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Neural Specialization With Generalizable Representations Underlies Children's Cognitive Development of Attention

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From childhood to adulthood, the human brain develops highly specialized yet interacting neural modules that give rise to nuanced attention and other cognitive functions. Each module can specialize over development to support specific functions, yet also coexist in multiple neurobiological modes to support distinct processes. Advances in cognitive neuroscience have conceptualized human attention as a set of cognitive processes anchored in highly specialized yet interacting neural systems. The underlying mechanisms of how these systems interplay to support children's cognitive development of multiple attention processes remain unknown. Leveraging developmental functional magnetic resonance imaging with attention network test paradigm, we demonstrate differential neurocognitive development of three core attentional processes from childhood to adulthood, with alerting reaching adult-like level earlier, followed by orienting and executive attention with more protracted development throughout middle and late childhood. Relative to adults, young children exhibit immature specialization with less pronounced dissociation of neural systems specific to each attentional process. Children manifest adult-like distributed representations in the ventral attention and cingulo-opercular networks, but less stable and weaker generalizable representations across multiple processes in the dorsal attention network. Our findings provide insights into the functional specialization and generalization of neural representations scaffolding cognitive development of core attentional processes from childhood to adulthood.

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continued

Public Significance Statement

Children exhibited differential neurodevelopment of three attentional processes, with alerting reaching adult-like level earlier, followed by orienting and executive attention maturing in middle-to-late childhood. In comparison to adults, children showed lower stability and weaker generalizability of neural representation across attentional processes. The interplay of neural specialization and generalization fosters children's cognitive development of attention.

Keywords: attention, cognitive development, specialization, generalizable representation

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From childhood to adulthood, the human brain undergoes protracted development, with prominent improvement in multiple attentional processes and cognitive capabilities. One long-standing question in the field of human developmental cognitive neuroscience is how exactly the brain develops highly specialized yet interacting neural modules that support nuanced attentional and cognitive functions. An interactive specialization view suggests that a given module can exist in multiple neurobiological modes to support different functions in development (Duncan, 2010; Johnson, 2011; Kragel et al., 2018). Advances in cognitive neuroscience have conceptualized human attention as a set of cognitive processes anchored in highly specialized yet interacting neural systems (Corbetta & Shulman, 2002; Moore & Zirnsak, 2017; Petersen & Posner, 2012; Posner & Petersen, 1990). Behaviorally, the dissociation of core attentional processes into alerting, orienting, and executive attention, the so-called trinity model, has been especially well characterized (Fan et al., 2002, 2009), making this domain an ideal model for studying the developmental pattern of highly specialized yet interacting neural modules that characterize children's multiple attention processes development.

The cognitive and behavioral characteristics of three attentional processes have been well characterized in both adults and children (Fan et al., 2002; Rueda et al., 2004), but their neurodevelopmental pathways need to be deciphered. Previous work has demonstrated developmental changes in behavioral performance (Rueda et al., 2004) and brain systems associated with the three attentional processes (Konrad et al., 2005). For instance, adults recruit dissociable neural systems for alerting, reorienting, and executive

attention, whereas children tend to show less focal engagement in frontoparietal and midbrain regions than adults (Konrad et al., 2005). This provides evidence for the immature and less pronounced dissociation of attention-related brain systems during childhood. Many neuroimaging studies have attempted to dissect attention-related brain regions into dorsal-attention, ventral-attention, and cingulo-opercular networks and characterize their developmental changes in structure and function (Corbetta & Shulman, 2002; Farrant & Uddin, 2015; Petersen & Posner, 2012; Posner & Petersen, 1990; Thiel et al., 2004). Recently, multiple lines of developmental cognitive neuroscience research converge onto the interactive specialization model, which highlights specialization and integration of specific brain systems as a fundamental principle in promoting children's cognitive development including attention domain (de Haan et al., 2002; Gauthier & Nelson, 2001; Johnson, 2001; Johnson et al., 2009; Neville et al., 1992). Therefore, investigating the specialization and integration of brain systems is critical to understand both typical and atypical neurodevelopment of human brain. However, it still remains elusive the underlying mechanisms of how distinct brain systems associated with three core attentional processes develop as the brain matures from childhood to adulthood and whether they undergo distinct developmental paces.

Through a developmental cascade, multiple brain systems must work in concert to yield nuanced attentional processes in support of ever-changing cognitive and environmental demands in a context-dependent manner (Atkinson & Braddick, 2012; Duncan, 2010; Duncan & Owen, 2000; Zelazo & Carlson, 2023). According to the multiple-demand

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Sha Tao played an equal role in supervision and resources. Qi Dong played a lead role in resources. Shaozheng Qin played a lead role in conceptualization, methodology, supervision, writing–original draft, and writing–review and editing.

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system model, there should be a latent system that supports the regulation of distinct yet highly intertwined attentional processes (Duncan, 2010). The essential function of such a system is to separate and integrate neural representations that are generalizable and flexible to meet ever-changing task demands. The common neural system in the frontoparietal cortex has been recognized as a multidemand system responsible for general recruitment to organize neural activity across diverse cognitive functions (Atkinson & Braddick, 2012), likely through compositional mechanism that can concomitantly separate, organize, and integrate multiple aspects of information (Cole et al., 2013; Yang et al., 2019). For the attention domain, in particular, the integrated dorsal attention network encompassing the frontal eye fields (FEF) and parietal cortex is linked to voluntary shifts of multiple attention-related tasks (Kane & Engle, 2002; Reverberi et al., 2012). It is thus conceivable that this system should be relevant to regulate the role of generalizability across three core attentional processes over development.

Neural ensemble activity is believed to serve as a possible mechanism that can give rise to a generalizable neural representation supporting multiple cognitive functions. Multivoxel pattern analysis, as a widely used approach in the neuroimaging community, allows to detect differences in neural representations between specific mental states or conditions by focusing on the analysis and comparison of corresponding distributed patterns of functional magnetic resonance imaging (fMRI) activity (Kriegeskorte et al., 2008; Sarma et al., 2016). We thus utilized multivoxel pattern analysis of task-dependent fMRI data, by computing pairwise correlations of distributed activity patterns between three attentional processes. This approach can not only parse process-specific multivoxel neural representations (Kriegeskorte et al., 2006, 2008) but also detect the stability of representational content across development in children and adults (Camacho et al., 2023; Qin, 2023; Qin et al., 2014). Furthermore, we implemented an innovative analytic approach that is capable of identifying latent shared multivariate representations that are generalizable across three attentional processes, with a hierarchical structure model using a construct-validation method grounded in psychometric theory (Kragel et al., 2018). This allows us to assess the generalizability of latent distributed representation patterns across multiple attentional processes by modeling the similarity structure of multivoxel activity of given region(s) within a compositional coding framework. Based on the multidemand system and compositional coding views, we hypothesized that the dorsal attention network would be responsible for mediating multivoxel representations generalizable across three attentional processes, most likely with weaker generalizability in children relative to adults.

Here we test the above hypotheses via implementation of an event-related fMRI paradigm with a child-friendly attention network test (ANT) combined with innovative analytic

approaches in a large sample of children and adults. We implement a set of univariate and multivariate analyses to assess age-related changes of specific attentional neural systems, distributed representation stability as well as generalizable representation across three attentional processes in task-general (i.e., commonly engaged in all three processes) and task-specific regions (i.e., separately engaged in one of the three processes).

Method and Materials

Transparency and Openness

All the necessary codes of this study are available from the GitHub link at <https://github.com/drhaol/Neurocognitive-Development-of-Attention>. The raw data are available from the corresponding author on reasonable request.

