

Neither Enhanced Nor Lost: The Unique Role of Attention in Children's Neural Representations

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A defining feature of children's cognition is the especially slow development of their attention. Despite a rich behavioral literature characterizing the development of attention, little is known about how developing attentional abilities modulate neural representations in children. This information is critical to understanding how attentional development shapes the way children process information. One possibility is that attention might be less likely to shape neural representations in children as compared with adults. In particular, representations of attended items may be less likely to be enhanced relative to unattended items. To investigate this possibility, we measured brain activity using fMRI while children (seven to nine years; male and female) and adults (21–31 years; male and female) performed a one-back task in which they were directed to attend to either motion direction or an object in a display where both were present. We used multivoxel pattern analysis to compare decoding accuracy of attended and unattended information. Consistent with attentional enhancement, we found higher decoding accuracy for task-relevant information (i.e., objects in the object-attended condition) than for task-irrelevant information (i.e., motion in the object-attended condition) in adults' visual cortices. However, in children's visual cortices, both task-relevant and task-irrelevant information were decoded equally well. What is more, whole-brain analysis showed that the children represented task-irrelevant information more than adults in multiple regions across the brain, including the prefrontal cortex. These findings show that (1) attention does not modulate neural representations in the child visual cortex, and (2) developing brains can, and do, represent more information than mature brains.

Key words: attention; cognitive neuroscience; development; fMRI

Significance Statement

Children have been shown to struggle with maintaining their attention to specific information, and at the same time, can show better learning of “distractors.” While these are critical properties of childhood, their underlying neural mechanisms are unknown. To fill in this critical knowledge gap, we explored how attention shapes what is represented in children's and adults' brains using fMRI while both were asked to focus on just one of two things (objects and motion). We found that unlike adults, who prioritize the information they were asked to focus on, children represent both what they were asked to prioritize and what they were asked to ignore. This shows that attention has a fundamentally different impact on children's neural representations.

Introduction

Attention is a critical system that can determine what the brain represents from the rich and complex sensory input that it receives (Posner and Petersen, 1990). Decades of research has shown that when adults attend to a particular item, sensory cortex shows attentional enhancement, a clearer neural representation, of the attended item, often at the expense of representing task-irrelevant information (Kamitani and Tong, 2005; Jehee et al., 2011). As yet, however, little is known about how such attentional enhancement develops, and how attention more generally impacts what is represented in children's brains. Do children's brains also enhance representations of attended information, as has been shown in adults? Or, given behavioral evidence showing late development of attentional abilities (Enns and Cameron,

Received Jan. 27, 2023; revised Apr. 4, 2023; accepted Apr. 7, 2023.

Author contributions: Y.J., D.B.W., and A.S.F. designed research; Y.J. and T.A.F. performed research; Y.J., D.B.W., and A.S.F. analyzed data; Y.J. wrote the first draft of the paper; Y.J., T.A.F., D.B.W., and A.S.F. edited the paper; Y.J., D.B.W., and A.S.F. wrote the paper.

This work was supported by Social Sciences and Humanities Research Council of Canada Insight Program Grant 435171493 (to A.S.F.) and the Natural Sciences and Engineering Research Council of Canada Grant RGPIN-2016-05 (to A.S.F.) and Discovery Grant RGPIN-2020-04097 (to D.B.W.). We thank the MRI user community at the University of Toronto (ToNI meeting group) for their helpful feedback across various stages of this project.

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The authors declare no competing financial interests.

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<https://doi.org/10.1523/JNEUROSCI.0159-23.2023>

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1987; Plude et al., 1994), might we observe reduced attentional modulation and possibly greater representation of unattended information as compared with adults? Here, we use fMRI in children and adults to address these questions.

Evidence from behavioral studies suggests that, unlike in adults, attention may not modulate neural representations in children, or at least not to the same extent. Indeed, a rich behavioral literature has demonstrated that selective attention is slow to mature (Enns and Cameron, 1987; Plude et al., 1994; Hanania and Smith, 2010; Plebanek and Sloutsky, 2017; Fisher, 2019). In particular, children appear to struggle with filtering out task-irrelevant information, showing worse filtering abilities than adults in both early (e.g., four to five years old) and middle childhood (e.g., seven to nine years old), with ongoing improvement until early adulthood (~18–20 years old; Hagen, 1967; Enns and Cameron, 1987; Plude et al., 1994). Furthermore, children also appear to process distracting information better than adults: they can both remember distractors better (Plebanek and Sloutsky, 2017) and show better learning of information that is present in distracting information (Frank et al., 2021). These findings suggest that there may be weaker neural evidence of attentional modulation in children, as a consequence of the ongoing development of filtering abilities and their greater sensitivity to distractors (Plude et al., 1994). Supporting this possibility, one neuroimaging study showed reduced attentional modulation in the visual cortex of children (8–13 years old; Wendelken et al., 2011). It is therefore possible that this reduced modulation would manifest in attention having a reduced impact on how well sensory cortex represents information, although this has not yet been tested.

It is also possible that attention may impact children's neural representations, especially when children are able to pay attention to task-relevant information just as well as adults. Indeed, despite ongoing development of attention, children still have significant attentional abilities: children, even young infants, can focus on a subset of available information (Amso and Scerif, 2015), and young children (~4.5 years old) can maintain their attention on a specific target (e.g., duck) throughout a task while ignoring distractors (e.g., turtles; Akshoomoff, 2002). Important further work has shown that expectation-driven top-down signals can modulate neural activity in infants' visual cortex (Emberson et al., 2015). Thus, attention may enhance children's neural representations, just as we typically observe in adults (Kamitani and Tong, 2005; Jehee et al., 2011).

In the current study, we directly test these possibilities, whether attention sharpens neural representations in children or not, by scanning children (ages seven to nine) and adults while they performed a one-back repetition detection task. All participants were asked to selectively attend to either objects (the object task) or motion direction (the motion task) and to indicate repetitions in only the cued dimension. We examined the neural activity patterns of object and motion across the different task conditions. We found that even when children can perform the task like adults, their visual cortex does not show enhanced neural representations of objects and motion through attention, suggesting that attention may have a fundamentally different impact on children's brains than on adults' brains. Our exploratory whole-brain analysis further shows that children's prefrontal cortex represents task-irrelevant information when adults' does not.

Materials and Methods

Participants

Twenty-six adults (mean age: 23.4 years; 281.3 months; 15 females) and 38 children (mean age: 8.9 years; 106.9 months, 18 females) participated

in the current study. Of 38 children who were recruited, 10 did not complete the functional portion of the scan (mean age: 8.7 years; 104.2 months, three females); seven of those children dropped out after a mock scan session, and three of them completed only the anatomical portion of the scanning session (T1 and diffusion spectrum imaging). Our preregistered target sample was 30 adults and 30 children, which was decided based on previous studies (Wendelken et al., 2011; Gomez et al., 2018; <https://osf.io/nuf2a>). While we did not meet this goal (having 26 adults and 28 children in the final sample), we decided to halt data collection before meeting this goal for logistic reasons (transition of institution of the first author followed by the onset of the COVID-19 pandemic); importantly, this decision was made before conducting analyses, both confirmatory and exploratory. All participants (and children's parents) consented before participation, and all aspects of the experiment were approved by the Research Ethics Board at the University of Toronto.

Exclusion criteria

Based on preregistered criteria, we excluded a total of two adults and two children for: having an IQ score, measured by Kaufman Brief Intelligence Test (KBIT), that was below 80 (one adult); having missed the target on >60% of target trials or a false alarm rate that was greater than their hit rate (one adult who also scored below 80 on the KBIT); and having excessive motion during scanning, defined as having >10% of scans with higher than 2 mm of framewise displacement (FD; one adult and two children).

