Attention network drives cortical maturation linked to childhood cognition

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Across the transition from childhood to adolescence the human brain experiences profound functional changes, shifting from an organizational framework anchored within somatosensory/motor and visual regions into one that is balanced through interactions with later-maturing aspects of association cortex[1-3]. Here, we provide consistent evidence linking this profile of large-scale functional reorganization to the development of attention network connectivity across independent datasets[4,5]. We demonstrate that maturational changes in cortical organization are preferential to the salience/ventral attention network[6-9] with heightened degree centrality and within-network connectivity, while connectivity within these network-linked vertices predicts cognitive ability such as fluid intelligence, perceptual reasoning and verbal ability[10]. Maturational refinement of the attention network closely links to the transition in cortical hierarchy, children with low ventral attention network connectivity exhibit adolescent-like topographical profiles, suggesting attentional systems may be critically important for understanding how brain functions are refined across development. These data highlight a core role for attention networks in supporting age-dependent shifts in cortical organization and cognition across childhood and adolescence, with the pruning in its between-network functional connections reflecting intricate interactions across multiple systems, rather than the segregation of an isolated network. The development of cortical hierarchy in children is driven by the ventral attention network, and the refinement of network connectivity within this system is linked to an accelerated pattern of cortical maturation.

Keywords: salience/ventral attention network, connectivity gradients, cortical organization, development, adolescence, intellectual ability

The human brain undergoes a series of staged developmental cascades across childhood and adolescence progressing from unimodal somatosensory/motor and visual regions through the transmodal association cortex territories that support complex cognitive functions[1,2,11]. Evidence for the scheduled timing of these neurodevelopmental events has emerged across biological scales, from regional profiles of cellular maturation[12], synapse formation and dendritic pruning[13], and intracortical myelination[14] through macro-scale morphological features including folding patterns[15] and associated areal expansion[16]. These processes are imbedded within age dependent anatomical changes across lifespan[17], particularly the prolonged development of association cortex territories. In parallel, substantial progress has been made characterizing the organization[6,18] and spatiotemporal maturation of large-scale functional systems across the cortex[19,20]. Here, *in vivo* imaging work strongly supports the development of a hierarchical axis, or gradient, of cortical organization, with association territories anchored at the opposite end of a broad functional spectrum from primary sensory and motor regions[3]. Despite clear evidence for age-dependent shifts in the macroscale organization of the cortex from childhood through adolescence, the manner and extent to which specific functional networks may contribute to the widespread process of cortical maturation remains to be determined.

The focused study of discrete functional circuits has provided foundational insights in core maturational processes. For example, discoveries have linked hierarchical changes within amygdala- and ventral striatal-medial prefrontal cortex (mPFC) circuitry to the development of emotional and social functioning in adolescence[1,11,21,22]. Yet, the maturational refinement of these subcortical-cortical circuits does not occur in isolation. Rather, they are embedded within a broad restructuring of functional systems across the cortical sheet[23]. Here, areal and network boundaries become more clearly defined throughout development[24], while the predominance of local connectivity patterns in childhood gradually gives way to long distance, integrative, connections in adolescence[19,25,26]. This reflects a developmental transition from an anatomically constrained organizational motif to a topographically distributed system[27]. In children, this complex functional architecture is situated within the unimodal cortex, between somatosensory/motor and visual regions. Conversely, adolescents transition into an adult-like gradient, anchored at one end by unimodal regions supporting primary sensory/motor functions and at the other end by the association cortex[3]. While the organizational profiles of large-scale cortical networks are distinct across childhood and adolescence[28], the extent to which developmental changes within select functional couplings may contribute to the drastic reorganization in the brain hierarchy is an open question. By one view, the developmental transition from unimodal through association cortices reflect the coordinated and shared influence of maturational changes across multiple functional systems spanning the entire connectome. An alternative, although not mutually exclusive, possibility is that specific brain networks may play a preferential role in the widespread developmental refinement of cortical connectivity.

Individual cortical parcels are functionally organized along a global gradient that transitions from somato/motor and visual regions at one end and multimodal association cortex at the other[29]. The hierarchical nature of these functional relationships reflects a core feature of brain organization in both adolescents[3] and adults[29]. Incoming sensory information undergoes a process of extensive elaboration and attentional modulation as it cascades into deeper layers of cortical processing. Visual system connectivity, as one example, moves along the dorsal and ventral visual streams, uniting within aspects of the dorsal and ventral attention networks including the anterior insula, superior parietal cortex, and operculum parietal before eventually filtering through multimodal convergence zones, particularly within the default network[30]. Although speculative, these data suggest a possible preferential role for sensory orienting and attentional systems in the integrity of the information processing hierarchies in the human brain. Intriguingly, there is mounting evidence to suggest the staged development of a ventral attention network, encompassing aspects of anterior insula, anterior prefrontal cortex and anterior cingulate cortex[6,31] (see also, cingulo-opercular network[8] and salience network[7]), that follows the age-dependent shifts in cortical organization across childhood and adolescence[3]. The salience/ventral attentional network, together with frontoparietal network, have been proposed to constitute a dual-network system for the 'top-down' and 'bottom-up' processing necessary for adaptive behavioral responses[8,9,32], supporting the functional propagation of information across primary somato/motor, visual, auditory cortex through the default network[30]. These dissociable attentional and control systems are interconnected in children but later segregate over the course of adolescence to eventually form the parallel architectures that support adaptive behavior in adulthood[24]. These data suggest that the attention system may play a preferential role in the transformative brain changes occurring throughout childhood and adolescence. Recent work has also revealed that the lateralization of functional gradients that may coincide with attention system lateralization[33]. As such, characterizing the relationships linking attention network connectivity and age-dependent changes in the macroscale brain organization would provide a tremendous opportunity to understand how the functional architecture of cortex is shaped and sculpted across the human lifespan. In turn, this would provide the opportunity to examine how the hierarchical reorganization of the cortical sheet may contribute to the emergence of cognitive and emotional abilities that characterize the transition from childhood to adolescence.