Participants

A total of 746 participants were recruited for this study, which consisted of 658 typically developing children (with 426 for behavioral sample, 272 in neuroimaging sample), and 88 young healthy adults (with 84 in behavioral sample, 75 in neuroimaging sample). Demographics of children and adults are listed in Table 1 and Supplemental Table S2. For other demographic variables such as parental education level, please refer to our previous studies from Children School Functions and Brain Development Project (Beijing Cohort; Wang et al., 2022; Xu et al., 2022). The study procedures were approved by ethical guidelines with the standards of the Declaration of Helsinki. Written informed consent was obtained from all participants before the experiment. For children, written informed consent was obtained from one of their parents or legal guardians. Participants reported no history of vision problems, no history of neurological or psychiatric disorders,

Table 1
Demographics of Children and Adults

Variable	Group	
	Children	Adults
All sample		
<i>N</i>	658	88
Age (<i>Mean ± SD</i>)	9.03 ± 1.41	21.91 ± 1.81
Gender	378M/280F	43M/45F
Ethnicity	Chinese Han	Chinese Han
Behavior sample		
<i>N</i>	426	84
Age (<i>Mean ± SD</i>)	9.14 ± 1.27	21.84 ± 1.81
Gender	242M/184F	41M/43F
Ethnicity	Chinese Han	Chinese Han
Imaging sample		
<i>N</i>	272	75
Age (<i>Mean ± SD</i>)	9.20 ± 1.22	21.85 ± 1.81
Gender	148 M/124F	32 M/43F
Ethnicity	Chinese Han	Chinese Han

Note. *N* = participants number; M = male; F = female.

and no current use of any medication or recreational drugs. Participants with mean accuracy for each cue and flanker conditions less than 50% or excessive head motion (max displacement > one voxel size) were excluded for further neuroimaging data analyses (Supplemental Figure S1).

Cognitive Tasks

We implemented a child-friendly version of the ANT consisting of six conditions, with four cue conditions and two target conditions (Figure 1a): (a) no-cue, (b) double-cue, (c) center-cue, (d) spatial-cue, (e) congruent flanker, and (f) incongruent flanker. Each trial started with a fixation cross at the central of the screen for random variable duration of between 400 and 1,000 millisecond (ms). Subsequently, on some trials, a warning cue was presented for 150 ms. A brief fixation period of 450 ms appeared after the disappearance of the cue. Thereafter, the target “fish” stimulus with either congruent or incongruent flankers was presented until participants made a button press or reached the time limit of 1,000 ms. The duration of the last fixation was 1,000 ms minus corresponding reaction time. For each trial, participants had to press either a left or right button to indicate the direction of the central fish as quickly and accurately as possible. The

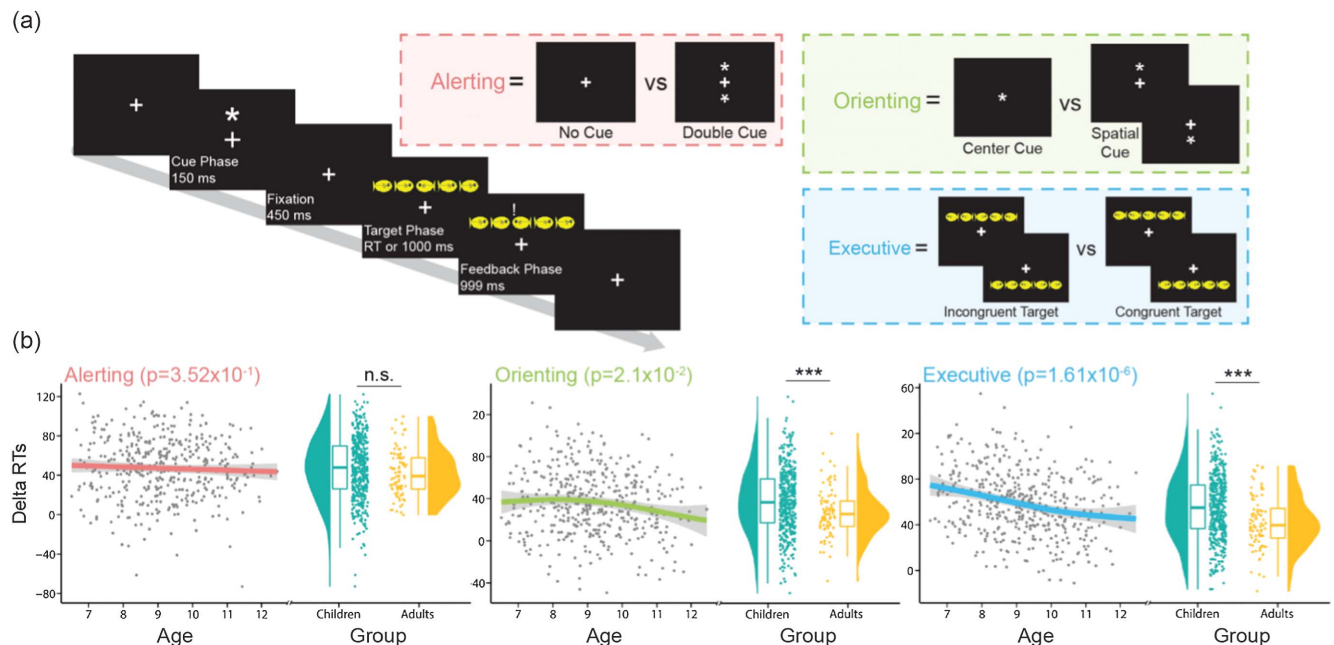
entire task was divided into two separate runs, and each run lasted approximately 6 min. Stimuli were presented via E-Prime 2.0 (<http://www.pstnet.com>; Psychology Software Tools, Inc.).

We computed three attentional scores for alerting, orienting, and executive attention after cleaning of behavioral data by the following preprocessing steps: (a) response times for incorrect responses were excluded from further analyses; (b) trials with RTs beyond 3 *SDs* were removed from each condition; and (c) mean RTs and accuracy for six different cue or target conditions were calculated to verify the validity of behavioral data. According to classic analytical methods (Fan et al., 2002; Konrad et al., 2005; Rueda et al., 2004), the operational definition of “alerting” score refers to the difference in RTs between no-cue and double-cue conditions, and “orienting” score as the difference in RTs between center-cue and spatial-cue conditions, and “executive attention” score refers as the difference in RTs between incongruent and congruent flanker conditions.

Behavioral Data Analysis

Participant demographic data and behavioral measures were analyzed in the R package (Version 3.5.1; platform:

Figure 1
ANT Paradigm and Behavioral Results



Note. (a) An example trial of the ANT, in which participants were required to decide as quickly and accurately as possible whether the central fish in a string of stimuli was pointing left or right. Three shaded boxes with dashed outlines depict the operational definitions of core attentional processes for alerting (light coral), orienting (light green), and executive (light blue) attention, respectively. (b) Left: Distinct developmental changes of attentional processes as a function of age from 7 to 12 years old in children. Colored curves represent the best fit using general additive model with shaded area indicating 95% confidence intervals. Right: Raincloud plots of behavioral scores of three core attentional processes in children and adults. Error bars = standard error of mean; n.s. = not significant; ANT = attention network test; RT = response time. See the online article for the color version of this figure.

+ fixation cross. * warning cue. *** $p < .001$.

apple-darwin15.6.0). We first performed separate t tests for behavioral data in three attentional processes between adults and children. Then, the general additive model (GAM) implemented in the R package “mgcv” (<https://cran.r-project.org/web/packages/mgcv/index.html>) was used to investigate age-related changes of three attentional abilities from 7 to 12 years old. This approach allows us to detect the linear or nonlinear age-behavior relation without defining a set of priori functions (i.e., polynomials). Importantly, the GAM estimates nonlinearities using restricted maximum likelihood and determines a penalty with increasing nonlinearity to avoid overfitting the data. We included sex as a covariate of no interest, because (a) no sex-related performance differences were found in our sample and (b) our primary focus was on the relation between age and distinct attention development. The final model for estimating age-related developmental effects on each attention score can be expressed as follows:

$$Y = \text{spline}(\text{age}) + \text{gender}, \quad (1)$$

where Y represents either alerting, orienting, or executive attention scores.