Thus, 24 adults (mean age: 23.1 years/278.8 months, range: 249–373 months, 14 females) and 26 children (mean age: 8.38 years/106.4 months, range: 85–123 months, 15 females) were included in the analysis.

Experimental design and stimuli

Attention task runs

The experiment consisted of three different attention task conditions: the object task, the motion task, and the baseline task. For all task conditions, one of four objects (bumble bee, car, chair, tree), superimposed with dots moving in one of four directions (up, down, right, left) were present on each trial, as shown in Figure 1A. Both the object and motion tasks took the form of a one-back working memory manipulation (Owen et al., 2005), in which participants were asked to press buttons corresponding with a repeat or no-repeat on each trial. For the object task, participants were asked to find objects repeating from one trial to the next, while ignoring the motion stimuli and, of course, any repeats in the motion direction (Fig. 1B). For the motion task, participants were asked to ignore the objects (including possible repeats) and find repeats in the motion direction (Fig. 1B). Repeats did not co-occur in the object and motion dimensions; when an object was repeated, motion direction was not repeated, and vice versa. For the baseline task, participants performed an oddball detection task on the fixation cross, detecting color changes in the fixation cross. Participants were asked to press corresponding buttons (white or pink) to indicate the fixation color on each trial. Before scanning, participants first practiced the one-back task separately for objects (without motion) and motion (without object), on the same stimuli as the main experiment. Then, participants practiced the object and the motion one-back tasks, as well as the baseline task, with both object and motion presented simultaneously, just like the main experiment in the scanner. They repeated the practice until they showed 75% or greater accuracy (hitting at least three out of four targets) for each task.

A mixed block/event-related design was used, where each task condition was embedded in each run as blocks, and each trial with an object image and motion stimulus was an event within each block. There were four total runs with three blocks per each run for each task condition and 16 trials/events per each block (exclusive pairs of four object categories and four motion directions). The order of the task blocks (object, motion, and baseline) was randomized per each run and each subject. There was a 12-s fixation block between the task blocks as well as one at the beginning and one at the end of each run.

All four object pictures subtended $\sim 8.1 \times 8.1^\circ$ of visual angle (Fig. 1A). Motion stimuli were created by using random-dot motion (RDM),

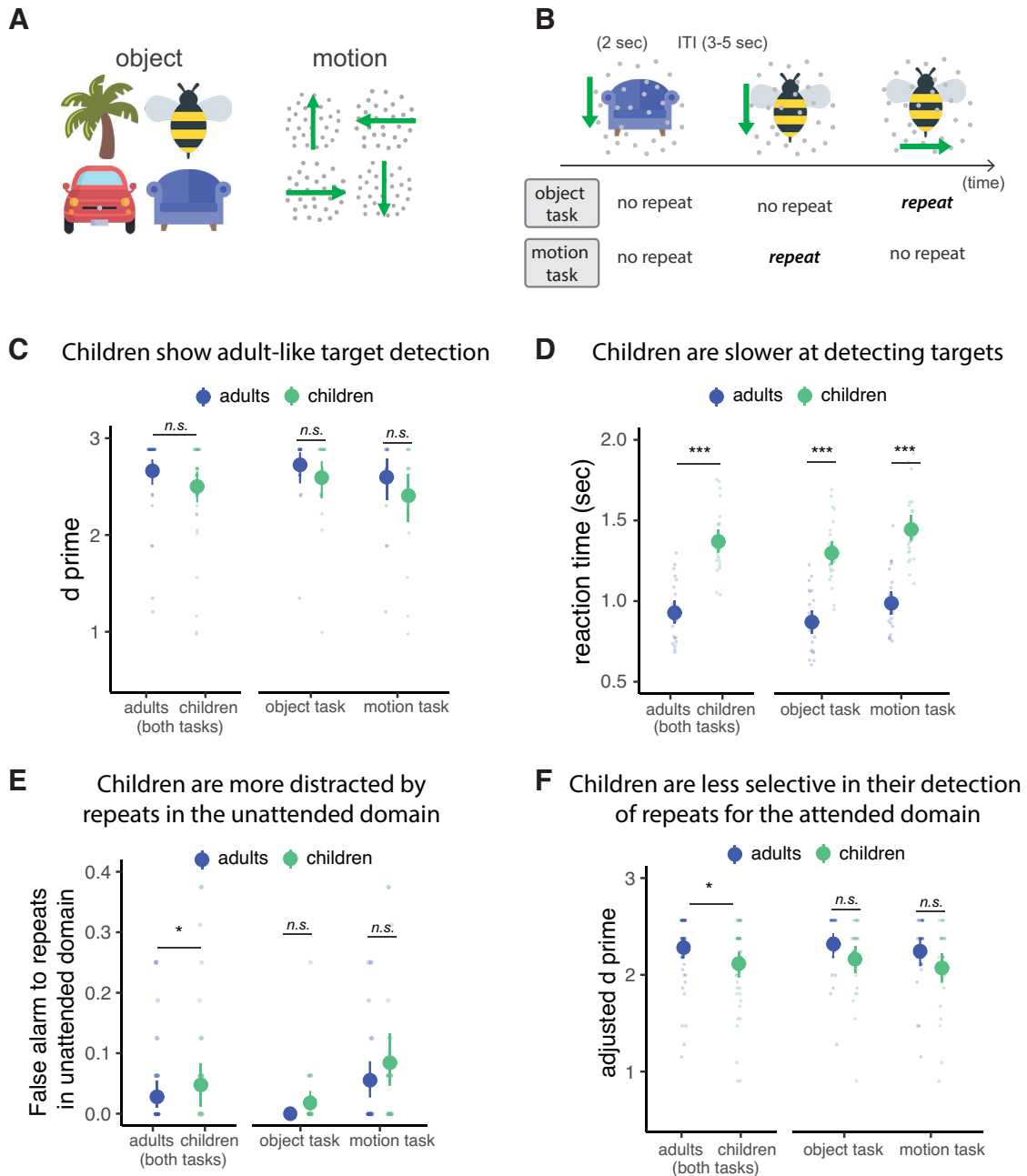


Figure 1. Stimuli and procedure of the experiment and behavioral performance. **A**, Object and motion stimuli. As shown in **B**, each 2-s trial consisted of one object with superimposed dots moving in one motion direction; for the object task condition (first row), participants were instructed to detect objects that repeated from the previous trial and ignore any possible repeats in motion; for the motion task (second row), participants were asked to detect repeating motion directions from the previous trial and ignore any possible object repeats. In each subsequent graph (**C–F**), adults’ (in blue) and children’s (in green) task performance, averaged across the task conditions, is plotted on the left, and their performance in each task condition is plotted on the right. Each colored dot indicates the mean of each group and the line indicates the estimated confidence interval (95%). Individual data are plotted in small colored dots. **C**, Sensitivity to target (repeats in the attended domain; d' prime) for adults (in blue) and for children (in green) in object and motion task conditions, $z(\text{hit rate}) - z(\text{false alarm to all nontarget trials})$. **D**, Reaction time in object and motion task conditions for adults (in blue) and children (in green). **E**, False alarms to repeats in the unattended domain (e.g., responding to repeats in motion in object task). **F**, Sensitivity to repeats in the attended domain, based on hit rate and false alarms to repeats in the unattended item (**E**), $z(\text{hit rate}) - z(\text{false alarm to unattended domain})$, $***p < 0.001$, $*p < 0.05$, $n.s. p > 0.05$.

which was presented within a large circular aperture ($10 \times 10^\circ$) at the center of the screen. Each dot was $\sim 0.2^\circ$ in diameter and moved with the speed of $4^\circ/s$ in one of the four cardinal directions, up, down, right, left, with 100% coherence (Fig. 1A). Each dot disappeared 200 ms after its creation or when it reached the boundary of the circular area. There were always 840 dots in the display; when any dot disappeared, a new dot was created at a random location within the circular display area. Importantly, the dots and the object stimulus were always presented together, with dots overlaying the object, across all three task conditions.