In the present study we examined the extent to which specific functional networks may serve to underpin the age-dependent maturation of functional gradient patterns across the cortical sheet. To directly address this open question, we first established the cortical territories exhibiting pronounced functional changes in a longitudinal sample of children and adolescents, revealing the preferential presence of developmental shifts within the ventral attention network. Follow-up analyses excluding regions exhibiting the maximal developmental change in children resulted in an accelerated maturation of adolescent-like gradient patterns, suggesting ventral attention territories play a core role in the expression of adolescent-like connectivity gradients. Moreover, across independent datasets, children with low ventral attention connectivity exhibited an accelerated profile of cortical maturation that closely resembles prior reports in adolescents and adults. Highlighting the importance of attention network connectivity in cognitive functioning, standardized measures of

intelligence linked with reduced attention network degree centrality in children and adolescents. Collectively, these data suggest that ventral attention system functioning in childhood and adolescence may underpin the developmental reorganization and maturation of functional networks across the cortical sheet.

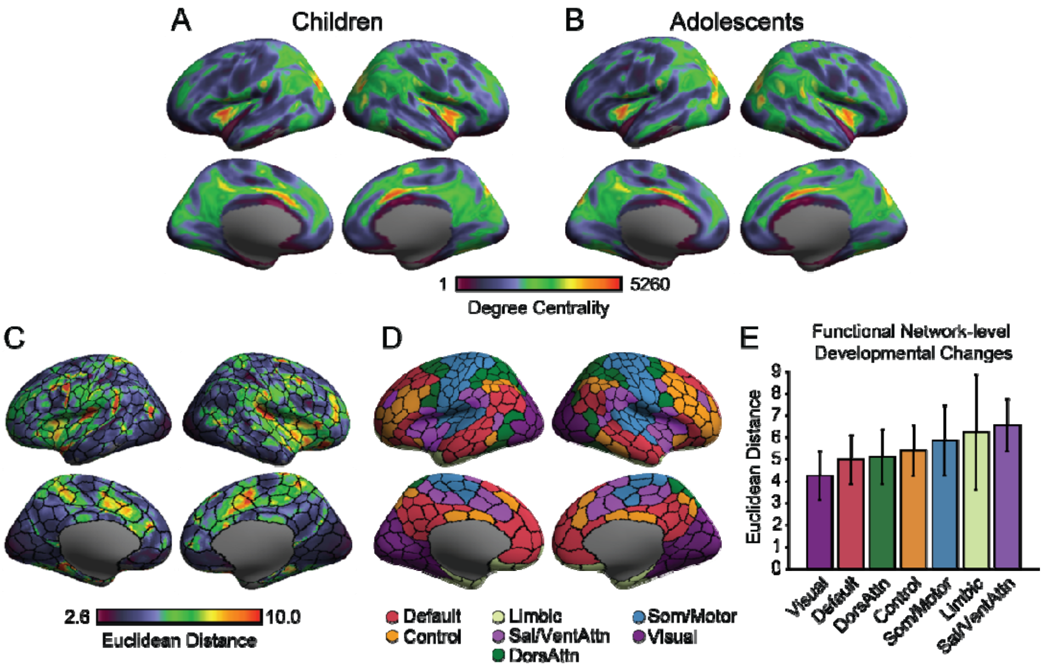

Figure 1. Salience/Ventral attention network areas demonstrate high population-level degree centrality but pronounced functional changes across development. Degree Centrality maps in children (A) and adolescents (B) reveal consistent dense connectivity in ventral attention network areas throughout development. Scale bar reflects the count of above threshold connections from a given vertex to all other vertices. Larger values indicate higher degree centrality. (C) Euclidean Distance of the functional connectome at each vertex between children and adolescents reveals a clear switch within the ventral attention network. Larger values indicate greater dissimilarity. (D) Regions based on the Schaefer et al., 400-parcel[34] atlas and colored by the Yeo et al., 7-network solution[6]. (E) Bar graph reflects changes in the Euclidean Distance of functional connectome at network level (mean network values ± standard error). The ventral attention network shows the largest developmental change while visual network and default networks are most stable between children and adolescents. DorsAttn, dorsal attention; Sal, salience; Som/Mot, somato/motor; and VentAttn, ventral attention.

High degree in attention network

Vertex-level functional connectivity (FC) matrices (20,484 × 20,484) were first generated using the data provided by the Chinese Color Nest Project (CCNP)[4,27]. In line with prior work[3,6,18], only the top 10% connections of each vertex were retained to enforce sparsity. Degree centrality maps for both children (6 to 12 y of age; n=202) and adolescents (12 to 18 years of age; n=176) were generated to characterize the broad organizational properties of the functional connectome across development (Figure 1A,B). Here, degree centrality reflects the count of above threshold connections for a given vertex to all other vertices (see Methods).

The observed profiles of degree centrality were highly similar between children and adolescents (Pearson r=0.947, $p_{spin} \leq 0.001$). Here, significance was established using permuted spin tests, which preserve the spatial autocorrelation structure of the data[35]. Heightened degree centrality values in both children and adolescents were preferentially evident in aspects of the ventral attention network, including portions of anterior insula, medial prefrontal cortex, and anterior cingulate cortex/midline supplementary motor area (Figure 1). Increased degree centrality was also present in adolescents within default network territories including portions of posterior inferior parietal lobule, posterior cingulate cortex, and precuneus. Additionally, visual system areas including superior and transverse occipital sulcus at the boundary between dorsal and visual network demonstrated high degree centrality values. Conversely, primary somatosensory and motor areas as well as regions within the lateral prefrontal cortex and temporal lobe exhibited relatively low degree centrality. Broadly, these data reflect the presence of dense connectivity within medial and posterior territories along the cortical sheet, while relatively low centrality was evident in lateral prefrontal and somato/motor areas, highlighting a stable pattern of degree centrality across childhood and adolescence.

Degree centrality broadly summarizes profiles of cortical connectivity, to examine developmental changes in functional connectivity strength at the vertex level, we calculated the associated Euclidean distance in functional connectivity similarity between children and adolescents (Figure 1C). Despite the presence of consistent population-level patterns of degree centrality, analyses revealed spatially non-uniform shifts in hub regions of functional connectivity across groups. The maximum developmental changes were anchored within the ventral attention network (Figure 1C-E), encompassing aspects of anterior and posterior insula as well as cingulate cortex. One-way ANOVA revealed the presence of between-network differences ($F=790.94$, $df=6$, $p \leq 0.001$), with increased Euclidean distance in the ventral attention network, relative to other networks (see multiple comparisons results in Supplemental Table 2). Prior work indicates that maturational age broadly follows the theorized hierarchy of cortical information processing[29], with somato/motor and visual networks maturing in childhood, while medial prefrontal aspects of default and limbic networks, peak later during adolescence[3,36]. However, in the present analyses, the default network exhibited relatively less developmental change in Euclidean distance between groups, followed by visual network (Figure 1E). Although speculative, these data suggest the presence of specific network-level similarities in connectivity between children and adolescents that may precede broader age-dependent shifts in the macroscale organization of cortex, highlighting the need to consider the manner, in which individual functional networks (e.g., default and attention) are embedded within the broader functional architecture of the brain.