Imaging Data Acquisition

Whole-brain images were acquired from Siemens 3.0T scanner (Magnetom Prisma syngo MR D13D, Erlangen, Germany) using a 64-head coil with a T2*-sensitive echo-planar imaging sequence based on blood oxygenation level-dependent contrast. Thirty-three axial slices (3.5 mm thickness, 0.7 mm skip) parallel to the anterior and posterior commissure line and covering the whole brain were acquired with the following parameters: repetition time (TR) 2000 ms, echo time (TE) 30 ms, flip angle (FA) 90°, voxel size $3.5 \times 3.5 \times 3.5 \text{ mm}^3$, field of view (FOV) $224 \times 224 \text{ mm}^2$. The ANT consisted of two runs, each with 177 volumes. Each participant’s high-resolution anatomical images were acquired through three-dimensional sagittal T1-weighted magnetization-prepared rapid gradient echo with a total of 192 slices, TR 2,530 ms, TE 2.98 ms, FA 7°, inversion time (TI) 1,100 ms, voxel size $1 \times 1 \times 1 \text{ mm}^3$, acquisition matrix 256×224 , FOV $256 \times 224 \text{ mm}^2$, BW 240 Hz/Px, slice thickness 1 mm.

fMRI Data Preprocessing

Brain images were preprocessed using statistical parametric mapping (SPM12, <https://www.fil.ion.ucl.ac.uk/spm/software/spm12>) based on MATLAB software platform (Version 8.1; MathWorks Inc., Natick, MA, USA). The first four volumes of functional images for each run were discarded for signal equilibrium and participants’ adaptation to scanning noise. Remaining images were corrected for slice acquisition timing and realigned for head motion correction. Subsequently,

functional images were coregistered with each participant’s gray matter image segmented from corresponding high-resolution T1-weighted image, then spatially normalized into a common stereotactic Montreal Neurological Institute space and resampled into 2 mm isotropic voxels. Finally, images were smoothed by an isotropic 3D gaussian kernel with a 6-mm full-width half maximum.

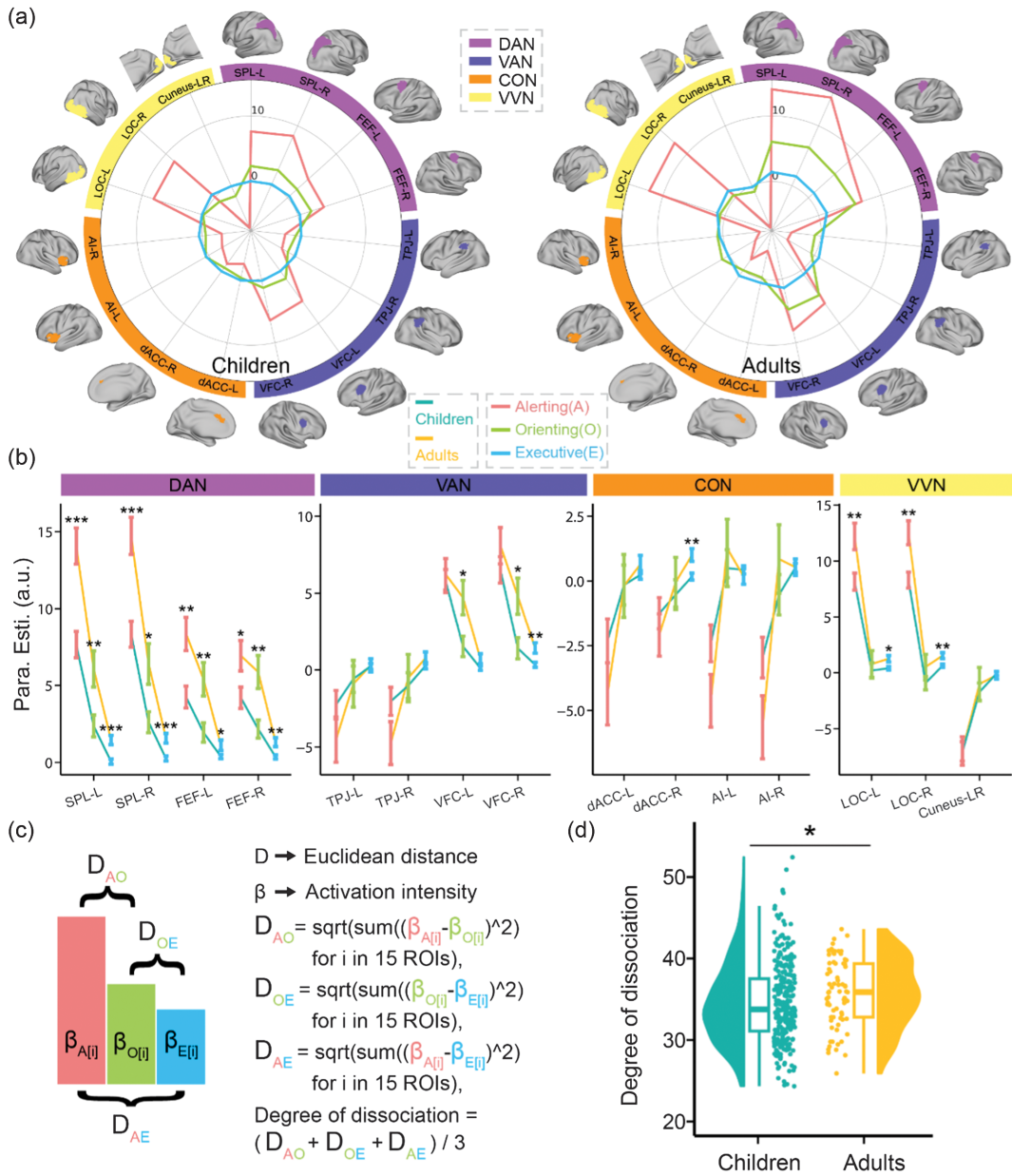
Univariate General Linear Model Analysis

To assess task-related brain responses in the ANT, we created six separate regressors (Supplemental Figure S2) to model task-invoked neural responses to four cues and two targets (Fan et al., 2005). These regressors were convolved with the canonical hemodynamic response function implemented in SPM12. In addition, each participant’s motion parameters from the realignment procedure were included to regress out effects related to head movement-related variability. We used high-pass filtering with a cutoff of 1/128 Hz and corrections for serial correlations using a first-order autoregressive model, AR (1) in the General Linear Model (GLM) framework. Relevant contrast parameter estimate images were initially generated at the individual-subject level for alerting, orienting, and executive attention.

Corresponding parametric contrast maps were submitted to a 2 (Group: children vs. adults) -by-3 (Process: alerting vs. orienting vs. executive) repeated-measures analysis of variance for treating participants as a random variable. We found a significant main effect of conditions (processes) at the group level (Supplemental Figure S4). We next defined a set of regions of interest (ROIs) according to F contrast, reflecting the main effect of conditions (processes). Significant clusters were determined by a stringent threshold of $q = .05$ (cluster size >45) false discovery rate (FDR) correction for multiple comparisons. These regions can be broadly classified into four distinct brain networks: (a) dorsal-attention network including superior parietal lobule (SPL) and FEF; (b) ventral-attention network including temporoparietal junction (TPJ) and ventral frontal cortex (VFC); (c) cingulo-opercular network including dorsal anterior cingulate cortex (dACC) and anterior insula; and (d) ventral visual network including lateral occipital cortex (LOC) and cuneus. To better clarify the relation between the ROIs and different attentional processes, we have summarized a table that defines each of these functional networks at both the behavioral and neural levels, along with corresponding brain regions (Supplemental Table S1). These ROIs were used for subsequent analyses (Figure 2a and 2b) to characterize developmental differences in brain activation patterns between children and adults by extracting parameter estimates (or β weights) from each ROI for alerting, orienting, and executive attention.

Separate one-way analyses of variance were conducted to the second-level group analysis to identify brain regions

Figure 2
Functional Dissociation of Brain Systems for Alerting, Orienting, and Executive Attention



Note. (a) Schematic polar plots showing weaker functional dissociation in dorsal-attention network (DAN), ventral-attention network (VAN), cingulo-opercular network (CON), and ventral visual network (VVN) in children (left) relative to adults (right). (b) Line graphs of activation intensity for alerting, orienting, and executive attention in children and adults. Significance with asterisk was obtained from separate comparisons between groups and conditions. (c) Schematic diagram of the degree of dissociation indicator calculation. (d) Bar plots show the difference for degree of dissociation across the three attention processes between children and adults. Error bars = standard error of mean; L = left; R = right; sqrt = square root; sum = summation; LOC = lateral occipital cortex; SPL = superior parietal lobule; FEF = frontal eye fields; VFC = ventral frontal cortex; dACC = dorsal anterior cingulate cortex; TPJ = temporoparietal junction; AI = anterior insula. See the online article for the color version of this figure. * $p < .05$. ** $p < .01$. *** $p < .001$.

associated with alerting, orienting, and executive attention in children (Supplemental Figure S5 upper), adults (Supplemental Figure S5 lower), and the combined two groups, respectively. Significant clusters were identified from

the group analysis and determined using the same threshold as noted above (FDR $q = .05$, cluster size >45) in brain regions of combined two groups. Additionally, we computed the sum of Euclidean distance between each pair of the

activation intensity in three attention processes under all 15 ROI as the overall index for the degree of dissociation (Figure 2c). The larger the value of this indicator represents the greater the degree of dissociation.

