Developmental refinements to neural attentional state during semantic memory retrieval through adolescence

Sagana Vijayarajah & Margaret L. Schlichting
Department of Psychology, University of Toronto, Canada, M5S 3G3

Corresponding Author: Margaret L. Schlichting; meg.schlichting@utoronto.ca

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Abstract

Despite the fact that attention undergoes protracted development, little is known about how it may support memory refinements in childhood and adolescence. Here, we asked whether people differentially focus their attention on semantic or perceptual information over development during memory retrieval. First, we trained a multivoxel classifier to characterize whole-brain neural patterns reflecting semantic versus perceptual attention in a cued attention task. We then used this classifier to quantify how attention varied in a separate dataset in which children, adolescents, and adults retrieved autobiographical, semantic, and episodic memories. All age groups demonstrated a semantic attentional bias during memory retrieval, with significant age differences in this bias during the semantic task. Trials began with a preparatory picture cue followed by a retrieval question, which allowed us to ask whether attentional biases varied by trial period. Adults showed a semantic bias earlier during the picture cues, whereas adolescents showed this bias during the question. Adults and adolescents also engaged different brain regions—superior parietal cortex and ventral visual regions, respectively—during preparatory picture cues. Our results demonstrate that retrieval-related attention undergoes refinement beyond childhood. These findings suggest that alongside expanding semantic knowledge, attention-related changes may support the maturation of factual knowledge retrieval.

Keywords: semantic knowledge; memory cues; autobiographical memory; children; parietal cortex

1. Introduction

Memory improves substantially over development, with gains being observed across a wide variety of tasks and for many types of content (Bauer et al., 2016; Ghetti et al., 2011; Ngo et al., 2018, 2021; Picard et al., 2009; Riggins, 2014; Rosen et al., 2019; Willoughby et al., 2012). While much work has documented how the refinement of encoding (e.g., Ghetti et al., 2010; Maril et al., 2011; Ofen et al., 2007; Rollins & Riggins, 2018; Shing et al., 2016) and retrieval (Brod et al., 2017; DeMaster & Ghetti, 2013; Selmeczy et al., 2019) mechanisms in the brain contribute to this improvement, relatively less is known about the role of attention in the emergence of adult-like memory retrieval. Here, we set out to characterize age-related differences in how particular attentional states are deployed as children, adolescents, and adults retrieve memories.

One type of attentional state with clear mnemonic consequences is attention to the deeper semantic or meaning-based aspects of experience rather than their surface-level perceptual features. Semantic attention has been associated with superior memory encoding at both the behavioural (Challis et al., 1996; Craik, 1977; Craik, 2010; Lockhart, 2002) and neural (Fliessbach et al., 2010, 2011; Kapur et al., 1994; Schott et al., 2013; Staresina et al., 2009) levels in adults, perhaps by encouraging elaboration (Addis & McAndrews, 2006; Staresina et al., 2009). Developmental work has shown that this memory benefit emerges behaviourally early in life, by 3 years of age: Both children (Ghetti & Angelini, 2008; Owings & Baumeister, 1979; Perlmutter et al., 1982; Puff et al., 1984) and adolescents (Andrade & Raposo, 2021; Owings & Baumeister, 1979) exhibit better memory when they focused on semantic as compared with perceptual features of stimuli during encoding, with the size of this memory boost increasing into young adulthood (Andrade & Raposo, 2021; Ghetti & Angelini, 2008; Owings & Baumeister, 1979; Perlmutter et al., 1982). Semantic versus perceptual attention at retrieval has also been shown to influence engagement of the hippocampus (Hashimoto et al., 2012), a key memory structure (Scoville & Milner, 1957); as well as improve the accuracy of memory decisions (Andrade & Raposo, 2021; Gallo et al., 2008; Ghetti & Angelini, 2008). Yet, how semantic versus perceptual attention is deployed during an unguided memory retrieval task, and whether this differs with development, remains unknown.

We reasoned that attending to the meaning of either the memory retrieval prompts or the reactivated contents of memory might be associated with better retrieval, particularly on tasks that might benefit from access to semantic information. However, we also anticipated developmental differences in how attention would be deployed. Broadly speaking, neural studies have shown differences in frontoparietal engagement during memory encoding (Chai et al., 2014; Maril et al., 2011; McAuley et al., 2007; Ofen et al., 2007; Shing et al., 2016) and retrieval (Brod et al., 2017; DeMaster & Ghetti, 2013; Fynes-Clinton et al., 2019; Ofen et al., 2012) between children and adults, consistent with the notion that attentional differences may at least in part explain age-related gains in memory (Ghetti & Fandakova, 2020). Given the protracted structural and functional development of the frontoparietal circuits (Dai et al., 2019; Fair et al., 2007; Farrant & Uddin, 2015; Wendelken et al., 2017) thought to underlie guided attention (Booth et al., 2003; Bowling et al., 2019; Corbetta et al., 2000; Kastner et al., 1998; Marshall et al., 2015; Shomstein et al., 2012), one might expect such differences to be quite protracted, potentially extending through adolescence. Yet, little work has been done on attention-memory interactions in development, especially during the adolescent period.

With respect to the deployment of semantic versus perceptual attention more specifically, we predicted that there might be developmental differences in either (a) the tendency to deploy semantic versus perceptual attention, and/or (b) the ability to guide one's attention in a top-down manner. With respect to the former, past work suggests that children may spontaneously focus on the perceptual aspects of experience (Badger & Shapiro, 2012; Gentner & Toupin, 1986; Sloutsky et al., 2007; Vendetti et al., 2015): For example, young children are more likely to make memory errors according to how a word sounds (i.e., along the phonological, perceptual dimension), whereas older age groups may tend to do so based on their meanings (i.e., along the semantic dimension; Brainerd & Reyna, 2007; Dewhurst & Robinson, 2004). Such a shifting bias from perceptual to semantic features may be related to children's tendency to focus on perceptual information (Badger & Shapiro, 2012; Brainerd & Reyna, 1998; Fisher, 2011; Gentner, 1990; Helo et al., 2017). As to the latter, children show reduced selective attention (DeMarie-Dreblow & Miller, 1988; Enns & Cameron, 1987) in that they seem to be unable to filter out task-irrelevant information (Deng & Sloutsky, 2016; Plebanek & Sloutsky, 2017; Sloutsky & Fisher, 2004). For this reason, children may be less apt to attend to one dimension (semantic, perceptual) over the other, and/or be less able than older participants to strategically guide or sustain their attention in accordance with current goals (Curtindale et al., 2007; Fisher et al., 2013; Lewis et al., 2017; Plebanek & Sloutsky, 2018). Such a reduced ability to modulate attention in a top-down fashion might in part explain why children benefit less from direction to attend to semantic features during memory encoding than do adults (Andrade & Raposo, 2021; Ghetti & Angelini, 2008; Owings & Baumeister, 1979).

