Neural Signatures of Semantic and Perceptual Memory Formation Become More Similar Across Development

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Abstract

In adults, the contribution of the prefrontal cortex and hippocampus to memory encoding varies depending on the type of information being learned. Because these regions are still developing in children, their contribution to the formation of memories for different types of associations may differ from that of adults. Here, we examined how semantic and perceptual similarity between items affects memory behaviour and neural engagement in children (6-7 years) and adults. Participants completed a pair learning task during functional magnetic resonance imaging, in which pairs were perceptually or semantically related. Memory was tested outside the scanner with cued recall. Semantic similarity facilitated recall in both age groups, but more so in adults. Neurally, semantic pairs elicited broad frontoparietal activity while perceptual pairs engaged ventral visual and lateral prefrontal areas. Children showed more distinct neural responses to semantic versus perceptual pairs than adults, as well as more engagement in anterior hippocampus for semantic than perceptual pairs. These findings suggest that semantic similarity provides a powerful scaffold for memory across development, with age-related changes in memory encoding marked by a shift toward reliance on more integrated neural systems.

Keywords: associative memory; children; fMRI

Introduction

The ability to bind different elements of experience is central to episodic memory, and it is particularly critical during development as children learn to integrate different types of information to construct representations of the world around them. This process is often studied in the lab using associative memory tasks, which have shown that the ability to learn and retrieve associations improves drastically during childhood (Guillery-Girard et al., 2013). These improvements have been linked to developmental gains in the strategic aspects of memory (Shing et al., 2008; 2010) as well as the more basic ability to bind pieces of information into an integrated representation (Ghetti & Fandakova, 2020; Lee et al., 2016).

Previous work has identified the hippocampus (Eichenbaum et al., 1992; Moscovitch et al., 2006) and prefrontal cortex (PFC; Blumenfeld & Ranganath, 2007) as being particularly important for associative memory, and shown that these regions also display marked changes in their activation profiles between childhood and adulthood (DeMaster & Ghetti, 2013; Ghetti & Bunge, 2012; Tang et al., 2018). For example, developmental increases in PFC engagement during encoding have been linked to better subsequent memory (Ofen et al., 2007; Wendelken et al., 2011), and are thought to reflect greater use of more controlled processes (e.g., memory strategies; Shing et al., 2010). By contrast, hippocampal engagement during memory encoding is thought to reflect the binding of elements within an experience (Davachi, 2006), and past work has found stability (Ofen et al., 2007), increases (Ghetti et al., 2010), and decreases (Maril et al., 2010) in engagement with age, suggesting that developmental change in hippocampal involvement in memory formation may depend on factors such as task demands, the type of information being encoded, and the specific hippocampal subregions examined.

Importantly, the processes by which we encode and store memories may differ depending on the nature of the information, which may in turn modulate the involvement of these different brain regions. Past work has demonstrated that similarity between items (e.g., perceptual, semantic) can support learning of new associations (Mathews, 1977), and that the brain regions subserving such learning can vary according to the nature of the items' similarity (Davis et al., 2021; Naspi et al., 2021a; 2021b). The encoding of semantically related information has been linked to semantic processing and elaboration in adults, and is supported primarily by prefrontal and temporal regions (Martin et al., 2018; Prince et al., 2005). Conversely, the encoding of visually similar items typically engages more parietal and occipital regions, which are linked to visual processing and attention (Uncapher & Wagner, 2009).

How these neural signatures emerge over childhood remains unclear, as frontotemporal, visual, and hippocampal regions follow distinct developmental timelines that could be consequential for memory encoding. Hippocampal volume is largely stable by age 4 (Gogtay et al., 2006), but volumetric changes in its anterior and posterior subregions continue into adulthood and have been separately linked to differences in episodic memory (DeMaster et al., 2014; Lee et al., 2020; Schlichting et al., 2017). The involvement of hippocampal subregions may also vary based on the type of association being encoded (Prince et al., 2005). The particularly protracted development of frontotemporal regions involved in semantic processing and elaboration (Sowell et al., 2004), coupled with the concurrent expansion of semantic

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knowledge (Fisher et al., 2015), may also influence the encoding of semantically related information. While visual regions, such as those in the ventral stream, mature relatively early in life, they become more integrated with semantic processing networks through childhood (Cohen et al., 2019; Grill-Spector et al., 2008). Thus, the ongoing development and integration of these brain regions may influence children's ability to encode semantically or perceptually similar items, leading children and adults to show distinct patterns of neural engagement and memory behaviour.

