the model. Although reported below, the results of these analyses should be treated as exploratory.

Results

Developmental differences in memory ability.

A model of memory performance in the scene-object task, selective encoding task, and the WRAML picture subtest in children demonstrated a significant positive correlation between age and memory ability, $r = .53$, $\chi^2 = 30.57$, $DF = 1$, $p < .001$ (Figure 1). A multi-group model including children and adults indicated that memory ability was significantly lower in children ($M_{\text{children}} = .67$) than in adults ($M_{\text{adults}} = .85$), $\chi^2 = 28.97$, $DF = 1$, $p < .001$. In line with these cross-sectional age differences, continuous time structural equation models revealed that memory ability increased significantly over time, $M = .27$, $SD = .03$, 95% CI: .21 to .34. Control analyses including children's age as a time-invariant predictor revealed that older children showed overall higher memory, $b = .36$, $SD = .07$, 95% CI: .23 to .49, and

less pronounced increase in memory over time, $b = -.15$, $SD = .03$, 95% CI: $-.23$ to $-.08$. Together, these results are consistent with protracted memory development and suggest that memory ability continues to improve in early adolescence.

Classification accuracy in adults and children.

Before examining MVPA classification accuracy in children, we first sought to establish whether the patterns of neural activity associated with the three different scenes in the present study can indeed reliably be decoded in adults from the ROIs involved in scene processing according to the Neurosynth meta-analysis (Figure 2A). We observed an above-chance classification accuracy in the parahippocampal/fusiform gyrus, retrosplenial cortex, and in the lateral occipital ROI (Figure 2B; Table 1). In contrast, classification accuracy in the anterior hippocampus was less consistent, and varied with the number of voxels included in the classification analysis (Table 1).

Similarly to adults, the three scenes could be reliably decoded from the parahippocampal, retrosplenial, and the lateral occipital ROIs in children (Figure 2C; Table 1). Classification accuracy did not differ significantly from chance in the anterior hippocampus (Figure 2C; Table 1). Thus, the regions that showed reliable differences in distributed activity patterns evoked by different scenes during memory encoding – parahippocampal, retrosplenial and lateral occipital areas – were the same in children and adults. At the same time, results in the hippocampus were less consistent across mask sizes. Consistent with these findings, whole-brain searchlight analyses revealed similar posterior brain regions in both children and adults, suggesting that the results are unlikely to be driven by the selection of ROIs (Supplementary Figure 2).

To directly compare age groups and brain regions, we conducted a mixed ANOVA on classification accuracy with group (children vs. adults) and ROI (anterior hippocampus vs. parahippocampal vs. retrosplenial vs. lateral occipital). We found a main effect of ROI ($F_{50 \text{ voxels}(3,387)} = 13.96$, $p < .001$, $\eta_p^2 = .05$; $F_{100 \text{ voxels}(3,387)} = 14.68$, $p < .001$, $\eta_p^2 = .10$), which was driven by lower classification accuracy in the anterior hippocampus compared to the remaining ROIs (all $p_{FDR} < .05$) along with higher classification accuracy in the occipital ROI compared to the parahippocampal ROI (all $p_{FDR} < .05$) and at a trend level compared to the retrosplenial cortex ($p_{FDR 50 \text{ voxels}} = .08$, $p_{FDR 100 \text{ voxels}} < .001$). There were no differences in classification accuracy between the parahippocampal and retrosplenial regions (all $p_{FDR} > .30$). We observed no main effects of age group ($p_s > .10$) or group x ROI interactions ($p_s > .45$). Control analyses confirmed that these results were not confounded by age differences in univariate activation. More specifically, there were no age differences in univariate scene-related activation (i.e., trial > baseline) at encoding in any of the ROIs (all $p_s > .15$). Univariate activation was not correlated with classification accuracy in the ROIs (all $r_s < .17$, all $p_s > .05$). When univariate activation was accounted for in age comparisons of classification accuracy, the results reported above did not change.

In sum, scene classification accuracy was similar across age groups, and was highest in the lateral occipital cortex. These results were replicated at T2 and T3 (Figure 2C), where children again demonstrated above-chance classification accuracy in the parahippocampal, retrosplenial and lateral occipital ROIs, but not in the hippocampus (Table 1).