Localizer runs

To localize object-selective regions in the brain, we performed two localizer runs where objects and scrambled-object images were presented in a blocked design (Malach et al., 1995). All participants performed the localizer runs after completing all four main task runs. There were four blocks for objects and four blocks of scrambled objects (18 s for each), and an object block and a scrambled block were always paired together, and this pair was embedded between the fixation blocks. The order of object/scrambled blocks in a pair were pseudorandomized so that for

half of the pairs, the object block came before the scrambled block and vice versa for the other half. In object or scrambled blocks, each picture of an object or a scrambled object was presented for 1 s with 600 ms Intertrial Interval (ITI). Participants were asked to watch the pictures without any explicit task. To ensure they watched all of the images, their eye gaze was monitored using an eye-tracking camera (without recording their eye movement). A 12-s fixation block was included at the beginning and end of each run.

fMRI scanning

All scanning was performed on a 3T Siemens Prisma MRI scanner with a 32-channel head coil at the Toronto Neuroimaging Facility at the University of Toronto. High-resolution anatomical images were acquired with a MPRAGE protocol with a multiband factor of 2. Images were then reconstructed using GRAPPA, with sagittal slices covering the whole brain (T1 = 1070 ms, TR = 2500 ms; TE = 2.9 ms; flip angle = 8°, voxel size = 1 × 1 × 1 mm; matrix size = 256 × 256 × 176 mm). This sequence includes a volumetric navigator (vNav) prospective motion correction system, which tracks and corrects for participants' head motion in real time (Tisdall et al., 2016). Functional images for the main and the localizer runs were recorded with a multiband acquisition sequence (TR = 2000 ms; TE = 30 ms; flip angle = 70°, voxel size = 2 × 2 × 2 mm; matrix size = 220 × 220 × 138 mm; multiband factor = 3; 69 slices).

Data analysis

Before data collection, three adults and three children participated in a pilot version of the current study. Parameters for data analysis, including the exclusion criteria regarding head movement and spatial and temporal smoothing, were determined based on this pilot data. Data from the pilot participants are not included in the presented analysis. The datasets generated during this study are available at <https://osf.io/kd74s/>.

Behavioral data

Task performance in the object task, the motion task, and the baseline task was quantified based on d-prime and the reaction time (RT). Hits ("repeat" responses to object-repeat trials in the object task condition) and false alarms ("repeat" responses to any trials where object was not repeated in the object task condition, applying the same symmetry for the motion task condition) were recorded for all tasks. D-prime scores were calculated as $z(\text{hit rate}) - z(\text{false alarm to all nontarget trials})$, where $z()$ refers to the inverse cumulative Gaussian distribution. To better assess the sensitivity to attended items and the susceptibility to the distractors (task-irrelevant items), we also determined an "adjusted d-prime" by calculating the sensitivity to unattended items, based on the hits to repeats in the task-relevant domain and false alarms to repeats in the task-irrelevant domain (e.g., repeating objects in the motion task condition).

We recorded reaction times (RTs) for all correct responses and excluded trials with RTs shorter than 200 ms or longer than the ITI (3–5 s, i.e., responded after the onset of next trial stimuli). Also, the RTs with larger or smaller than the mean ± 2 SD within each participant were excluded. Based on these criteria, 12.97% of the trials were excluded in adults, and 22.2% of the trials were excluded in children.

MRI data: preprocessing

Preprocessing of anatomical and functional data were performed using fMRIPrep (version 20.0.0) and AFNI functions (version 20.3.02). Anatomical T1w images were corrected for intensity nonuniformity (INU) with N4BiasFieldCorrection distributed with ANTs 2.2.0 (Avants et al., 2014) and then skull-stripped using antsBrainExtraction (ANTs 2.2.0), followed by visual inspection for accuracy. A whole-brain mask was created for each participant using their skull-stripped anatomical T1w image for further analyses. Functional data were corrected for susceptibility distortion estimated from the fieldmap using fugue (FSL 5.0.9), co-registered to a T1w reference using bbrregister (FreeSurfer), which was configured with six degrees of freedom, and corrected for head-motion using mcflirt (FSL 5.0.9). Volumes with movement > 2 mm were corrected via interpolation between the nearest nonaffected

volumes to reduce abrupt signal changes caused by head motion (3dDespike, AFNI). No spatial smoothing was applied to the functional data of the main experiment runs. Functional data of the localizer runs were spatially smoothed with a Gaussian kernel with 4-mm full width at half maximum (FWHM) using 3dmerge in AFNI. For both the main experiment and the localizer data, temporal smoothing was performed to remove frequencies above 0.2 Hz. Head-motion parameters with respect to the BOLD reference were estimated before any spatial or temporal smoothing.

Quality control of child MRI data

We observed that children moved more than adults during the scanning. The average framewise displacement (FD) was higher in children than in adults, $t_{(46,537)} = 3.602$, $p < 0.001$, $d = 0.66$. However, any differences that we observe in the neural data are not likely because of differences in data quality across the two groups for the following reasons. First, in both LOC, and MT, we found that the temporal SNR (tSNR) does not differ in adults and children; in LOC, $t_{(46,918)} = 1.318$, $p = 0.194$, $d = 0.37$; in MT, $t_{(47,576)} = 1.396$, $p = 0.1692$, $d = 0.4$. Second, when we matched the FD values between adults and children by excluding 11 adults who stayed very still during the scanning, $t_{(27,003)} = 1.109$, $p = 0.276$, $d = 0.36$, we still observe the same patterns of the neural data that we do without the exclusion of the adults who moved less (Fig. 2). Finally, when we examined the univariate contrast between either of the task conditions and the baseline condition as a sanity check, we saw similar contrasts in adults and children; both adults and children show activation in the fronto-parietal regions (Fig. 3).

Regions of interest

The lateral occipital complex (LOC) was defined using data from the localizer runs. After preprocessing, functional data from the localizer runs were processed using a general linear model (GLM; 3dDeconvolve in AFNI) with regressors for the two types of images (object, scrambled objects) with six nuisance regressors of motion derivatives. The LOC was defined as continuous clusters of voxels with significant contrast of objects $>$ scrambled objects, $q < 0.05$, corrected using false discovery rate (FDR; Westfall and Young, 1993).

The middle temporal area (MT) was defined using the probabilistic atlas provided by Wang et al. (2015), which was created using functional data from a large cohort of adults. First, the probabilistic MT map was thresholded at $p > 10\%$ in the MNI152 space to ensure that the atlas region was large enough to cover individual differences but still did not cross the borders between areas. The binarized map was then registered into each subject's anatomical space using 3dNwarpApply in AFNI, which served as a template for each individual. Any voxels within the template were excluded if they were also included in the LOC mask. Within this template space, voxels were rank ordered using the GLM contrast of the functional data from the baseline condition; functional data from the baseline condition was modeled using 3dDeconvolve in AFNI with four regressors for each of four dot motion directions as well as six nuisance regressors of subject motion derivatives. We first determined the ideal number of voxels for MT by using cross-validation within the baseline condition data. Voxels were first ranked from highest to lowest F statistic of a one-way ANOVA of the activity of each voxel with dot motion direction as the main factor, and this rank order was used when selecting voxels. Then, we performed leave-one-run-out (LORO) cross validation with the number of voxels varying from 50 to 500 in increments of 50. The number of voxels that provided the best decoding accuracy was used for the main analysis (object attend condition, and motion attend condition). If there were ties, we selected the smallest number of voxels. On average, we selected 141.87 voxels as a result of this procedure. One adult participant did not show any motion selectivity in the MT parcel from the baseline data and thus was excluded from the MT analysis.