Here, we characterized developmental differences in how children, adolescents, and adults engaged semantic versus perceptual attention during memory retrieval. We trained a pattern classifier to identify neural "states" associated with semantic versus perceptual attention using data from a separate task in which adults were alternately cued to attend to each type of information (Vijayarajah & Schlichting, 2023). We then applied this trained classifier to neural data from a developmental sample (Fynes-Clinton et al., 2019) to quantify how they deployed attention during each of three retrieval tasks probing autobiographical, semantic (factual), and episodic (picture) memory, respectively. Given children's difficulty aligning attention in accordance with task goals, we expected age-related increases in the engagement of attentional states most related to the retrieved content—i.e., semantic attention during semantic retrieval, as these questions required consideration of meaning; and perceptual attention during the retrieval of episodic memories, which focused on perceptual details of pictures. With respect to autobiographical memories, we anticipated that children may show a perceptual and adults a semantic bias given these memories typically include a mixture of semantic and episodic details (King et al., 2022; Levine et al., 2002).

As a secondary question, we also asked whether the particular timecourse of attentional engagement differed over development. Retrieval trials were structured such that questions were preceded by picture cues that hinted at the topic of the upcoming question. We reasoned that children may be less apt to leverage these cues than adults, in line with prior work (Hasselhorn, 1990; Heisel & Ritter, 1981; Kobasigawa, 1974; Mistry & Lange, 1985). Such a pattern would also be consistent with cognitive control research, which has shown age-related increases in the tendency to engage proactive (versus reactive) processes across many cognitive domains (Chatham et al., 2009; Niebaum et al., 2021), including in memory (Paz-Alonso et al., 2009). Specifically, we predicted that while older participants (adults, adolescents) may proactively engage attentional states in preparation for retrieval, younger ones (children) may instead wait for the particular memory question to evoke them.

2. Method

We used two independent functional magnetic resonance imaging (fMRI) datasets to ask how semantic versus perceptual attention supports successful retrieval over development. In one dataset (hereafter, termed the "Attention Localizer"), young adults were cued to alternate between attending to semantic and perceptual features of pictures during scanning (Vijayarajah & Schlichting, 2023). We used this dataset to define neural semantic and perceptual attentional states, which were then compared with neural patterns evoked in the second dataset ("Memory Retrieval"; publicly available data from Fynes-Clinton, Marstaller, & Burianová, 2019) to quantify attention-related engagement in children, adolescents, and adults performing a series of retrieval tasks. Our predictions and analysis plan for this investigation were preregistered (https://osf.io/bhg3d), with deviations (largely for simplicity) and follow-up exploratory analyses indicated throughout the paper. We also present analyses exactly as preregistered in the **Supplementary Materials**; briefly, they do not meaningfully differ from those in the main paper.

2.1. Participants

All participants (from both datasets) met the following criteria: right-handed; free from a diagnosis of mental illness, neurological disorders, and vision or hearing impairments; and had no MRI contraindications. All participants also provided consent (parents or legal guardians provided consent for participants under 17 years of age) and were compensated for their time ($25 CAD per hour for Attention Localizer; $30 AUD per hour for Memory Retrieval).

2.1.1. Attention Localizer

This experiment included 46 young adults (18-35 years old) from a previous investigation (Vijayarajah & Schlichting, 2023). Four participants were excluded from the final sample for pilot analyses (N=1), illness in the scanner (N=1), and poor performance on a memory test not considered here (N=2). These exclusions yielded a final sample size of 42 participants (28 females, 14 males; mean=19.80 years; 18-30 years old), which was determined *a priori* to both achieve 80% power to detect an effect size of Cohen’s d=0.45 estimated from previous work (Aly & Turk-Browne, 2016) and also ensure an equal number of participants in each of the six counterbalancing groups.

2.1.2. Memory Retrieval

This publicly available dataset (Fynes-Clinton et al., 2019) included 21 children (8 females, 13 males; mean=10.90 years; 10-12 years old), 20 adolescents (11 females, 9 males; mean=15.25 years; 14-16 years old), and 21 young adults (11 females, 10 males; mean=26.71 years; 20-35 years old). We excluded the first three adults (based on their participant number) from the final sample to serve as pilot participants for the refinement of our analysis plan with this dataset.

Participants all met a head motion inclusion criterion of having a framewise displacement (FD) that was less than 2mm on average (set by Fynes-Clinton et al., 2019). Yet, even among this low-motion group of participants there were age-related decreases in motion (FD; children versus adolescents: t=2.56, p=0.02, Cohen's d=0.81; children versus adults: t=4.01, p=2.95 x 10^{-4}, d=1.30; adolescents versus adults: t=2.57, p=0.01, d=0.84). We therefore performed control analyses to ensure age-related differences in head motion did not impact our main results (see **Supplementary Materials**: Accounting for age-related differences in framewise displacement).

2.2. Procedure

2.2.1. Attention Localizer task

A full description of the task design can be found in Vijayarajah & Schlichting (2023). Briefly, participants viewed 144 storybook-style illustrations organized into 18 blocks of eight illustrations each. Prior to each block, participants were cued with a simple shape (pre-trained to be associated with a particular task; shape-task mapping counterbalanced across participants; 2500ms followed by a 500ms inter stimulus interval [ISI]) to orient to either the semantic meaning (story) or perceptual (artist style) features of the upcoming illustrations by detecting repeats along the corresponding dimension (nine artist blocks, nine story blocks; assignment of blocks to conditions was counterbalanced across participants). Illustrations were presented one at a time

(2500ms, 500ms ISI), and each block contained at least one repeat along each the story (consecutive illustrations that depicted the same story, but were created by different artists) and artist style (different stories, same artist) dimensions. Participants indicated with a button press whether each illustration was or was not a repeat along the cued dimension.

The experiment was divided into three scanning runs of equal length, with three blocks from each condition per run. We included fixation time at the beginning (3000ms) and end (9000ms) of each run to account for stabilization and lag of the MR signal, respectively. Participants also completed blocks from an orthogonal baseline task which asked them to indicate which of three squares (left, middle, or right) a dot appeared in each of the eight baseline task trials (2500ms, 500ms ISI) in a block.

2.2.2. Memory Retrieval task

Fynes-Clinton, et al. (2019) designed the retrieval tasks to investigate whether shared or differentiated brain networks support autobiographical, semantic, and episodic retrieval over development. Here, we used their dataset to ask a novel question—how neural attentional states (defined in the Attention Localizer) are engaged during the successful retrieval of these different types of content in development.

An in-depth description of the tasks can be found in the original paper (Fynes-Clinton et al., 2019). For consistency, we use the same task names as Fynes-Clinton et al. (2019). To summarize, participants performed autobiographical, semantic, and episodic retrieval tasks that each consisted of 25 trials made up of picture cues depicting general topics (4000ms with a 1000ms ISI; e.g., a picture of a dentist checking their patient's teeth) followed by retrieval questions (8000ms with a jittered 800–1200ms