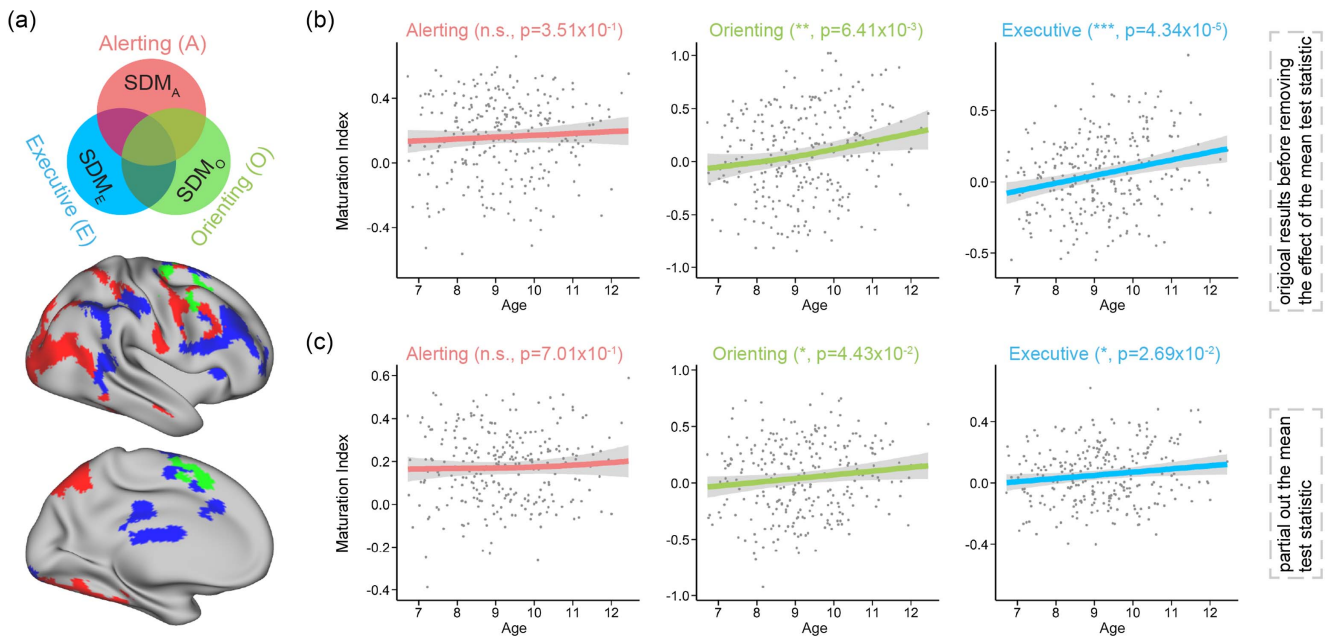
Multivariate Maturation Index

Multivariate maturation index is a spatial correlation approach to characterize developmental differences in distributed brain activity patterns (Cai et al., 2019). This index represents the degree of multivoxel activity pattern involved in a certain process in children as relative to that in adults, namely “adult-like” maturation activity pattern in literature (Cai et al., 2019; Stoeklein et al., 2020; Truelove-Hill et al., 2020). To investigate age-related changes in separate neural activity patterns associated with distinct attention during childhood, we computed a multivariate maturation index for each of three attentional processes using representation similarity analysis (Kriegeskorte & Kreiman, 2012; Sarma et al., 2016). We created three specific symmetric difference masks (SDMs; i.e., “disjunctive union” in mathematics) based on the brain activation map specific to each process while excluding the other two processes. The SDM of three processes was generated by significant clusters (FDR $q = .05$, cluster size >45) in adults involved in alerting

(A), orienting (O), and executive (E) attention, respectively (Figure 3a). For instance, the mask for alerting was created by the formula as following: $SDM_A = Mask_A \& \sim Mask_O \& \sim Mask_E$. Next, each process-specific neural representation vector was extracted using each SDM from different attention processes in each child, and averaged neural representations for each process were created by averaging corresponding patterns across adults. Then, we computed the maturation index using Pearson correlation between the process-specific pattern vector in each child and the corresponding averaged pattern vector across adults (Figure 4a). The maturation index for each process was represented by the similarity of each child’s specific SDM pattern vector relative to the mature pattern represented by an averaged pattern vector in the corresponding SDM across adults. Besides, to mitigate potential confounds according to solutions provided by previous studies (Coutanche, 2013; Davis et al., 2014; Tomparý & Davachi, 2017; Xue et al., 2013), several steps were undertaken: (a) demeaning and normalizing of task-invoked activity intensity across voxels in a given ROI for each participant and (b) implementing a partial correlation approach to regressing out the mean test statistic in an SDM for each child to compute spatial correlation or pattern similarity. We used the GAM with the penalized splines to estimate age-related changes of neural maturation index for

Figure 3

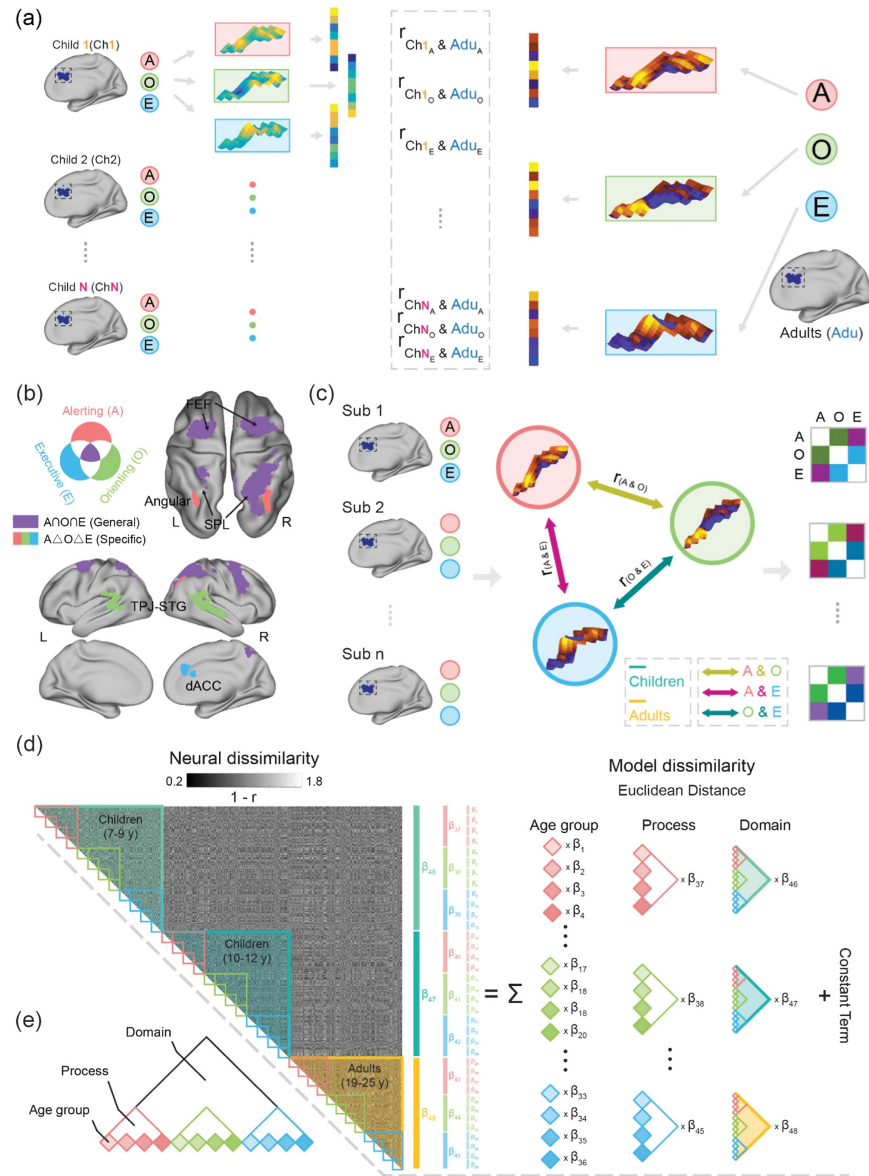
Differential Developmental Patterns of Brain Systems Involved in Core Attentional Processes



Note. (a) The symmetric difference mask (SDM) for alerting (red), orienting (green) and executive (blue) attention. (b) Scatter plots depict distinct age-related changes as a function of age for alerting, orienting, and executive attention in children from 7 to 12 years old. Colored curves represent the best fit from a general additive model (GAM) with shaded area indicating 95% confidence intervals. (c) Scatter plots depict distinct age-related changes as a function of age for alerting, orienting, and executive attention in children from 7 to 12 years old when regressing out the mean test statistic of activation it. n.s. = not significant. See the online article for the color version of this figure.