Decoding analysis

Decoding analysis was performed separately for each task condition and for each type of stimuli. First, for object decoding, we trained a linear support vector machine (SVM; using BrainIAK package and Scikit-learn libraries; Pedregosa et al., 2011; Kumar et al., 2020) to assign the correct

Adults whose FD values are matched to children’s ($n = 13$, right) show the same pattern of the decoding results as the entire adult group

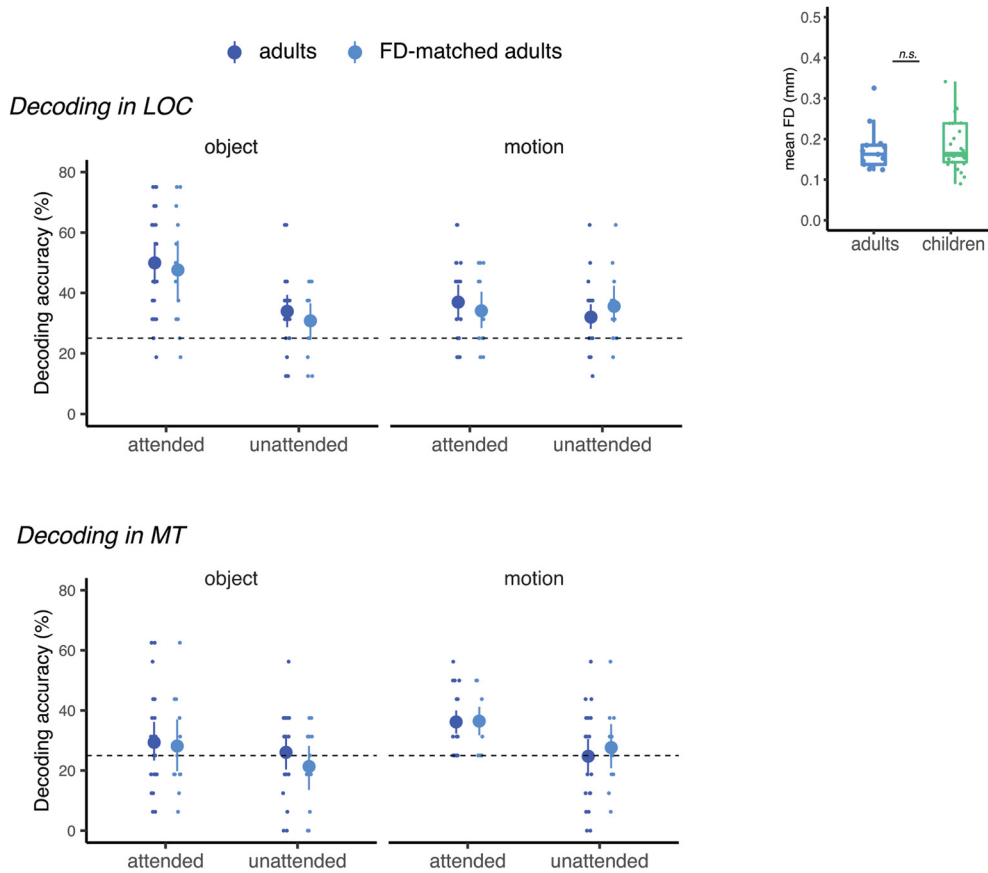


Figure 2. A subset of adults ($n = 13$; plotted in light blue) whose FA values are matched to those in children (plotted on the right; children’s data are plotted in green) showed similar patterns of decoding as the full adult sample (plotted in darker blue). *n.s.* $p > 0.05$.

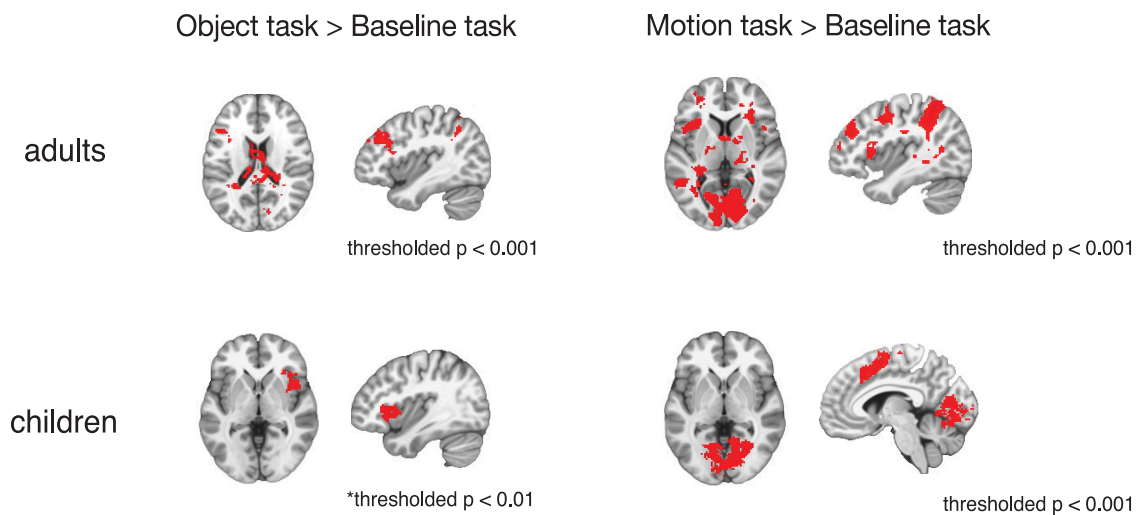


Figure 3. Univariate analyses showing the contrast between the object task (e.g., attending to the objects) and the baseline task (left), and the contrast between the motion task (e.g., attending to motion) and the baseline task (right), in adults (upper panel), and in children (lower panel). Adult show greater activation when attending to either object or motion in fronto-parietal regions, including the middle frontal gyrus (MFG), the frontal eye field (FEF), and the superior parietal lobule, and also in visual cortex. In children, the MFG shows greater activation in the object task. The MFG, the FEF, and the visual cortex show greater activation when attending to motion.

labels to the neural activity patterns, which were the β estimates of each object (bumblebee, car, chair, tree), inside an region of interest (ROI), using all runs except one (leave-one-run-out; LORO cross-validation). The SVM decoder produced predictions for the labels of the left-out

data. This cross-validation was repeated so that each run was tested once, providing predictions for object categories in each ROI and for each subject. The same procedure was performed for motion direction (up, down, right, left), resulting in decoding accuracy (a fraction of

correct predictions) for object and motion in each task condition. Note that given high hit rates in both adults and children, all of the trials were used to train and test the classifier regardless of whether it was correctly answered or not in all of the analyses.

Group-level statistics were computed over all participants in each group (child and adult) using one-tailed t tests, determining whether decoding accuracy was significantly greater than chance level (25% for both object and motion). To compare the decoding performance across the conditions within each group, paired two-tailed t tests were performed. Finally, to test how decoding performance varied across conditions between adults and children, repeated-measures ANOVAs with group as a between-subjects variable, and task condition as a within-subjects variable were performed. Importantly, because we were interested in the effect of our attention manipulation (task condition) in each group, we set out to explore the simple effect of task condition (e.g., differences between attended vs unattended) in each group even when group by task condition interaction was not significant. Note that this simple effect of task condition is especially crucial to better understand whether children's brains represent task-relevant and task-irrelevant information similarly.

Searchlight analysis

To explore representations of objects and motion outside of the predefined ROIs, we performed a searchlight analysis using a cubic searchlight of size $7 \times 7 \times 7$ voxels (343 voxels in volume). The searchlight was centered on each voxel within the whole-brain mask, and LORO cross-validation was performed within each searchlight location using a linear SVM classifier separately for object and motion decoding in each task condition (using BrainIAK; Kumar et al., 2020). Decoding accuracy at a given searchlight location was assigned to the central voxel.