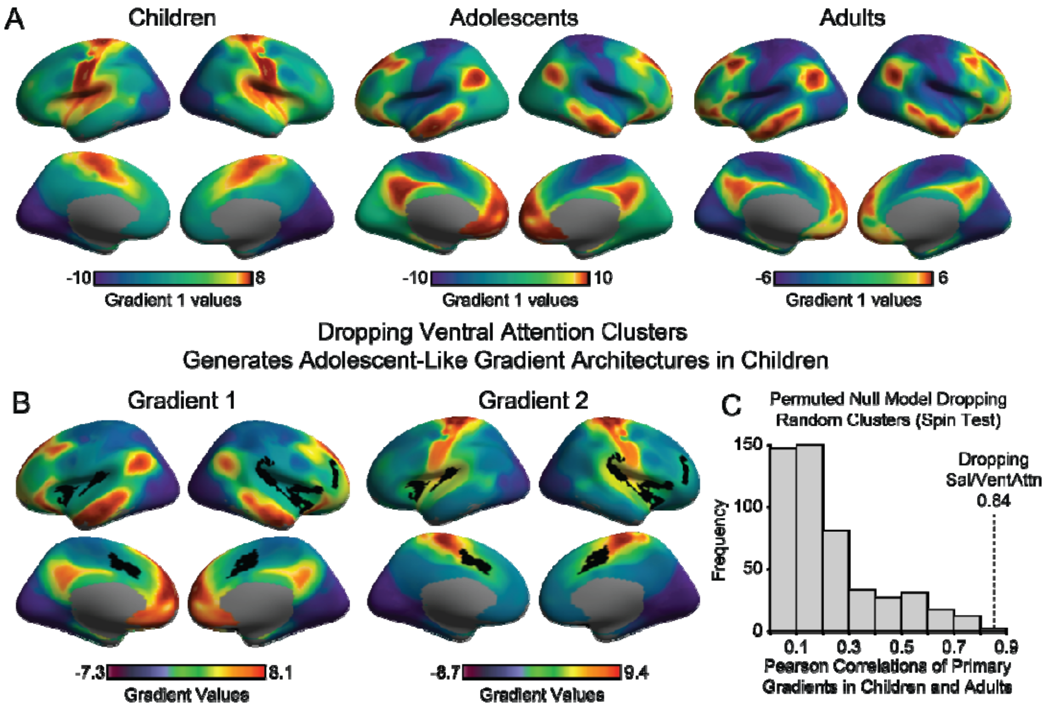

Figure 2: Ventral attention territories play a core role in the expression of adolescent-like connectivity gradients. (A) The principal cortical gradients of connectivity in children, adolescents (data from Dong et al., 2021[3]) and adults (data from Margulies et al., 2016[18]). (B) Clusters with maximum developmental changes in Euclidean Distance were extracted (Figure 1c), denoted as black on the cortical surface. Associated vertices were then dropped from the cortical connectome in the child group prior to rederiving the gradients. Results reveal that default and visual networks anchor the extremes along the principal gradient (Gradient 1), mirroring the principal gradient in both adolescents (r=0.68, $p_{spin} \leq 0.001$) and adults (r=0.84, $p_{spin} \leq 0.001$). In children, the rederived second gradient (Gradient 2) revealed a unimodal architecture separating somatosensory network from visual network, which closely corresponds on the second gradient in both adolescents (r=0.66, $p_{spin} \leq 0.001$) and adults (r=0.85, $p_{spin} \leq 0.001$). (C) To further assess the significance of the results, we constructed a permuted null model in the present data. Clusters with same size and shape as (B) but shuffled locations on the cortical sheet were generated and excluded from analyses in child group 500 times. For each shuffle, the principal gradient

was extracted and compared with the principal gradient in adults. The permuted null model shows only 1 case revealing a higher correlation than that observed in the real data, the x-axis indicates the absolute correlation values, the y-axis indicates the frequency of correlations, dotted line refers to the hypothesis being tested.

A core network during development

The transition from childhood to adolescence is marked by pronounced changes in the functional organization of cortex[3,28]. Broadly, this is reflected in the presence of age-dependent transitions across macroscale gradients that extend from unimodal (somato/motor and visual) regions through the cortical association areas that support complex cognition[2,11,21,22](Figure 2A). Next, we examined whether age-dependent alterations in ventral attention network connectivity might partly account for the maturation of the cortical processing hierarchy as reflected in these overlapping organizing axes, or gradients. Brain areas with maximum differences in Euclidean distance were extracted (See Methods; Figure 2B), and then removed from brain connectivity matrix while we rederived the functional gradients. Here, diffusion map embedding[18,37,38] was used to decompose participant-level connectivity matrices into a lower dimensional space. The resulting functional components, or gradients, reflect dissociable spatial patterns of cortical connectivity, ordered by the variance explained in the initial functional connectivity matrix[3,18].

As identified in our prior study[3], the primary gradient in children closely matches the second gradient in adolescents and adults. Here, dropping ventral attention areas (a simulation of ‘lesion’) generates adolescent- and adult-like gradient architectures in children. The removal of ventral attention network regions led to the formation of a primary gradient in children that closely assembles the first gradient in both adolescents ($r=0.68$, $p_{spin} \leq 0.001$) and adults ($r=0.84$, $p_{spin} \leq 0.001$). The rederived second gradient in children most closely assembled the second gradient in both adolescents ($r=0.66$, $p_{spin} \leq 0.001$) and adults ($r=0.85$, $p_{spin} \leq 0.001$). However, while the primary gradient derived from ventral attention network lesioned data in children broadly recapitulated the primary gradient in adults[18], several inconsistencies were observed. Notably, in the ‘lesioned’ data from the child group, one end of the primary gradient of connectivity was anchored in the visual areas, with the regions at the other end encompassed broad swaths of the association cortex. Prior work in adults has revealed visual territories along with somato/motor and auditory cortex serve to anchor one end of the primary cortical gradient[18]. Additionally, although the second gradient derived from ventral attention network lesioned data in children closely resembles the second gradient in adults, a muted default network profile can still be observed. While the dropped clusters are not anchored at the extreme end of the primary gradient in children (Figure 2A), it is densely connected and spatial adjacent with somato/motor territories. Further control analysis revealed that areas within ventral attention network primarily contributed to the reversal in gradients (Supplemental Figure 1). Although speculative, dropping of ventral attention vertices from the gradient analyses may decrease the number of functional connections attributed to somato/motor network, indirectly shifting its position along the gradient spectrum.