* $p < .05$. ** $p < .01$. *** $p < .001$.

Figure 4
Illustration of the Process and Model Construction of Multivariate Analysis



Note. (a) Schematic illustration of the maturation index defined as the degree of multivoxel pattern similarity for each child's process-specific brain activity pattern relative to corresponding averaged brain activity pattern across adults. The Venn diagram on the right is the definition visualization of symmetric difference mask (SDM) of each process. (b) Schematic illustration of task-general and task-specific brain regions defined as the intersection (light violet: task-common) and symmetric difference (light magenta: task-specific) of activation associated with three attentional processes. (c) Schematic illustration of multivariate pairwise neural representation stability for alerting, orienting, and executive attention. (d) Decomposing multivariate neural representation dissimilarity into three hierarchical levels of age group, process, and domain. The graphical formula shows how the observed neural dissimilarity (spatial distance) across neural representation from each process in each participant was modeled as a weighted summation of theoretical dissimilarity (Euclidean distance) matrices constructed according to age group (36 parameters), process (six parameters), and domain (three parameters) membership, in addition to a constant term. The matrix shows the dissimilarity of neural representation across three attentional processes in all participants from three age groups in a given region. Each row represents one participant under three processes, and each element of the dissimilarity in activity patterns for pairwise individuals. Colored bars indicate corresponding levels in the functional hierarchy of dissimilarity. (e) Dendrograms convey theoretical groupings of brain activity at three levels of age group, process, and domain. Colored grids illustrate model-based partitioning of neural dissimilarity into components that generalize across participants (bottom, unique to an age group), age groups (middle, unique to a condition), and processes (top, unique to a domain). dACC = dorsal anterior cingulate cortex; FEF = frontal eye fields; SPL = superior parietal lobule; TPJ = temporoparietal junction; STG = superior temporal gyrus. See the online article for the color version of this figure.

alerting, orienting, and executive attention separately:

$$\text{Maturation index} = \text{spline}(\text{age}) + \text{gender}. \quad (2)$$

Neural Representation Stability Across Three Attentional Processes

Representational similarity analyses were utilized to separately assess the pairwise similarity of multivoxel activity patterns associated with three attentional processes within both task-general and task-specific ROIs, which allows us to quantify the stability of neural activity patterns in the multivoxel space evoked by alerting, orienting, and executive attention (Zhuang et al., 2022). We first identified task-general regions that were commonly engaged in three attentional processes and task-specific regions that were engaged in only one of the attentional processes. We created separate activation maps for each of the three attentional processes ($q = .05$, FDR correction): that is, including $i1$ (alerting), $i2$ (orienting), and $i3$ (executive), respectively. We then obtained task-general and task-specific ROIs by two following formulas: (a) task-general ROIs = $i1$ & $i2$ & $i3$ to select the most representative regions involving the FEF and SPL and (b) task-specific ROIs for each of three attentional processes, with $i1$ & $\sim i2$ & $\sim i3$ for alerting to select angular, $\sim i1$ & $i2$ & $\sim i3$ for orienting to select TPJ extending to STG, or $\sim i1$ & $\sim i2$ & $i3$ for executive attention to select dACC (Figure 4b). Pairwise spatial correlations were computed for task-general regions (i.e., FEF, SPL and their combined ROIs) and task-specific regions (i.e., angular, TPJ-STG and dACC). Such similarity metrics were used to quantify the pairwise pattern stability of alerting, orienting, and executive attention (Figure 4c). We compared pairwise representational similarity analyses scores for three attentional processes between children and adults to examine developmental changes in neural representation stability. Additionally, we computed the sum of pattern stability between each pair of the three attention processes under each ROI as the index for overall stability.

We also implemented a whole-brain searchlight approach to assess developmental changes in neural representation stability in children and adults. Using a searchlight mapping method (Kriegeskorte et al., 2006, 2008), a 6-mm spherical ROI (so-called the “searchlight”) centered on each voxel was first selected, and then stability scores between each pair of attentional processes were computed using Pearson’s correlation. The averaged similarity scores were assigned to the central voxel and run through every voxel across the whole brain to create participant-specific searchlight maps. These maps were subsequently submitted to independent-sample T tests to determine developmental changes in neural representation stability between adults and children.

Generalizable Neural Representations Across Attention Processes

An innovative analytic approach with hierarchical structure modeling was implemented to assess the generalizability of task-evoked neural representations across attentional processes. The generalizability metrics were then submitted to further analyses to investigate age-related changes in generalizable neural representations across three attentional processes in children and adults. To gain the homogeneity of the whole brain across different age groups, we split children into two subgroups of middle childhood (7–9 years-old, $N = 136$) and late childhood (10–12 years-old, $N = 136$), and unified all adults ($N = 75$) into one single group. We modeled neural representations of three attentional processes within a given ROI from the three age groups in a hierarchical structure (Figure 4d). This model was organized into a three-level hierarchical structure, including age groups as the first level, attentional processes as the second level, and generalizable attention as the highest level (Figure 4e). The representational dissimilarity matrix (RDM) represents the observed neural dissimilarity (Y) with spatial distance measured by 1 minus the Pearson correlation coefficient between pairs of spatial patterns in different attentional processes from participants. The GLM was modeled as a weighted summation of theoretical dissimilarity (X) according to the three levels, including Euclidean distance of model dissimilarity matrices derived from binary vectors indicating the membership of age groups (36 RDMs) on the first level, attentional processes (nine RDMs) on the second level, and generalizable domain (three RDMs) on the third level, as well as a constant term (C ; Figure 4d right). This GLM formula is defined as follows:

$$Y = \sum_{i=1}^{48} (X_i \cdot \beta_i) + C, \quad (3)$$

where Y represents the spatial distance of the RDM of observed neural dissimilarity, X_i represents the Euclidean distance of each theoretical dissimilarity in each level of model, β_i represents the parameter estimates of each X_i that means of neural representation generalizability, and C represents a constant term. This approach allowed us to investigate the generalizability of interactive neural representations and test the validity of the shared multidemand mechanism underlying alerting, orienting, and executive attention. Parameter estimates (β) from the hierarchical structure model provide estimates of neural representation generalizability.

In the present study, we mainly focused on parameter estimates from the third level representing the generalizable domain. Separate regressors on this level assess the degree of generalizability across different attentional processes. Positive values indicate shared spatial patterns across different processes, providing evidence for a coherent

domain-general pattern. Notably, inference on parameter estimates (β) was made using a bootstrapping procedure by rebuilding all participants' neural activity patterns. This procedure involved repeatedly rebuilding observed neural dissimilarity (Y) for all participants' neural activity patterns over 5,000 iterations. In each rebuilding, a new RDM was constructed using neural activity pattern and corresponding GLM was estimated. Then, parameter estimates (β) were generated in each bootstrap as a sample distribution, and significance was defined as the ratio of less than the full hypothesis with 0 by using normal approximation for inference. To investigate developmental changes, we compared corresponding parameter estimates between children and adults over 1,000 times. Each time, we randomly selected 100 values from the 5,000 iterations for comparison by using an independent T test and acquired a p value. The corresponding significance is defined as the number of significant results ($p = .001$) divided by 1,000.

Results

Distinct Developmental Profiles of Children's Alerting, Orienting, and Executive Attention

We first investigated developmental changes in behavioral performance for the alerting, orienting, and executive attention between children and adults. Given a priori hypotheses derived from previous studies (Rueda et al., 2004), alerting, orienting, and executive attention reflect relatively independent processes on a behavioral level. We thus conducted separate t tests to examine developmental differences in three attentional processes between adults and children. These tests revealed no reliable difference in alerting performance, $t(508) = 1.41$, $p = .079$, Cohen's $d = .17$, Jeffreys, Zellner, and Siow Bayes factor (JZS-BF) = .62, but lower performance for orienting, $t(508) = 3.02$, $p = .001$, $d = .36$, JZS-BF = 19.67, and executive attention, $t(508) = 3.92$, $p < .001$, $d = .47$, JZS-BF = 369.67, in children than adults (Figure 1b).