Here, we had children and adults study pairs of items during fMRI scanning, and then tested memory for those pairs outside the scanner using cued recall. Item pairs were either semantically or perceptually related, allowing us to test how the nature of an association influences the neural engagement it elicits during successful encoding. Based on the relatively slower development of the frontotemporal regions that support semantic processing, we expected age group differences to be greatest for semantic associations. We also expected hippocampal subregions to make distinct contributions to semantic and perceptual encoding across development, given evidence that subregions follow different developmental trajectories and may be differentially involved in memory for semantically and perceptually related information in adults (Prince et al., 2005).

Method

Participants

The behavioural sample included 35 children aged 6-7 years (*M* = 7.34; *SD* = 0.45) and 36 adults (25-35 years; *M* = 29.37, *SD* = 3.04). Twelve children were excluded from fMRI analyses due to head motion (N = 11; see fMRI Preprocessing) and technical issues during data acquisition (N = 1), yielding an fMRI sample of 23 children (*M*=7.37; *SD* = 0.42). No adults were excluded from fMRI analyses. All participants were right-handed with normal or corrected-to-normal vision, and had no history of psychological or psychiatric disorders. Children were screened for subclinical behavioural problems using the Child Behavior Checklist (parent-completed; CBCL/6-18; Achenbach & Rescorla, 2001). Consent was provided by all adult participants and parents of child participants; all child participants provided assent. Participants were compensated $20 CAD per hour.

Task and Procedure

Neuroimaging data were collected during the pair learning task (Figure 1A), which was the final run of a larger fMRI study. On each of the 48 trials, a pair of images was presented for 3s, with a jittered interstimulus interval of 1.5, 3, or 4.5s. Items within a pair were either semantically (e.g., basketball, basketball players) or perceptually similar (e.g., basketball, pumpkin). Previous exposure to the items from earlier in the study was equated across pairs. Participants were instructed to study the pairs by creating a story relating the two items. Whether an image appeared on the left or right side of the pair was counterbalanced, and trial order was randomized across counterbalancing groups. A fixation cross was shown at the beginning of the run for at least 3000ms to allow the MR signal to stabilize, and for 9000ms at the end of the run to account for signal lag. The run lasted 4.98 minutes.

After completing the pair learning task, participants exited the scanner and, after a brief break (2-5 minutes), began the cued recall task. On each trial in the recall task, one item from a previously studied pair (i.e., the cue) was presented (Figure 1B). Participants were instructed to tell the experimenter verbally what item the cue had been paired with and/or any details that they could remember about the item. All previously studied pairs were tested, yielding 48 trials. The task was self-paced, and responses were transcribed manually by the experimenter and coded for accuracy after the session. Trial order was randomized across counterbalancing groups.

MRI Data Acquisition

MRI data were collected with a 3.0T Siemens Prisma MRI scanner. Sixty-nine functional slices were collected at orientations that maximized brain coverage, using a multi-band echo-planar imaging (EPI) sequence (repetition time [TR] = 1500ms, echo time [TE] = 28ms, 220x220x138mm matrix, 2mm isotropic voxels, flip angle = 71°, simultaneous multi-slice factor = 3). A structural T1-weighted 3D fast gradient echo volume (MPRAGE; 256x256x176mm matrix, 1mm isotropic voxels) was collected for co-registration and spatial normalization to a standard template space, along with a field map to correct for susceptibility distortion (TR = 700ms, TE = 4.92/7.38ms, flip angle = 60°, 220x220x138mm matrix, 2mm isotropic voxels).

