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ORIGINAL ARTICLE

Associations between cortical thickness and parasympathetic nervous system functioning during middle childhood

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Abstract

Positive associations have been found between cortical thickness and measures of parasympathetic cardiac control (e.g., respiratory sinus arrhythmia, RSA) in adults, which may indicate mechanistic integration between neural and physiological indicators of stress regulation. However, it is unknown when in development this brain–body association arises and whether the direction of association and neuroanatomical localization vary across development. To investigate this, we collected structural magnetic resonance imaging and resting-state respiratory sinus arrhythmia data from children in middle childhood ($N = 62$, $M_{age} = 10.09$, range: 8.28–12.14 years). Whole-brain and exploratory ROI analyses revealed positive associations between RSA and cortical thickness in four frontal and parietal clusters in the left hemisphere and one cluster in the right. Exploratory ROI analyses revealed a similar positive association between cortical thickness and RSA, with two regions surviving multiple comparison correction, including the inferior frontal orbital gyrus and the Sylvian fissure. Prior work has identified these cortical areas as part of the central autonomic network that supports integrative regulation of stress response (e.g., autonomic, endocrine, and behavioral) and emotional expression. Our results suggest that the association between cortical thickness and resting RSA is present in middle childhood and is similar to the associations seen during adulthood. Future studies should investigate associations between RSA and cortical thickness among young children and adolescents.

KEYWORDS

cortical thickness, middle childhood, respiratory sinus arrhythmia, structural MRI

1 | INTRODUCTION

Neuroimaging has contributed to our understanding of neurovisceral mechanisms underlying psychological well-being and dysfunction (Carnevali et al., 2018). In adults, positive associations have been found between measures of parasympathetic nervous system regulation of the heart and brain morphology in frontal and temporal cortices (Koenig et al., 2021; Thayer et al., 2012; Winkelmann et al., 2017; Woodward et al., 2008; Yoo et al., 2018). These positive associations are thought to indicate cross-level integration between measures of neural and physiological health and may serve as a putative biological mechanism of resilience against stress-related disorders

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(Beauchaine, 2015; Carnevali et al., 2018). Although these brain–body associations are well studied in adults, little is known about when in development they arise. To address this question, we examined the associations between two measures of regulatory health in a group of 8- to 12-year-old children. Specifically, we used respiratory sinus arrhythmia (RSA) at rest as our measure of parasympathetic cardiac control and cortical thickness as our measure of brain morphology. Furthermore, our goal was to elucidate whether the neuroanatomical localization and direction of association between these measures in children was comparable to those seen among adults.

1.1 | The role and mechanistic coupling of respiratory sinus arrhythmia and cortical thickness

Both RSA and cortical thickness have been identified as predictors of emotional health (Beauchaine, 2015; Fonseka et al., 2016; Luby et al., 2016), but while resting RSA findings have been relatively consistent across studies, cortical thickness-related findings have been mixed. Cortical thickness is an index of gray matter morphology and is calculated as the shortest distance between the pial surface and the gray-white matter cortex boundary (Fischl & Dale, 2000). Rich evidence suggests that areas of the parietal and the prefrontal cortex support emotion regulation (Buhle et al., 2014; Gross, 1998; Kim & Hamann, 2007; Ochsner et al., 2002; Ochsner & Gabrieli, 2002; Ochsner & Gross, 2005; Pan et al., 2018), and the thickness of these regions is a meaningful predictor of risk for emotional disorders in youth (Gold et al., 2017). However, the literature regarding the direction of the association between cortical thickness and emotional well-being is mixed, with some studies suggesting that thicker (Dimanova et al., 2022; Fonseka et al., 2016) or thinner cortices (Taylor et al., 2021) are associated with greater mental health risk, whereas others argue that the direction of association may depend on when in development this association is studied (Ducharme et al., 2014) or the conditions under which children are raised (Korom et al., 2021). Two intervention studies extend these findings. One correlational study suggested that thicker cortices in parietal and occipital areas at pre-intervention may indicate better treatment response in anxious youth (Gold et al., 2017). Another randomized clinical trial found that thicker than normal cortices in adults may attenuate depressive symptoms at pre-intervention, and that treatment may lead to cortical thinning as symptom severity decreases (Bansal et al., 2018). Overall, these results indicate that thicker cortices may support less vulnerability or better odds for recovery from emotional disorders.