For group-level analysis, we first coregistered each participant's anatomical brain image to the MNI 152 template using a nonlinear transformation warping (3dQWarp, AFNI). We then used the same transformation parameters to register individual decoding accuracy maps to MNI space using 3dNWarpApply (AFNI), followed by spatial smoothing with a 4-mm FWHM Gaussian filter. We performed one-tailed t tests to test whether decoding accuracy at each voxel was above chance (25%) using 3dMEMA (AFNI). After thresholding at $p < 0.05$ (one-tailed) from the t test, we conducted a cluster-level correction for multiple comparisons. We used 3dClustSim in AFNI to conduct α probability simulation for each participant. The estimated smoothness parameters computed by 3dFHMx (AFNI) were used to conduct the cluster simulation with a p value of 0.05 as the threshold. In the simulations, a corrected α of 0.05 was used to determine the minimum cluster size. We used the average of the minimum cluster sizes (216 voxels) across all participants as the cluster threshold.

Results

Behavior

As shown in Figure 1C, target information was well-attended in both groups, with children showing adult-like target detection performance in both task conditions. D-prime was also not different in adults and children across the task conditions, $F_{(1,96)} = 1.294$, $p = 0.258$, $\eta p^2 = 0.001$. Nonetheless, children showed greater sensitivity to task-irrelevant information (repeats in the unattended items) than adults (Fig. 1E, left): false alarms to repeats in the unattended domain were more frequent in children as compared with adults when data were combined across the task conditions, $F_{(1,96)} = 4.721$, $p = 0.032$, $\eta p^2 = 0.05$. Correspondingly, as shown in Figure 1F, children showed poorer selectivity for attended items using our index of adjusted d-prime [$z(\text{hit rate}) - z(\text{false alarm to unattended domain})$] as compared with adults, $F_{(1,96)} = 4.523$, $p = 0.036$, $\eta p^2 = 0.04$. Therefore, despite matched performance across age groups in target sensitivity (d-prime; Fig. 1C), children showed more errors to repeating "lures" in the unattended domain

than adults, suggesting their greater processing of these irrelevant distractors (Fig. 1E,F).

Importantly, since the adjusted d-primes (using only unattended lures to calculate false alarm rate) from both groups were significantly greater than zero (adults: $t_{(23)} = 36.611$, $p < 0.001$; children: $t_{(25)} = 33.39$, $p < 0.001$; Fig. 1F), it is clear that both adults and children were able to follow task instructions and prioritize the detection of repeats in the target stimulus class (e.g., repeating objects in the object task) over repeats in the stimulus class they were instructed to ignore (e.g., repeating motion in the object task).

As expected (Pelegrina et al., 2015), children (mean RT: 1.32 s, SD = 0.218) were also slower than adults (mean RT: 0.92 s, SD = 0.187) when detecting targets across task conditions (Fig. 1D, left), $F_{(1,96)} = 11.958$, $p < 0.001$, $\eta p^2 = 0.55$, both in the object, $F_{(1,48)} = 66.14$, $p < 0.001$, $\eta p^2 = 0.58$, and motion condition, $F_{(1,48)} = 68.1$, $p < 0.001$, $\eta p^2 = 0.59$.

Object and motion representation in the visual cortex

Having characterized behavior, we next turned to the neural analysis. Before addressing our primary question about attention, we first aimed to establish that specific objects and different motion directions can be discriminated in children's visual cortices that are specialized for these categories of information (objects in LOC and motion in MT, as has been shown in adults; Kamitani and Tong, 2006; MacEvoy and Epstein, 2009) as this has not previously been done in children. To do so, we performed a multivoxel pattern analysis to decode object categories (bumble bee, car, chair, and tree) and motion direction (up, down, rightward, leftward) regardless of whether they were attended or not, combining across the object and the motion task conditions.

We found sensitivity for the relevant stimulus class in both children and adults. In particular, we were able to decode objects in the LOC better than chance (25%) in both adults (mean accuracy = 41.92%; $t_{(23)} = 6.924$, $p < 0.001$, $d = 1.41$) and children (mean accuracy = 31.97%; $t_{(25)} = 4.48$, $p < 0.001$, $d = 0.88$), replicating previous work in adults (MacEvoy and Epstein, 2009) and extending this to children. Likewise, we were able to decode motion direction better than chance in the MT in both adults (mean accuracy = 30.45%; $t_{(22)} = 2.86$, $p = 0.008$, $d = 0.59$) and children (mean accuracy = 32.87%; $t_{(24)} = 4.523$, $p < 0.001$, $d = 0.90$), replicating previous work in adults (Kamitani and Tong, 2006; Seymour et al., 2009), and showing for the first time that motion direction can be decoded in children's MT.

Attentional modulation in sensory cortex

Decoding in LOC

We next tested how attention modulates neural representations in the child visual cortex, and how this modulation may differ from adults, looking first at LOC and then MT. As shown in Figure 4B, in LOC, the task impacted adults' and children's object representations differently: there was a significant interaction between group (adults, children) and attention condition (attended vs unattended) in the decoding of objects, $F_{(1,48)} = 6.983$, $p = 0.011$, $\eta p^2 = 0.127$. Specifically, adults showed significantly greater decoding of objects when objects were attended (mean decoding accuracy when attended = 50%, SD = 18.1%; mean decoding accuracy when unattended = 33.85%, SD = 10.6%), $t_{(41,83)} = 3.553$, $p < 0.001$, $d = 1.025$. However, in children, the attentional manipulation had no impact on object decoding, $t_{(49,89)} = 0.896$, $p = 0.374$, $d = 0.988$ (mean decoding when attended = 34.85%, SD = 12.27%, mean decoding accuracy when unattended = 31.73%, SD = 12.86%).

Children represent both attended and unattended items, unlike adults who prioritize attended information