fMRI Preprocessing

Volumes were preprocessed with fMRIprep (version 20.2.1; Esteban et al., 2019). Structural images were normalized to the 2mm MNI152NLin2009cAsym template (Fonov et al., 2009). Motion correction (FSL MCFLIRT) and susceptibility distortion correction (FSL FUGUE) were applied to the functional data, which were registered nonlinearly to the template space (ANTs antsApplyTransforms with Lanczos interpolation; boundary-based registration; six degrees of freedom; FreeSurfer BBREGISTER; Greve & Fischl, 2009). Realignment parameters from fMRIprep were used to compute framewise displacement (FD) and the standardized derivative of the root mean square variance over voxels (DVARS) for each functional volume. Participants exceeding an FD threshold of 0.5mm and/or standardized DVARS threshold of 1.5 in more than 33% of volumes were excluded.

fMRI Analysis

fMRI data were analyzed using fMRI Expert Analysis Tool (FEAT) version 6.0.0, part of FMRIB's Software Library (FSL) Version 6.0.7.3 (Smith et al., 2004). Before univariate analyses, we applied spatial smoothing with a 4mm Gaussian kernel and high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, σ = 100s) to the functional data. The data were modelled using a general linear model (GLM). Pairs were modelled as 3s events and convolved with a double-gamma haemodynamic response function. Pairs were split according to pair type and subsequent memory, yielding remembered semantic, forgotten semantic, remembered perceptual, and forgotten perceptual events. Motion parameters and their temporal derivatives, FD, and DVARS were included as confound regressors. Group maps were generated by combining contrast of parameter estimate images (COPEs) for each participant using FMRIB's Local Analysis of Mixed Effects (FLAME) 1+2, which were cluster corrected with a z threshold of 3.1 to define contiguous clusters and a cluster probability threshold of $p < .05$.

Given our interest in the neural correlates of memory for semantic versus perceptual associations across development, we performed functional region of interest (fROI) analyses on clusters that were more engaged (i.e., active) for remembered semantic versus perceptual pairs and vice versa, collapsing across age groups. We then extracted and z scored the average COPE estimates within each cluster for each participant, and tested for differences in the activation profiles of each cluster between age groups.

Small Volume Correction in Hippocampus Given the hippocampus' well-documented role in memory (e.g., DeMaster et al., 2014; Eichenbaum et al., 1992), we also examined whether engagement in hippocampal subregions was influenced by the type of similarity between pairs using small volume correction. Hippocampus was delineated by hand on a 1mm MNI152 anatomical template. Because we did not collect scans optimized for landmark-based subregion definition (i.e., a T2-weighted image oriented perpendicular to the hippocampal long axis) and the MNI template is not ideal for visualizing the anatomical landmarks that delineate the hippocampal head, body, and tail, we opted to divide the hippocampus into thirds according to the number of slices along the longitudinal axis (12 per subregion). We considered only the anterior and posterior segments as they may be particularly sensitive to the type of association being encoded (i.e., semantic versus perceptual; Prince et al., 2005), which were registered nonlinearly to the MNI152NLin2009cAsym template using ANTs. AFNI's 3dFWHMx function was used to estimate smoothness within left and right anterior and posterior hippocampus using residuals from each participant's first-level GLM, and these smoothness estimates were averaged to produce a group-level estimate. Using AFNI's 3dClustSim with an alpha of $p < .05$ and a cluster size threshold of $p < .001$, the minimum cluster extents were determined to be 2 voxels in each subregion.

Statistical Analysis

In the behavioural and fROI data, we tested for age group and pair type differences in memory behaviour using (generalized) linear mixed-effects models in R (R statistical package version 4.3.1; R Core Team, 2023; lme4 package version 1.1-35.1; Bates et al., 2015). Fixed effects included age group, pair type, and the age group by pair type interaction. Only participants were treated as random effects in the behavioural model, as the inclusion of by-participant random slopes for pair type did not significantly improve model fit ($\chi^2(2) = 1.75$, $p = .418$). Statistical significance of fixed effects was assessed using a Wald chi-square test (Type III sum of squares; car package version 3.1-2; Fox & Weisberg, 2019). Marginal contrast analyses were used to conduct pairwise comparisons between model predictors (modelbased package version 0.8.6; Makowski et al., 2020), and the Holm method was used to correct p-values for multiple comparisons across the pairwise contrasts of interest within each model's fixed effects. fROI analyses primarily focused on clusters showing either a significant main effect of age group, or an age group by pair type interaction.