Previous research has implicated the posterior hippocampus in scene processing and contextual memory (cf. Ranganath & Ritchey, 2012). In control analyses, we therefore examined whether the hippocampal body and tail showed above-chance classification accuracy. We did not find evidence for consistently reliable decoding from the hippocampal body or tail across mask sizes in children and adults (see Supplementary Figure 3 for details).

Scene representation distinctiveness and memory ability.

Children demonstrated substantial heterogeneity in classification accuracy in scene-processing regions (Figure 3A). To further examine whether this variability was associated with individual differences in children's memory performance, we computed a composite score representing average classification accuracy across parahippocampal, retrosplenial, and lateral occipital ROIs, from which scene information could be decoded reliably. Next, we related this composite score to the latent factor of episodic memory capacity.

A model combining memory and classification accuracy in children demonstrated an acceptable fit to the data (*50-voxel mask*: $\chi^2 = 0.32$, $DF = 2$, $RMSEA = .00$; *100-voxel mask*: $\chi^2 = 0.14$, $DF = 2$, $RMSEA = .00$). There was a significant correlation between scene representation specificity and memory ability (Figure 3B), such that children with higher classification accuracy across scene processing regions showed better memory, ($r_{50 \text{ voxels}} = .40$, $\chi^2 = 9.02$, $DF = 1$, $p = .003$; $r_{100 \text{ voxels}} = .51$, $\chi^2 = 14.84$, $DF = 1$, $p < .001$). Similar results were obtained when participants' age was included in the model ($r_{50 \text{ voxels}} = .32$, $\chi^2 = 6.97$, $DF = 1$, $p = .008$; $r_{100 \text{ voxels}} = .40$, $\chi^2 = 18.65$, $DF = 1$, $p = .001$). If, instead of using a composite score across ROIs, classification accuracy for each ROI was independently correlated with memory, the relation was primarily driven by the parahippocampal ROI ($r_{50 \text{ voxels}} = .46$; $r_{100 \text{ voxels}} = .42$, $ps < .005$), with lower positive values in lateral occipital ($r_{50 \text{ voxels}} = .13$, $p = .17$; $r_{100 \text{ voxels}} = .33$, $p = .01$) and retrosplenial regions ($r_{50 \text{ voxels}} = .15$, $p = .16$; $r_{100 \text{ voxels}} = .32$, $p = .02$). Thus, children's memory ability tracked representational specificity, particularly in parahippocampal cortex.

Continuous time structural equation models revealed that classification accuracy across scene-processing regions did not change significantly over time in children, $M_{50 \text{ voxels}} = .022$, $SD_{50 \text{ voxels}} = .06$, 95% CI: $-.096$ to $.14$; $M_{100 \text{ voxels}} = .03$, $SD_{100 \text{ voxels}} = .057$, 95% CI: $-.08$ to $.15$. Notably, we observed a positive correlation between the memory ability intercept and the classification accuracy intercept, $r_{50 \text{ voxels}} = .67$, 95% CI: $.21$ to $.94$; $r_{100 \text{ voxels}} = .65$, 95% CI: $.32$ to $.92$, suggesting that children with overall greater neural distinctiveness in the scene-processing network had overall better memory. At the same time, we did not find evidence that neural specificity was related to change in memory over time, all $ps > .05$. Thus, representational specificity helped to explain individual differences among participants, but not improved memory over middle childhood.

Control analyses including children's age revealed that older children showed higher classification accuracy ($b_{50 \text{ voxels}} = .22$, $SD_{50 \text{ voxels}} = .097$, 95% CI: $.03$ to $.41$; $b_{100 \text{ voxels}} = .20$, $SD_{100 \text{ voxels}} = .10$, 95% CI: $.01$ to $.40$), and a tendency for less pronounced change in classification accuracy over time ($b_{50 \text{ voxels}} = -.14$, $SD_{50 \text{ voxels}} = .07$, 95% CI: $-.27$ to $-.09$; $b_{100 \text{ voxels}} = -.11$, $SD_{100 \text{ voxels}} = .06$, 95% CI: $-.23$ to $.01$). Importantly, including age as a

time-invariant covariate did not change the observed positive relation between individual differences in classification accuracy and memory, $r_{50 \text{ voxels}} = .60$, 95% CI: .04 to .93; $r_{100 \text{ voxels}} = .62$, 95% CI: .28 to .91.