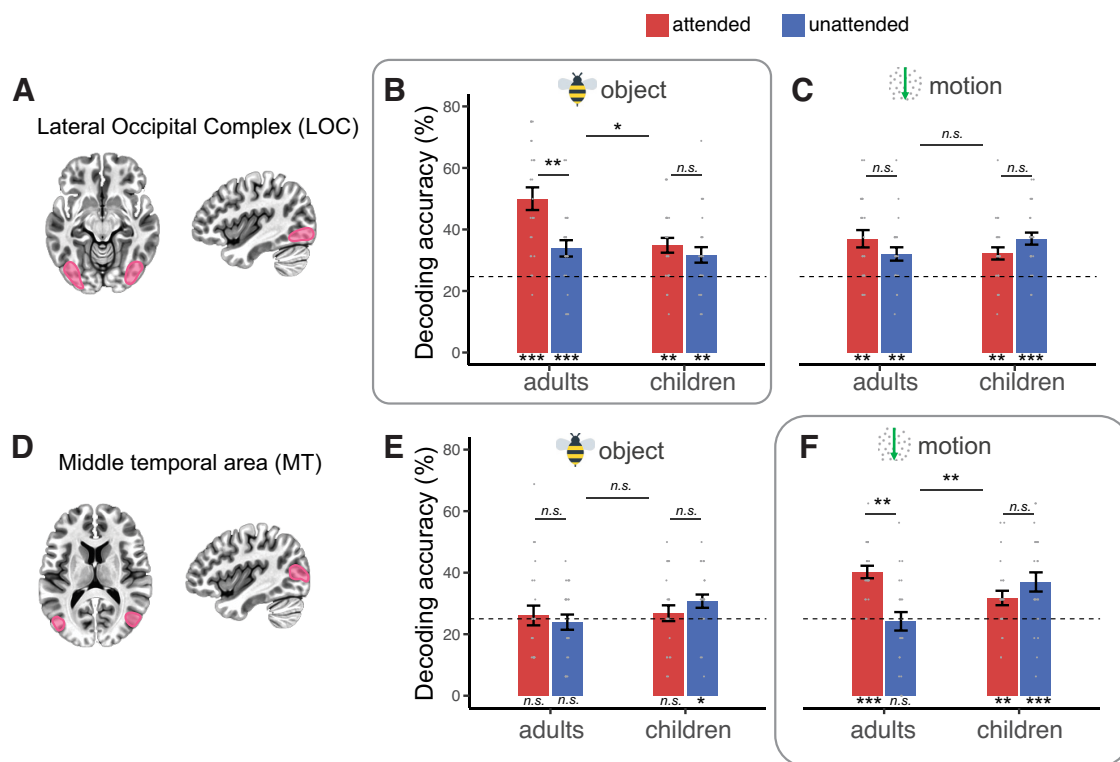


Figure 4. Decoding of object and motion in regions of interest. **A**, The lateral occipital cortex (LOC) is visualized, and all data plotted in this top panel (**B**, **C**) are from this region of interest. In **B** and **C**, decoding accuracy is plotted for objects (**B**) and motion directions (**C**), separately for adults and children (*x*-axes) when each stimulus class (objects in **B**, motion in **C**) is attended (red) or unattended (blue). Since the LOC is selective for object information, the object data are highlighted by the inclusion of a pink box around graph **B**. Decoding accuracy that is significantly greater than chance level is marked at the bottom of the plot (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$), and significant comparisons between adults and children as well as their interactions with task condition are noted at the top of each plot (* $p < 0.05$). Individual data are plotted as small opaque dots, and error bar indicates SEM. For object decoding, greater decoding of attended information observed only for adults but not in children in LOC (**C**), and this interaction between group and attention condition is not observed for motion (**C**). **D**, The middle temporal area (MT) is visualized, and all data plotted in the bottom panel (**E**, **F**) are from this region of interest. In **E** and **F**, decoding accuracy is plotted for the four objects (**E**) and the four motion directions (**F**), separately for adults and children (*x*-axes) when each stimulus class was attended (red) or unattended (blue). In the MT, we observe successful decoding of motion directions only when motion was task-relevant in adults. However, children's MT represent motion both when motion was task-relevant or irrelevant.

Along with the interaction, there was a significant main effect of group in the decoding of objects, where adults' decoding accuracy was significantly greater than children's, $F_{(1,48)} = 7.427$, $p = 0.009$, $np^2 = 0.134$. Simple comparisons reveal that this main effect is driven by stronger decoding in adults when objects were attended ($t_{(40.081)} = 3.441$, $p = 0.001$, $d = 0.988$), as there was no significant difference between adults' and children's decoding accuracies when objects were not attended, $t_{(47.578)} = 0.579$, $p = 0.565$, $d = 0.164$.

For motion information (Fig. 4C), a stimulus class for which LOC is not specialized, we found that motion can be decoded above chance in both adults and children, which was unexpected (see Discussion), but as expected there was no significant interaction between group and attention condition, $F_{(1,48)} = 2.534$, $p = 0.118$, $np^2 = 0.05$. Neither adults' nor children's decoding accuracies for motion differed by attention in this object-specialized region: adults, $t_{(42.79)} = 0.774$, $p = 0.442$, $d = 0.22$ (mean decoding accuracy when attended = 35.15%, SD = 13.14%; mean decoding accuracy when unattended = 32.55%, SD = 9.9%); children, $t_{(49.99)} = -1.725$, $p = 0.091$, $d = 0.48$ (mean decoding accuracy when attended = 32.21%, SD = 10.1%; mean decoding accuracy when unattended = 37.01%, SD = 9.9%). Thus, for adults, attentional enhancement of visual representation appears to occur only for objects, for which the LOC is specialized. Critically,

this attentional enhancement does not happen at all in the child LOC.

Decoding in MT

In MT (Fig. 4D), we observed a significant interaction between group and attention condition in the decoding of motion (Fig. 4F), $F_{(1,47)} = 13.169$, $p < 0.001$, $np^2 = 0.219$. We found that adults showed better decoding of motion when they attended to motion, $t_{(38.70)} = 4.422$, $p < 0.001$, $d = 1.3$ (mean decoding when attended = 40.21%, SD = 9.7%; mean decoding when unattended = 24.18%, SD = 14.38%), suggesting that attention enhances motion representations in the adult MT. Indeed, in adults, motion was not decoded above chance level when motion was not attended, $t_{(23)} = -0.271$, $p = 0.605$, $d = -0.057$. In children, however, motion decoding did not differ between attention conditions, $t_{(46.23)} = -1.319$, $p = 0.193$, $d = -0.37$ (mean decoding when attended = 31.49%, SD = 11.1%; mean decoding when unattended = 36.3%, SD = 14.89%). Thus, in adults, attention to motion modulates its representation. This is not the case in children: attention toward motion does not impact neural representations in children's MT, and children's MT, unlike in adults, represents motion direction even when motion is not relevant to the task, $t_{(25)} = 3.867$, $p < 0.001$, $d = 0.758$ (Fig. 4F).

For object decoding, a stimulus class for which MT is not specialized, there was no significant interaction between group and attention condition in MT, $F_{(1,47)} = 2.448$, $p = 0.124$, $np^2 = 0.05$, echoing analyses in the LOC (for motion). In adults' MT, object information was not represented regardless of the attention condition (attended: mean decoding accuracy = 26.08%, SD = 15.38%, $t_{(22)} = 0.338$, $p = 0.369$, $d = 0.07$; unattended: mean decoding accuracy = 23.91%, SD = 11.86%, $t_{(22)} = -0.439$, $p = 0.667$, $d = -0.09$), and decoding did not differ across the two attention conditions, $t_{(42.7)} = 0.742$, $p = 0.462$, $d = 0.21$. In children, however, object categories could be decoded in MT when they were unattended, mean decoding accuracy = 30.76%, SD = 10.14%, $t_{(23)} = 2.90$, $p = 0.003$, $d = 0.57$, indicating that child MT can represent object information greater than chance, but adult MT does not. Interestingly, however, this object decoding in child MT was not observed when children attended to objects, mean decoding accuracy = 26.92%, SD = 12.08%, $t_{(25)} = 0.811$, $p = 0.212$, $d = 0.16$, although object decoding did not differ across the task conditions (attending to object vs attending to motion), $t_{(48.53)} = -1.242$, $p = 0.219$, $d = 0.3$.

Taken together, these data show that children's visual cortex is unresponsive to attentional manipulations, decoding of the relevant stimulus class is not improved with attention. This is in stark contrast to adults' visual cortex, which shows greater decoding with attention to the relevant stimulus class in both the LOC and MT. Furthermore, in MT, children appear to represent motion information greater than chance when motion was task-irrelevant, whereas adults' MT does not, which may be related to children's sensitivity to task-irrelevant information (Fig. 1E,F). In subsequent analyses, we perform direct comparisons across age groups to ask whether children represent more task-irrelevant (unattended) information than adults across the brain.

Whole-brain analysis

To this end, we examined motion and object representations across the brain using a searchlight analysis. Similar to the ROI-based analysis, we here examined how objects and motion are represented when they are attended and not attended, in adults and in children. As we are interested in attentional relevance regardless of stimulus dimension (object or motion), we combined the data across object and motion decoding and explored how attended and unattended information is represented in adults and children. We first explored interactions between attentional relevance (attended vs unattended) and groups (adults vs children), and then we explored how adults and children represent attended and unattended information, respectively.