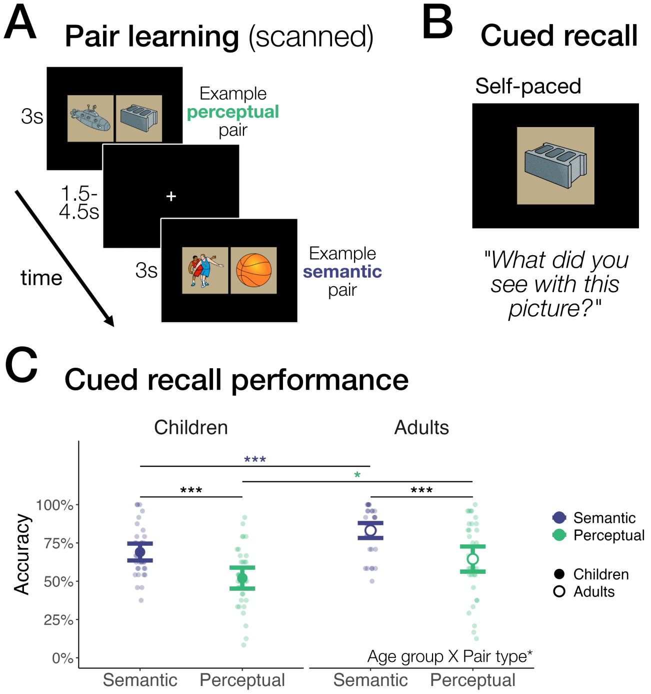

Figure 1: (A) Pair learning and (B) cued recall tasks. Black rectangles represent screens. (C) Cued recall accuracy in children and adults on semantic (blue) and perceptual (green) pairs. Translucent dots represent individual participants, and larger central dots represent group means. Error bars represent 95% confidence intervals. *$p < .05$, ***$p < .001$

Results

Semantic Similarity Benefits Memory

With respect to subsequent memory, adults outperformed children ($\chi^2(1) = 11.08$, $p < .001$), and memory was better for semantic than perceptual pairs ($\chi^2(1) = 143.09$, $p < .001$). Moreover, age differences were especially pronounced for semantic pairs ($\chi^2(1) = 4.71$, $p = .030$; predicted age difference for semantic pairs = 0.98, 95% CI = [0.47, 1.49], $z = 3.78$, $p < .001$; predicted age difference for perceptual pairs = 0.62, 95% CI = [0.13, 1.11], $z = 2.49$, $p = .013$; Figure 1C).

Distinct Patterns of Engagement for Successful Encoding of Semantic and Perceptual Pairs

Given that memory in both age groups was influenced by whether the association was semantic or perceptual, we next asked which brain regions were differentially engaged during the encoding of remembered associations that were either semantically or perceptually related (Figure 2A). Of the regions in which follow-up fROI analyses revealed no evidence of developmental differences, several bilateral frontoparietal and lateral temporal regions were more engaged for remembered semantic than perceptual pairs . By contrast, the regions that were more engaged for remembered perceptual than semantic pairs were left-lateralized and spanned inferior frontal gyrus (IFG), lateral occipital cortex (LOC), and superior parietal lobule (SPL).