Discussion

The present study investigated the neural specificity of scene representations in childhood, and how it contributes to memory performance across a variety of tasks. In both children (7–12 years) and adults, distributed activity patterns evoked by different complex scenes could be reliably decoded from cortical regions implicated in scene processing, including the parahippocampal and fusiform cortex, retrosplenial cortex, and lateral occipital cortex. Classification accuracy of the scene-specific neural patterns during memory encoding was above chance and similar across age groups. Notably, children with higher levels of neural item-level specificity for scene representations – particularly in parahippocampal cortex – demonstrated better memory. At the same time, we found no evidence that neural specificity was related to longitudinal memory improvements in the transition from childhood to adolescence.

During memory encoding, we demonstrated that different scenes could be reliably decoded from several cortical regions in children. Moreover, we found similar levels of within-category classification accuracy across children and adults, indicating that the neural representation of complex scenes is relatively developed by middle childhood. To ensure that the present analysis was not biased by a particular group, we performed voxel selection within each individual for each ROI; this is likely to minimize age differences relative to studies in which areas are defined based on group results. While this result – similar classification accuracy between middle childhood and adulthood – is consistent with some studies examining univariate activity (e.g., Menon et al., 2005; Ofen et al., 2007), it is seemingly at odds with other studies demonstrating age-related increases in univariate activity in the parahippocampal place area during successful scene encoding (e.g., Chai et al., 2010; Golarai et al., 2007). It should be noted, however, that differences in distributed patterns of neural activity do not necessarily correspond to differences in average activity across a group of voxels (Rissman & Wagner, 2012). Critically, age-invariant classification accuracy points to the possibility that sensory information necessary to form episodic memories is successfully represented during this age period, and that developmental differences observed in univariate activity, including longitudinal changes in task-related activity (e.g., Fandakova et al., 2018; Selmecky et al., 2018), may reflect the development of memory processes associated with committing incoming information to memory, not in the fidelity with which item-level sensory and contextual information is represented at encoding.

Neural representations of incoming information over distributed cortical networks represent key building blocks of memory. In adults, the fidelity of neural representations has been linked to the success of memory formation at the trial level (e.g., Xue et al. 2010; Favila et al., 2016). Additionally, higher category-level neural specificity has been associated with better memory performance in the same task (e.g., Kuhl, Rissman, & Wagner, 2012). At the behavioral level, lower fidelity of item-level representations, especially with visually complex stimuli, may result in lower memory accuracy and greater susceptibility to false

memories (e.g., Ye et al., 2016). Here, we provide evidence that the distinctiveness with which information about different complex scenes is represented during encoding in cortical regions associated with scene processing is related to better memory in childhood. Of note, representational specificity was correlated with memory ability beyond the specific task in which neural specificity was assessed, suggesting that this measure may capture a more general property related to the ability to form distinct representations for complex scene stimuli.

What might be a possible neural mechanism underlying the relation between neural specificity and individual differences in memory? Li and colleagues (2001) proposed a neurocomputational model linking age-related cognitive deficits in later adulthood to decreases in dopaminergic modulation. In this model, simulating decline in dopaminergic modulation resulted in lower neuronal responsivity and led to increased neural noise and less distinctive neural activation patterns. Although comparable evidence in childhood is missing, dopamine levels have been shown to increase during childhood (e.g., Goldman-Rakic & Brown, 1982) and adolescence (Hoops & Flores, 2017; Luciana, Wahlstrom, Porter, & Collins, 2012) in humans and non-human primates. These changes are multifaceted in nature, including changes in dopamine receptor density and dopamine concentration. In addition, the exact trajectory of dopaminergic change is a matter of debate with some evidence of linear increase from childhood to adolescence vs. a concentration peak in adolescence (cf. Wahlstrom et al., 2017). Consistent with the model proposed by Li and colleagues (2001), it is possible that individual variability in neural specificity may, at least to some extent, reflect individual differences in dopaminergic modulation (cf. Luciana et al., 2012) that contribute to heterogeneity in memory performance. The present results are consistent with empirical findings from aging - age-related reductions in neural specificity have been related to declines in cognitive performance across a variety of tasks (e.g., Park et al., 2010; Zheng et al., 2017). Interestingly, correlations between different tasks and cognitive domains are higher in children and older adults than in younger adults, likely because individual differences are driven primarily by domain-general rather than domain-specific factors (e.g., Baltes, Lindenberger, & Staudinger, 2006). To the degree to which neural specificity reflects neural responsiveness regulated via dopaminergic pathways, representation fidelity may represent a domain-general mechanism contributing to individual differences in cognition.