We next examined the extent to which the observed elimination of age-dependent shifts in the macroscale organization of the cortex is specific to the removal of ventral attention network-dominated vertices. Here, we generated 500 null models in the child group with clusters dropped at random locations but with shapes and sizes that match the ventral attention network vertices (reflecting the maximum differences in Euclidean Distance between children and adolescents). For each random model, the first and second gradients of child group were extracted and correlated with the corresponding first and second gradients in adults. Providing evidence for the role of the ventral attention network in the formation of adult-like gradient architectures in children, for the primary gradient the observed correlation was greater than the correlations from the null distribution ($p \leq 0.002$) across 499/500 permutations (Figure 2C). For the second gradient the observed correlation was greater than the correlations from the null distribution ($p \leq 0.001$) across all 500 permutations. While the present analyses are consistent with a core role for the ventral attention network in age-dependent changes in the macroscale organization of the cortex, longitudinal future work should examine possible relationships linking large-scale gradient transitions with shifts in attention network functioning across development.

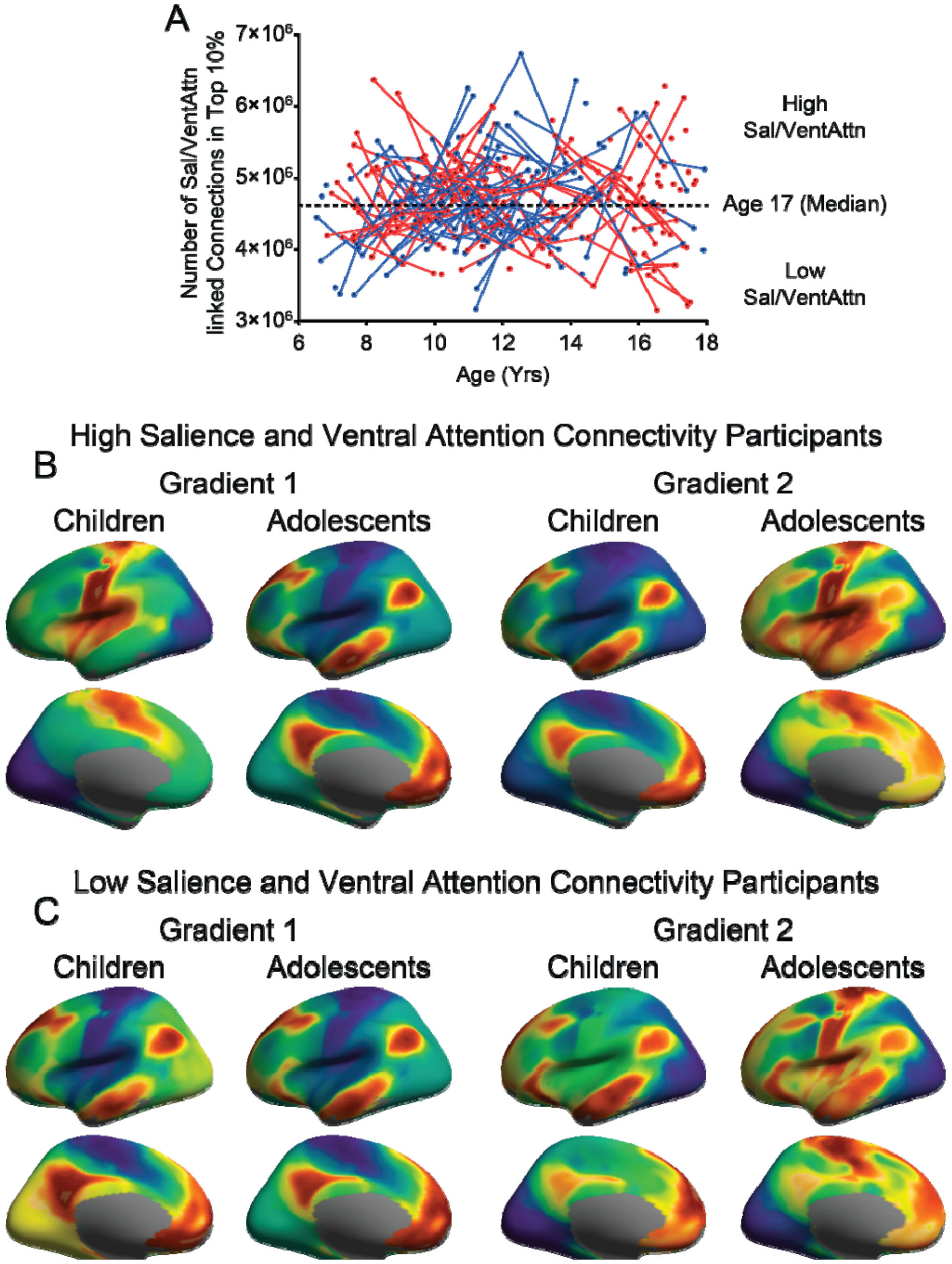

Figure 3: Individual differences in ventral attention network connectivity reveal accelerated cortical maturation in some children. (A) The number of functional connections linked with ventral attention network at individual level. Male participants are marked in blue, female participants are marked in red. Repeated imaging sessions within the same participants are linked by lines. The x-axis represents age range from 6 to 18 years. The y-axis reflects the number of connections that are linked to the ventral attention network following thresholding. Participants were divided into high and low ventral attention

connectivity groups according to the median value in age 17-year-old participants (dotted line). (B) The gradient maps in high ventral attention connectivity groups reveal typical patterns identified in our previous work in both children and adolescents[14]. (C) The gradient maps in low ventral attention connectivity groups reveal an accelerated maturation process in children, with both the primary and secondary gradients demonstrated a transmodal architectures. Functional organization was broadly preserved across the high and low attention groups in adolescents, with a subtle muting of the ventral attention gradient values in the low attention participant group.