To characterize the developmental profiles of alerting, orienting, and executive attention from 7 to 12, we implemented a GAM to test for linear or nonlinear relations between age and behavioral metrics (Baum et al., 2017). Children's alerting performance showed no significant change with age ($p = .352$). However, we observed a monotonic developmental pattern as a function of age in orienting ($p = .021$) and a linear decrease in executive attention ($p < .001$), which indicates improvement in performance (Figure 1b). The raw RTs in each condition were presented in Supplemental Table S3. These results indicate distinct developmental profiles of children's attentional processes, with alerting reaching an adult-like level by Age 7, and a protracted development of orienting and executive attention throughout middle and late childhood.

Weaker Functional Dissociation of Brain Systems for Children's Attention

To further investigate developmental changes in functional dissociation of brain systems involved in alerting, orienting, and executive attention, we conducted a whole-brain 2 (Group: children vs. adults) by 3 (Process: alerting vs. orienting vs. executive attention) analysis of variance. We found the main effect of process in the occipital, temporal, parietal, and frontal cortices (Supplemental Figure S4 and Table S4), and we defined ROIs from these cortices, which belong to different attentional networks, for extracted activation intensity. As shown in Figure 2a and Supplemental Figure S2a, children show weaker functional dissociation, both in the activation patterns across brain regions and the intensity of activation in three distinct attentional processes. Further statistical analyses revealed no significant differences in the TPJ, anterior insula, left dACC, and cuneus between children and adults, $-1.103 \leq t(345) \leq 1.858$, $p \geq .065$, but significantly weaker dissociation in distributed regions of the SPL, FEF, VFC, right dACC, and LOC in children than adults, $-4.441 \leq t(345) \leq -2.299$, $p \leq .02$, $-.525 \leq d \leq -.278$, $1.669 \leq BF \leq 241.919$; FDR correction, $q = .05$; Figure 2b and Supplemental Table S5. To further investigate developmental differences in functional dissociation of these brain systems involved in three attentional processes, we conducted the degree of dissociation analysis for above 15 ROIs, by computing the sum of Euclidean distance between each pair of brain activation in these processes. This analysis revealed significant differences, $t(345) = -2.155$, $p = .033$, between children and adults (Figure 2d).

Distinct Developmental Profiles of Brain Systems for Children's Attention

Next, we investigated the developmental profiles of brain systems involved in children's alerting, orienting, and executive attention. Separate whole-brain analyses for activation maps were conducted to identify brain systems involved in distinct attention processes in each age group of children and adults. We observed age-related changes in task-evoked univariate brain responses in children from 7 to 12 years old (Supplemental Figure S3b, FDR $q = .05$, cluster size > 45).

We then investigated the developmental trajectories of brain systems associated with alerting, orienting, and executive attention, by computing an overall multivariate maturation index (Figure 4a). As shown in Figure 3b, our further generalized additive model analyses revealed no significant age-related change in the maturation index for alerting ($p = .351$), a monotonic developmental pattern for orienting with an initial flat trend and a subsequent increase at age 9 ($p = .006$), and a linear increase in executive attention throughout middle and late childhood ($p < .001$). Given differences in univariate activation of a given SDM that could affect the multivariate maturation (between-participant spatial correlation) measure, we therefore conducted

additional analyses by regressing out the mean test statistic of univariate activation in an SDM for each participant. Again, these analyses still revealed a similar pattern of age-related increase in multivariate maturation index for orienting ($p = .044$) and executive attention ($p = .027$, Figure 3c). These results indicate differential maturation profiles of brain systems associated with three core attention processes, with alerting reached an adult-like level by Age 7 and protracted development of orienting and executive attention in middle and late childhood.

Less Stable and Weaker Generalizable Neural Representation Across Multiple Attentional Processes in Childhood

To investigate age-related changes in neural representation associated with multiple attentional processes, we implemented two multivariate analytic approaches to assess the stability and generalizability of task-related neural representation across three attentional processes in children and adults. Given our hypotheses at issue, we mainly focused on task-general regions of the FEF and SPL that were commonly engaged in three attentional processes and task-specific regions of the angular gyrus, dACC, and TPJ extending to STG that were engaged in only one of the attentional processes (Figure 4b). Two independent-sample t tests revealed lower neural representation stability within pairwise processes in children relative to adults, only for task-general regions in the dorsal-attention network, $-4.635 \leq t(345) \leq -2.691$, $p \leq .008$, $-.627 \leq d \leq -.402$, $12.075 \leq JZS-BF \leq 6288.504$; FDR correction, $q = .05$; Figure 5a and Supplemental Table S6. Interestingly, however, this did not emerge for task-specific regions of the angular, dACC, and TPJ, $-1.748 \leq t(345) \leq -.301$, $p \geq .083$; Supplemental Table S6. In the neural representation stability analysis, we observed significant differences between children and adults with overall stability in task-general regions but not found in task-specific regions, FEF + SPL: $t(345) = -4.783$, $p < .001$; FEF: $t(345) = -5.209$, $p < .001$; SPL: $t(345) = -3.863$, $p < .001$; Figure 5b. We also conducted additional whole-brain parallel analyses using a searchlight algorithm, which again revealed weaker pairwise neural representation stability primarily in regions of the dorsal-attention network in children than adults, with most prominent effects in the SPL and FEF (Figure 5c).

To assess the developmental changes in the generalizability of task-evoked neural representation across three attentional processes, we further implemented an innovative analytic approach utilizing a hierarchical structure for both task-general (i.e., FEF, SPL, and their combination) and task-specific regions (i.e., angular, dACC, and TPJ-STG). As shown in Figure 6a and 6b, we observed that adults exhibited significantly higher generalizable neural representation across three attentional processes than the permutation chance level in task-general regions of dorsal-attention

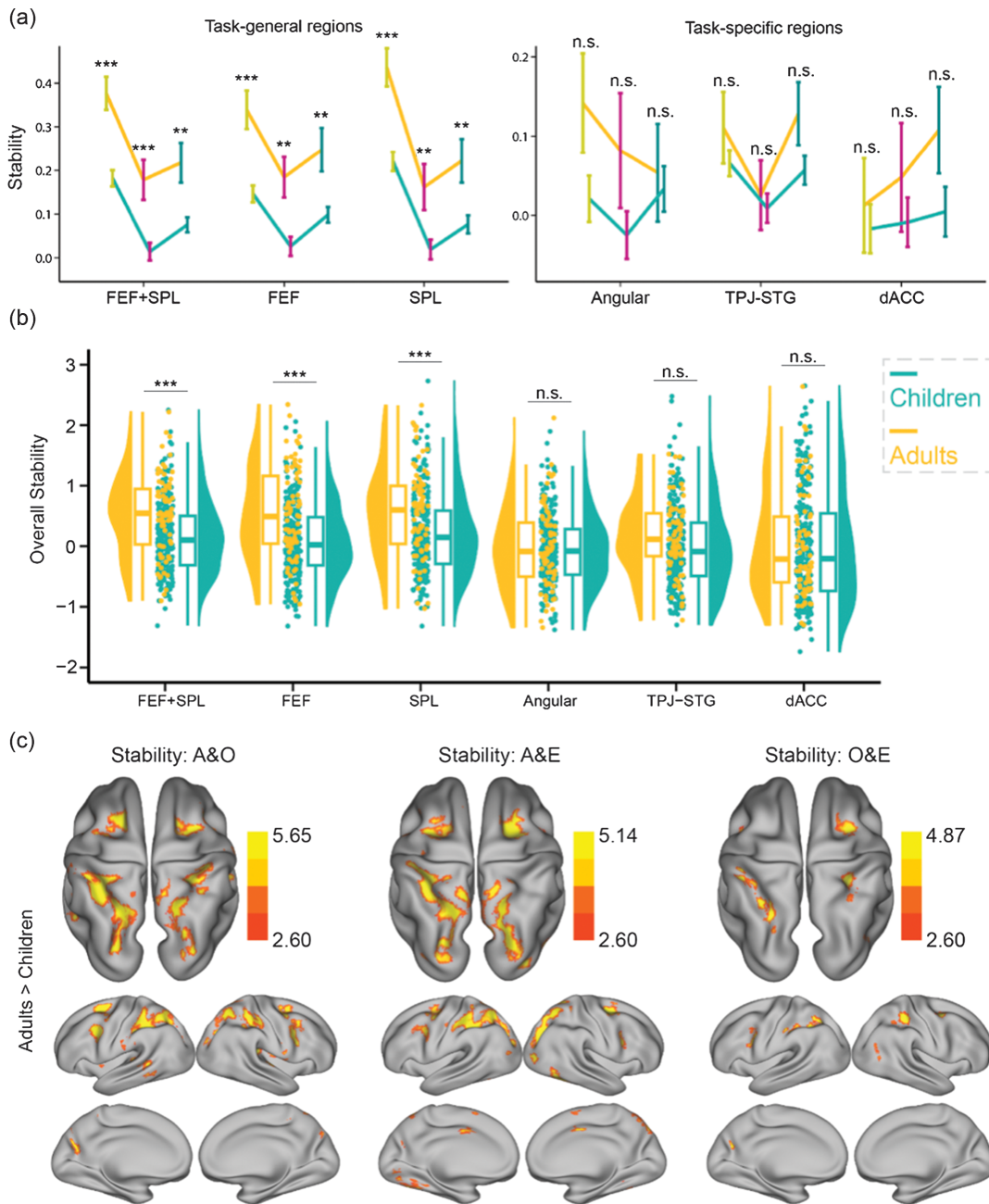
network (FEF + SPL: $p = .018$), especially for the FEF ($p = .005$), but not in task-specific regions of angular, TPJ-STG and dACC (all $p \geq .096$). In contrast, we observed no reliable differences in all of the regions in young children (all $p \geq .084$ by the permutation test). Subsequently, we then examined developmental changes in the generalizability indices for task-general regions between children and adults using a bootstrapping approach. These analyses revealed that children exhibited weaker generalizability of neural representations across three attentional processes in task-general regions, with the most prominent effect in the dorsal-attention network (FEF + SPL: $p < .001$) and especially in the FEF ($p < .001$; Figure 6a). Together, these results indicate that children exhibit less stability and weaker generalizable neural representation patterns across three attentional processes in core regions of the dorsal-attention network.