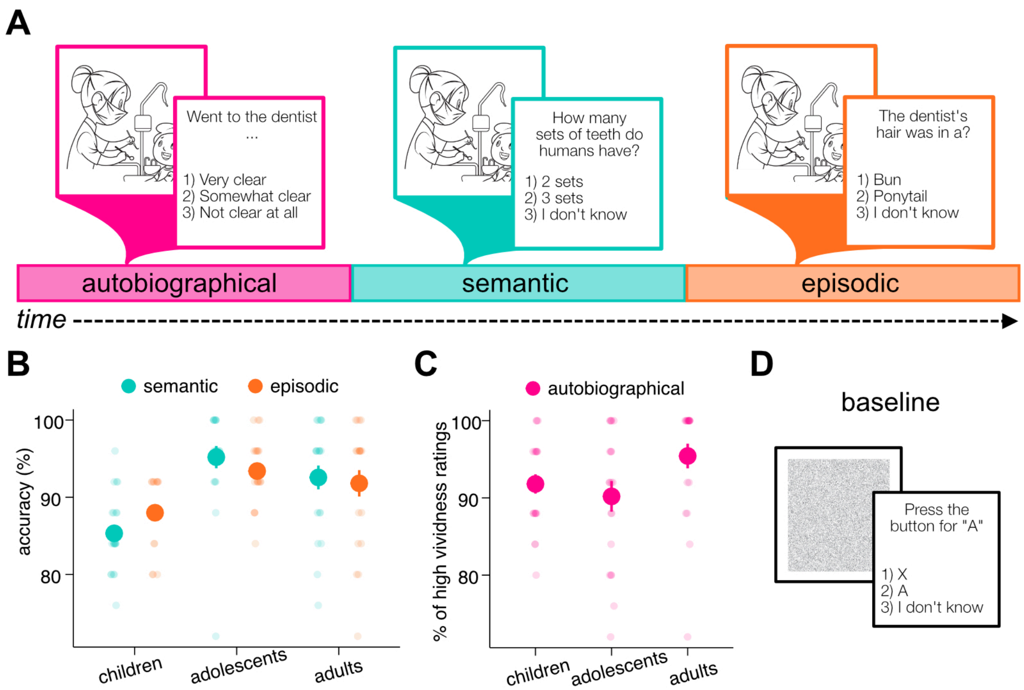

Figure 1. Memory Retrieval tasks and behaviour. (A) Task paradigm based on the figure by Fynes-Clinton et al. 2019. Participants first performed an autobiographical task (fuchsia) where they retrieved past experiences related to the picture cue (the dentist visit; this picture cue did not appear in the real experiment and is solely presented here for descriptive purposes) and rated the vividness of the retrieved memory. In the second scanning run, participants were provided the same picture cues and asked to retrieve a related general knowledge fact (semantic task; teal). In the final scanning run, participants were asked about details from the picture cue which had been presented twice before this task (episodic task; orange). Intermixed in each run were baseline task trials (depicted in D). (B) The percentage of correct trials in the semantic and episodic tasks with age group on the x-axis and accuracy as a percentage on the y-axis. The larger circles represent group mean; points are individual participants; intervals are standard error around the group mean. (C) The percentage of retrieved autobiographical memories rated with high vividness depicted as in B. (D) The baseline task showed a scrambled image cue followed by a simple perceptual judgment.

inter-trial interval; mean jitter=1000ms) that prompted the retrieval of task-related content. Autobiographical questions prompted the retrieval of a past experience, and participants rated the retrieved memory for vividness. Semantic questions tested participants' factual knowledge with multiple-choice questions. Episodic questions tested participants' memory for details from the picture cue stimuli which had appeared in all three tasks, also in a multiple-choice format (**Figure 1**).

The retrieval tasks were separated into three different scanning runs and appeared in a fixed order, with the autobiographical task in the first run, followed by the semantic task in the second run, and lastly the episodic task in the third run. The episodic task was completed last because the original authors reasoned this order would encourage participants to rely on their long-term memory for the picture cues from the preceding tasks as opposed to their visual working memory (Fynes-Clinton et al., 2019). Furthermore, because all trials in a given run were from the same task, participants could always anticipate the type of retrieval question that would appear. Participants also performed five trials from a baseline task that were intermixed with retrieval trials in each task. The baseline task had the same structure as retrieval trials, but instead presented scrambled pictures as cues followed by non-memory-based perceptual matching questions.

2.3. MRI data acquisition and preprocessing

2.3.1. Attention Localizer parameters

Functional volumes were acquired with a multi-band echo-planar imaging (EPI) sequence that collected 69 oblique axial slices (repetition time [TR]=1500ms, echo time [TE]=28.0ms, flip angle=71°, 220 x 220 x 138mm matrix, 2mm isotropic voxels, multiband acceleration factor=3, GRAPPA factor=2). One T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) volume (256 x 256 x 160mm matrix, 1mm isotropic voxels) was acquired for spatial normalization, followed by a field map for susceptibility distortion correction (TR=700ms, TE=4.92/7.38ms, flip angle=60°, 220 x 220 x 138mm matrix, 2mm isotropic voxels).

2.3.2. Memory Retrieval parameters

Raw MRI data were retrieved from OpenNeuro (Markiewicz et al., 2021;

https://openneuro.org/datasets/ds001748/versions/1.0.4). Functional volumes were collected with an EPI sequence that consisted of 45 slices (2.5mm isotropic voxels; TR=3000ms; TE=30ms; FOV=190mm). A T1-weighted MPRAGE (1mm isotropic voxels; FOV=256mm) volume was also acquired. More acquisition details can be found in Fynes-Clinton et al. (2019).

2.3.3. MRI preprocessing

Both datasets were preprocessed with the same fMRIprep pipeline (version 1.1.4; Esteban et al., 2018), with functional volumes from the Memory Retrieval dataset additionally resampled to the 2mm isotropic dimensions used in the Attention Localizer for our subsequent analyses. In this pipeline, T1-weighted volumes were skull-stripped through the ANTs brain extraction tool (Avants et al., 2011), and segmented for cerebrospinal fluid, white-matter, and gray-matter (GM) with FSL FAST (Zhang et al., 2001). These volumes were then normalized to MNI152NLin2009cAsym space with ANTs nonlinear registration. Functional data were corrected for motion using FSL MCFLIRT and normalized to the 2mm isotropic template space using nonlinear registration via the T1 anatomical (boundary-based registration; 9 degrees of freedom; using BBREGISTER in FreeSurfer; Greve & Fischl, 2009). All transformations were computed, concatenated, and applied in a single step using antsApplyTransforms and Lanczos interpolation in ANTs.

2.3.4. Nuisance regressors

We calculated motion nuisance regressors using fMRIprep and custom scripts. The standard six motion parameters (x, y, z, yaw, pitch, roll) and framewise displacement (FD) for each functional volume were derived from motion correction of functional scans during preprocessing. We additionally calculated the temporal derivative for the standard six motion parameters and FD for each volume using custom Python scripts. Lastly, we included the six anatomical CompCor motion components (Behzadi et al., 2007) derived during preprocessing.

2.3.5. Anatomical mask

We characterized attention-related neural engagement within a group whole-brain grey-matter (GM) mask derived from participants in both datasets. This group GM mask was made by first creating participant-specific GM masks using the T1-weighted GM tissue-probability maps generated during preprocessing by FSL FAST (in fMRIprep). The masks were then thresholded at 0.5 to restrict to voxels with 50% or greater probability of being located within GM. Participant-specific masks were then resampled to the 2mm functional data dimensions using nearest neighbour interpolation, combined, and thresholded again to include only voxels that were in GM for at least 50% of all participants for the final group mask. Subsequent analyses in both datasets were restricted to voxels within this group mask.

2.4. Leveraging the Attention Localizer to quantify attentional states in memory retrieval

We first characterized semantic versus perceptual attentional states from the Attention Localizer, and then used these states to ask how children, adolescents, and adults from the Memory Retrieval dataset evoked attention during successful retrieval.

2.4.1 Data preparation

Prior to performing the attentional state analyses, we shifted the condition onsets in each scanning run from both datasets by 6s to account for hemodynamic lag in the fMRI signal. To ensure our state analyses were restricted to task-related neural patterns, we also excluded non-task fixation time from the data. In the Attention Localizer specifically, we excluded three TRs at the onset of each attention cue to remove data associated with cue-to-condition transition periods.