Accelerated cortical maturation

The analyses above provide evidence for a specific relationship between ventral attention network connectivity and the formation of adult-like gradient architectures in children. Significant connectome-level changes were also observed in heightened within-network functional connectivity and degree centrality of ventral attention network. (Supplementary Figure 2). However, it is not yet clear the extent to which individual variability in attention network functioning may link with the accelerated maturation of gradient architectures across development. To examine this potential relationship, we divided participants into subgroups based on their individual ventral attention network connection counts (Figure 3A). Here, the group split was determined based on the median connection count in the oldest participants (>17 years of age; dotted line in Figure 3a). Participants with fewer connections than this median value were assigned to a low ventral attention group (child n=95 adolescent n=76), all other participants were assigned to a high ventral attention group (child n=107; adolescent n=100). The gradients were then rederived for high and low attention groups across both children and adolescents. No significant associations were observed between the high and low attention groups in age (p=0.45), gender (p=0.82) and head motion (p=0.87).

In adolescents, both the primary (r=0.98, $p_{spin} \leq 0.001$) and secondary (r=0.99, $p_{spin} \leq 0.001$) gradient architectures were consistent within the low and high ventral attention network participants (Figure 3B,C). For children with high salience and ventral attention connectivity, their functional organization follows the typical pattern of brain maturation[3] (Figure 2A). Here the primary gradient in the high ventral attention children matched the secondary gradient in both adolescents (r=0.89, $p_{spin} \leq 0.001$) and adults (r=0.91, $p_{spin} \leq 0.001$), while the second gradient in high ventral attention children matched the primary gradient in both adolescents (r=0.89, $p_{spin} \leq 0.001$) and adults (r=0.91607, $p_{spin} \leq 0.001$). In these children, somato/motor areas were anchored at the opposite extreme from visual regions, revealing a unimodal dominant gradient architecture. However, in children with low ventral attention connectivity we observed a developmentally accelerated pattern of gradient organization that broadly matches the primary and secondary gradients previously identified in both adolescents (Gradient 1: r=0.93, $p_{spin} \leq 0.001$; Gradient 2: r=0.92, $p_{spin} \leq 0.001$) and adults (Gradient 1: r=0.68, $p_{spin} \leq 0.001$; Gradient 2: r=0.65, $p_{spin} \leq 0.001$).

If the salience/ventral attention network contributes to the maturation of cortical hierarchy, the functional integrity of attentional systems may also associate with changes in cognitive and behavioral performance. To examine this hypothesis, we next assessed the relationship between standardized measures of cognitive functioning (IQ) and the degree centrality of the ventral attention network with a Linear Mixed Effect (LME) model. LME models for IQ subdomain scores in verbal, perceptual reasoning, working memory, processing speed, and a composite total score were constructed separately. Age, gender, head motion and the vertex-level connectivity counts with ventral attention network were fed into each LME model as fixed effects, repeated measurements were set as the random effect. Results revealed significant negative associations between the ventral attention network and verbal ($p \leq 0.05$), perceptual reasoning ($p \leq 0.01$) and the composite IQ scores ($p \leq 0.05$). Associations with participant age and verbal score ($p \leq 8 \times 10^{-6}$), perceptual reasoning score ($p \leq 0.05$) and total score ($p \leq 0.001$), as well as associations with gender and verbal score ($p \leq 0.05$), perceptual reasoning score ($p \leq 0.05$), and total score ($p \leq 0.05$) were also observed. Suggesting that this pattern was not due to variability in data quality, no significant associations between IQ scores and head motion were evident ($p > 0.05$; see LME results in Supplemental Tables 3-7 for each IQ subdomain score).

Collectively, these results demonstrate that individual variability within the attention network in children associates with dissociable motifs of connectivity across the functional connectome and covaries with the cognitive functioning. Here, children with low ventral attention connectivity exhibit an accelerated profile of cortical maturation that closely resembles prior reports in adolescents and adults. These data suggest a fundamental relationship between individual variability within the ventral attention network and the age-dependent changes in the macroscale properties of human brain organization and cognitive ability.