Discussion

In the present study, we investigated the development of cognitive components in children's attentional processes from 7 to 12 years old, as well as functional specialization and generalization across brain systems in children relative to adults. Behaviorally, children's alerting ability reached an adult-like level early on, though their orienting and executive attention exhibited more protracted development throughout middle and late childhood. Relative to adults, children exhibited less pronounced functional dissociation involved in these three attentional processes. In parallel with behavior results, we found distinct developmental profiles of attentional brain systems, with alerting reaching an adult-like level by Age 7, and orienting and executive attention coming on board later in middle childhood. Critically, children showed adult-like neural representation in regions of the ventral-attention and cingulo-opercular networks but lower stability and weaker generalizability of neural representations in regions of the dorsal-attention network, especially in the FEF. Our findings highlight the distinct development of children's attentional processes and further suggest that specialization and generalization of neurofunctional modules underlie the development of attention.

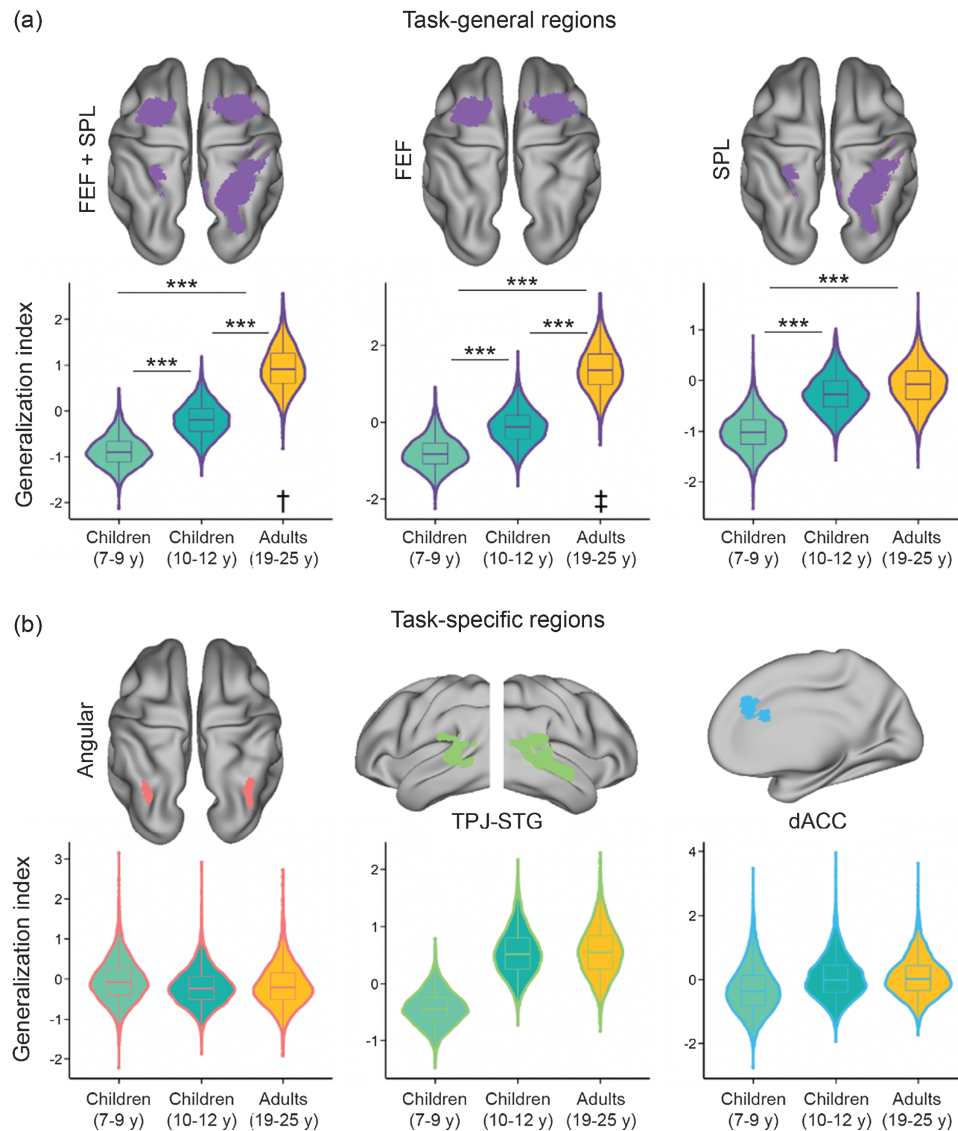
At the behavioral level, children's alerting ability matures earliest, while orienting and executive attention were not yet adult-like, and underwent protracted development from 7 to 12 years old. Since alerting has been linked to the arousal system that mediates wakefulness as well as the autonomic nervous systems (Eysenck, 2012; Posner & Petersen, 1990; Robbins & Everitt, 1995; van de Weijer-Bergsma et al., 2008). One may speculate that an earlier adult-like level of alerting may serve as a scaffold for the later development of the other two processes. Interestingly, we observed a monotonic increase of children's orienting ability, with an initial flat trend and a subsequent increase beginning at age 9 years old. Considering

Figure 5
Developmental Changes in Attention-Related Neural Representation Stability



Note. (a) Line graphs depict neural representation stability between children and adults in task-general and task-specific regions. (b) Bar plot for the difference between children and adults with overall stability in task-general and task-specific regions. (c) Representative views of significant clusters showing significantly lower pairwise neural representation stability measure for alerting (A), orienting (O), and executive (E) attention between children and adults, derived from the whole-brain searchlight analyses. Color bars indicate *t* values. Significant clusters were determined using the threshold of FDR $q = .05$ and cluster size >45 . Error bars = standard error of mean; n.s. = not significant; FEF = frontal eye fields; SPL = superior parietal lobule; dACC = dorsal anterior cingulate cortex; TPJ = temporoparietal junction; STG = superior temporal gyrus; FDR = false discovery rate. See the online article for the color version of this figure.
 ** $p < .01$. *** $p < .001$.

Figure 6
Generalizable Representation Across Three Attentional Processes in Children and Adults



Note. (a) Violin plots illustrate the generalizability index in task-general regions including the FEF and SPL in three age groups. (b) Violin plots illustrate the generalizability index in task-specific regions including the angular, dACC, and TPJ extending to STG in three groups. *y* = years old; FEF = frontal eye fields; SPL = superior parietal lobe; dACC = dorsal anterior cingulate cortex; TPJ = temporoparietal junction; STG = superior temporal gyrus. See the online article for the color version of this figure.

