



Cerebellum-cingulo-opercular network connectivity strengthens in adolescence and supports attention efficiency only in childhood

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ABSTRACT

Posterior cerebellar lobules are active during executive function (EF) tasks and are functionally connected to EF-associated cortical networks such as the fronto-parietal network (FPN) and cingulo-opercular network (CON). Despite evidence that EF and cerebello-cortical connectivity develop on a similar time scale, developmental relationships between EFs and cerebello-cortical connectivity have not been directly investigated. We therefore examined relationships between cerebello-cortical connectivity and EF performance in a typically developing sample ages 8 – 21. Resting-state functional connectivity between posterior cerebellum and FPN (middle frontal gyrus, posterior parietal lobules)/CON (anterior cingulate, insula) was computed using independent components analysis. Using conditional process models, we tested the hypothesis that cerebellum – PFC connectivity would mediate the relationship between FPN/CON and EF, and that cerebello-cortical connectivity, and connectivity – EF relationships, would become stronger with increasing age. Cerebellum – CON connectivity strengthened with age, but a relationship between cerebellum – anterior cingulate cortex (ACC) connectivity and attention efficiency was significant only in younger children. Results suggest that during childhood, the posterior cerebellum and ACC may support sustained and executive attention, though age has a stronger effect on EF. These findings may help to guide further studies of executive dysfunction in neurodevelopmental disorders.

1. Introduction

The cerebellum has a unique, uniform, structure and function that allow it to participate in many motor and cognitive processes, modulating aspects of movement and cognition that originate in the cortex (E et al., 2014; Schmahmann et al., 2019; Stoodley and Schmahmann, 2009). Tracing studies have illustrated multisynaptic, closed-loop anatomical connections between the cerebellum and contralateral cortical areas that generate motor or cognitive commands (Bostan et al., 2013; Hoshi et al., 2005). Such loops begin in the cortical regions that

create motor plans or thoughts (e.g. primary motor cortex, prefrontal cortex), synapse in the pons or red nucleus, and then synapse on the cerebellar cortex (Ramnani, 2006). The cerebellum likely performs similar operations on whatever data it receives and then sends processed information back to the cerebral cortex via the cerebellar deep nuclei and thalamus (Ito, 2008; Ramnani, 2006), making cognitive and motor processes more efficient and automatic (Koziol et al., 2009; Ramnani, 2014).

Whereas the cerebral cortex generates movement or thought, the cerebellum uses internal models to modulate information that originates

Abbreviations: EF, executive function; PFC, prefrontal cortex; FPN, fronto-parietal network; CON, cingulo-opercular network; ACC, anterior cingulate cortex; MFG, middle frontal gyrus; PNC, Philadelphia Neurodevelopmental Cohort; CNB, Computerized Neurocognitive Battery; PCPT, Penn Continuous Performance Test; LNB, Letter N-Back; PCET, Penn Conditional Exclusion Test; FD, framewise displacement; ICA, independent components analysis; IC, independent component; FNC, functional network connectivity; FDR, false discovery rate.

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in the cortex (Koziol et al., 2009). Generally, the anterior cerebellum (lobules I-V) is active during motor tasks, whereas the posterior cerebellum (lobule VI, Crus I/II [subdivisions of lobule VIIa], lobule VIIb) is active during cognitive tasks, and there is a secondary motor representation in lobules VIIa/b that may also perform cognitive functions (Guell, Gabrieli et al., 2018; Krienen and Buckner, 2009; Stoodley and Schmahmann, 2010). Meta-analyses of neuroimaging data demonstrated consistent posterior cerebellar activity during cognitive tasks, including language, music, timing, working memory, and executive function (E et al., 2014; McKenna et al., 2017; Schmahmann et al., 2019; Stoodley and Schmahmann, 2009). Koziol et al. (2009) argued that executive functions (EFs) are specific cognitive functions that rely on the cerebellum for smooth and efficient processing, which has been demonstrated by functional magnetic resonance imaging (fMRI) studies showing significant cerebellar activity during complex cognitive tasks (Balsters et al., 2014; Clark et al., 2020; E et al., 2014; Niendam et al., 2012; Stoodley and Schmahmann, 2009).

It is generally agreed upon that EFs come “on line” in childhood, and that *accuracy* and *efficiency* of EFs continue to improve throughout adolescence (Anderson, 2002; Lee et al., 2013; Luna et al., 2010). Basic abilities to use working memory, inhibit prepotent responses, and switch cognitive sets appear to come on line relatively early, but precision, accuracy, and performance monitoring of these EFs continue to improve throughout adolescence (Lee et al., 2013; Luna et al., 2010). Specific EF abilities appear to reach adult-level performance between the ages of 15 and 21, with task-specific differences (Crone and Steinbeis, 2017; Gur et al., 2012; Huizinga et al., 2006; Luna et al., 2004). Some have argued that “basic” stimulus- and rule-driven EF tasks, such as attention allocation and working memory, mature before “complex,” conscious and deliberative, EF tasks such as reasoning and problem-solving (Crone and Steinbeis, 2017; Nigg, 2017); however, tasks studied vary widely. Large studies from the Philadelphia Neurodevelopmental Cohort (PNC), the dataset used for the current study, have shown that accuracy and speed on EF measures of attention, working memory, and cognitive flexibility significantly increased with age across a range of 8 – 21 years, with the largest increase for attention performance (Gur et al., 2012). In addition, within-individual variability decreased for accuracy and showed a U-shaped curve for speed across this age group, suggesting refinement of these skills and echoing the cerebellum’s function in coordinating cognition (Roalf et al., 2014).

Neurodevelopmental trajectories of the prefrontal cortex (PFC) and posterior cerebellum structures are similar to each other, and parallel trajectories of EFs. Specifically, anterior cerebellum (motor) lobules mature earlier than the posterior (cognitive) areas, like the PFC matures later than motor cortex (Gogtay et al., 2004; Tiemeier et al., 2010; Wierenga et al., 2014). Thus, the maturation of PFC and posterior cerebellum may underlie maturation of EF, consistent with the idea that development of motor skills, cognitive skills, and prefrontal – cerebellar circuits are closely intertwined (Diamond, 2000; Gottwald et al., 2016; Koziol and Lutz, 2013).