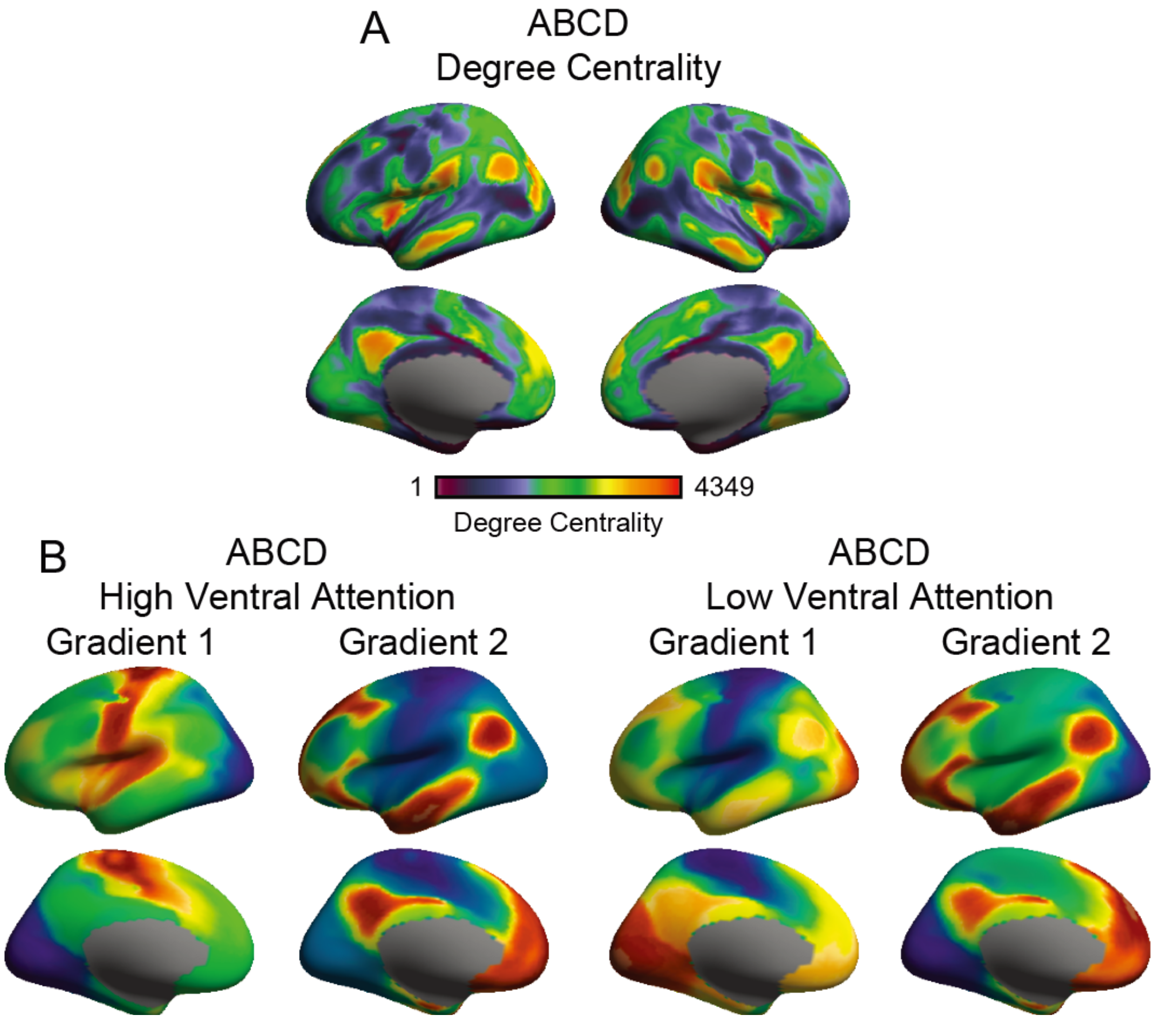

Figure 4: Relationship between ventral attention network connectivity and accelerated cortical maturation reliable across independent datasets. (A) Degree Centrality maps in children (9~11 years old, n=2186) from the ABCD project reveals dense connectivity in ventral attention network areas in a pattern that is consistent with the CCNP participants (Figure 1A). Scale bar reflects the count of above threshold connections from a given vertex to all other vertices. Larger values indicate higher degree centrality. (B) The gradient maps in the ABCD high ventral attention connectivity groups reveal typical patterns identified in our previous work in children[14] as well as the CCNP high ventral attention group (Figure 3B,C children). (C) The gradient maps in the ABCD low ventral attention connectivity groups closely resemble accelerated maturation process in children in the CCNP sample.

Generalizability across cohorts

The analyses above reveal a relationship between ventral attention network connectivity, the functional maturation of the cortical connectome, and cognitive functioning in a population of healthy developing children and adolescents from the Chinese Color Nest Project[4]. To examine the generalizability of the above results, we utilized 2186 participants from the ABCD[5] study, where participant data differed from the CCNP in sample population, study site, MRI scanner and acquisition parameters. Here, the ABCD data was limited to participants between 9 to 11 years old. Highlighting the robustness of the analyses reported above, we observed a profile of heightened degree centrality in ventral attention network areas that was consistent with the CCNP analyses (Figure 1A). Broadly, the ABCD degree centrality map demonstrated a lower degree centrality distribution along the cortex than the CCNP dataset (Figure 4A). Here, the inferior parietal gyrus and supramarginal gyrus, together with middle anterior cingulate cortex exhibited highly connected architecture. Hub regions of default network including the angular gyrus, middle temporal gyrus, and post cingulate cortex also revealed heightened degree centrality in the ABCD data, which might again indicate the raising of default network as a significant cortical core at the transition to adolescence.

Next, we assessed the reliability of a relationship linking the maturation of functional gradient architecture of the cortical sheet with individual variability in ventral attention connectivity across populations. To do so, we split the children in the ABCD study in a manner consistent with the CCNP analyses to examine whether the ventral attention network connections are coupled with the functional gradient maturation. Consistent with our findings in the CCNP children group, the gradient profiles of children with high ventral attention network connectivity in the ABCD study (n=1367) displayed the developmentally typical gradient profile (Figure 4B). In this group, the primary visual and somatosensory areas occupied the ends of the primary gradient, matched the second gradients in CCNP adolescents ($r=0.896$, $p_{spin} \leq 0.001$) and HCP adults ($r=0.93$, $p_{spin} \leq 0.001$); while the second gradient revealed transmodal organization matching the first gradients in CCNP adolescents (r=0.918, p_{spin}≤0.001) and HCP adults (r=0.944, p_{spin}≤0.001). An accelerated developmental profiles was revealed in the ABCD children with low ventral attention network links (n=819), broadly matching the primary and secondary gradients previously identified in CCNP adolescents (Gradient 1: r=0.865, p_{spin}≤0.001; Gradient 2: r=0.856, p_{spin}≤0.001), and demonstrating a hybrid organization comparing with HCP adults (correlations between the first gradient in ABCD low attention group and gradients in HCP adults: r=0.61, p_{spin}≤0.001, r=0.73, p_{spin}≤0.001; correlations between the second gradient in ABCD low attention group and gradients in HCP adults: r=0.71, p_{spin}≤0.001, r=0.62, p_{spin}=0.002). These data provide converging evidence, across independent collection efforts, of an association between attention system connectivity and the broader functional organization and maturational properties of cortex.

As a final step we repeated the behavior association analysis in the ABCD project. Here, NIH toolbox scores were used to access the cognitive abilities including crystallized (picture vocabulary and oral reading recognition) and fluid components (pattern comparison processing speed, list sorting working memory, picture sequence memory, flanker test and dimensional change card sort)[10]. As above, a linear regression model was conducted to examine the relationship between the degree centrality of the ventral attention network and cognitive functioning. Age, sex and head motion were set as covariates in the model. Consistent with our CCNP results, these analyses revealed the functional connections of ventral attention network were significantly associations with cognition total composite standard score (p=0.0024), crystallized composite standard score (p=0.022), cognition fluid composite standard score (p=0.0058), picture vocabulary (p=0.0048), and list sorting working memory (p=0.0025). Other significant associations are reported in the Supplemental Tables.

The replication analysis in the ABCD dataset highlight a key role for the ventral attention network in the maturation process of both cortical hierarchy and cognitive ability. Notably, speaking to the robustness of the observed results, the differences across datasets are quite substantial, including but not limited to participant race, ethnicity, culture, and environment as well as scanner, scanning parameters, socioeconomic factors, and education. Here, we applied the connection counts with ventral attention network derived from the CCNP dataset directly on the children in the ABCD dataset, and revealed consistent findings. Across sample collections, children with high ventral attention network connectivity demonstrated typical developmental patterns in functional gradients, while those with lower relative connectivity exhibited adolescents- and adult-liked gradients. The degree centrality of the ventral attention network is significantly associated with similar cognitive components in the CCNP and ABCD datasets. Collectively, our replication analysis suggests a close and generalizable relationship between the ventral attention network and the maturation process of cortical hierarchy. These data support the hypothesis that the ventral attention network preferentially drives the refinement in the macroscale organization of cortex and cognitive ability during the transition from childhood to adolescence.