Based on the well-established contributions of dopamine to cognitive control (e.g., Cools, 2008), we should also consider that stimulus-specific processing can be enhanced through the engagement of top-down cognitive control processes in children and adults (e.g., Wendelken, Baym, Gazzaley, & Bunge, 2011). Further research is needed to examine how neural specificity for stimuli of different types and complexity interacts with these modulatory top-down effects.

We did not find evidence that neural specificity was related to individual differences in memory improvement over time. Variability in memory improvement over time may therefore be driven primarily by other developmental forces, such as the ability to bind different features of an event in an integrated memory representation (e.g., Ghetti & Bunge, 2012), the ability to regulate encoding and retrieval in line with ongoing task demands

dependent on fronto-parietal development (e.g., Fandakova et al., 2018; Simmonds, Hallquist, & Luna, 2017; Yu et al., 2018), the increasing influences of pubertal changes (e.g., Selmečzy et al., 2018), or the increasing importance of motivational factors (e.g. Davidow, Foerde, Galván, & Shohamy, 2016). Future research is needed to directly test the influence of these different factors against each other.

The present study corroborates and extends the few previous studies that examined the relevance of scene processing for subsequent memory in childhood (Chai et al., 2010; Wendelken et al., 2011). Furthermore, a recent study (Rosen et al., 2018) reported that encoding-related activity in the fusiform face area and in the lateral occipital lobe predicted associative memory for face-object pairs in 6- to 19-year-olds after controlling for age differences. This and other prior studies demonstrated the relevance of individual differences in the recruitment of sensory processing areas for memory formation in childhood (e.g., Natu et al., 2016). The present study extends these findings by examining multivariate patterns of activity in childhood and demonstrating that representational specificity plays an important role for individual differences in memory ability.

More generally, multivariate approaches might provide further insights on the development of category-specific areas. For example, some studies suggested that object recognition in the lateral occipital complex is mature prior to age 8 (e.g., Golarai et al., 2007), whereas others demonstrated age-related increases in activity up to late adolescence (e.g., Rosen et al., 2018). Similarly, it is yet unclear whether age-related increases in the lateral occipital complex, as well as in the fusiform area for faces, reflect the development of modulatory effects of top-down attention or further development in neural specificity.

We acknowledge several limitations in the present study. First, we selected regions of interest that represent key nodes of the scene-processing network based on a Neurosynth meta-analysis. Although this procedure ensured that ROIs were defined independently of the task in which neural specificity was examined, the present design did not allow to determine ROIs based on localizer tasks specific to individual participants. Thus, it is possible that our results do not fully capture the development of neural specificity and its relevance for behavior. Our approach to select either 50 or 100 most informative voxels specific for each participant along with the whole-brain searchlight analyses likely attenuate this problem, but future research should complement these findings by using localizer tasks. Related to this, the task in which we examined neural specificity was not a pure scene task, but rather a scene-object association task. Thus, scene-object binding processes at encoding may have contributed to lower classification accuracy than would have been observed in a pure scene task. Even though the relation with memory performance speaks to the role of improved fidelity of scene representation (e.g., Xue, 2018), we cannot completely rule out that scene-object binding may have contributed to individual differences in classification accuracy. Second, due to the developmental focus of the study, our adult sample was relatively small and demonstrated uniformly high memory performance, thereby precluding us from examining the contributions of neural specificity to memory in adults. Finally, future studies should examine younger children to test whether, based on the modulatory role of dopamine, age differences in neural specificity may be pronounced earlier in development. Here, different measures of memory performance that vary systematically on relevant dimensions

such as encoding-retrieval delay, incidental vs, intentional encoding, and that extend beyond scenes should be included.