Functional neuroimaging has also revealed likely neurodevelopmental changes in brain connectivity between the cerebellum and the cerebral cortex, though very few studies have investigated the cerebellum during childhood and adolescence. Many extant cerebellar findings are incidental, due to including the cerebellum (or parts of the cerebellum; often the imaging bounding box eliminates the lower portions) in whole-brain studies, but the cerebellum is typically not investigated directly or discussed in the text. Nevertheless, whole-brain resting-state functional connectivity studies have demonstrated that between childhood and early adulthood, cerebellar nodes appeared to become more integrated into traditionally cortical large-scale networks (Dosenbach et al., 2010; Fair et al., 2007, 2009, 2013; Kolskär et al., 2018; Kundu et al., 2018; Solé-Padullés et al., 2016). Importantly, head motion likely accounts for much variance in distance effects (Fair et al., 2013; Satterthwaite et al., 2019); however, studies showed that after motion correction, general cerebellum-PFC connections remain, though

reduced in strength (Fair et al., 2013; Satterthwaite, Wolf, Ruparel et al., 2013). Taken together, evidence suggests that cerebello-cortical connectivity likely strengthens at least until adolescence, and increasing integration of spatially distributed large-scale networks may even be driven by posterior cerebellar regions (Kundu et al., 2018).

EF development may depend on better coordinating executive abilities and increasing their efficiency, suggesting a potential role of the cerebellum in facilitating these processes (Chevalier, 2015; Koziol and Lutz, 2013). Evidence thus far shows cerebellar involvement in working memory, but cerebello-cortical relationships with other EFs are less clear. One functional connectivity study of the PNC found that the cerebellum, fronto-parietal network (FPN), and cingulo-opercular network (CON) acted as connectivity hubs that predicted working memory performance (Kolskär et al., 2018). In addition, load-dependent age-related differences in connectivity were observed in a fronto-parietal-cerebellar network during a working memory task (van den Bosch et al., 2014). Similarly, another PNC study showed neural activation in frontal, parietal, and posterior cerebellar regions, including Crus I and II, that increased with visual N-back load (Satterthwaite, Wolf, Erus et al., 2013). A similar pattern was demonstrated in an fMRI study of verbal working memory (O’Hare et al., 2008). Some prior work has shown that the cerebellum is likely involved in networks underlying EFs (e.g., FPN, CON); however, findings were either simply included in whole brain results, or studies did not investigate connectivity *between* the cerebellum and prefrontal cortex. While these investigations did not target the cerebellum specifically, they suggest a network including fronto-parietal cortex and posterior cerebellum underlies working memory performance, and these relationships likely become stronger with age.

One study that did specifically study the cerebellum in relation to EF showed that better working memory performance was associated with greater gray matter volume in right Crus I and II and right lobule VIIb; better set shifting was associated with greater gray matter in bilateral lobules VIIb and VIIa and left Crus II (Moore et al., 2017). In addition, a moderating effect of age was observed: older children in this study demonstrated better working memory performance and more gray matter in right lobule VIIa/b, whereas this relationship was weaker in younger children. Cerebellar morphology was also associated with general cognitive function and psychopathology in a PNC sample (Moberget et al., 2019).

The activation and functional connectivity studies conducted thus far suggest that cerebello-cortical connectivity will increase throughout adolescence, predicting EF performance more strongly with increasing age. However, most studies of functional connectivity still consider the cerebellum to be a separate network to cortical networks, and thus do not always test for correlations between the cerebellum and cortical regions. To our knowledge, no studies of EFs that directly investigate resting-state connectivity between the cerebellum and cortical executive networks have yet been completed.

Studying cerebello-cortical connectivity and EFs may have an impact on future work involving neurodevelopmental disorders and potential treatments for executive dysfunction. Many neurodevelopmental disorders are associated with cerebellar dysfunction, so findings related to typical development may help to inform studies of attention deficit/hyperactivity disorder (ADHD), autism spectrum disorder (ASD), psychosis, and other disorders (Satterthwaite et al., 2015; Stoodley, 2015; Wolf et al., 2015). Additionally, noninvasive cerebellar stimulation studies have shown promise for cerebellar stimulation impacting cognitive functions (Ferrucci and Priori, 2014; Grimaldi et al., 2016). Thus, understanding typical development of cerebello-cortical circuits can inform this work in clinical populations and may have therapeutic benefits.

Altogether, research suggests that the cerebellum becomes integrated with, and more strongly connected to, nodes of large-scale cortical networks from childhood to adolescence, potentially acting as a mediator between the “primary processor” in the prefrontal cortex and

executive functioning. Concomitantly, the age range over which this integration takes place corresponds roughly to the age range at which executive functions mature (Dosenbach et al., 2010; Fair et al., 2009; Huizinga et al., 2006; Kundu et al., 2018; Lee et al., 2013; Luna et al., 2004; Uddin et al., 2010). Developmental changes in functional network connectivity appear to coincide with, and may even drive, changes in cognitive abilities (Grayson and Fair, 2017; Kundu et al., 2018). However, because no studies have taken a direct approach to investigate relationships among age, EF performance, and cerebello-cortical functional connectivity in a targeted and data-driven way, a critical piece of proposed neurodevelopmental models of executive functioning may be missing (Clark et al., 2021).

As evidenced in Clark's et al. (2021) review, the literature indicating that the cerebellum is a modulator of executive functions across neurodevelopment is extremely heterogeneous and largely not designed to study the cerebellum, precluding any firm conclusions about developmental patterns of cerebello-cortical connectivity and involvement in EFs. Even studies that have used a purportedly "whole brain" approach may be missing parts of the cerebellum due to the bounding box or other scanning parameters (which typically prioritize frontal lobes over the cerebellum). The PNC, the dataset used for this study and in Kolskär et al. (2018) and Satterthwaite et al. (2013), used scanning parameters to include the full cerebellum in as many participants as possible (Satterthwaite et al., 2014), and even so, as detailed in our methods, we excluded numerous participants' data (12%) for incomplete cerebellar coverage. Unless explicitly stated in the methods that imaging included the full cerebellum and quality assurance was performed for full coverage (which was not detailed by any study reviewed here), it cannot be assumed of "whole brain" studies that the full cerebellum was tested in all participants. Further, most studies that investigated whole brain connectivity used a graph theoretical approach with predefined spherical regions of interest; these included only a select few regions in the cerebellum, none of which included the inferior portions of the cerebellum (e.g., Dosenbach et al., 2010, Fair et al., 2007, 2009). Therefore, because extant evidence based on heterogeneous study design and unclear cerebellar coverage suggests developmental changes in cerebello-cortical connectivity and associations with EFs, we sought to study the cerebellum and EFs *directly* using data-driven methods and ensuring full cerebellar inclusion, so as to begin to paint a clearer picture of relationships between cerebello-cortical connectivity and EFs during childhood and adolescence.

We hypothesized that because the posterior cerebellum is thought to modulate cognitive functions, posterior cerebellum (e.g., lobules VI, VII (Crus I/Crus II/VIIb), lobule VIII) – PFC (e.g., anterior cingulate, middle frontal gyri) connectivity would mediate the relationship between cortical networks and EF performance. We also hypothesized that age would moderate all three paths of the mediation, showing both increasing cerebellar integration with cortical networks and stronger connectivity – EF relationships with age. Age was investigated as a moderator because previous research demonstrated that the relationship between EF performance and cerebellar structure/function is not consistent at all age groups (Kolskär et al., 2018; Moore et al., 2017; Satterthwaite et al., 2013; van den Bosch et al., 2014). Rather, increasing age was predicted to enhance the relationship between EF performance and functional connectivity.