Functional connectome propagation

Although the attention regions identified in the present analyses are recognized as a single system at a coarse scale[39,40], this broad functional architecture is comprised of multiple spatial adjacent but functionally dissociable networks[6,7,14,41]. This complex architecture underpins a cascade of functions supporting information processing, from the control of stimulus driven attention[39] to the initialization of task sets and maintenance of sustained attention during goal pursuit[9]. The hierarchical flow of information from sensory regions to deeper levels of cortical processing is also reflected in the spatial continuity of associated functional parcels along cortical surface, for example, the salience network[7,31], spanning orbital fronto-insular and dorsal anterior cingulate areas through broad posterior areas of insula and dorsal anterior cingulate cortex[9,31]. Broadly, information propagates along posterior to anterior as well as dorsal to ventral axes across cortex and the associated organization of functionally linked parcels is reflected through the presence of continuous functional gradients[3,18]. Here, the ventral attention network is situated at an intermediate position along this functional spectrum transiting from primary sensory/motor networks to the default network that anchors association cortex. Converging evidence for this hierarchical functional motif has been revealed through analyses of step-wise connectivity. Consistent with classic theories regarding the integration of perceptual modalities into deeper layers of cortical processing[29], functional relationships spread from primary somato/motor, visual and auditory cortex before converging within ventral attention territories, and eventually the default network[30]. As a whole, these data provide clear evidence situating the ventral attention network between primary unimodal and association cortices, highlighting a key role for attention systems in the functional propagation of sensory information to the multimodal regions that support higher-order cognitive functions.

The cingulo-opercular/ventral attention network, together with frontoparietal network, have been proposed to constitute a parallel architecture of executive functioning and cognitive control, supporting adaptive goal pursuit and flexible behavioral adjustments[32]. Although the frontoparietal network, encompassing aspects of dorsolateral prefrontal, dorsomedial prefrontal, lateral parietal, and posterior temporal cortices, is functionally dissociable from cingulo-opercular/ventral attention network in adulthood, studies in developmental populations have revealed that they are functionally linked prior to adolescence[24]. Moreover, in children, the ventral attention network possesses a broad distributed connectivity profile with reduced segregation from salience networks[42], perhaps reflecting fluid community boundaries in those areas. Anterior prefrontal cortex is shared by the two networks in children but later segregated into ventral attention network in early adolescence, with dorsal anterior cingulate cortex incorporated into frontoparietal network in adulthood[24]. This aspect of network development is consistent with evidence for increased, but more diffuse, patterns of task-evoked activity in children relative to adults[43], reflecting the presence of scattered pattern of community assignments in prefrontal territories, particularly those supporting attentional processes[28].

A core driver of cortical restructuring

Accumulating evidence has revealed a dramatic restructuring in the macroscale organization of the cortex across development and suggested the scheduled maturation of functional gradient patterns may be critically important for understanding how cognitive and behavioral capabilities are refined across development. Here, by first localizing the significant maturational changes in functional connectome across childhood and adolescence, we demonstrate that the ventral attention network, which is both activated by external stimuli (i.e., salience network[7]) as well as the execution of cognitive control (i.e., cingulo-opercular network[9]), plays a critical role in onset of the age-dependent shifts that characterize the macroscale organization of cortex across development. Children with fewer functional connections within the ventral attention network exhibited an accelerated maturation of gradient architecture and higher IQ scores. Although the process of brain maturation emerges from a host complex interaction of biological systems that span genes and molecules through cells, networks, and behavior, the current findings suggest a core role for attention network-linked territories. The manner through which the development of ventral attention network functioning interacts with the complex developmental relationships that span multiple biological systems and link with associated with behaviors across health and disease, remains an open question to be answered in future work.

Methods

Datasets

Chinese Color Nest Project (CCNP): CCNP is a five-year accelerated longitudinal study across the human life span[4,27,44]. A total of 176 adolescents and 202 typically developing children were included in the analysis, details of the dataset and exclusion criteria can be found in our previous work[14]. All MRI data was obtained with a Siemens Trio 3.0T scanner at the Faculty of Psychology, Southwest University in Chongqing. The reported experiments were approved by the Institutional Review Board from Institute of Psychology, Chinese Academy of Sciences. All participants and their parents/guardians provided written informed consent before participating in the study.

Adolescent Brain Cognitive Development Study (ABCD): ABCD is a multi-site longitudinal cohort following the brain and cognition development of over ten thousand 9~10 years old children. MRI scans including T1-weighted, T2-weighted and resting-state fMRI was obtained with 3T Siemens Prisma, General Electric 750 and Phillips scanners across 21 sites, details of the scan parameters can be found in reference[5]. Here, we unitized the MRI baseline data from 2186 children (female 54.4%, mean age 10.01 years old) for the reproducibility analysis. The study was approved by the Institutional Review Board from the University of California, San Diego[45]. All participants and their parents/guardians provided written informed consent[46].

MRI Data Preprocessing

CCNP dataset: Anatomical T1 images were visually inspected to exclude individuals with substantial head motion and structural abnormalities. Next, T1 images were fed into the volBrain pipeline (http://volbrain.upv.es)[47] for noise removal, bias correction, intensity normalization and brain extraction. All brain extractions underwent visual inspection to ensure tissue integrity. After initial quality checks, T1 images were passed into the Connectome Computation System (CCS)[48] for surface-based analyses. CCS pipeline is designed for preprocessing multimodal MRI datasets and integrates publicly available software including SPM[49], FSL[50], AFNI[51] and FreeSurfer[52]. Resting-state fMRI data preprocessing included a series of steps common to intrinsic functional connectivity analyses: (1) dropping the first 10s (4 TRs) for the equilibrium of the magnetic field; (2) estimating head motion parameters and head motion correction; (3) slicing time correction; (4) time series de-spiking; (5) registering functional images to high resolution T1 images using boundary-based registration; (6) removing nuisance factors such as head motion, CSF and white matter signals using ICA-AROMA[53]; (7) removing linear and quadratic trends of the time series; (8) projecting volumetric time series to surface space (the *fsaverage5* model with medial wall masked out); (9) 6mm spatial smoothing. All preprocessing scripts are publicly available on GitHub (https://github.com/zuoxinian/CCS). Any resting-state scan with a mean head motion above 0.5 mm was exclu5ded from further analysis. The demographic information of subjects included in the analyses is listed in Supplemental Table 1.