Echoing the findings from the ROI-based analysis where we observed greater attentional enhancement in adults, we observed several clusters showing greater attentional modulation in adults as compared with children. Specifically, the clusters in the middle frontal gyrus, the inferior frontal gyrus, and the basal ganglia show greater attentional modulation in adults than children (Fig. 5A; Table 1). In line with the ROI-based findings (where we previously looked at each stimulus class separately by attention condition), we also found a cluster showing greater attentional modulation in adults in visual cortex (Fig. 5A, left). These findings indicate that attention does not have the same impact on children as it does on adults, not just in the visual cortex but also

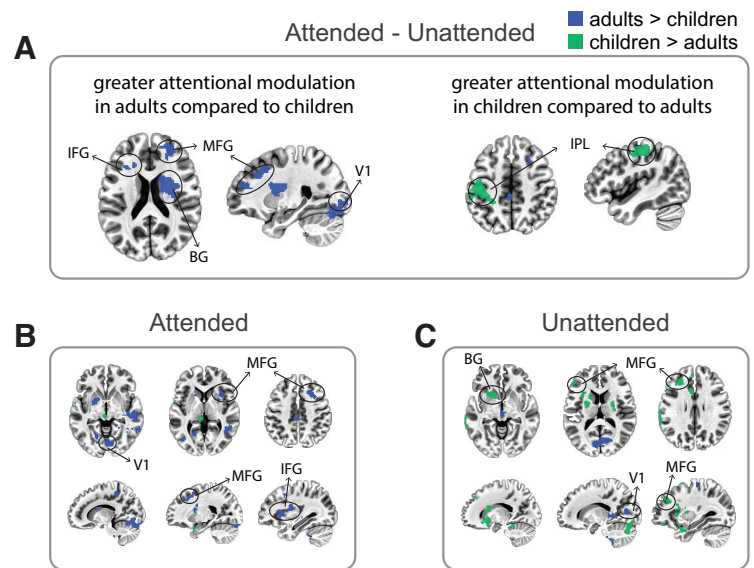


Figure 5. Comparison of searchlight maps between adults and children. Blue clusters indicate better decoding in adults than children, and green clusters indicate better decoding in children than adults. **A**, Contrast between adults and children for attentional modulation (attended–unattended; both for object and motion). **B**, **C**, Contrast between adults and children for attended (**B**) and unattended (**C**) searchlight maps (both for object and motion). Both maps are thresholded at $p < 0.05$ and cluster-wise correction was conducted for multiple comparisons (minimum cluster size, 226 voxels).

in the prefrontal cortex (the middle frontal gyrus and the inferior frontal gyrus) and basal ganglia. Interestingly, children did show greater attentional modulation (e.g., greater decoding through attention) as compared with adults in the inferior parietal lobule (Fig. 5A, right), suggesting a possible greater reliance on this earlier to develop (relative to prefrontal regions; Lenroot and Giedd, 2006) part of the association cortex for attentional processes.

To further understand how adults and children represent attended and unattended information, we then compared adults' and children's decoding, first, for attended information and then for unattended information, again with object and motion combined.

For attended information, adults show better decoding than children in multiple locations across the brain, including the early visual cortex, the middle frontal gyrus, and the inferior frontal gyrus. Indeed, most of the clusters in this contrast map show better decoding in adults than children (see Fig. 5B; Table 2). However, when information was unattended, we see a very different pattern (Fig. 5C; Table 3): Figure 5C shows quite a lot of green (greater in children) and very little blue (greater in adults). Specifically, in the anterior part of the brain, including the middle frontal gyrus and the basal ganglia, children show better decoding of unattended information than adults (Fig. 5C, green clusters), although the opposite pattern is present in the early visual cortex (Fig. 5C, blue clusters).

These findings demonstrate two interesting patterns. First, although children can attend to information in a particular domain with the presence of distractors (Fig. 1C), the adult brain shows clearer representations of attended information than the child brain (Fig. 5B). Second, the child brain, especially their prefrontal cortex, represents unattended information more clearly than the adult brain (Fig. 5C).

Discussion

We found that information is represented in seven- to nine-year-old children's visual cortex regardless of attentional relevance,

Table 1. Comparison between adults and children for attentional modulation (differences in attended–unattended)

| | Peak MNI coordinate | | | Differences between adults and children (%) | Volume (ml) | Description |
|-------------------|---------------------|-------|-------|---|-------------|--|
| | x | y | z | | | |
| Adults > children | −39.5 | 62.5 | −30.5 | 8.97 | 13,648 | Right middle occipital gyrus, right fusiform gyrus, right inferior occipital gyrus |
| | 20.5 | −7.5 | −10.5 | 9.05 | 9736 | Left inferior frontal gyrus, left putamen |
| | −35.5 | 0.5 | 13.5 | 7.12 | 6456 | Right putamen, right insula |
| | 4.5 | 34.5 | 47.5 | 6.84 | 3280 | Left precuneus, left middle cingulate cortex |
| | −23.5 | −23.5 | 35.5 | 7.51 | 3216 | Right cingulate gyrus, right medial frontal gyrus |
| | −31.5 | −47.5 | 17.5 | 5.69 | 2056 | Right middle frontal gyrus, right superior frontal gyrus |
| Children > adults | 38.5 | 30.5 | 53.5 | 7.66 | 12,576 | Left parietal lobule, left postcentral gyrus |
| | −7.5 | 22.5 | 65.5 | 6.84 | 2792 | Right medial frontal gyrus, right superior frontal gyrus |
| | 60.5 | 4.5 | −28.5 | 5.77 | 2040 | Left inferior temporal gyrus, left middle temporal gyrus |
| | 0.5 | 20.5 | −0.5 | 6.16 | 1936 | Left thalamus |

Table 2. Comparison between adults and children for decoding of attended information

| | Peak MNI coordinate | | | Differences between adults and children (%) | Volume (ml) | Description |
|-------------------|---------------------|------|-------|---|-------------|--|
| | x | y | z | | | |
| Adults > children | −9.5 | 80.5 | −6.5 | 5.34 | 10312 | Right calcarine gyrus, right lingual gyrus, V1, V2, V3 |
| | −35.5 | 2.5 | 15.5 | 3.72 | 7904 | Right inferior frontal gyrus, right insula |
| | −45.5 | 52.5 | 9.5 | 4.22 | 7760 | Right superior temporal gyrus, right middle temporal gyrus |
| Children > adults | 52.5 | 10.5 | −38.5 | 3.64 | 3048 | Left inferior temporal gyrus |
| | 32.5 | 14.5 | 69.5 | 3.85 | 2848 | Left superior frontal gyrus, left middle frontal gyrus |

Table 3. Comparison between adults and children for decoding of unattended information

| | Peak MNI coordinate | | | Differences between adults and children (%) | Volume (ml) | Description |
|-------------------|---------------------|-------|-------|---|-------------|--|
| | x | y | z | | | |
| Adults > children | −1.5 | 72.5 | 11.5 | 3.68 | 5536 | Right/left calcarine gyrus, middle occipital gyrus |
| | 32.5 | 24.5 | 65.5 | 2.78 | 1920 | Left precentral gyrus |
| Children > adults | −39.5 | 64.5 | −24.5 | 3.8 | 9952 | Right cerebellum, right fusiform gyrus |
| | 28.5 | 4.5 | 7.5 | 3.43 | 9760 | Left inferior frontal gyrus, left putamen |
| | 66.5 | 22.5 | −16.5 | 3.05 | 4328 | Left middle/inferior temporal gyrus |
| | 44.5 | −19.5 | 45.5 | 3.58 | 3784 | Left middle frontal gyrus |
| | 10.5 | −53.5 | −22.5 | 2.93 | 3728 | Left superior frontal gyrus, left superior orbital gyrus |
| | 62.5 | 40.5 | 39.5 | 2.9 | 3640 | Left parietal lobule |

which was shown in both LOC and MT. In addition, while adults showed attentional enhancement, that is, better decoding in LOC and MT when the relevant class was attended (e.g., object for LOC), decoding in LOC and MT was similar in children regardless of whether the relevant class was attended or not. Related to this lack of attentional modulation in children's visual cortex, children's MT appears to represent task-irrelevant information, unlike adults. Extending these findings, the exploratory whole-brain analysis shows that children's prefrontal cortex (especially, the middle frontal gyrus) and basal ganglia represent task-irrelevant information more strongly than in adults. This greater representation of task-irrelevant information in children's brains is likewise reflected in behavior: children showed greater behavioral sensitivity to task-irrelevant information (Fig. 1*F,E*), despite not differing from adults in their target-sensitivity overall. Taken together, these findings indicate that the information that is represented in children's brains is determined by their task goals to a lesser extent than in adults. In particular, children do not prioritize or enhance their representations of task relevant information and, critically, they represent more information that is not task-relevant.