2.4.2. Classifier cross-validation and training (Attention Localizer dataset)

Because our ultimate goal involved defining neural states in one group of participants and applying them to another (i.e., the Memory Retrieval dataset), we focused on identifying attentional states that generalized across different individuals. To do this, we had a sparse multinomial logistic regression (SMLR) classifier (PyMVPA; default parameters; no feature selection was performed; Hanke et al., 2009) decode semantic versus perceptual attentional states across all 42 participants in the Attention Localizer using leave-one-participant-out-cross-validation. In this cross-validation, we trained the classifier on condition-labeled TRs from the semantic (story) and perceptual (artist style) attention conditions from all but six participants—holding out one from each of the six counterbalancing groups—and tested the accuracy of the classifier's predictions on the six held-out participants. This decision was made to ensure the training dataset was balanced in terms of the assignment of cues to condition. We repeated this process seven times (42/6) so that the classifier was tested on each participant once. We found that we could decode semantic versus perceptual attentional states across different participants significantly above chance (mean=0.64; 95% CI [0.62, 0.66]; t-test versus 0.50; $t=13.20$, $p=2.23 \times 10^{-16}$, $d=2.04$).

We used a classifier trained on neural data from all 42 participants to interrogate attentional states evoked in the Memory Retrieval dataset. We additionally included baseline task neural data in this classifier training solely to reduce dependency in the neural patterns characterized as semantic versus perceptual attention across people. This classifier could decode neural patterns reflective of semantic attention, perceptual attention, and the baseline task across different participants significantly above chance (mean=0.75; 95% CI [0.74, 0.76]; t-test versus 0.33; $t=61.20$, $p=6.90 \times 10^{-42}$, $d=9.42$) using the same cross-validation approach.

2.4.3. Classifier application to memory retrieval (Memory Retrieval dataset)

We applied the trained classifier to functional data from each retrieval task to test for age- and task-related differences in attentional states. This classifier yielded prediction probabilities for both attentional states on a TR-by-TR basis for each participant, and for each retrieval task. These prediction probabilities were then log odds transformed to correct for non-normality in the distribution of raw classification probabilities for all TRs (as done in Richter et al., 2016; using the logit function a part of the car package; Fox & Weisberg, 2015), and averaged across TRs within the same trial to derive one classifier estimate for each attentional state for every trial. We additionally restricted our analysis to baseline and retrieval task trials that were correct—or in the case of the autobiographical task, rated with high vividness—to capture attentional state engagement associated with successful retrievals.

2.4.4. Testing age group differences in attention during retrieval

We used (generalized) linear mixed-effects models (lme4 package version 1.1-26; Bates et al., 2015) implemented in R version 4.0.4 (Team, 2021) to test whether classifier evidence for semantic versus perceptual attentional states varied as a function of (1) memory retrieval (across all three retrieval tasks) versus the baseline task in each age group, (2) the different retrieval tasks (autobiographical, semantic, episodic) in each age group, and (3) the different age groups within each retrieval task. Each model predicted the difference between classifier evidence for semantic versus perceptual attentional states (semantic-perceptual evidence) to ask whether there was reliable evidence for a semantic (semantic>perceptual, or semantic-perceptual difference score above 0) or perceptual (perceptual>semantic; semantic-perceptual below 0) attentional bias, while accounting for within-participant random effects using random intercepts (when interrogating differences within the same task) or slopes (when interrogating task differences). Models that interrogated age group differences in attention also included age group as an ordered categorical predictor (adults>adolescents>children) to test changes in attention over development. We performed follow-up pairwise comparisons with the estimated marginal means from these models (calculated with the emmeans package; Searle et al., 2023) to test for reliable evidence of attentional bias (i.e., a difference score significantly above or below 0), age group differences, and condition differences. Our focus on results predicting the difference between classifier evidence for semantic versus perceptual attention rather than evidence for each state is a deviation from our preregistered analysis. Our reasons for this deviation were to both simplify our results section and ensure independence of the observations going into our mixed models—such that each correct retrieval trial contributed exactly one data point within the model. We report our preregistered analysis of semantic versus perceptual evidence as separate levels of a categorical predictor in the **Supplementary Materials**.

In our preregistered follow-up analyses, we examined whether there were age-related differences in how semantic versus perceptual attentional states were evoked when considering different trial periods within each task—i.e., in preparation for retrieval (picture cue) versus during retrieval prompts (retrieval question).

2.5. Exploratory general linear model (GLM) analyses for univariate engagement during retrieval trial periods

We used univariate contrasts to identify brain regions that mirrored the age-related attention differences in semantic retrieval we uncovered in the classification analysis that separately considered picture cue and question periods. To do this, we modeled univariate engagement separately for picture cues and retrieval questions in correct versus incorrect trials from the semantic task. Picture cues were modeled for a duration of 4000ms while question periods were modeled for an 8000ms duration; all events were then convolved with the double-gamma hemodynamic response function. We also included temporal derivatives for all task regressors along with the 18 volume-wise nuisance regressors derived during preprocessing in these GLMs. Temporal autocorrelation correction was performed using FILM prewhitening. These GLMs resulted in participant-specific statistic images for each trial period in correct and incorrect trials from the semantic task and the baseline task. With these statistic images we modeled our contrasts of interest (semantic task picture cue>retrieval question and retrieval question>picture cue, both restricted to correct trials) in each participant.

Parameter estimates for these contrasts were then submitted to higher-level FEAT GLMs (Woolrich et al., 2004) that estimated the univariate response for each contrast across participants, while accounting for between-participant variance (mixed-effects FLAME 1). These higher-level GLMs were tested for the interaction of age group on voxels activated for picture cues versus retrieval questions, at the whole brain level (correction for multiple comparisons was performed using cluster-based Gaussian random field theory [Worsley et al., 2002], with a cluster-forming threshold of $z \geq 3.1$ and whole-brain corrected cluster significance level of $p<0.05$). For the clusters that emerged at this threshold, we extracted their cluster activation from each trial period and age group in order to perform follow-up pairwise t-tests that revealed the condition differences that contributed to the age group and trial period interaction.

3. Results

3.1. Behaviour

3.1.1. Attention Localizer

For an in-depth description of participants' performance in this experiment see Vijayarajah & Schlichting (2023). To summarize, participants could perform both the artist and story conditions well above chance (discrimination [d']; Banks, 1970; story: $t=8.24$, $p=3.07 \times 10^{-10}$, $d=1.27$; artist: $t=13.65$, $p<2.2 \times 10^{-16}$, $d=2.11$), such that they correctly responded more to repeats along the cued dimension than repeats along the uncued dimension. This suggests that participants successfully oriented their attention in response to the cues as instructed.