Developmental Differences in Engagement We next considered regions in which follow-up fROI analyses revealed reliable age group differences that did not interact with pair type. Among the regions that were more engaged for semantic than perceptual pairs, adults showed greater engagement than children in right early visual cortex ($\chi^2(1) = 8.52$, $p = .004$), and left LOC ($\chi^2(1) = 4.99$, $p = .026$; Figure 2B). By contrast, children showed stronger engagement than adults in more anterior ROIs, including right precentral gyrus ($\chi^2(1) = 4.12$, $p = .042$), right medial prefrontal cortex (inferior cluster: $\chi^2(1) = 10.38$, $p = .001$; superior cluster: $\chi^2(1) = 8.74$, $p = .003$), right lateral temporal cortex ($\chi^2(1) = 4.47$, $p = .035$), and right frontal pole ($\chi^2(1) = 7.43$, $p = .006$; Figure 2C). In clusters showing greater activation for perceptual pairs, adults recruited left LOC ($\chi^2(1) = 21.57$, $p < .001$) and bilateral inferior parietal lobule (IPL; left: $\chi^2(1) = 5.40$, $p = .020$; right: $\chi^2(1) = 13.02$, $p < .001$) more than children, while children showed stronger engagement in right anterior temporal cortex ($\chi^2(1) = 40.64$, $p < .001$). Thus, irrespective of whether pairs were semantically or perceptually related, adults showed greater recruitment of visual and parietal regions during successful encoding than children, who in turn showed greater engagement than adults in frontal and temporal clusters.

To better understand how particular regions contribute to distinct memory outcomes across development, we next considered clusters that displayed significant interactions between age group and pair type. This included one cluster in right superior frontal gyrus from the remembered semantic > perceptual contrast (Figure 3A), and six clusters from the reverse contrast, spanning right IFG (two clusters; Figure 3B), right SPL (two clusters; Figure 3C), right IPL (Figure 3D), and right LOC (Figure 3E; all $p < .05$). Marginal contrast analyses revealed that all interactions were driven by children showing a larger difference in engagement between semantic and perceptual pairs than adults. Notably, the more anterior IFG and SPL clusters also showed significant main effects of age group. The IFG cluster showed a developmental decrease in engagement irrespective of pair type ($\chi^2(1) = 6.10$, $p = .014$), and the same trend was marginal in the more posterior IFG cluster ($\chi^2(1) = 3.79$, $p = .052$). By contrast, there was an age-related increase in engagement in the more anterior SPL cluster, driven by adults recruiting the region more than children for both semantic (predicted age difference = -0.83, 95% CI = [-1.20, -0.46], $t(74) = -4.44$, $p < .001$) and perceptual pairs (predicted age difference = -0.43, 95% CI = [-0.80, -0.05], $t(74) = -2.29$, $p = .025$). Together, these results highlight a trend toward less distinct neural responses to semantic and perceptual associations with age, such that the mechanisms supporting successful memory encoding become more general between childhood and adulthood.