2. Methods

2.1. Participants

The Philadelphia Neurodevelopmental Cohort (PNC) is a population-based sample of children and adolescents ages eight to 21. The PNC is a collaboration between Children's Hospital of Philadelphia (CHOP), the Center for Applied Genomics, and the University of Pennsylvania (Penn). Please see previous publications about the characteristics of the PNC for greater detail on study methods (Satterthwaite et al., 2014,

2016). Parental consent and participant assent were obtained during the original study. We received permission to download and use the data for this project through the National Center for Biotechnology Information (NCBI) database of Genotypes and Phenotypes (dbGaP). The data and analyses presented in the current project are based on the use of study data downloaded from the dbGaP web site, under phs000607.v2.p2.

Both resting-state functional magnetic resonance imaging (rs-fMRI) and valid neurocognitive data were available for 1397 participants. Participants were excluded for the following reasons: medical condition with probable central nervous system involvement ($n = 338$), no information about medical conditions ($n = 50$), inpatient psychiatric hospitalization ($n = 35$), use of drugs or alcohol resulting in adverse effects ($n = 74$), and invalid neuropsychological performance ($n = 57$). Participants were also excluded for unusable imaging data ($n = 7$), high in-scanner head motion (mean framewise displacement (FD) > 0.5 mm; $n = 109$), and inadequate coverage of the cerebellum ($n = 173$). Thus, 554 participants were included in this study. Participant demographic details are presented in Table 1.

2.2. Assessments

The Penn Computerized Neurocognitive Battery (CNB) was used to measure cognitive function (Gur et al., 2010, 2012). The Penn CNB consists of 14 computerized neuropsychological tests (Moore et al., 2015). Because the original CNB was developed for use in healthy adult populations, measures were adapted for use with children and adolescents (i.e. simplifying instructions, reducing the number of trials on some measures; Gur et al., 2012).

Three individual tests from the Executive-Control factor were used for this study: the Penn Continuous Performance Test (PCPT), a measure

Table 1
Participant demographic information and task performance.

Variable	Mean	Standard Deviation	Minimum	Maximum
Age	14.10	3.18	8	21
Years of Education	7.77	3.13	1	15
Mother's Years of Education	14.22	2.47	2 ^a	20
Father's Years of Education	13.88	2.65	5	20
Estimated IQ (WRAT)	103.03	17.03	70	145
Mean Framewise Displacement (mm)	0.180	0.106	0.033	0.498
PCPT Number of True Positives	51.64	7.55	11	60
PCPT Median RT for True Positives (ms)	489	64	370	788
Attention Efficiency	0	1.59	-6.30	2.71
LNB Total Correct 2-Back Responses	8.31	1.58	2	10
LNB Median RT for Correct 2-Back Responses (ms) ^b	563	167	305	1760
Working Memory Efficiency ^b	0	1.47	-9.27	2.50
PCET Accuracy	1.93	0.69	0.04	3.27
PCET Median RT for Correct Responses (ms)	2424	896	1196	9256
Flexibility Efficiency	0	1.62	-7.88	2.93
Gender		Race		
Male	Female	Caucasian	African American	Other/Mixed
216	338	221	271	62

$N = 554$; WRAT, Wide Range Achievement Test, PCPT, Penn Continuous Performance Test; LNB, Letter N-Back; PCET, Penn Conditional Exclusion Test; RT, reaction time.

^a This is the number reported in the original data; the modal value is 12 so it is possible this is an error, but removing this value does not change the mean.

^b Significant difference between males and females (two sample t-test).

of attention/vigilance, the Letter N-Back (LNB), a measure of working memory, and the Penn Conditional Exclusion Test (PCET), a measure of abstraction and cognitive flexibility. The three tests were treated separately in these analyses because studies of executive function in children and adolescents show only modest correlations between flexibility and working memory domains, and the factor structure of EFs changes over the course of adolescence (Huizinga et al., 2006; Lee et al., 2013; Miyake et al., 2000). In addition, many studies using these data have used measures separately, as each measure was chosen to tap into a specific neurocognitive function (Gur et al., 2012; Satterthwaite et al., 2015; White et al., 2017). Accuracy and speed scores on each measure were combined into an efficiency score for this study, as in Moore et al. (2015). This was achieved by computing standardized (z) scores for accuracy and speed based on the entire sample, multiplying the speed z -score by -1 (so that higher scores indicated faster responses, to align with accuracy), and summing $z(\text{accuracy})$ and $-z(\text{speed})$. We computed attention efficiency from the PCPT, working memory efficiency from the 2-back performance on the LNB, and flexibility efficiency from the PCET.

2.3. Neuroimaging

Neuroimaging was acquired on a single scanner, a 3 T Siemens TIM Trio whole-body scanner located in the hospital of the University of Pennsylvania operating under the VB17 revision of the Siemens software. Signal excitation and reception were obtained using a quadrature body coil for transmit and a 32-channel head coil for receive. Participants completed a mock scanning session including recorded scanner noise prior to MRI acquisition to acclimate to the MRI environment and learn to remain still during scanning. Feedback regarding head motion was provided by the MoTrack motion tracking system (Psychology Software Tools, Inc, Sharpsburg, PA). Resting-state fMRI and structural MRI scans were used for this study.

Structural images were obtained using a magnetization prepared, rapid-acquisition gradient-echo (MPRAGE) sequence (TR = 1810 ms, TE = 3.5 ms, 160 1 mm slices). Resting-state BOLD scans were acquired with a single-shot, interleaved multi-slice, gradient-echo, echo planar imaging (GE-EPI) sequence. Scanning parameters were as follows: TR = 3000 ms, voxel resolution $3 \times 3 \times 3$ mm, 46 interleaved slices, 124 volumes. Total scanning time was 6.2 min. During the resting-state scan, participants were instructed to stay awake, keep their eyes open, fixate on a cross hair, and remain still. For further neuroimaging details please see Satterthwaite et al. (2014).

2.4. Preprocessing

Images were preprocessed using a standard pipeline implemented in the Data Processing Assistant for fMRI, Advanced Edition (DPARSFA; (Yan and Zang, 2010)) and SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). Preprocessing steps included the following: removal of the first five timepoints to account for scanner stabilization, slice timing correction with the middle slice as a reference, realignment, co-registration to T1, normalization to the Montreal Neurological Institute (MNI) template using the unified segmentation algorithm, and smoothing with a 6 mm full width half maximum Gaussian kernel. Images were inspected manually for full cerebellar coverage and participants whose cerebellum was not included or had mean FD > 0.5 were excluded ($n = 282$).