3.1.2. Memory Retrieval

Behavioural performance was reported in Fynes-Clinton et al. (2019). In brief, there were age group differences in accuracy and response times in the semantic (accuracy: $F=14.00$, $p=1.00 \times 10^{-3}$, $\eta 2=0.32$; response times: $F=7.50$, $p=1.00 \times 10^{-3}$, $\eta 2=0.20$) and episodic tasks (accuracy: $F=4.82$, $p=0.01$, $\eta 2=0.14$; response times:

$F=8.10$, $p<0.01$, $\eta2=0.22$), along with age group differences in baseline task response times ($F=19.40$, $p<1.00 \times 10^{-3}$, $\eta2=0.40$); there were no reliable age group differences in vividness ratings or response times in the autobiographical task (both $p>0.07$). In the semantic task, children were reliably less accurate and slower to make correct responses in comparison to adolescents (accuracy: $t=5.52$, $p=2.43 \times 10^{-6}$, $d=1.72$; response times: $t=3.67$, $p=7.30 \times 10^{-4}$, $d=1.15$) and adults (accuracy: $t=3.84$, $p=4.28 \times 10^{-4}$, $d=1.19$; response times: $t=3.16$, $p=3.02 \times 10^{-3}$, $d=0.97$). Behaviour in the episodic task showed a similar pattern: Children were reliably less accurate in comparison to adolescents ($t=2.02$, $p=0.01$, $d=1.26$), and slower to make these responses in comparison to both adolescents ($t=3.86$, $p=4.14 \times 10^{-4}$, $d=1.21$) and adults ($t=2.41$, $p=0.02$, $d=0.74$). Adults and adolescents did not differ in their accuracy or response times in both of these tasks (all $p>0.11$). With respect to the baseline task, children were slower to make correct responses than the older age groups (versus adolescents: $t=5.56$, $p=2.10 \times 10^{-6}$, $d=1.74$; versus adults: $t=3.35$, $p=1.76 \times 10^{-3}$, $d=1.03$) and adults were slower to make these responses in comparison to adolescents ($t=3.35$, $p=1.78 \times 10^{-3}$, $d=1.05$).

3.2. Memory retrieval is associated with semantic attentional states

We first examined whether there were differences in the types of attentional states that support memory retrieval overall—specifically, whether there was a consistent semantic or perceptual attentional bias across retrieval tasks. All age groups demonstrated reliable differences in attentional bias during memory retrieval versus the baseline task (children: $\beta=0.31$, $SE=0.09$, $t=3.43$, $p=1.49 \times 10^{-3}$; adolescents: $\beta=0.32$, SE=0.10, t=3.35, $p=1.98 \times 10^{-3}$; adults: β=0.29, SE=0.11, t=2.65, p=0.02; **Figure S1**), driven by a significant semantic bias during memory retrieval in all age groups (children: t=4.31, $p=4.00 \times 10^{-4}$; adolescents: t=7.10, $p<1.00 \times 10^{-4}$; adults: t=4.20, $p=5.00 \times 10^{-4}$). There were no significant attentional biases during the baseline task in all age groups (all p>0.13), but numerically greater perceptual than semantic attention evoked in this task (estimated marginal means; children=-0.24; adolescents=-0.11; adults=-0.22). There were also no reliable age-related differences in these attentional biases (all p>0.86). Therefore, all age groups showed a significantly greater semantic attentional bias during memory retrieval processes in comparison to non-memory (baseline task) judgments.

3.3. Age-related changes in attentional states during the semantic retrieval task

We next examined whether there were age group differences in the engagement of this semantic attentional bias within each retrieval task. We found age-related increases in this bias between children and adolescents during the semantic retrieval task (β=0.36, SE=0.17, t=2.06, p=0.04); there was no reliable difference between adults and either adolescents or children, (p>0.17; **Figure 2**). Moreover, both adolescents (t=4.74, $p=1.00 \times 10^{-4}$) and adults (t=2.16, p=0.03) but not children (p=0.10) showed a

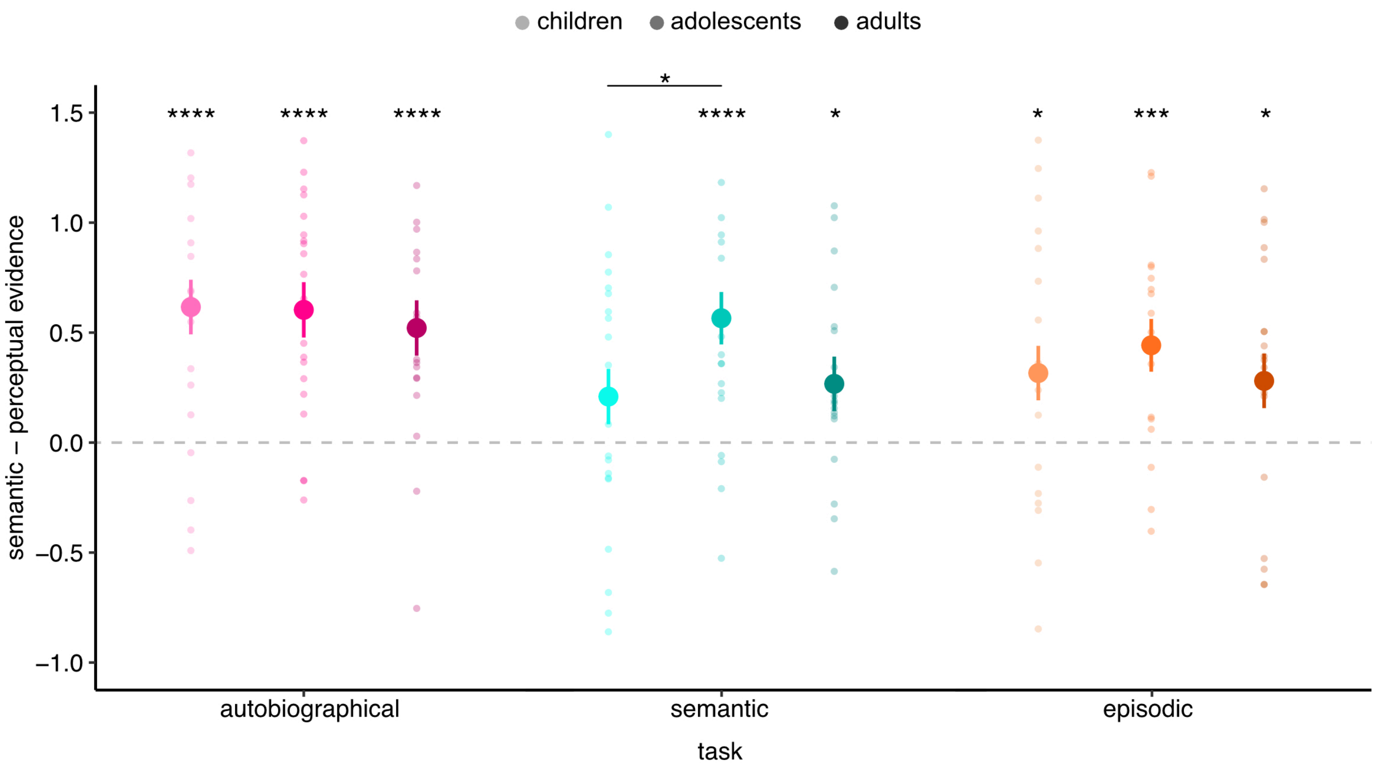

Figure 2. Age-related differences in attentional bias during each retrieval task. Attentional bias (y axis) is depicted as a function of the retrieval tasks (x axis; autobiographical in fuchsia, semantic in teal, and episodic in orange) and age group (children in light colours, adolescents in medium-dark colours, and adults in dark colours). Larger circles represent the group estimated marginal means; points are individual participants; intervals are standard error around the estimated marginal mean. Asterisk denotes the significant age group difference in attentional bias within the semantic task. Asterisk above the age group means denote significant evidence of an attentional bias in that task. ** p<0.05, *** p<0.001, **** p<0.001*

reliable semantic attentional bias in this task. By contrast, there was no evidence of age-related differences in attentional bias during the autobiographical or episodic tasks (all $p>0.33$), and all ages demonstrated reliable semantic attentional biases in both (autobiographical, children: $t=4.96$, $p<1.00 \times 10^{-4}$; autobiographical, adolescents: $t=4.80$, $p<1.00 \times 10^{-4}$; autobiographical, adults: $t=4.14$, $p=1.00 \times 10^{-4}$; episodic, children: $t=2.55$, $p=0.01$; episodic, adolescents: $t=3.69$, $p=3.00 \times 10^{-4}$; episodic, adults: $t=2.27$, $p=0.02$).