Compared to cortical thickness, resting RSA outcomes have been more reliably linked to emotional health outcomes. RSA is a measure of parasympathetic nervous system cardiac control, as indexed by oscillations in the amplitude of heart rate at the frequency of spontaneous respiration (Mulkey & du Plessis, 2019). The function of the parasympathetic nervous system is to maintain homeostasis at rest and recover flexibly at times of increased environmental demands (Calkins, 1997; Propper & Moore, 2006). Given its role in stress regulation, resting RSA is a transdiagnostic, peripheral biomarker of emotion regulation, with higher RSA at rest consistently associated with better emotion regulation than lower resting RSA (Beauchaine et al., 2007; Calkins et al., 2019). Taken together, both RSA and cortical thickness are meaningful predictors of regulatory health, with resting RSA being a more reliable biomarker than cortical thickness.

The mechanistic associations between RSA and cortical thickness are well studied in adult populations. In adults, resting RSA is regulated by a complex network of cortical, subcortical and medullary brain regions, including the anterior cingulate cortex (ACC), parietal cortex, insula, orbitofrontal, and ventromedial PFC, amygdala, hypothalamus, periaqueductal gray, and ventrolateral and medial regions of the medulla (Benarroch, 1993; Mulkey & du Plessis, 2019; Palma & Benarroch, 2014; Saper, 2002). The regulation of RSA at rest is achieved by inhibitory efferent pathways that link the prefrontal cortex with the peripheral nervous system via the vagus nerve that exert top-down control over the cardiac excitatory signals of the limbic system and brainstem (Lewis & Todd, 2007). Through this mechanistic link between central and peripheral nervous system functioning, PFC activation translates into resting RSA as a peripheral index of executive control (Beauchaine, 2015). Since PFC is mechanistically linked to RSA in the mature brain, impaired functioning of the PFC also affects resting RSA. This functional coupling between RSA and PFC is substantiated by mounting evidence showing that most forms of psychopathology are characterized by both PFC dysfunction and low resting RSA (Beauchaine, 2015). In addition to the PFC, altered cortical thickness and activation patterns of the parietal cortex have been implicated in emotional wellbeing, as well as respiratory and cardiac health. Specifically, Gold et al. (2017) found that thinner cortices in the parietal and occipital lobe were predictive of worse treatment outcomes in anxious youth. Furthermore, diminished activation in the fronto-parietal network has been linked to depressive symptoms (for reviews, see Brzezicka, 2013 and Teixeira et al., 2014). Considering the parietal lobe's role in integrating cognitive, sensory, visuomotor, and working memory functions, reduced activation and

cortical thinning may lead to poor cognitive flexibility (e.g., rumination) during times of distress, breakdown of information integration, and inflexible allocation of cognitive resources, possibly due to inadequate exchange of information between the prefrontal and parietal regions (Brzezicka, 2013; Teixeira et al., 2014). Functional MRI studies have also shown that slow breathing techniques increase the activation of not only the PFC, but also the parietal and supplementary motor cortices (Critchley et al., 2015; Yu et al., 2011). Furthermore, the presence of an infarction in the left parietal lobe has been found to increase the risk of adverse cardiac outcomes, such as cardiac death, more so than an infarction in the PFC (Rincon et al., 2008). Taken together, rich evidence demonstrates that PFC function and RSA are mechanistically linked during adulthood and that the parietal cortex meaningfully contributes to the regulation of cardiac and respiratory functioning, but it is yet to be established when in development these functional associations emerge.