ICA-AROMA (Pruim et al., 2015) was then used to minimize the effects of head motion on each participant's imaging data. ICA-AROMA uses independent components analysis (ICA) via MELODIC to identify signal that is consistent with head motion, white matter, and cerebrospinal fluid (CSF), based on realignment parameters, edge fraction, CSF fraction, and high-frequency content. These components that are identified as noise are then regressed out of the images to create denoised images using ordinary least squares regression (see Pruum et al., 2015 for

full details). Denoised images were used in all further analyses.

ICA-AROMA was chosen as the preferred motion correction method because it reduces distance dependence between regions in functional connectivity analysis, and would thus minimize the effects of head motion on the long-range connections we were investigating (Satterthwaite et al., 2019). While global signal regression (GSR) and timepoint censoring have also been recommended for motion correction in connectivity studies, GSR has the potential to introduce anti-correlations (Murphy and Fox, 2017) and it was unclear how that may have impacted our interpretation of ICA analyses. In addition, group ICA requires that all datasets contain identical timepoints. Murphy and Fox (2017) suggest that regressing out non-neural signal (such as white matter and CSF) is an appropriate alternative method to remove unwanted noise related to "global signal." By using ICA-AROMA first for motion correction and then group ICA to identify functional networks containing optimal signal-to-noise ratio, it was felt that sufficient noise would be removed and distance effects would be reduced without removing timepoints or introducing anticorrelations.

2.5. Functional network connectivity analysis

The Group ICA of fMRI Toolbox (GIFT; <http://mialab.mrn.org/software/gift/index.html>) version 4.0b was used to compute group independent components analysis (GICA) for all participants using the Infomax algorithm and 20 ICASSO permutations. The number of independent components (ICs) was set to 100, as previous studies have shown that 100 components provide effective parcellation of known functional networks without creating extreme parcellations of visual and cerebellar areas (Nomi et al., 2017; Wu et al., 2018).

Following GICA, all independent components were visually inspected to determine which ICs represented brain signal (Allen et al., 2011). Based on previously identified cortical networks associated with cognitive processing (Allen et al., 2011), ICs corresponding to the nodes of fronto-parietal and cingulo-opercular networks, as well as posterior cerebellum, were selected for further analysis (see Fig. 1 for visual representation of selected components). Based on findings of our unpublished analyses with this dataset, we chose specific components to limit multiple comparisons. FPN components included bilateral middle frontal gyrus (MFG; BA 9/46) and right inferior parietal lobule. CON components included dorsal anterior cingulate (ACC) and bilateral anterior insula. Cerebellar components included left Crus I/II and left lobule VI/Crus I/Crus II/lobule VIIb/lobule VIII (these components will be hereafter labeled as left VI/VII/VIII for brevity, as Crus I and II are part of lobule VII). An anterior cerebellum component (bilateral lobule IV/V) and primary motor cortex were also selected as control regions, as anterior cerebellar components were not expected to correlate with EFs. In total, 6 components of interest and 2 control components were used for primary analyses.

We chose right FPN (MFG and right IPL) and left Crus I/II for fronto-parietal network analyses because our prior (unpublished) work showed left Crus I/II – MFG had a trend-level positive relationship with age, but right Crus I/II – MFG did not, and right FPN showed a trend-level relationship with age. Also, Reineberg et al. (2015) found that connectivity between left Crus I/II and right FPN predicted general EF ability. We also chose CON components and left VI/VII/VIII – ACC for the cingulo-opercular network analyses for consistency. There is no literature to suggest there should be lateralized differences in these cerebello-cortical networks, and the PFC components are bilateral, so these specific components were chosen to reduce multiple comparisons. The lobule VI/VII/VIII component was chosen for analysis with the cingulo-opercular network components and Crus I/II component was chosen for analysis with the fronto-parietal components because past work in adults has shown more anterior/medial parts of the posterior cerebellum to be connected to the CON and more posterior/lateral parts of the posterior cerebellum to be connected to the FPN (Buckner et al., 2011; Marek et al., 2018; Seitzman et al., 2020).

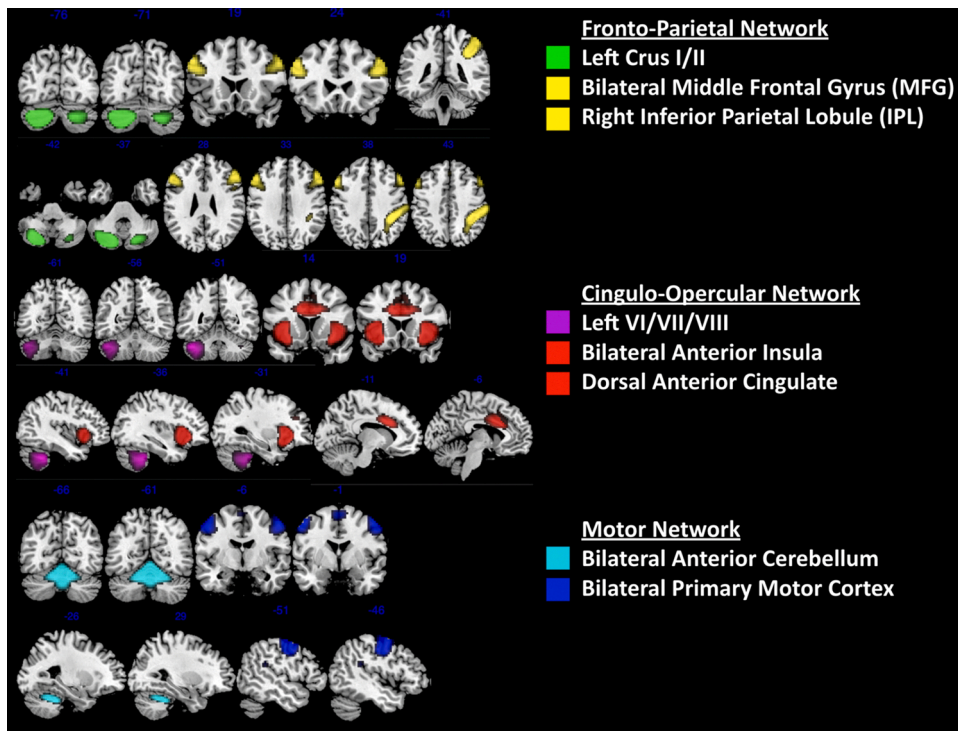


Fig. 1. Selected Components. Components were plotted on the Single Subject T1 brain template in MRICron. Images are thresholded at an arbitrary threshold for illustrative purposes to show areas of maximum intensity.