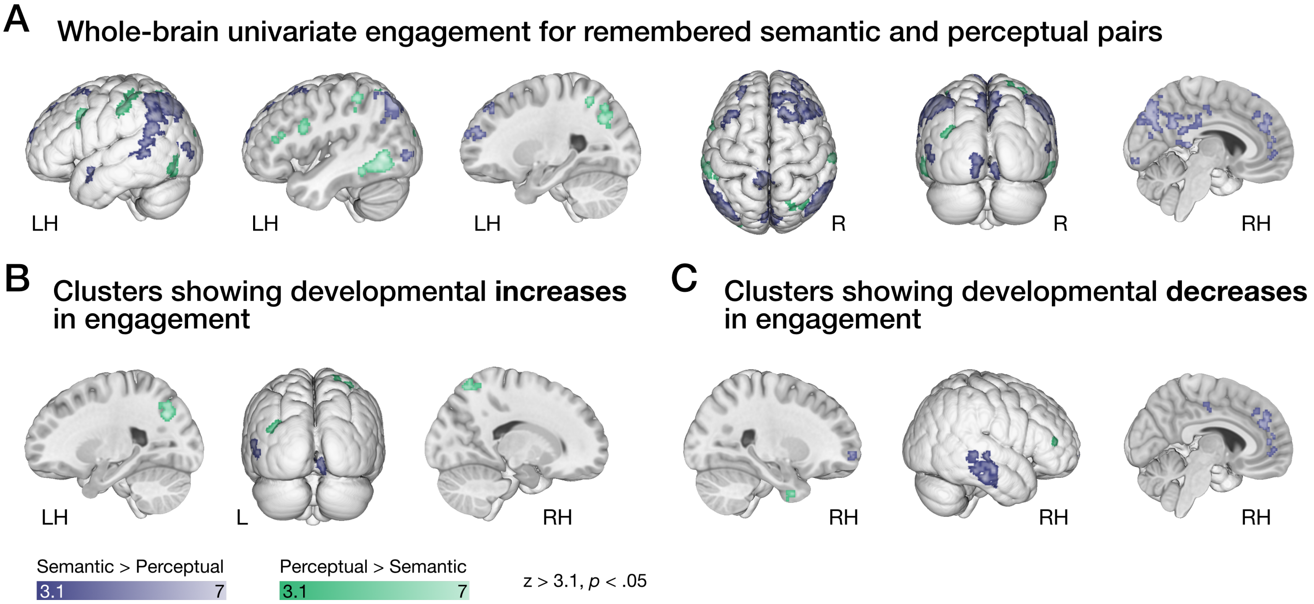

Figure 2: (A) Significant clusters in the across age group univariate contrasts for remembered semantic > perceptual pairs (blue on maps) and remembered perceptual > semantic pairs (green on maps). Of these clusters, those in which functional ROI analyses revealed significant main effects of age group at $p < .05$ are displayed beneath, with (B) displaying clusters where adults' engagement was greater than children's and (C) displaying clusters where children's engagement was greater than adults'. Maps in (B) and (C) are masked versions of the maps in (A).

Hippocampal Subregions No clusters were significant in the perceptual > semantic contrast, but one significant cluster (6 voxels) emerged in the remembered semantic > perceptual contrast in left anterior hippocampus. Overall engagement within this cluster did not differ between children and adults ($\chi^2(1) = 0.39$, $p = .532$), but there was a marginal interaction between age group and pair type ($\chi^2(1) = 3.65$, $p = .056$). Only children showed significantly stronger engagement for semantic than perceptual pairs (predicted pair type difference = 0.81, 95% CI = [0.36, 1.25], $t(57) = 3.61$, $p < .001$; adults: $p = .151$), suggesting that anterior hippocampus shifts from a bias toward semantic encoding in childhood to a more general role in memory encoding in adulthood (Figure 3F).

Discussion

In this study, we investigated how semantic and perceptual similarity influence memory behaviour and neural engagement during successful encoding of item pairs in children and adults. We found that semantic similarity facilitated memory in both age groups, and, consistent with expectations, was more beneficial for adults' memory than children's. At the neural level, successful semantic encoding elicited greater engagement in superior prefrontal and lateral parietal cortices, while perceptual encoding recruited more lateral prefrontal and ventral visual regions. Developmental increases in engagement—irrespective of whether pairs were semantically or perceptually related—were observed in occipital and parietal regions, while developmental decreases in engagement occurred in frontal and temporal regions. Compared to children, adults also showed less distinct neural responses to semantic and perceptual associations across several frontoparietal regions. Analyses of hippocampal subregions further revealed that anterior hippocampus displayed a similar shift from a bias toward greater involvement in semantic encoding in childhood to a more general role in memory encoding in adulthood.

Several regions showed developmental consistency in their bias toward semantic or perceptual encoding. For example, bilateral precuneus showed a bias toward semantic encoding across both age groups, aligning with past work implicating the region in successful memory formation across development (Chai et al., 2010; Ofen et al., 2007). Left IFG and left IPL were the only clusters showing a bias toward perceptual encoding that did not vary across age groups, which stood in contrast to right IFG and right IPL, where the difference in engagement between pair types decreased with age. Others have observed laterality differences in both IPL and IFG's involvement in memory encoding across