Our findings address for the first time how task-irrelevant information is represented in both adults' and children's brains.

Previous studies looking at attentional modulation in children's brains explored attentional enhancement or competition for the attended information (Wendelken et al., 2011; Kim et al., 2021). However, these studies have not looked at how attention impacts representations of unattended information in children. What we found using multivariate analysis is rather striking. Along with no attentional modulation in the visual cortex, we also show that children's prefrontal cortex and basal ganglia represent task-irrelevant information even better than adults'. These findings suggest that children's brains, especially their prefrontal regions, can represent information that adults' brains do not (Fig. 5*C*).

Children's greater neural representation of task-irrelevant information is also well aligned with previous work in children demonstrating their greater learning of and behavioral sensitivity to task-irrelevant information (Plude et al., 1994; Sloutsky and Fisher, 2004; Plebanek and Sloutsky, 2017; Darby et al., 2021; Frank et al., 2021). These findings have been interpreted as being linked to the ongoing development of attention making children more likely to process and therefore remember task-irrelevant information than adults (Best et al., 2013; Plebanek and Sloutsky, 2017). Our findings reveal how this might be possible in the developing brain. By representing more task-irrelevant information, children have more opportunity to learn about it in the

longer term. It should be noted, however, that the current experiment does not measure learning and memory directly. Future work is needed to link our important neural findings to differences in learning and behavior. Indeed, as expected given the overall low number of false alarms to distractors we did not observe a direct link between children's sensitivity to task-irrelevant information (their greater false alarm rate to lures in the unattended dimension) and their neural representation of the irrelevant in the current study, either during the object task (correlation between decoding in the MT and false alarms to motion: $r = -0.28$, $p = 0.167$), or the motion task (correlation between decoding in LOC and false alarms to objects: $r = -0.282$, $p = 0.162$). This is likely because the current study was designed to observe possible attentional modulation of the neural representations of objects and motion, not optimized to observe behavioral differences in the learning of specific items, for which a greater number of distractors and trial-unique items would be ideal.

Importantly, we matched the task performance (Fig. 1C) between adults and children in the present study to ensure any neural differences we observe in adults and children are *not* because of differences in their abilities to focus on the target or to follow task instructions. It is important to note, however, that possible differences in task strategy could still be at play. For example, adults and children could be deploying attention at different points in the task (e.g., while viewing stimuli and/or making decisions about them). Having observed these important age-differences with matched task performance, future work can now ask how attention impacts these neural patterns in both children and adults when asked to deploy different task-strategies and under varying degrees of task difficulty.

It is also important to highlight that, along with the lack of attentional modulation in children's visual cortex, we show, for the first time, that children's visual cortex represents visual stimuli with high specificity, measured with distinct neural activity patterns for different exemplars, as typically shown in adults (MacEvoy and Epstein, 2009). Previous fMRI studies looking at children's visual cortex have mainly focused on when and how domain-selective regions emerge across development, such as the fusiform face area for faces, the parahippocampal place area for scenes, and the LOC for objects (Golarai et al., 2007; Scherf et al., 2007). These studies show that domain-specific regions in visual cortex appear to mature relatively early in life, demonstrating adult-like properties (e.g., sizes or domain specificity) in school-aged children (six to eight years old; Golarai et al., 2007; Scherf et al., 2007) if not earlier (Deen et al., 2017; Kosakowski et al., 2022). Extending these previous findings, the current study shows that the LOC can also display distinct neural activity patterns for different exemplars (e.g., tree or bumble bee) within a specific domain (objects) in children, just as has been shown in adults (MacEvoy and Epstein, 2009; Haxby, 2012), and that children's MT can represent the direction of motion, just like adults' MT (Kamitani and Tong, 2006). Any attentional modulation effects notwithstanding, the fact that these individual exemplars can be decoded from children's brains demonstrates that fine-grained representations of stimuli are present in LOC and MT in children, alongside their domain selectivity.

It is also important to note that our whole-brain analyses revealed insights about the development of the prefrontal cortex. Along these lines, there is a large body of work which demonstrates immature prefrontal cortex's function through weaker neural activation related to attention, working memory, or cognitive control (Bunge et al., 2002; Crone et al., 2006; Thomason

et al., 2009; Wendelken et al., 2011; Vogan et al., 2016). This paints a picture of the immature prefrontal cortex as doing much less than its more mature counterpart in adults, and rightly so. Our findings add some important depth to this picture, however, by showing that the immature prefrontal cortex is also doing more than the mature prefrontal cortex; it is representing unattended information more.

While this may be counterintuitive given the especially slow maturation of the prefrontal cortex (Bunge et al., 2002; Gogtay et al., 2004), these findings contribute to a growing and renewed focus on the function of the prefrontal cortex in young children which shows greater functional capabilities than previously assumed (for instance, Raz and Saxe, 2020). The present work suggests that we need to rethink what maturity means from a representational perspective, in which representing less information may be more mature. Indeed, a hallmark of neural immaturity is redundancy: juveniles have more redundant synapses and more neurons (e.g., thicker cortices) across the developing brain (Huttenlocher, 1990; Chechik et al., 1999), which are pruned as the brain matures. While much work is needed to establish any links in these structural terms, it could be that representing more is made possible by having more neural resources, such as more neurons or synapses.

The possible implications of the prefrontal cortex representing more irrelevant information in children are far reaching. In particular, the prefrontal cortex may be especially important for abstract and multimodal representations. Indeed, recent work has shown that the adult prefrontal cortex represents both acoustic and visual aspects of scenes (Jung et al., 2018; Jung and Walther, 2021) and, unlike sensory cortex, the prefrontal cortex can represent stimuli more abstractly, that is independent of the modality in which they were originally presented (also see Kumar et al., 2017). This leaves open questions about what the greater representation of irrelevant information in children's prefrontal cortex means: could the developing prefrontal cortex also be representing these items in a more abstract way, like in adults? And if so, how might this shape children's learning or ability to generalize in novel circumstances? This is an interesting and important avenue for future work to better understand how representations in prefrontal cortex develop.

Future investigations notwithstanding, the current study has uncovered a fundamental difference in the role of attention in shaping adults' and children's neural representations: unlike in adults, attention does not modulate neural representations of attended information in children, who actually show better neural representation of irrelevant information as compared with adults in their prefrontal cortex. These findings are critical when thinking about how children may process and learn information differently from adults, as they reflect how information is prioritized differently in the developing human brain. Indeed, the present data indicate that compared with adults, children are sensitive to more information in the environment, beyond their immediate goals, and such sensitivity can be helpful when children need to learn about multiple aspects of our information-rich world at once, or when their goals change.

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