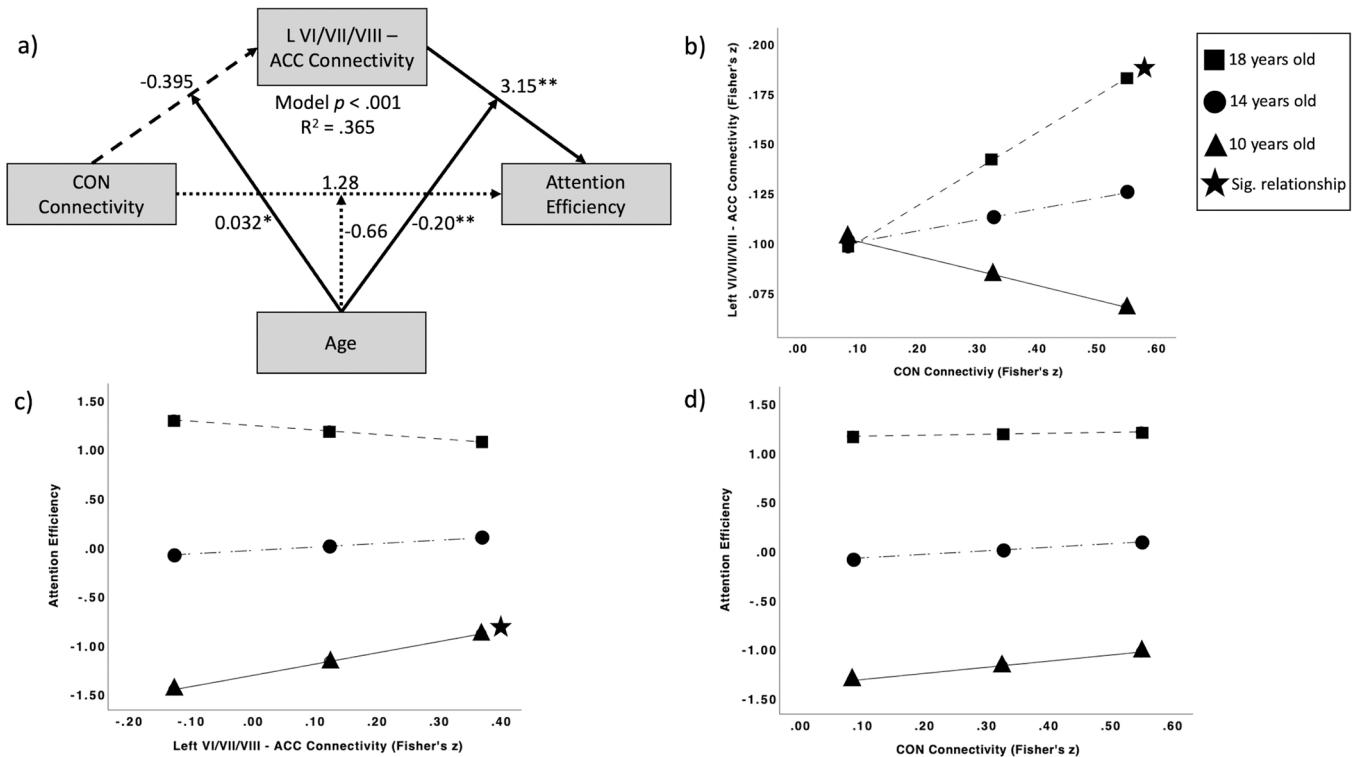


Fig. 2. Significant moderated mediation results. Solid arrows represent significant relationships at a false discovery rate corrected α , dashed arrows represent significant relationships at an uncorrected p -value, and dotted arrows represent nonsignificant relationships. Figure a) shows the theoretical model and significant relationships. Figures b, c, and d show conditional effects of the three paths in the mediational model, at the 16th 50th, and 84th percentiles of age. Figure b) shows the relationship between CON connectivity and left VI/VII/VIII - ACC connectivity; c) shows the relationship between left VI/VII/VIII - ACC connectivity and attention efficiency; and d) shows the relationship between CON connectivity and attention efficiency. Unstandardized coefficients are reported.

See [Supplementary Figure 1](#) for the current components overlaid on Buckner's parcellation.

Functional network connectivity (FNC) between these ICs of interest was computed within the MANCOVAN toolbox in GIFT. MANCOVAN calculates Pearson's correlations between time courses of components, computes the Fisher's Z transformation, and generates a matrix of FNC

values. These FNC values were extracted for use in regression analyses. We extracted FNC between cortical nodes of the FPN and CON and between posterior cerebellum and prefrontal cortex nodes of FPN and CON. We also extracted FNC between anterior cerebellum and motor cortex.

Table 2

Moderated mediation results. Model 59 was specified in the PROCESS macro implemented in SPSS. All values are bootstrapped with 5000 samples. Bolded outcomes show significant relationships at a false discovery rate corrected significance level. Raw *p* values are presented.