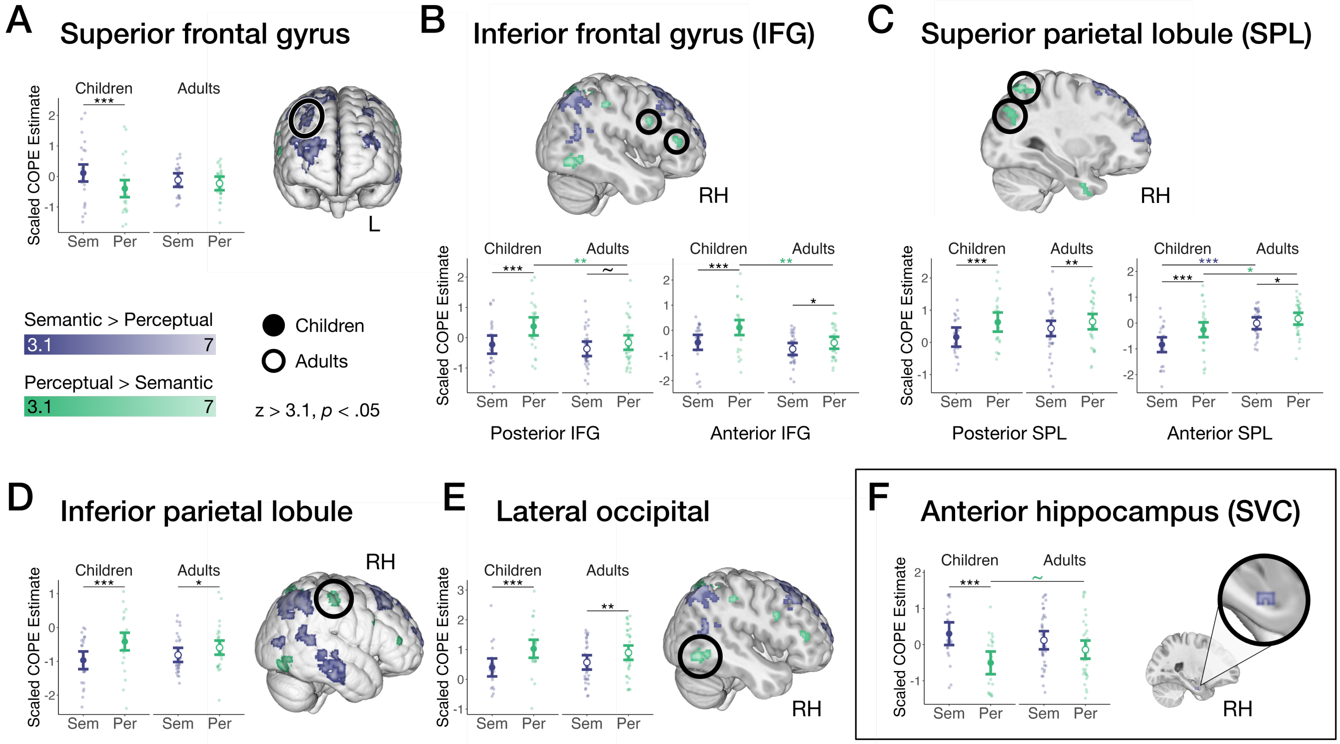

Figure 3: Clusters from the across age group univariate contrasts for remembered semantic > perceptual pairs (blue on maps) and remembered perceptual > semantic pairs (green on maps) in which fROI analyses revealed significant age group by pair type interactions (not marked on scatterplots). Maps are the same as those in Figure 2A. Scatterplots display *z* scored COPE estimates within the circled clusters. Translucent dots represent participant COPE estimates for remembered semantic (blue) and perceptual (green) pairs, while larger central dots represent model predicted COPE estimates (scaled). Error bars represent 95% confidence intervals of the model predictions. Cluster in anterior hippocampus (F) was significant after small volume correction, but not in the whole-brain contrast. ~$p < .1$, *$p < .05$, **$p < .01$, ***$p < .001$

development (Tang et al., 2018; 2020), and the age group consistency in left IFG and IPL here may relate to the left hemisphere's relative specialization for linguistic and conceptual processing. This specialization could make these regions less sensitive to age-related changes in visuospatial and perceptual processing, which are typically more right-lateralized and thus may face heightened demands in tasks like ours that use pictorial stimuli (Corballis, 2003).