1.2 | Development of respiratory sinus arrhythmia and cortical thickness

Resting RSA and cortical thickness have unique developmental trajectories. Resting RSA undergoes maturation between infancy and childhood. It rapidly increases during the first 3 years of life (Alkon et al., 2006; Bar-Haim et al., 2000; Bornstein & Suess, 2000; Calkins & Keane, 2004) but then decelerates between 3 and 7 years of age, and levels off or decreases after age 8 (El-Sheikh, 2005; Salomon, 2005). These developmental changes in resting RSA suggest that early childhood is the most formative period of one's resting RSA development (Alkon et al., 2003; Marshall & Stevenson-Hinde, 1998), but it may remain malleable to increased environmental demands, such as chronic stress (Mulkey & du Plessis, 2019). The first years of life are also critical to children's cortical development but, in contrast to resting RSA, ACC and OFC show a protracted structural development with the most intensive pruning of synapses occurring during adolescence, followed by a slow, gradual pruning throughout adulthood (Frangou et al., 2022; Lenroot & Giedd, 2006). Although it is unknown how the maturational patterns of resting RSA, PFC, and parietal cortex thickness relate to one another before adulthood, some evidence points to possible meaningful associations between the two during adolescence (Koenig, Parzer, et al., 2018). However, due to methodological limitations in Koenig and his colleague's project, such as small sample size and only girls being involved in the study, greater investigation of the developmental associations is warranted. Overall, emerging evidence suggests that the association between RSA and cortical thickness is indicative of cross-communication between the brain and the body to support emotional health; yet, it remains unknown when in development children can rely on it for effective emotion regulation.

1.3 | The importance of middle childhood in the integration of brain–body mechanisms

Middle childhood represents a transitional period between early childhood and adolescence that is rich in physical, social, emotional, and cognitive changes and learning opportunities. Some of these changes include gaining gradual independence from parents (Lengua, 2003; Skinner & Zimmer-Gembeck, 2016), developing better regulating emotion (Underwood & Hurley, 1999), and learning to better manage conflicts with peers (Holmes et al., 2016; Underwood et al., 1999). The successful navigation of these tasks is dependent on the child's neurobiological and physiological systems that support regulatory, cognitive, and affective output (Zimmer-Gembeck & Skinner, 2016). These systems have their unique regulatory roles, timelines, and feedback mechanisms, but they rely on shared biological structures that allow for coordinated, flexible, and efficient orchestration of biological and behavioral responses to environmental demands (for a review, see Joëls & Baram, 2009 and Skinner & Zimmer-Gembeck, 2016). Given the importance of this developmental period in children's emerging emotion and self-regulation, mechanistic associations between measures of regulatory health, including RSA and cortical thickness, may already be established or may be in the process of forming to support adaptive functioning; however, more data are needed to determine if this is indeed the case.

1.4 | Study aims and hypotheses

The aim of the present study was to investigate the association between parasympathetic cardiac control and brain morphology, as indexed by resting RSA and cortical thickness respectively, during middle childhood. More specifically, we examined whether the neuroanatomical localization and direction of association between these biological outcomes were comparable to those seen during adulthood. We hypothesized that an RSA–cortical thickness association would be observed in frontal and parietal cortical regions that aid children's regulatory independence and health. We also hypothesized that we would find a positive RSA–cortical thickness association, given the mounting evidence that higher resting RSA is more

adaptive (Beauchaine, 2015) and thicker cortices are associated with less vulnerability to mental health problems (Gold et al., 2017).

2 | METHOD

2.1 | Participants

Participants included children between the ages of 8 and 12 years from the mid-Atlantic region of the United States enrolled in a larger longitudinal study. The inclusion criteria for this substudy were an IQ score higher than 70, no history of serious neurological disorders, and the successful completion of an electroencephalography (EEG) assessment prior to the MRI scan. The EEG assessment was introduced as an inclusion criterion to maximize the success of the MRI scan, with the assumption that participants who successfully completed the non-invasive EEG task were more likely to successfully complete the MRI scan as well. A total of 80 children participated in a T1-weighted structural MRI scan. Data from five participants were excluded due to failed processing in FreeSurfer (Version 6, http://surfer.nmr.mgh.harvard.edu). Data from an additional five participants were excluded due to poor data quality, resulting in a sample size of 70 usable MRI scans. Of these 70 children, 8 children had missing RSA data (reasons described below), resulting in an analytical sample of 62 participants.