Predictor	Unstandardized Coefficient	SE	<i>p</i>	95CI
<i>Outcome: L VI/VII/VIII – ACC, R² = .136, p < .001</i>				
CON	-0.395	0.182	.031	-0.75 – 0.04
Age	0.003	0.005	.541	-0.01 – 0.01
Gender	-0.029	0.020	.149	-0.07 – 0.01
FD	-0.667	0.10	< 0.001	-0.86 – 0.48
CON × Age	0.032	0.020	.011	0.008 – 0.06
<i>Outcome: Attention Efficiency, R² = .365, p < .001</i>				
CON Direct Effect	1.282	1.038	.217	-0.76 – 3.32
L VI/VII/VIII – ACC	3.152	1.038	.003	1.01 – 5.19
Age	0.339	0.031	< 0.001	0.28 – 0.40
Gender	0.080	0.112	.478	-0.14 – 0.30
FD	0.482	0.565	.394	-0.63 – 1.59
CON × Age	-0.066	0.072	.360	-0.21 – 0.08
L VI/VII/VIII – ACC × Age	-0.200	0.071	.005	-0.34 – 0.06
<i>Outcome: Working Memory Efficiency, R² = .136 p < .001</i>				
CON Direct Effect	-0.509	1.134	.654	-2.73 – 1.72
L VI/VII/VIII – ACC	1.196	1.133	.292	-1.03 – 3.42
Age	0.124	0.033	< 0.001	0.06 – 0.19
Gender	0.461	0.122	< 0.001	0.22 – 0.70
FD	0.253	0.618	.683	-0.96 – 1.47
CON × Age	0.054	0.079	.491	-0.10 – 0.21
L VI/VII/VIII – ACC × Age	-0.060	0.078	.438	-0.21 – 0.09
<i>Outcome: Flexibility Efficiency, R² = .028, p = .027</i>				
CON Direct Effect	-0.192	1.308	.883	-2.76 – 2.38
L VI/VII/VIII – ACC	0.357	1.307	.785	-2.21 – 2.92
Age	0.049	0.038	.205	-0.03 – 0.12
Gender	0.238	0.141	.093	-0.04 – 0.52
FD	0.466	0.712	.513	-0.93 – 1.86
CON × Age	0.051	0.091	.571	-0.13 – 0.23
L VI/VII/VIII – ACC × Age	-0.008	0.089	.927	-0.18 – 0.17
<i>Outcome: L Crus I/II – MFG, R² = .062, p < .001</i>				
R FPN	0.264	0.179	.141	-0.09 – 0.19
Age	0.009	0.004	0.02	0.001 – 0.02
Gender	-0.015	0.019	.444	-0.05 – 0.02
FD	-0.425	0.090	< 0.001	-0.60 – 0.25
R FPN × Age	-0.018	0.012	.134	-0.04 – 0.01
<i>Outcome: Attention Efficiency, R² = .356, p < .001</i>				
R FPN Direct Effect	-0.051	1.073	.962	-2.16 – 2.06
L Crus I/II – MFG	1.824	1.187	.125	-0.51 – 4.16
Age	0.305	0.024	< 0.001	0.26 – 0.35
Gender	0.070	0.113	.535	-0.15 – 0.29
FD	0.137	0.545	.802	-0.93 – 1.21
R FPN × Age	0.027	0.073	.718	-0.12 – 0.17
L Crus I/II – MFG × Age	-0.117	0.081	.148	-0.28 – 0.04
<i>Outcome: Working Memory Efficiency, R² = .115, p < .001</i>				
R FPN Direct Effect	1.256	1.161	.280	-1.03 – 3.54
L Crus I/II – MFG	1.722	1.285	.181	-0.80 – 4.25
Age	0.159	0.026	< 0.001	0.11 – 0.21
Gender	0.461	0.122	< 0.001	0.22 – 0.70
FD	0.040	0.590	.947	0.12 – 1.20
R FPN × Age	-0.061	0.079	.439	-0.22 – 0.09
L Crus I/II – MFG × Age	-0.096	0.087	.272	-0.27 – 0.08
<i>Outcome: Flexibility Efficiency, R² = .027, p = .039</i>				
R FPN	1.621	1.343	.228	-1.02 – 4.26
L Crus I/II – MFG	-0.247	1.486	.868	-3.17 – 2.67
Age	0.080	0.031	.009	0.02 – 0.14
Gender	0.230	0.141	.104	-0.05 – 0.51
FD	0.236	0.683	.730	0.110 – 1.58
R FPN × Age	-0.109	0.092	.234	-0.29 – 0.07
L Crus I/II – MFG × Age	0.046	0.101	.647	-0.15 – 0.24

L, Left; R, Right; FPN, Fronto-Parietal Network; CON, Cingulo-Opercular Network; MFG, Middle Frontal Gyrus; ACC, Anterior Cingulate Cortex; FD, Framewise Displacement; SE, standard error; 95CI 95% confidence interval.

2.6. Statistical analyses

The FNC values extracted from GIFT were entered into conditional process (moderated mediation) models in SPSS version 25. Simple correlations were run to explore relationships among variables. For our main hypothesis, a conditional process model was specified (Model 59) using the PROCESS macro to characterize whether and how relationships between connectivity and EFs differ with age. This model tests for simple mediation and for moderation of all paths in the mediation (the model is illustrated in Fig. 2). FPN or CON connectivity was entered as the predictor, EF efficiency was entered as the outcome (attention, working memory, or flexibility efficiency), and posterior cerebellum – PFC (either MFG or ACC) connectivity was entered as the mediator. Age was entered as a moderator of all three paths of the model. Gender and FD were included as covariates. Indirect effects were bootstrapped with 5000 iterations.

A conditional effect would be present if relationships between cerebello-cortical connectivity or between connectivity and EFs differed in strength at different ages. In total, we ran six moderated mediational models to investigate EF efficiency. To correct for multiple comparisons, we computed FDR-corrected significance for an α -value of .05 using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). We also ran supplementary analyses to test for specificity of our findings: the six models of interest were re-run with finger tapping speed as an added covariate to investigate whether adding motor speed accounted for a significant amount of variance in our models and changed our results.

3. Results

Previous work showed significant relationships between age and all EF measures (Gur et al., 2012), and we replicated these findings in this sample of the PNC in our exploratory analyses, showing the strongest relationship for attention efficiency (attention efficiency $r = 0.592$, $p < .001$; working memory efficiency $r = 0.290$, $p < .001$; flexibility efficiency $r = 0.126$, $p = .003$). All EF measures were modestly correlated (attention – working memory $r = 0.399$; attention – flexibility $r = 0.227$; working memory – flexibility $r = 0.327$). Anterior cerebellum – motor cortex connectivity did not correlate with any cognitive measures in preliminary analyses and thus it was not used in conditional process models.

All conditional process models except for CON predicting flexibility efficiency showed a significant main effect of age, and there was also a significant main effect of gender on working memory efficiency (males were more efficient; Table 2). No indirect effects or conditional indirect effects were significant in any model (i.e., no mediation). Age moderated the relationship between CON and left VI/VII/VIII – ACC connectivity at an FDR-corrected threshold ($B = 0.032$, $p = .011$); connectivity was stronger in older participants (Fig. 2b). An interaction probe using three age groups at the 16th, 50th, and 84th percentiles of age (10, 14, and 18 years) revealed that the relationship between CON connectivity and posterior cerebellum – ACC connectivity was not significant in younger participants, but significantly positive in the 18-year-old group ($t = 2.90$, $p = .004$).

Age also moderated the relationship between left VI/VII/VIII – ACC connectivity and attention efficiency at an FDR-corrected threshold ($B = -0.200$, $p = .005$). An interaction probe revealed that the focal relationship between left VI/VII/VIII – ACC connectivity and attention efficiency was positive for the youngest age group ($t = 2.99$, $p = .003$), and the relationship was nonsignificant in adolescents and young adults (Fig. 2d). We also observed a direct effect of left VI/VII/VIII – ACC connectivity on attention efficiency ($B = 3.152$, $p = .003$). No significant mediation or moderation were observed for models predicting working memory or flexibility efficiency. In addition, models predicting attention efficiency accounted for larger amounts of variance than models predicting working memory or flexibility: attention models $R^2 = .35 - .36$, working memory and flexibility models $R^2 = .02 - .13$.

To test the specificity of our findings and identify whether motor speed was accounting for variance in the model, we re-ran analyses with bilateral finger tapping as a covariate, and results remained similar to our original results, with p values equal to our computed FDR cutoff. Thus, while motor speed did account for a significant amount of variance in the models, the direct and conditional effects remained, though slightly reduced in strength. Age continued to moderate the relationship between CON and left VI/VII/VIII – ACC connectivity ($B = 0.033$, $p = .009$). Age also still moderated the relationship between left VI/VII/VIII – ACC connectivity and attention efficiency ($B = -0.177$, $p = .010$). We also observed a direct effect of left VI/VII/VIII – ACC connectivity on attention efficiency ($B = 2.66$, $p = .008$). Therefore, our findings show unique variance in attention efficiency was accounted for by cerebello-cortical connectivity and the interaction between age and cerebello-cortical connectivity, despite motor speed also accounting for significant variance.