Taken together, our results indicate that neural specificity of the distributed activity patterns evoked by different scenes is relatively mature by middle childhood, and is associated with memory ability in the transition between childhood and adolescence. Future research should test the extent to which these contributions reflect direct effects via different levels of distinctiveness in neural representations, possibly related to dopaminergic modulation, or indirect effects via biasing the engagement of still developing cognitive control operations. Thus, examining multivariate patterns of activity may contribute to our understanding of episodic memory development in childhood and beyond.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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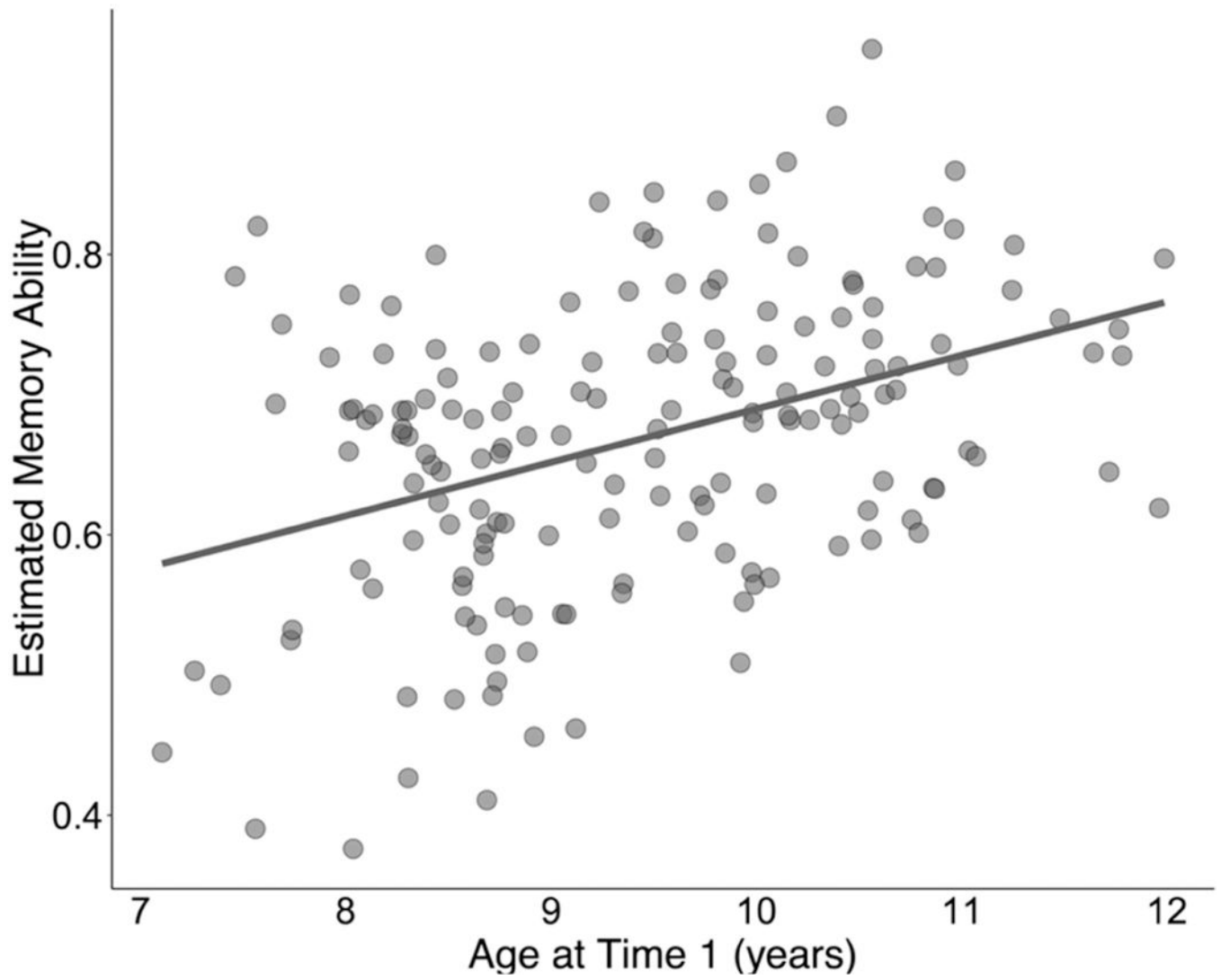


Figure 1. Estimated memory ability in children based on a latent factor of the scene-object task, selective encoding task, and the WRAML picture subtest. Older children demonstrated higher memory than younger children.