The participant pool was racially diverse and included children with and without early childhood risk for caregiver adversities. Forty-one children (24 female) and their families were referred to the study by Child Protective Services (CPS) following allegations of maltreatment during early childhood. As part of a diversion from foster care programs, families participated in one of two parenting interventions (Attachment and Biobehavioral Catch-up or Developmental Education for Families) before children turned 2 years old. A group of twenty-one children (10 female) with no history of CPS involvement were recruited from the community when they were 8 years old. Exclusion criteria in this low-risk group included prior history of CPS involvement, homelessness, or family history of drug misuse at the time of enrollment.

Children with and without adversity exposure did not differ in age ($t(60) = .68$, $p = .49$) or gender distribution ($\chi^2(1, N = 62) = .30$, $p = .58$). See Table 1 for information on age, sex, race, ethnicity, income, and parental education of the participant pool. To examine whether the association between cortical thickness and resting RSA differed between the CPS-involved and low-risk groups, as well as between the two intervention groups, we completed robustness moderation analyses.

TABLE 1 Demographic information.

Sex, No. (%)	Female = 34 (54.83%) Male = 28 (45.17%)
Race, No. (%)	African American = 41 (66.13%) Biracial = 12 (19.35%) White = 7 (11.29%) Hispanic = 1 (1.61%) Other = 1 (1.61%)
Ethnicity, No. (%)	Hispanic = 11 (17.74%) Non-Hispanic = 51 (82.26%)
Age (*SD*, range)	
Avg. age at MRI data collection	10.09 years (.82; 8.28–12.14)
Avg. age at RSA data collection	9.443 years (.35; 8.19–10.07)
Avg. age difference between MRI and RSA data collection	0.647 years (.79; −1.00 – 2.38)
Parental education[a] (*SD*)	
Avg. Parental Education	2.81 (1.14)
Income (*SD*; range)	
Avg. income in USD	$34,478 ($31,260; $1903–$175,000)

Note: $N = 62$.

[a]Educational background was measured on a scale of 6 (1 = did not complete high school; 2 = GED; 3 = high school diploma; 4 = some college; 5 = 4-year college degree; 6 = postgraduate degree (MA, MBA, PhD, JD, MD)).

2.2 | Procedure

2.2.1 | Physiological data collection and processing

The James Long Company hardware and software were used for physiologic data acquisition, cleaning, and processing (James Long Company, Caroga Lake, NY, USA). Heart rate and respiration data were used to calculate RSA. Heart rate data were collected using two disposable electrocardiography (ECG) electrodes placed on the rib cage (one on the left and one on the right) and one grounding electrode placed on the chest (a bipolar configuration). Respiration data were collected using a pneumatic bellows belt fastened around the midsection. Following sensor placement, parents and children were instructed to complete a three-minute paced breathing task to measure baseline autonomic data (Butler et al., 2006; Grossman & Taylor, 2007).

The software algorithm identified heartbeats, calculated interbeat intervals (IBIs) as the difference in milliseconds between the beats and identified IBIs with unusual values for visual verification or correction. Misidentified heartbeats were manually corrected. Consistent with previous work in children (Woody et al., 2016), ECG data

were excluded if 10% or more of the heart beats required manual correction, resulting in eight child's ECG data being excluded from analyses. RSA was estimated using the peak-to-valley method, which accounts for the difference in IBIs during respiratory inspiration and expiration (Grossman et al., 1990). RSA levels were averaged across the three-minute resting baseline task.

2.2.2 | MRI data collection and processing

Children who passed the MRI safety screener were invited for an MRI scan while accompanied by a parent or caregiver. Prior to scanning, children participated in a mock MRI scan to familiarize children with and assess their comfort in the scanner. Following the mock scan, children completed a series of structural and functional MRI scans, with the T1-weighted scan being the first sequence in the scanning protocol. Children were provided with cartoons or movies to watch during the structural scan. The Institutional Review Board at (deleted for review) approved the study protocol.