We performed control analyses to ensure age-related changes in head motion (FD) and task response times did not fully account for age group differences in attentional bias during the semantic retrieval task (these analyses can be found in the

Supplementary Materials). Briefly, this age group effect was robust to both control analyses. Together, these results are consistent with the idea that there are age-related changes in attentional states that support semantic factual retrieval beyond childhood.

3.4. Age-related differences in attentional states during picture cues versus question periods in the semantic task

We reasoned that one possibility for why children do not show a reliable attentional bias in the semantic task may be that they are slower to engage attentional states in comparison to older age groups. In particular, adults and adolescents may use the picture cues to proactively guide their retrieval-related attention while children may instead do so when provided the question. To test this possibility, we examined whether age-related differences in attentional bias also varied by the different trial periods—i.e., during picture cues versus the factual questions that followed the cues. We focus on attentional bias (semantic-perceptual evidence) in this analysis as well instead of considering semantic versus perceptual evidence separately as we had preregistered; the preregistered analysis can be found in the **Supplementary Materials**.

Indeed, attentional bias varied by age group and trial period in the semantic task ($F=3.27$, $p=0.04$; **Figure 3**)—an overall interaction that was driven by adults showing a pattern that was significantly different from adolescents ($\beta=-0.20$, $SE=0.09$, $t=-2.30$, $p=0.02$; interaction when excluding the child group) and marginally so from children ($\beta=-0.18$, $SE=0.09$, $t=-1.96$, $p=0.05$; interaction when excluding the adolescent group); children and adolescents were not significantly different from one another when adults

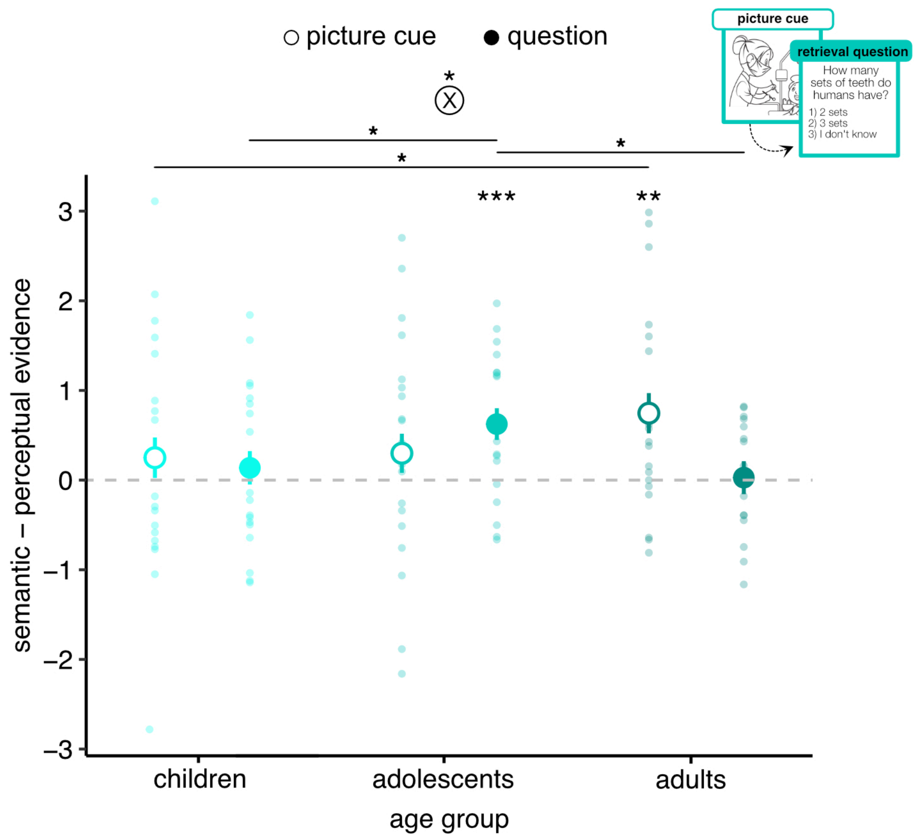

Figure 3. Age group differences in attentional bias during the semantic task trial periods**.** Attentional bias is depicted as a function of the semantic task trial periods (picture cue with open circles, retrieval question as closed circles) and age with colour (children in light teal, adolescents in medium-dark teal, and adults in the darkest teal). Larger circles represent group estimated marginal means; points are individual participants; intervals are standard error around the estimated marginal mean. Tensor product symbol denotes significant interaction of age group and trial period on attentional bias. Asterisks above the trial period means denote significant evidence of an attentional bias in that trial period, for that age group. * *p<0.05, ** p<0.01, *** p<0.001*

were dropped from consideration (p=0.35). Specifically, adults demonstrated a reliable semantic attentional bias during the picture cue (t=3.33, p=1.50 x 10^{-3}) but not question period (p=0.88), while adolescents demonstrated the opposite pattern, showing a semantic bias during the question period (t=3.53, p=6.00 x 10^{-4}) but not picture cue (p=0.10). Children did not show a reliable attentional bias at either trial period (both p>0.28). Moreover, comparing across age groups revealed that adolescents showed significantly greater semantic bias during the question period when compared to the other age groups (adults: t=2.38, p=0.01; children: t=1.99, p=0.05). During the picture cue, adults showed a greater semantic bias relative to children (t=2.23, p=0.03) but not adolescents (p=0.23).

Age-related differences in the timecourse of attentional bias were only observed in the semantic task: There was no interaction of age group and trial period on attentional bias in the autobiographical ($p=0.33$; **Figure S2**) or episodic ($p=0.75$; **Figure S3**) tasks. Instead, attentional bias varied by trial period in the autobiographical task ($\beta=-0.43$, $SE=0.08$, $t=-5.56$, $p=2.78 \times 10^{-5}$), with all ages showing a significant semantic attentional bias during the question period (children: $t=6.03$, $p<1.00 \times 10^{-4}$; adolescents: $t=5.01$, $p<1.00 \times 10^{-4}$; adults: $t=4.69$, $p<1.00 \times 10^{-4}$) but not picture cue (all $p>0.42$). There was no effect of trial period on attentional bias in the episodic task ($p=0.47$).

Furthermore, the semantic task results were also robust to control analyses that account for age group differences in head motion and response times (reported in the **Supplementary Materials**). Therefore, despite no reliable difference between adolescents and adults in either semantic task behaviour (**Figure 1**) or attentional biases when we considered the entire semantic retrieval trial as a whole (**Figure 2**), separately considering picture cue and retrieval questions showed that the two groups evoked this bias at different periods to retrieve the same factual knowledge.