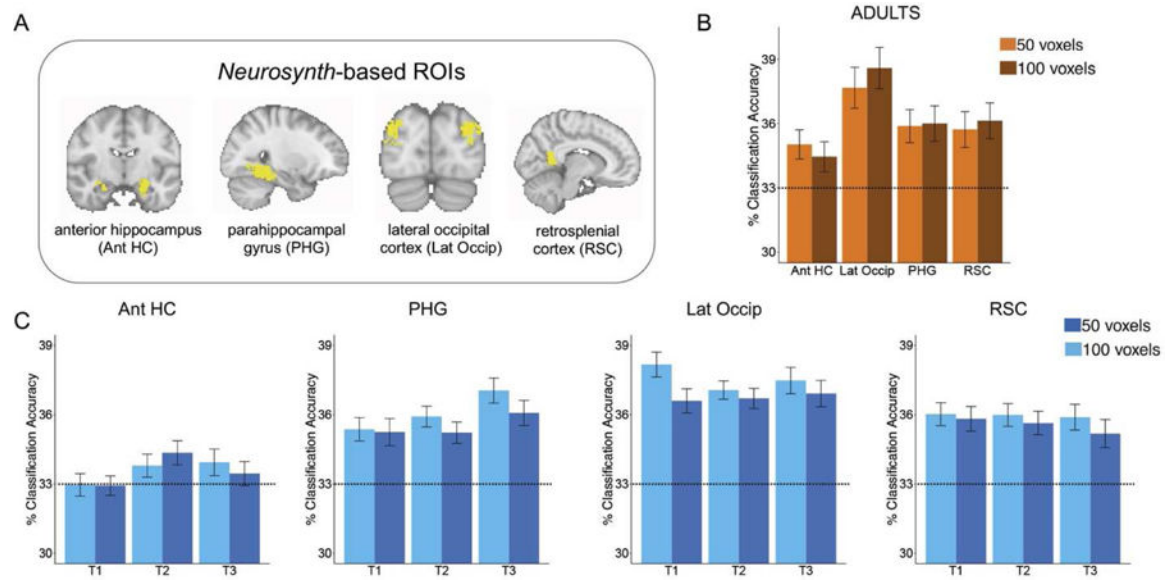


Figure 2.

Classification accuracy in scene-processing regions. **A.** Scene-processing ROIs based on Neurosynth meta-analysis. All ROIs were bilateral. **B.** Classification accuracy in adults. **C.** Classification accuracy in children across ROIs and time points. With three scenes chance levels for classification accuracy are at 33.3% (dotted line). T1 = Time 1; T2 = Time 2; T3 = Time 3