We collected T1-weighted MPRAGE scans (1 × 1 × 1 mm isometric voxels) at the Center for Biomedical and Brain Imaging at the University of Delaware using a 3-Tesla Siemens MAGNETOM Prisma Fit scanner and a 20-channel head coil for multiband capability. We used FreeSurfer's standard, recon-all pipeline, including cortical mantle reconstruction and spatial smoothing of 10 mm full width at half maximum (FWHM). Technical details of the FreeSurfer procedures are described elsewhere (Dale et al., 1999; Fischl et al., 2002, 2004; Fischl & Dale, 2000).

Of the 80 brains, 75 were successfully processed with FreeSurfer, followed by two rounds of quality control. First, a trained graduate student rated the quality of each image on a scale of one to four (1 = great segmentation, no motion, include; 2 = good segmentation, some motion, include; 3 = satisfactory segmentation, substantial motion, include; 4 = poor segmentation, extensive motion, exclude) based on Afacan et al.'s (2016) guidelines. Secondary quality assessment was performed using the Qoala-T supervised-learning tool (Klapwijk et al., 2019). Of the 75 processed brains the same five scans were recommended for exclusion by the trained rater and Qoala-T. As noted earlier, eight children did not have usable RSA data, which resulted in 62 anatomical scans in our analytical sample. The average motion on these 62 scans was 2.218 ($SD = .708$) according to the graduate student's scores and the average Qoala-T score was ($M = 76.849$, $SD = 9.144$). The correlation between the two ratings was significant ($r(60) = -.406$, $p = .001$), suggesting convergent validity between the two quality control assessments. The risk groups did not differ from each other significantly in terms of their quality assessment scores (Qoala-T: ($F(1, 60) = .194$, $p = .661$)); graduate student's score: ($F(1.60) = .614$, $p = .437$). The MRI images were not edited manually to avoid the introduction of unsystematic noise.

2.3 | Data analytic approach

2.3.1 | Primary analyses

Vertex-wise general linear models were performed in FreeSurfer's Qdec toolbox—a specialized software for examining whole-brain cortical morphology—to investigate the main effect of RSA on cortical thickness across the entire cortical mantle. We used a Gaussian kernel of 10 mm FWHM to spatially smooth the data. The vertex-wise threshold of significance was $p < .05$. We corrected for multiple comparisons using Monte Carlo simulations with a cluster-wide corrected threshold of $-\log10(p)$ (Hagler et al., 2006). Clusters that survived multiple comparisons corrections were then used as masks to calculate mean cortical thickness in that region for each study participant, which then were entered into a regression model and were visualized in R. Only the clusters that survived multiple comparisons correction are reported. All statistical models included the image quality score, sex, and age at the time of scanning to follow the example of previous studies on brain morphology (Korom et al., 2021; VanTieghem et al., 2021).

2.4 | Secondary analyses

Finally, given that our participant pool included typically developing low-risk children, as well as children with a history of CPS involvement, we completed follow-up group X RSA moderation analyses to examine if group (CPS-involved vs. low risk) status interacted with RSA in predicting children's cortical thickness outcomes.

2.5 | Exploratory analyses

We completed exploratory region-of-interest (ROI) analyses using FreeSurfer outputs based on two cortical atlases: the Desikan-Killiany Atlas (DK-A; Desikan et al., 2006) and the Destrieux Atlas (Des-A; Destrieux et al., 2010). DK-A is a cortical parcellation scheme that subdivides the cortex into 34 gyral-based, standard neuroanatomical regions per hemisphere. Des-A subdivides the cortex into 74 gyral and sulcal regions per hemisphere, the limit between sulcal and gyral regions

being the curvature value of the surface (Destrieux et al., 2010). As opposed to DK-A, where both visible gyral and hidden sulcal areas are included in single ROIs, Des-A separates gyral ROIs visible on the brain's surface from hidden cortical regions (banks of sulci). An important strength of the latter parcellation scheme is its fine anatomic resolution that follows the cytoarchitecture of the cortex. By comparing the results between the two parcellation atlases, we can make inferences about the impact of researchers' methodological choices on CT-RSA associations.