† Permutation $p = .05$. ‡ Permutation $p = .01$. *** $p = .001$.

many cognitive abilities pertaining to attention (e.g., reading) undergo substantial changes in school-aged children at 9–10 years old (Anderson, 2002; Chugani, 1998; Kail, 1986), this may in part account for our observed developmental effect on the orienting process. Moreover, children's executive attention exhibited a prominent linear increase in performance from 7 to 12 years old, in line with one longitudinal study in 7–11 years old children (Suades-González et al., 2017), and it is consistent with findings in the literature that executive attention still

remains immature in middle-to-late childhood (Zelazo & Müller, 2002). Our behavioral data from a large sample size extends previous findings on children's attention development, which is relevant for better understanding different aspects of attentional deficits that manifest in children with attention-deficit hyperactivity disorder and other developmental disorders.

At the neuroimaging level, four innovative aspects of our results demonstrate immature neural specialization,

heterogeneous neurodevelopment, less stability, and weaker generalization of three attentional processes during middle-to-late childhood. First, children exhibited less pronounced functional dissociation among widespread brain systems compared to adults. In line with predictions by the interactive specialization model (Johnson, 2000, 2001, 2011), these data suggest that brain systems of three distinct attentional processes may not be fully specialized during this age range. Specifically, children's lower specialization across three processes localized to core nodes of the dorsal-attention network encompassing FEF and SPL (Corbetta & Shulman, 2002; Petersen & Posner, 2012). The lower specialization in alerting and orienting processes also involves the LOC within the ventral-visual network and the VFC, respectively. For executive attention, the prominent effects are localized at not only the dACC but also the VFC and LOC. The VFC is believed to mature relatively late due to its involvement in higher order cognitive functions (Johnson, 2000, 2001), whereas the dACC, a core node of the cingulate-opercular network critical for executive attention and cognitive control, is known to undergo protracted development until early adulthood (Fjell et al., 2012; Hao et al., 2015). Notably, we observed a prominent involvement of the dorsolateral prefrontal cortex (DLPFC) in executive attention but less pronounced in alerting and orienting in adults, indicating its specific effect to this process in adulthood. However, we did not observe reliable DLPFC engagement in children, suggesting that executive attention still remains immature in middle-to-late adulthood (Zelazo & Müller, 2002). One possibility is that the domain-general role of DLPFC may still not emerge in this age range, or rather supporting executive attention within executive functions (Zelazo & Carlson, 2023) but not acting as a domain-general role in the attention domain. According to the interactive specialization model, functional brain development is a process of differential specialization among multiple coactivation cortical regions responding to specific stimuli (Johnson, 2000). For instance, weaker activation and less functional dissociation in face- and place-selective regions have been linked to immature specialization associated with the visual perception of faces and places, respectively (Kanwisher et al., 1997). Our findings shed light on the differential developmental pathways of three core attentional processes, elucidating relatively specialized brain systems underlying the development of sophisticated attention processes from childhood to adulthood.

Second, children's alerting-related multivariate brain maturation metric reached adult-like levels in childhood at 7–12 years old, coinciding with their behavioral developmental pattern. Interestingly, the maturation metrics for both orienting and executive attention showed a protracted increase from Age 7 to 12. Such correspondence between behavioral and neurodevelopmental patterns across three attentional processes suggests that each system and its neurofunctional organization may undergo a developmental

process at different paces. Our findings thus provide important implications into the heterogeneous neurodevelopment of children's attentional processes during childhood (Blonder, 1992; Paus, 2005). Notably, our maturation index measures capture multivoxel activity patterns corresponding to each attentional process. This approach provides an overall quantitative analysis of the neurodevelopmental profiles of each attentional process, reflecting more comprehensive brain-level descriptions of mental processes (Cai et al., 2019; Woo et al., 2017). Thus, our findings indicate the heterogeneity of developmental pathways to specific brain systems engaged by distinct attentional processes, extending findings on developmental changes in attention-related brain structure and function within isolated regions (Berman & Friedman, 1995; Farrant & Uddin, 2015; Johnson, 1990; Konrad et al., 2005; Westlye et al., 2011).

Third, children also exhibited less stability and weaker generalizability of neural representation in the dorsal-attention system than adults. Even though each attentional process appears to commonly recruit these brain regions, the multivoxel activity patterns within these regions are less stable in children than adults. Such finding may reflect immature refinement of neural representations within task-general regions, which concurs with predictions by the interactive specialization theory (Johnson, 2011) and the dorsal-stream vulnerability theory (Atkinson & Braddick, 2012). Functional integration of multiple systems is believed to support children's cognitive development (Fair et al., 2009; Kundu et al., 2018). The FEF and SPL, as core parts of the frontoparietal multidemand system, are linked to top-down regulation of attentional processes (Atkinson & Braddick, 2012). Thus, immature refinement of attentional systems may explain children's lagging behavioral performance, requiring nuanced coordination of these neural systems (Atkinson & Braddick, 2012; Duncan, 2010).

Fourth, through the utilization of a hierarchical modeling of the similarity structure of neural representations, we furthermore identified weaker generalizability across three attentional processes in the dorsal-attention network (especially the FEF) in children. Based on the multidemand system and compositional coding views (Atkinson & Braddick, 2012; Duncan, 2010; Kane & Engle, 2002; Reverberi et al., 2012), along with empirical evidence for the frontoparietal system as a latent shared construct underlying multiple cognitive domains, it is thus conceivable that FEF may play a key "tutor-like" role in promoting the development of attentional brain network from childhood to adulthood. Indeed, a common infrastructure of multiple attentional processes has been previously suggested (Corbetta et al., 1998), specifically for regions of the dorsal-attention network critical for top-down control of attentional processing (Corbetta & Shulman, 2002). This again speaks to the dorsal-attention network appears to act as a critical hub to promote functional integration of multiple attentional

processes throughout development. Our observed developmental effects in the univariate and multivariate measures are not mutually exclusive from each other. Rather, they may reflect two parallel aspects of the same developmental cascade, suggesting initial immature specialization and integration of attentional brain networks. At the univariate activation level, this system participates in three different attentional processes with weaker functional dissociation in children than in adults. At the multivoxel activity level, this system may coexist in multiple neurobiological modes to support distinct attentional processes, but with less stable neural representations during each attention process and weaker generalizability across these modes in children relative to adults. The latter likely reflects the immature organization of spatial patterns of task-related activity distributed over voxels that resemble process-specific neuro-functional signatures for alerting, orienting, and executive attention (Kane & Engle, 2002; Kriegeskorte et al., 2006, 2008; Reverberi et al., 2012). Building on the interactive specialization theory and related developmental models, our findings point toward a framework through which specialized and generalizable neural representations underlie the development of multiple attentional processes from childhood to adulthood. We emphasized that the dorsal-attention network may play a pivotal role in the generalizability of neural representations across multiple processes over development. Our data suggest the possibility of a population-based compositional coding mechanism by which the dorsal-attention network may act as a latent interface to scaffold the refinement, specialization, and integration of multiple neural modules that support nuanced attentional processes during development.

There are several limitations in our present study. First, our observed differential developmental patterns of three attentional processes were derived from a cross-sectional design, which is required for further investigations using longitudinal designs to capture developmental effects as the brain matures. We used conventional approaches for spatial normalization, which rely on a standard adult template rather than pediatric or age-specific templates. Second, the mechanisms underlying generalizable neural representations across three attentional processes detected here remain elusive, and future studies with novel designs are needed to address this question and resolve the subtraction logic for these processes. Delineating finer-grained neuronal representations requires advanced neuroimaging techniques with higher spatiotemporal resolution. Third, the uneven age distribution of children sample with less participants in Ages 7, 11, and 12 may circumvent the statistical estimation of age-related effects in our present study. Future studies with even age distribution are helpful to address this issue. Finally, the DLPFC was considered as one of the important regions in executive attention by previous studies; future studies are required to better disentangle its developmental pathways to attentional processes and domain-general executive functions.

In conclusion, our study demonstrates the development of cognitive components in children's core attentional processes and highlights both immature specialization and generalization of their associated neural systems. Our findings also suggest a potential neurodevelopmental mechanism through which the interplay of neural specialization and generalization promotes the development of highly specialized yet interacting attentional modules that may apply to other domains of children's cognitive development.

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