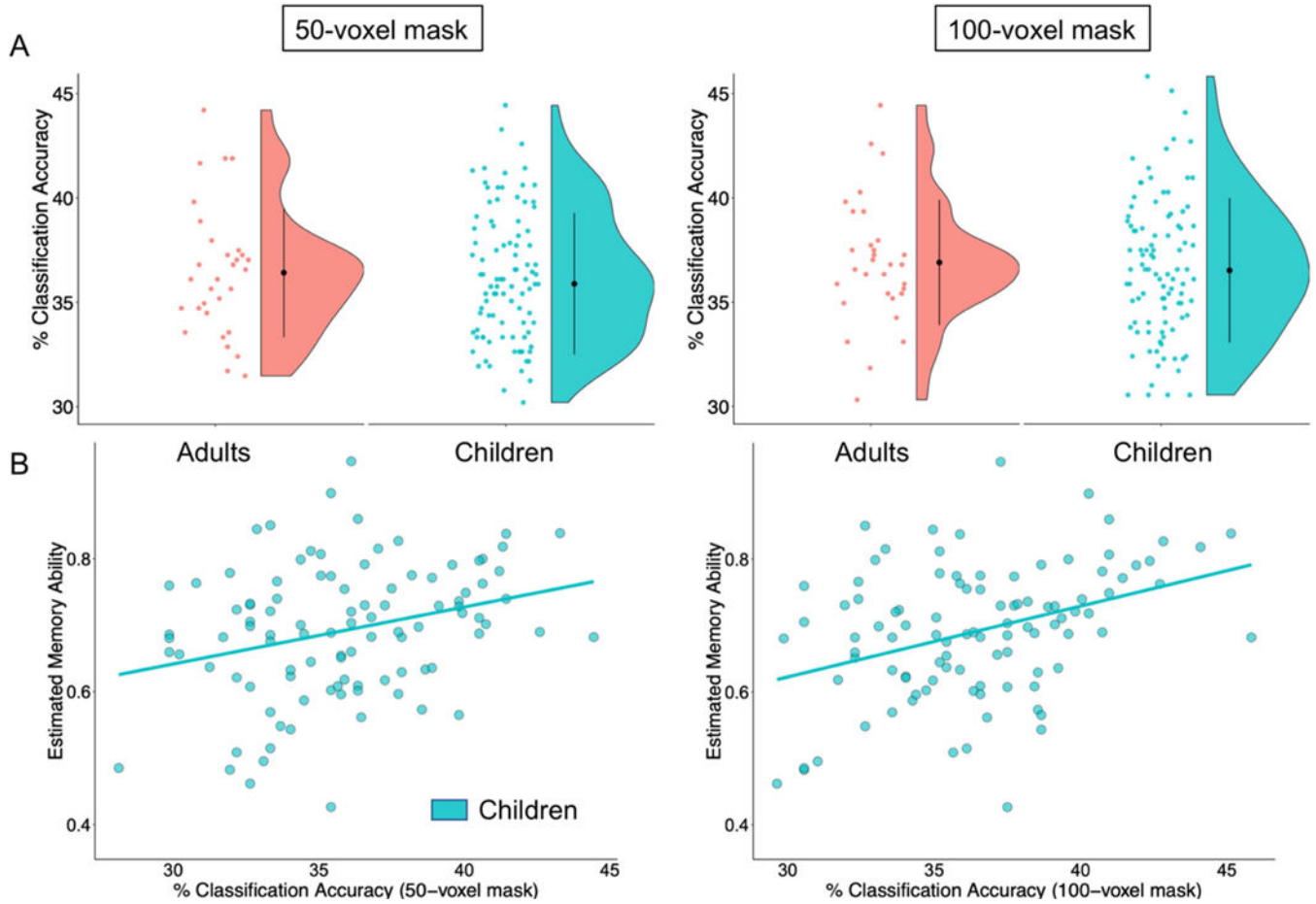


Figure 3. Individual differences in classification accuracy in the 50-voxel mask (left) and the 100-voxel mask (right) is related to memory ability at Time 1. **A.** Individual differences in classification accuracy across scene-processing regions (i.e., composite score of lateral occipital, parahippocampal, and retrosplenial ROIs which showed above-chance scene classification in both groups). Black dots represent average classification accuracy in children and adults. **B.** Correlation between classification accuracy and estimated memory ability in children. With three scenes chance levels for classification accuracy are at 33.3%.

Table 1.

Results of tests of classification accuracy against chance in adults and children at each time point. Reported p-values are corrected for multiple comparisons using an FDR correction.

Neurosynth ROI	50-voxel mask	100-voxel mask
Parahippocampal		
Children		
- <i>Time 1</i>	t(99) = 3.28, p _{FDR} = .001	t(99) = 4.01, p _{FDR} < .001
- <i>Time 2</i>	t(92) = 4.08, p _{FDR} < .001	t(92) = 5.75, p _{FDR} < .001
- <i>Time 3</i>	t(73) = 5.04, p _{FDR} < .001	t(73) = 6.84, p _{FDR} < .001
Adults	t(30) = 3.31, p _{FDR} = .004	t(30) = 3.23, p _{FDR} = .005
Retrosplenial		
Children		
- <i>Time 1</i>	t(99) = 4.67, p _{FDR} < .001	t(99) = 5.38, p _{FDR} < .001
- <i>Time 2</i>	t(92) = 4.53, p _{FDR} < .001	t(92) = 5.1, p _{FDR} < .001
- <i>Time 3</i>	t(73) = 3.04, p _{FDR} = .004	t(73) = 4.63, p _{FDR} < .001
Adults	t(30) = 2.86, p _{FDR} = .01	t(30) = 3.37, p _{FDR} = .004
Lateral occipital		
Children		
- <i>Time 1</i>	t(99) = 6.28, p _{FDR} < .001	t(99) = 4.01, p _{FDR} < .001
- <i>Time 2</i>	t(92) = 7.74, p _{FDR} < .001	t(92) = 9.50, p _{FDR} < .001
- <i>Time 3</i>	t(73) = 6.29, p _{FDR} < .001	t(73) = 7.28, p _{FDR} < .001
Adults	t(30) = 4.53, p _{FDR} < .001	t(30) = 5.46, p _{FDR} < .001
Anterior hippocampus		
Children		
- <i>Time 1</i>	t(99) = 0.95, p _{FDR} = .40	t(99) = 0.75, p _{FDR} = .46
- <i>Time 2</i>	t(92) = 1.95, p _{FDR} = .06	t(92) = 0.94, p _{FDR} = .46
- <i>Time 3</i>	t(73) = 0.23, p _{FDR} = .82	t(73) = 1.06, p _{FDR} = .34
Adults	t(30) = 2.49, p _{FDR} = .02	t(30) = 1.59, p _{FDR} = .12