We chose the ROIs from both atlases based on the results of a recent mega-analysis by Koenig and his colleagues (2021). From the DK-A atlas, the bilateral ROIs included the insula, lateral OFC, rostral medial frontal gyrus (MFG), medial OFC, caudal ACC, superior frontal gyrus, and rostral ACC. Corresponding areas selected from the Des-A atlas included the orbital gyrus, H-shaped orbital sulcus, medial orbital sulcus/olfactory cortex, orbital rectus gyrus, suborbital gyrus, lateral orbital sulcus, superior frontal gyrus, superior frontal sulcus, middle ACC gyrus and sulcus, rostral ACC gyrus and sulcus, Sylvian fissure, inferior orbital frontal gyrus, middle frontal gyrus, middle frontal sulcus, fronto-marginal gyrus and sulcus, and 5 subregions of the insula (superior-, inferior-, and anterior circular sulcus, insular short gyrus, and long insular gyrus and central insular sulcus).

We completed false discovery rate (FDR) multiple comparison adjustments for the ROI analyses in R, using the "p.adjust" command in R's *stats* package. See Table 3 for all the ROIs where significant uncorrected associations were found, along with the *p* values following FDR correction. For a visualization of the selected ROIs on the group average brain, compared between the two atlases, see Figure 1. All the ROI analyses were completed in R (Version 3.6.1).

3 | RESULTS

3.1 | Primary analyses

Our primary analyses aimed to test the main effect of RSA on cortical thickness across the cortical mantle. See Figure 2 for visual representation of our significant findings on the group average cortex. In the right hemisphere, one cluster survived Monte Carlo multiple comparison corrections, with a cluster peak in the right hemisphere pars triangularis of the inferior frontal gyrus (encompassing areas of the inferior frontal gyrus and orbital gyrus). In the left hemisphere, four clusters survived Monte Carlo multiple comparisons corrections, with cluster peaks in the pars opercularis (encompassing areas of the inferior frontal sulcus, inferior part of the precentral sulcus, and