ABCD dataset: Minimally preprocessed T1 images[54] were fed into Freesurfer[52] for surface reconstruction. Resting-state fMRI data[54] preprocessing included a series of steps as following: (1) dropping the initial frames for the equilibrium of the magnetic field; (2) estimating head motion parameters and voxel-wise differentiated signal variance (DVARS) and head motion correction; (3) registering functional images to high resolution T1 images using boundary-based registration; (4) Scrubbing the frames with FD□>□0.3□mm or DVARS□>□50, along with one volume before and two volumes after. (5) removing nuisance factors such as global signal, head motion, CSF and white matter signals; (6) band-pass filtered (0.009□Hz□≤□f□≤□0.08□Hz); (7) projecting volumetric time series to surface space (the fsaverage5 model with medial wall masked out); (8) 6mm spatial smoothing. Full details of data preprocessing can be found in previous study[55]. All preprocessing scripts are publicly available (https://github.com/ThomasYeoLab/ABCD_scripts) on GitHub. Any resting-state scan with a max head motion above 5 mm and over half of their volumes censored was excluded from further analysis.

Degree Centrality Mapping. Functional connectivity (FC) matrices and the corresponding Fisher-z transformed values were first generated for each resting-scan per visit. Then the two test-retest FC fisher-z (FCz) matrices within one visit were averaged to increase signal-to-noise ratio for generating individual FCz matrix for each visit, which was later averaged across individuals to form group-level FCz matrices. For the group-level FCz matrices, only the top 10% functional connenctivities of each vertex were retained, other elements and negative FCs in the matrix were set to 0 to enforce sparsity, yielding an asymmetrical matrix, of which the rows are corresponding to the connectome of each vertex. Degree centrality map was obtained by counting the non-zero elements in each column of the FCz matrix. We then calculated the cosine distance between any two rows of the FCz matrix and subtracted from 1 to obtain a symmetrical similarity matrix, this similarity matrix was later used to derive the gradients.

Euclidean Distance. To characterize the developmental changes between children and adolescents, the Euclidean distance was computed for each row of the cosine distance matrix between children and adolescents. Then most changed clusters were extracted according to the following two criteria: the top 10% in Euclidean distance map and the cluster size above 500 vertexes. One-way ANOVAs were performed to test the statistical differences between networks.

Gradients Analysis. The extracted clusters and their FCs were firstly dropped in the initial FCz matrix of children group, and then cosine similarity matrix was calculated. Diffusion map embedding[18,38] was implemented on the similarity matrix to derive gradients (https://github.com/NeuroanatomyAndConnectivity/gradient_analysis). Pearson correlations were computed between the derived gradients in children and adults. To examine the statistical significance of the observed Pearson correlations, null distributions were generated by randomly rotated the locations of the extracted clusters across the cortical surface while keeping the shape and size fixed. For each permutation, the gradients and correlations were rederived. A total of 500 permutations were performed to generate the null model.

Circos Plot. Circos Plot was utilized to demonstrated the differences in numbers of functional connectivity between children and adolescents at network level. For each vertex, its connectome was represented as the corresponding row in the FCz matrix. The associated number of network-level connections was obtained by counting the non-0 elements in each network according to the Yeo 7-network solution, generating a matrix with dimension 20484 (number of vertex) by 7 (number of networks). Vertexes were grouped into networks to generate the final network to network FC matrix (7 by 7). The rows of this network-to-network matrix are displayed as the links from right half circus with larger radius to the left smaller half circus, referring to the FCs with networks in its own connectome, the opposite links from left to right circus represent the columns in the network-to-network matrix, referring to the FCs of each network that were existed in other networks' connectome (Supplementary Figure 2).

High and Low Ventral Attention Network Group Definition. Ventral attention network linked connections were extracted as the corresponding column in network-to-network matrix, referring to the functional connectivity other networks linked with ventral attention network. Then we take the median value of functional connectivity number in 17-year-old age group. Any single scan with a connectivity number above the threshold was assigned to the "high" ventral attention subgroup, other scans were assigned to the "low" ventral attention group. The gradients were then rederived for each group.

Association Analysis with IQ Score in the CCNP Dataset. Linear Mixed Effect (LME) model was applied to estimate the association between connections number with ventral attention network and IQ scores. IQ scores were obtained by Wechsler Children Intelligence Scale IV, including scores in following subdomains: verbal, perception reasoning, working memory, processing speed ability. LME was conducted using the following formula:

$$\mathrm{IQ\_score} \sim 1 + \mathrm{Age} + \mathrm{Gender} + (\mathrm{Ventral\ attention})\_\mathrm{DC} + \mathrm{HeadMotion} + (1 \mid \mathrm{Subid})$$

Here (Ventral attention)_DC refers to the connections with ventral attention network, together with age, gender, head motion and the intercept set as the fixed effect factor. Subid refers to the participant IDs, multi measurements for a single participant were coded as an identical nominal variable, set as the random effect factor. LME models were applied for the total IQ and subdomain scores separately.

Linear regression model was applied to estimate the association between connections number with ventral attention network and cognitive scores in the ABCD dataset. Cognitive scores were accessed by NIH toolbox, including scores in following domains: crystallized (picture vocabulary and oral reading recognition) and fluid components (pattern comparison processing speed, list sorting working memory, picture sequence memory, flanker test and dimensional change card sort)[10]. The model was conducted using the following formula:

$$\mathrm{Cognitive\_score} \sim 1 + \mathrm{Age} + \mathrm{Gender} + (\mathrm{Ventral\ attention})\_\mathrm{DC} + \mathrm{HeadMotion}$$

Developmental Effects on Degree Centrality of Ventral Attention Network. Linear Mixed Effect (LME) model was also applied to estimate the association between connections number with ventral attention network and age, gender head motion. LME was conducted using the following formula:

$$(\mathrm{Ventral\ attention})\_\mathrm{DC} \sim 1 + \mathrm{Age} + \mathrm{Gender} + \mathrm{HeadMotion} + (1 \mid \mathrm{Subid})$$

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Data Availability: Data from the CCNP dataset used here are available at https://ccnp.scidb.cn/en. The ABCD data used in this report came from ABCD BIDS Community Collection (ABCC; NDA Collection 3165) and the Annual Release 2.0: https://doi.org/10.15154/1503209.

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