4. Discussion

We investigated relationships between typically developing cerebello-cortical functional connectivity and executive function measures across childhood and adolescence. Our original hypothesis was that posterior cerebellum – PFC connectivity would mediate the relationship between cortical networks and EF performance, and age would moderate all three paths of the mediation, showing conditional effects: we predicted both increasing cerebellar integration with cortical networks and stronger connectivity – EF relationships with age. Results showed a conditional effect of age on connectivity, as predicted, as connectivity between posterior cerebellum and anterior cingulate cortex (CON model) was stronger at older ages. The same relationship was not observed for the FPN model. Moreover, in younger participants, cerebellum – ACC connectivity predicted attention efficiency, but CON connectivity did not, suggesting a possible role for the posterior cerebellum, specifically, in facilitating attentional vigilance in childhood. Thus, our hypothesis was only partially supported, as mediation was not observed. However, the finding linking posterior cerebellum and attention adds to the growing literature implicating the posterior cerebellum in cognitive functions, including during childhood (Buckner et al., 2011; Caligiore et al., 2017; Clark et al., 2020, 2021; E et al., 2014; Guell, Gabrieli et al., 2018; Ito, 2008; Stoodley and Schmahmann, 2009).

Spatially, the cerebellar component most strongly associated with attention efficiency encompassed multiple lobules—most of left lobule VI, VIIb, and VIII, and the more anterior parts of left Crus I/II. In adulthood, lobules VI, VII, and VIII have consistently been associated with the cingulo-opercular network, which has been identified as crucial for sustained task performance and tonic alertness (Buckner et al., 2011; Coste & Kleinschmidt, 2016; Dosenbach et al., 2006; Marek et al., 2018; Sadaghiani & D'Esposito, 2015; Seitzman et al., 2020). Posner, Rothbart, and Voelker (2016) refer to the CON as the “executive attention network,” highlighting its role in attentional control, error and conflict detection, and performance monitoring. Dosenbach and colleagues (2006) showed that posterior cerebellar regions were active with the CON, especially during errors, and much work has demonstrated that both the cerebellum and ACC participate in conflict monitoring and error-based learning (Becerril & Barch, 2013; Botvinick et al., 2004; Dosenbach et al., 2006; Ide & Li, 2011; Ito, 2008; Sokolov et al., 2017). Becerril and Barch (2013) also suggested that the dorsal ACC responds to errors, whereas the left lateral and inferior cerebellum are associated with conflict monitoring. Similarly, Ide and Li (2011) related the dorsal ACC to error occurrence and the inferior cerebellum to post-error slowing (i.e. performance monitoring and adjustment) on a stop signal task. The dorsal ACC has also been implicated in updating internal models of task performance, as it was active when participants were updating spatial predictions during a saccade task (Kolling et al., 2016; O'Reilly et al., 2013). Thus, the posterior cerebellum and ACC may be

responsible for creating and updating internal models, respectively, for efficient performance on tasks that require “executive attention.” This study adds to the adult literature by suggesting that these relationships are present and show unique developmental patterns in childhood and adolescence.

While we did observe a conditional effect of cerebello-cortical connectivity on attention efficiency, this study revealed that age is a more robust predictor of attention than is cerebello-cortical connectivity. Attention efficiency had the strongest association with age, and the largest increase was in younger children (Gur et al., 2012); thus, age may represent an omnibus marker for co-development of cerebello-cortical connectivity and attention efficiency in this age group. This co-development may be neurobiologically driven and/or experience or learning driven.

Nevertheless, the interactions we observed indicate interesting developmental relationships between cerebello-cortical connectivity and cognition that should be explored further in future research. As predicted, age demonstrated a conditional effect on cerebello-cortical connectivity, in line with previous studies (Dosenbach et al., 2010; Fair et al., 2007, 2009, 2013; Kolskár et al., 2018; Kundu et al., 2018; Solé-Padullés et al., 2016). The relationship between the CON and posterior cerebellum – ACC connectivity was strongest in adolescents and young adults, suggesting that the posterior cerebellum becomes more integrated into the cingulo-opercular network across this age group. This finding agrees with extant literature demonstrating that cerebellum – PFC functional connections strengthen with age and the cerebellum becomes integrated into functional networks (even when controlling for motion; Dosenbach et al., 2010; Fair et al., 2007, 2009, 2013; Kundu et al., 2018). However, we saw this relationship only for the cingulo-opercular network and not the fronto-parietal network.

In this study, the relationship between left Crus I/II – MFG connectivity and FPN connectivity showed no significant simple or conditional effects on EFs. Stronger cerebellum – FPN connectivity in childhood compared to adulthood was also observed by Kipping et al. (2017), possibly suggesting FPN cerebello-cortical connections strengthen earlier than the CON, which continues into adolescence and young adulthood. The cingulo-opercular network was shown to be crucial for development of attention into adolescence in previous work, whereas similar changes were not observed in the fronto-parietal network (Kolskár et al., 2018; Marek et al., 2015; Posner et al., 2016). Our findings support Marek et al.’s (2015) assertion that major cortical networks are relatively organized by adolescence, but that the CON specifically continues to integrate with subcortical regions, supporting executive attention. We extend this hypothesis to include the cerebellum.

Additionally, the relationships between connectivity and attention efficiency were strongest in the younger participants, despite weaker cerebello-cortical connectivity in this age group. Though relationships did not strengthen with age as cerebello-cortical connectivity did, findings are consistent with some past work that found a plateau of prefrontal/cerebellar gray matter at approximately age 12 – 15 (Giedd et al., 1999; Gogtay et al., 2004; Tiemeier et al., 2010; Wierenga et al., 2014) and adult-level performance on “basic” EF tasks in childhood or early adolescence (Anderson, 2002; Lee et al., 2013; Luna et al., 2010). This effect may be strongest in younger children because this is the period over which attention performance improves most robustly (Gur et al., 2012; Luna et al., 2010).

Though we hypothesized that the relationship between cerebello-cortical connectivity and EF efficiency would increase further into young adulthood, it is possible that executive attention relies more on the cerebellum as internal models are being formed and refined in childhood; in later adolescence and adulthood less engagement between these regions may be required as the cerebellum is more integrated into the CON network. This integration may reflect a change in “baseline” connectivity (Gusnard and Raichle, 2001) over development that becomes less consistent with task performance at older ages. Resting-state connectivity may therefore be less related to performance in later

adolescence, whereas task-evoked connectivity is, assuming a new baseline. Ramnani argued that the cerebellum helps to transition neural systems from “controlled” to “automatic” processing (Kozioł et al., 2014; Ramnani, 2014). This may be the reason the cerebellum is more engaged in the younger children when it is “teaching” the prefrontal cortex to anticipate outcomes through error-based learning and these connections are strengthening (Caligiore et al., 2019; Kozioł and Lutz, 2013). The executive attention required for the PCPT may be more automatic in later adolescence, as the internal models are established, requiring less cerebellar support.