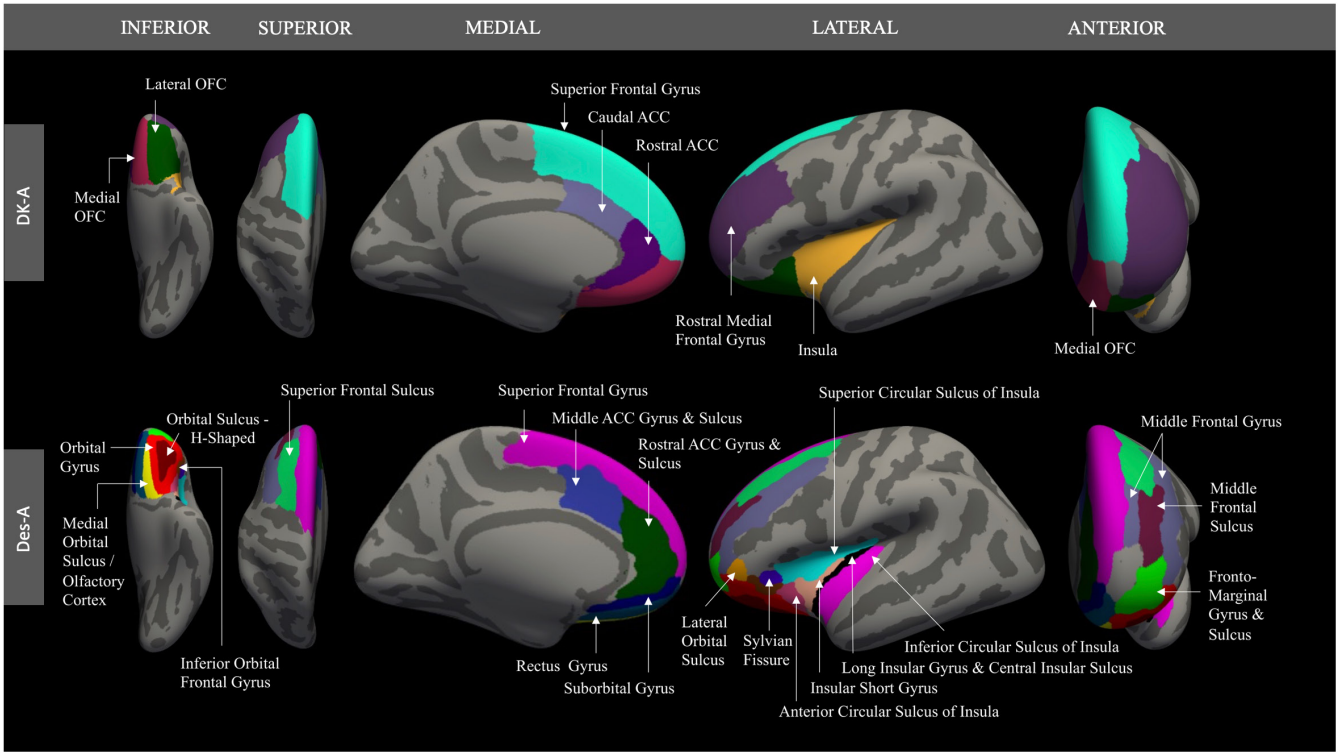

FIGURE 1 Selected ROIs shown on the left hemisphere of the group average brain. Des-A, Destrieux atlas; DK-A, Desikan-Killiany atlas.

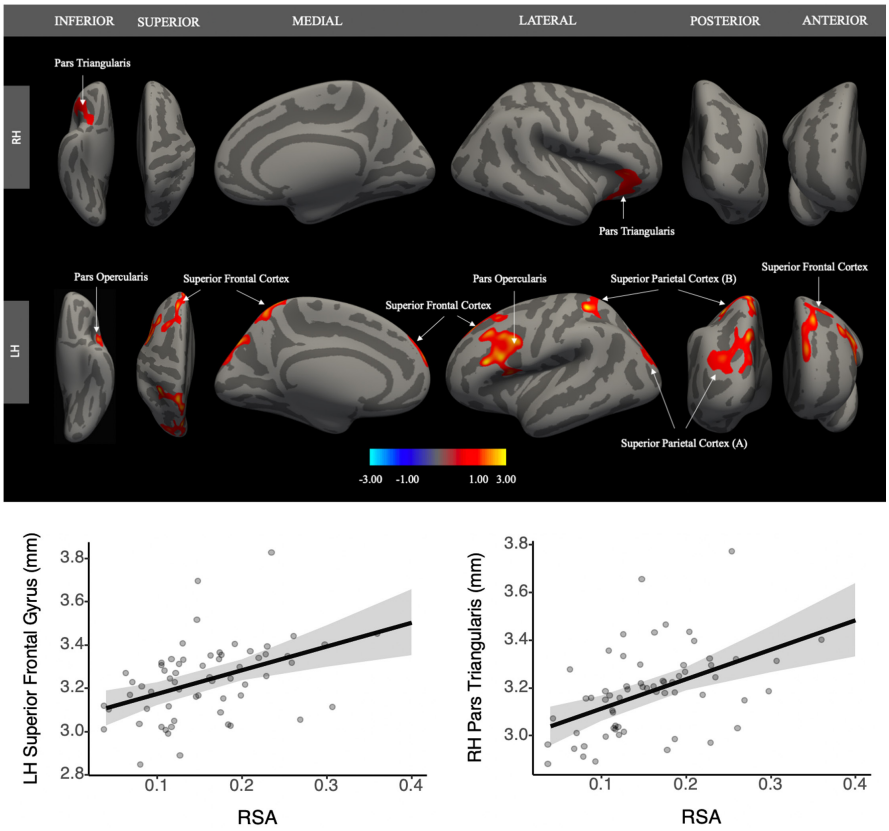

FIGURE 2 Significant main effect of respiratory sinus arrhythmia (RSA) on cortical thickness (CT) in Qdec. (a) Significant cortical areas are shown in red on the group average brain, following Monte Carlo multiple comparison corrections in both hemispheres. (b,c) Scatter plots represent prototypical positive associations between RSA and cortical thickness in both hemispheres. The model controlled for age, sex, and image quality. LH, left hemisphere; RH, right hemisphere. RH—pars triangularis; LH—pars opercularis; LH—superior parietal cortex A; LH—superior parietal cortex B; LH—superior frontal cortex.