Across regions that preferentially responded to both semantic and perceptual pairs, we observed developmental decreases in engagement in frontal and temporal clusters and increases in occipital and parietal clusters. While the decreases in frontal engagement conflict with some previous work (Ofen et al., 2007; Wendelken et al., 2011), this pattern could reflect developmental change in the broader organization of neural memory systems, as encoding strategies become less effortful and more automatized. For example, the greater medial PFC engagement in children than adults for semantic pairs observed here may reflect children's greater difficulty integrating them with existing schemas, with mPFC engagement compensating for their less efficient access to prior knowledge (Brod et al., 2013). The increases in engagement observed in occipital and parietal regions may reflect greater recruitment of visual and attentional networks to support the integration of perceptual and semantic information (Golarai et al., 2007). Past work has linked age-related increases in engagement of visual processing regions to developmental improvements in memory (Rosen et al., 2018), with secondary sensory areas in occipital and parietal cortices thought to play a key role in the processing of subsequently remembered stimuli. Additionally, because the hippocampus receives sensory input from both occipital and parietal regions, the extent to which regions like SPL and LOC faithfully represent that input could influence the robustness of the resulting memory traces (Fandakova et al., 2019; Inhoff & Ranganath, 2017).

The developmental trend toward reduced neural differentiation between semantic and perceptual encoding in regions like IFG, parietal cortex, and LOC adds further nuance to this picture. For example, while anterior SPL showed stronger engagement for perceptual than semantic pairs in both age groups, adults' engagement was stronger than children's during both semantic and perceptual encoding, indicating that while this region's contribution to memory encoding may increase with age, it also becomes more general, possibly through greater involvement in top-down attentional processes (Uncapher & Wagner, 2009). This and the analogous patterns observed in other clusters could also be indicative of adults' tendency to rely on more distributed neural systems, where children's reliance on particular regions to encode particular types of associations gives way to more integrated networks in adulthood that can support more varied forms of memory encoding. It is also possible that the manipulation had a stronger influence on how children engaged with the pairs during encoding, such that adults were more likely to use both semantic and perceptual information regardless of pair type. This possibility is consistent with models holding that cognitive development entails access to a more varied set of strategies (Siegler, 1998), and while it is not mutually exclusive with a greater reliance on more distributed and integrated neural systems, it does highlight the possibility that children's more distinct neural responses to semantic and perceptual pairs reflects a compensatory process involving more selective or specialized encoding strategies.

Anterior hippocampus showing a semantic bias in children and playing a more general role in adults points to developmental shifts in the more basic mechanisms supporting memory encoding. Past work in adults indicates that anterior hippocampal activity supports the abstraction of overlapping features or themes across events (Ghetti & Fandakova, 2020; Poppenk et al., 2013). Children's greater engagement for semantic pairs could therefore reflect a reliance on this region to extract or integrate meaning, which adults can achieve through more distributed cortical networks. Alternatively, anterior hippocampus may simply play a more general role in memory encoding in adults, as past adult work has suggested that the region may extract general perceptual and semantic themes from incoming input to support the formation of broad memories (Vijayarajah & Schlichting, 2023). Thus, future work should seek to clarify whether age group differences in the engagement of hippocampal subregions reflect distinct strategies for encoding different types of information, or differences in their underlying neural circuitry.

Together, these findings shed light on the developmental trajectory of memory for semantically and perceptually similar associations, revealing distinct patterns of neural engagement across age groups. Our results suggest that development is associated with an increase in reliance on occipital and parietal regions—linked to attention and visual processing—during memory encoding, while the role of specific regions like IFG, SFG, LOC, and anterior hippocampus becomes more general and less influenced by the type of associations being encoded. While these univariate findings provide insight into where semantic and perceptual biases occur during encoding, future research using multivariate methods will be needed to characterize the nature of the underlying representations and the way that they support memory across development. Prior work suggests that memory may benefit from more distinctive representations, particularly in visual areas (e.g., Bowman et al., 2019), and that semantic and perceptual representations change across development in distinct ways (e.g., Naspi et al., 2023). However, the types of representations that are most beneficial for children's memory remain unclear, and identifying the mechanisms that underlie their ability to form memories for different types of associations will help clarify how more integrated memory systems emerge over development.

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