3.5. Neural mechanisms that mirror attentional state differences in picture cues versus question periods from the semantic task

We carried out follow-up exploratory analyses (that were not pre-registered) to identify brain regions that may underlie the observed interaction between age group and trial period on attentional biases in the semantic task (**Figure 3**). Specifically, we performed a univariate whole-brain contrast to determine where in the brain univariate engagement varied by this interaction (i.e., age [adults versus adolescents] x trial period

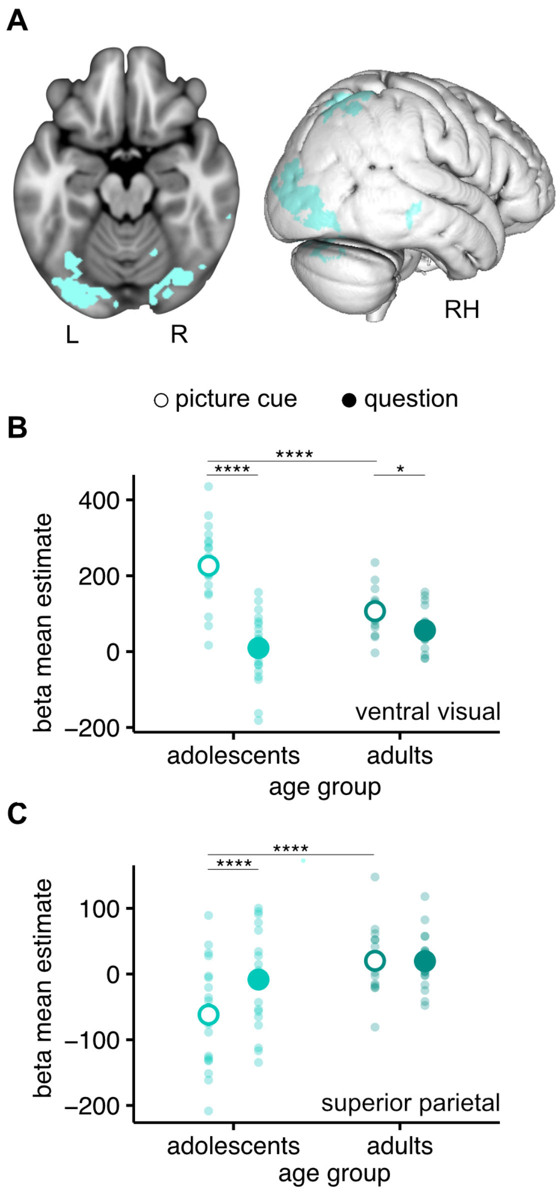

Figure 4. (A) Functional ventral visual (left) and right superior parietal cortex (right) regions. Depicted are clusters showing significant univariate engagement differences between adults and adolescents as a function of the semantic task trial periods (picture cue versus question period). Activation (beta means) from the ventral visual (B) and superior parietal cortex (C) functional clusters shown as a function of age group (x axis; adolescents in teal and adults in the darker teal) and trial period (open circles for picture cues, closed circles for the question period). Follow-up pairwise comparisons to describe the nature of the interaction are depicted on each chart. Larger circles represent group beta means; points are individual participants; intervals are standard error around the beta mean. * *p<0.05, **** p<0.0001*

[picture cue versus question period]). We focused on comparing only adolescents and adults as these were the only two groups to show a significant semantic attentional bias during either trial period. This analysis revealed two clusters sensitive to these age group differences: one spanning ventral visual and lateral temporal cortex, and the other in right superior parietal cortex (**Figure 4A**). While both age groups engaged ventral visual regions more during the picture cue than question period (adolescents: t=5.18, p=5.39 x 10^{-5}, d=1.16; adults: t=2.52, p=2.15 x 10^{-2}, d=0.03), adolescents engaged this region more than adults during the picture cue (t=4.57, p=5.29 x 10^{-5}, d=1.46; **Figure 4B**). In contrast, adolescents engaged right superior parietal cortex more during the question versus picture cue (t=5.18, p=5.39 x 10^{-5}), while adult showed no reliable activation difference between these trial periods (p=0.92). However, adults did recruit this region more during the picture cue than adolescents (t=3.90, p=3.88 x 10^{-4}, d=1.25; **Figure 4C**). These findings show that adolescents and adults differently engaged ventral visual and superior parietal cortex regions during the preparatory picture cue period of semantic factual retrieval trials.

4. Discussion

Here, we characterized how attention shapes the development of successful memory retrieval. We first identified semantic versus perceptual attentional states that successfully generalized across different individuals. With these attentional states, we examined age group differences in attention during the successful retrieval of autobiographical memories, semantic factual knowledge, and episodic picture details in an independent group of children, adolescents, and adults. All age groups demonstrated a semantic attentional bias during memory retrieval compared with non-memory judgments in the baseline task. However, there were age-related changes in this bias during the semantic retrieval task, such that a reliable semantic bias was observed in adolescents and adults but not in children during semantic factual retrieval. There were also age group differences in the timecourse of this attentional engagement during semantic retrieval: Adults evoked a semantic bias during picture cues that preceded the question while adolescents instead evoked this bias during the question. This timecourse effect was mirrored in the univariate engagement of superior parietal cortex and ventral visual regions. Adults recruited superior parietal cortex more during the picture cue than adolescents who instead engaged ventral visual regions during the cue more than adults. These results underscore how both the nature and timing of attention during memory retrieval shows developmental refinement through adolescence.

All age groups evoked greater semantic meaning versus perceptual attention during memory retrieval in comparison to the baseline task. There are a couple of speculative possibilities as to why we observed this semantic attentional bias across tasks. First, it is possible that the semantic meaning states we characterized may reflect memory elaboration processes that have been previously linked to meaning-based attention (Challis et al., 1996; Craik & Lockhart, 1972; Lockhart, 2002). Enhanced attention to semantic meaning across retrieval tasks may therefore index broader elaboration processes that support memory retrieval overall, irrespective of the nature of the content to be remembered. This aligns with previous work that shows elaboration processes recruit a neural profile that overlaps with prefrontal cortex and hippocampus regions that support episodic, semantic, and autobiographical memory (Cohen & Eichenbaum, 1993; Davachi et al., 2003; Davachi & Wagner, 2002; Poldrack et al., 1999; Ranganath et al., 2004; Thompson-Schill et al., 1997; Wagner et al., 2001). Another possibility is that engagement with highly familiar information such as repeated picture cues and/or question prompts about familiar past experiences may evoke semantic meaning biases. Broadly consistent with this idea, it has been shown that word meaning is extracted faster when linked to familiar versus unfamiliar information (Markman & Wachtel, 1988; Pomper & Saffran, 2019). Therefore, familiar information in the task trials and/or within cued memory retrieval tasks in general may evoke semantic attentional biases across age groups. Importantly, it does not appear that the semantic bias across retrieval tasks is due to our classifier labeling any new neural patterns as semantic attention, since this semantic bias was not observed in the baseline task.