Notably, this particular attention task may have shown somewhat of a ceiling effect in older participants, as there was more variability in accuracy and speed at younger ages. The task was administered over a total of 3 min (half that of the adult measure; Gur et al., 2010, 2012), and thus may have not consisted of enough trials, or may not have been attentionally challenging enough, to fully tap into executive attention in older participants. This task was designed to be simple and short enough for 8-year-olds, and to be a relatively quick task of attention. Therefore, it is possible that if performance on the shortened version of the task reaches a ceiling in late childhood, then the cerebello-cortical system may not be as engaged in older participants when the task appears easier, less sustained attention is required, and task performance is more automatic. Importantly, it is plausible that relationships between connectivity and attention performance will be significant on more attentionally challenging adult-level tasks, or when using measures of intra-individual variability.

Our findings that cerebellum – ACC connectivity is associated with attention efficiency specifically (and not working memory or flexibility) likely reflects the cerebellum’s (and the ACC’s) role in executive attention or cognitive control broadly, rather than a role in higher level facets of executive function (Botvinick et al., 2004; Kolling et al., 2016; Lee et al., 2013). This finding is in line with a study showing that white matter integrity between cerebellum and PFC was associated with auditory attention performance but not working memory (Ailion et al., 2020). Further, successful performance on the attention task (PCPT) requires vigilance, sustained attention, performance monitoring, and error detection, which fall under Posner and colleagues’ (2016) definition of executive attention. The notion that the cerebellum is involved in these “lower level” executive processes (Nigg, 2017) aligns with Schmahmann’s Universal Cerebellar Transform theory, which argues that the cerebellum performs the same operation on any information it receives, thus acting as a domain-general processor (Schmahmann et al., 2019). Regarding its role in executive functioning and within the cingulo-opercular network, its domain-general role may therefore be facilitating executive attention, which may also affect other cognitive processes.

Further, the PCPT requires quick responding more than the other measures do, and the cerebellar component associated with attention efficiency included part of lobule VIII, a secondary motor lobule (Guell, Gabrieli et al., 2018). Guell and colleagues’ (2018) work has revealed that lobule VIII is engaged in “motor processes that require higher task focus (p. 12),” and lobule VIII is thought to be less involved in “extreme” or direct motor processing, based on both lesion and fMRI studies (Guell, Schmahmann et al., 2018; Stoodley et al., 2016). Attention efficiency may thus be more strongly associated with VI/VII/VIII – ACC connectivity because the PCPT required more focused attention/vigilance and motor speed than the other tasks. Notably, however, our supplemental analyses including finger tapping as a covariate showed that our findings were not solely related to motor function. Though finger tapping speed did account for a significant amount of variance in the model, cerebello-cortical connectivity and the interaction continued to account for unique variance in attention efficiency.

There are important limitations in this work that should be considered. The publicly available PNC dataset did not include item-level responses, which would be helpful for determining relevant measures such as intra-individual variability and non-responding to target stimuli, and

may be especially relevant to study cerebellar function (Kozioł et al., 2009). Regarding neuroimaging, data collected from children are notoriously noisy due to motion (Satterthwaite et al., 2012). To minimize these effects, we controlled for head motion using conservative measures at the subject level, excluded participants with excessive head motion, and included mean FD in our statistical models at the group level as recommended by recent neurodevelopmental studies (Satterthwaite et al., 2019). In addition, Marek et al. (2018) demonstrated that cerebellar resting state functional connectivity is more variable than cortical networks, and this effect may be amplified in children and adolescents and thus impact cerebello-cortical connectivity. Marek et al. (2020) also showed that large sample sizes (e.g. $N > 2000$) are necessary for showing reproducible brain-behavior relationships; while our sample is large compared to many neurodevelopmental imaging studies, statistical power is still limited and results should be replicated in a larger sample. Finally, our interpretations are limited by the fact that we used resting-state instead of task-based fMRI. However, resting-state fMRI is particularly adaptable for children and is thought to capture the underlying neural architecture that correlates with task-evoked networks (Guell et al., 2018; Uddin et al., 2010). Our goal was to investigate how this network architecture relates to executive function, so using resting-state was also appropriate for our aims.

The current findings may help to lay a foundation for studies and treatment of neurodevelopmental disorders. Numerous developmental disorders affecting cerebellar structure are associated with EF deficits, as well, such as Spina Bifida Myelomeningocele, Chiari malformation (Kozioł & Barker, 2013; Steinberg et al., 2020) and pediatric cerebellar tumors (Cantelmi et al., 2008; Fox et al., 2021; King et al., 2019) and could be used to further understand such relationships. In addition, neurodevelopmental disorders such as ASD, ADHD, dyslexia, and congenital heart disease have been associated with deficits in cerebellar structure and/or function (Clark et al., 2021; Semmel et al., 2018; Stoodley, 2015). ADHD may be especially relevant, given our finding that cerebellum – ACC connectivity is related to executive attention. Thus, the cerebellum's role within the cingulo-opercular network might be important to study in these populations during sensitive periods in which disruption of cerebello-cortical circuitry makes individuals vulnerable (Fair et al., 2013; Wang et al., 2014). Further, cerebellar stimulation may be therapeutic for improving cognitive functions in clinical populations (Ferrucci and Priori, 2014; Grimaldi et al., 2016).

In summary, this study showed the predicted strengthening of the relationship between cerebellum – ACC and CON connectivity throughout adolescence, but this strengthening did not predict all aspects of EF. Posterior cerebellum – ACC resting state connectivity was associated with attention efficiency more strongly in younger children than adolescents, but age was an overall stronger predictor of attention performance than was resting-state functional connectivity. Cerebellum – ACC connectivity did predict attention efficiency in younger participants, so the cerebellum may influence executive attention more in childhood during the greatest increase in attention and working memory performance and the establishing of internal predictive models. Future work utilizing more sensitive measures of task variability, change over time, practice effects, and task-based fMRI would be helpful to further probe how the cerebellum may fit into the development of the CON and executive functions. This study contributes to the understanding of how cerebello-cortical functional connections develop and are related to age and executive functioning and can provide a further foundation to guide future research questions regarding different clinical groups.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data utilized in this study are publicly available through the National Center for Biotechnology Information (NCBI) database of Genotypes and Phenotypes (dbGaP), phs000607.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2022.101129.

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