Age group differences in attention between children and adolescents were observed during the retrieval of semantic facts. Given we only considered correct trials, these results might suggest that age-related refinement in attention during factual retrieval persists even *after* the relevant knowledge has been formed. Our findings extend previous work showing age-related differences in the degree to which cued attention to semantic features supports memory formation (Andrade & Raposo, 2021; Ghetti & Angelini, 2008; Perlmutter et al., 1982) by demonstrating similar changes in the spontaneous (uncued) deployment of semantic attention during successful memory retrieval. We suggest that differences in the attentional states that support semantic factual retrieval from childhood to adolescence may reflect immaturity in how children's general knowledge is structured, how accessible relevant knowledge is during retrieval, or a combination of both. While such protracted development may seem inconsistent with previous frameworks that suggests semantic structures mature first to lay the foundation for highly contextual episodic and autobiographical memories (Conway & Pleydell-Pearce, 2000; Keresztes et al., 2017), the nature of the semantic content participants retrieved here aligned more with specialized factual knowledge that is slowly accumulated over one's lifetime (Conway & Pleydell-Pearce, 2000; Lin & Murphy, 2001; Voss et al., 1986). Less experience with the specialized knowledge domains tested in the semantic task may contribute to age group differences in how this knowledge is structured (Favarotto et al., 2014; Gobbo & Chi, 1986; Siew & Guru, 2023) and the accessibility of this knowledge during retrieval (Horgan & Morgan, 1990). Unlike previous work that assessed age-related differences in knowledge structure using participants' self-report responses (e.g., Lin & Murphy, 2001; Unger et al., 2016; Unger & Fisher, 2019), here, we demonstrate developmental changes in this knowledge using objective measures that were characterized in a completely different experiment and set of participants.

Age-related differences in semantic attention during factual knowledge retrieval were also evident in its timecourse. Despite adults and adolescents showing no reliable difference in accuracy or response times on average in the semantic task, these age groups engaged attention during different periods to access the same knowledge: Adults proactively engaged semantic attention in preparation for knowledge retrieval (i.e., showed significant evidence of a semantic attention bias during the picture period) while adolescents instead engaged these states when provided the retrieval question. While it may be puzzling that adults and adolescents demonstrate different neural approaches during factual knowledge retrieval yet achieve similar behaviour, one possibility is that high performance on this task (average accuracy in adults and adolescents=93.85%) obscures our ability to characterize behavioural differences between these age groups that relate to the observed neural differences. Future work using a semantic task that encourages more errors in adults and/or adolescents may reveal nuanced relationships between semantic retrieval behaviour and the neural changes characterized here.

This timecourse difference between adolescents and adults is consistent with work demonstrating age-related increases during childhood in the proactive engagement of control mechanisms for many different cognitive tasks (Chatham et al., 2009; DeMarie-Dreblow & Miller, 1988; Niebaum et al., 2021; Paz-Alonso et al., 2009), but also extends this idea by demonstrating that such improvements continue into adolescence (Calabro et al., 2020; Larsen & Luna, 2018; Luna et al., 2010; Ravindranath et al., 2020) and in the domain of memory. One potential explanation as to why we see these proactive versus reactive retrieval-related attention differences is the protracted development of frontoparietal control networks (Crone, 2009; Hwang et al., 2010; Rohr et al., 2018; Tooley et al., 2022) that broadly support the strategic deployment of attention in service of task goals (Scolari et al., 2015; Szczepanski et al., 2013) and the retrieval of semantic information (Martin et al., 2023; Thompson et al., 2017). We speculate that while adolescents may possess the knowledge required to answer the factual questions, underdeveloped attention control mechanisms may prevent easy access to this information, such that specific retrieval prompts are necessary for this semantic attentional engagement.

Adults and adolescents also engaged superior parietal cortex and ventral visual regions differently over the timecourse of factual knowledge retrieval. Adolescents engaged ventral visual regions during picture cues more than adults, which may reflect their enhanced perceptual processing (e.g., Fisch et al., 2009; Hiramatsu et al., 2011; Kim et al., 2020) of the cue over using its content to guide their attention. Adults instead engaged superior parietal cortex more during the picture cue in comparison to adolescents. Adults' enhanced recruitment of parietal cortex during these preparatory retrieval periods could potentially reflect their use of parietal mechanisms that support (1) memory searches through past knowledge for the relevant information (Humphreys & Lambon Ralph, 2015), (2) the reactivation of the related knowledge (Jonker et al., 2018; Kuhl et al., 2013; Kuhl & Chun, 2014), and/or (3) internal memory signals about the degree to which the relevant information has been successfully retrieved (Vilberg & Rugg, 2008). In contrast, adolescents may not be able to leverage the same mechanisms because of immaturity in their parietal-based cognitive control networks (Chai et al., 2017; Ciesielski et al., 2006; Farrant & Uddin, 2015; Solis et al., 2021), memory retrieval systems (Daugherty et al., 2017; Keresztes et al., 2017; Lee et al., 2014, 2020; Ofen et al., 2007; Schlichting et al., 2022; Selmeczy et al., 2019), or the interaction of both.

One limitation of this work is that we characterized semantic attentional states within a group of adults. Potentially, children may not demonstrate reliable differences in attention during factual retrieval in the current experiment because they evoke a more age-group specific semantic cognitive state our classifier was not trained to detect. Given our approach relies upon the generalization of attentional states across age groups, we are not poised to detect if these states were specific to a particular age group. However, it is important to note that our classifier did successfully generalize to attentional states evoked by children for some retrieval types. More specifically, children demonstrated a reliable semantic bias during memory retrieval (collapsed across all three retrieval tasks) in comparison to the orthogonal baseline task (**Figure S1**).

Furthermore, there were no reliable age group differences in this attentional bias in the autobiographical or episodic tasks. These findings suggest that our classifier trained on adult states could successfully characterize attentional states in children, with age group differences in these states observed during semantic knowledge retrieval. Nevertheless, it is possible that the nature of our classifier trained on adult data can at least in part explain why we saw no evidence of a semantic bias in children during the semantic task. Namely, it might be that: (1) children are simply more variable in their neural semantic retrieval states, leading to a null effect on average; (2) semantic retrieval states in children may not be generalizable because of differences in factual knowledge; and/or (3) children may leverage a very different approach to perform the semantic task that does not map onto our attentional states. Future work that examines how age-specific semantic attentional states relate to successful retrieval is needed to test these possibilities.

4.1. Conclusions

Our novel approach of characterizing developmental changes in the types of attention that support retrieval revealed nuanced differences in semantic retrieval that persisted through adolescence. Specifically, we found continued refinement in attention during the retrieval of factual knowledge from childhood to adolescence, in comparison to episodic and autobiographical retrieval that did not show these age group differences. Developmental refinement was also observed in the timecourse of semantic retrieval: Adults evoked attention in preparation for this retrieval while adolescents used explicit retrieval prompts to guide their attention, with this timecourse difference reflected in differential engagement of superior parietal cortex and ventral visual regions. Both the accumulation of general knowledge and the maturation of cognitive control mechanisms may bolster the development of attentional states that support general knowledge retrieval in the mature brain. Despite semantic knowledge accrual beginning early in life, there is continued refinement in the attentional mechanisms that support access to this knowledge through adolescence.

CRediT authorship contribution statement

Sagana Vijayarajah: Conceptualization; Data Curation; Formal Analysis; Investigation; Methodology; Project Administration; Software; Visualization; Writing—Original Draft Preparation; Writing—Review & Editing. Margaret Schlichting: Conceptualization; Funding Acquisition; Methodology; Resources; Software; Supervision; Visualization; Writing—Review & Editing.

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