TABLE 2 Left and right hemisphere cluster characteristics that survived multiple comparisons correction.

Cortical region	Cluster size (mm^2)	Peak within cluster	Approximate coordinates in MNI space (x, y, z)		
		t	x	y	z
Left hemisphere					
Pars opercularis	2139.08	2.899	−44.1	23.0	19.8
Superior parietal cortex A	1656.74	2.700	−18.4	−78.3	36.8
Superior parietal cortex B	1278.49	3.072	−35.8	−42.3	57.5
Superior frontal cortex	1130.45	2.609	−16.2	39.9	42.9
Rights hemisphere					
Pars triangularis	1257.49	3.617	45.0	29.4	0.6

inferior frontal gyrus), two clusters in the superior parietal cortex (cluster A on Figure 2 encompassing areas of the middle and superior occipital gyrus, superior occipital and transversal sulcus, cuneus, and parieto-occipital sulcus, and cluster B encompassing areas of the precuneus, superior parietal gyrus, intraparietal sulcus, and the postcentral sulcus), and the superior frontal cortex (encompassing areas of the frontal middle gyrus, and superior frontal gyrus and sulcus). For information on cluster characteristics (size, Montreal Neurological Institute [MNI] coordinates and peak), see Table 2. In all five clusters, higher RSA was associated with thicker cortices. For simple slope effects, see Table 3.

3.2 | Secondary analyses

Our secondary analyses examined whether group status (CPS-involved vs. low-risk) moderated the association between RSA and cortical thickness. We completed these analyses at the whole-brain level in Qdec, as well as after the values were extracted from the significant clusters

TABLE 3 Significant main effects of RSA on cortical thickness in the Qdec and at exploratory ROIs.

Cortical region	Intercept	B	SE	t	*p* value	FDR
Whole-brain analyses in Qdec						
Left hemisphere						
Pars opercularis	2.788	1.083	.240	4.503	–	–
Superior parietal cortex A	2.427	.919	.261	3.520	–	–
Superior parietal cortex B	2.554	1.419	.338	4.196	–	–
Superior frontal cortex	3.076	1.098	.300	3.657	–	–
Right hemisphere						
Pars Triangularis	2.908	1.233	.302	4.079	–	–
Exploratory analyses—Desikan-Killiany atlas						
Left hemisphere						
Rostral ACC	3.688	.900	.445	2.020	.048	.672
Superior frontal gyrus	3.140	.514	.245	2.095	.040	.567
Rostral middle frontal gyrus	2.846	.462	.230	2.010	.049	.687
Exploratory analyses—Destrieux atlas						
Left hemisphere						
Rostral ACC	3.688	.900	.445	2.020	.048	1.00
Superior frontal gyrus	3.315	.694	.273	2.538	.013	.111
Middle frontal gyrus	3.171	.728	.276	2.633	.010	.109
Right hemisphere						
Inferior frontal orbital gyrus	2.667	1.183	.369	3.207	.002	**.044**
Orbital gyri	3.201	.898	.329	2.725	.008	.109
Sylvian fissure	2.492	1.446	.350	4.123	.001	**.004**

Note: The estimates reflect unstandardized regression coefficients. The "*p* value" and "FDR" columns reflect uncorrected and FDR-corrected *p* values, respectively, for the exploratory ROI analyses. All whole-brain results were corrected for multiple comparisons in Qdec at the $p < .05$ level.

described in the Primary Analyses section. No significant moderation effects were found at the whole-brain level or at any of the significant clusters ($p > .05$), suggesting that the groups did not differ significantly in their RSA–cortical thickness associations.

3.3 | Exploratory analyses

See Table 3 for the magnitude of the uncorrected main effect of RSA on cortical thickness at the ROIs where significant effects were found, as well as the FDR-corrected *p* values. Bold values denote statistical significance at the FDR corrected $p < .05$ level.

3.3.1 | Desikan-Killiany atlas

Significant positive associations were found at the rostral ACC, superior frontal gyrus, and the rostral middle frontal gyrus in the left hemisphere at the uncorrected $p < .05$ level. No significant effects were found in the right hemisphere. We controlled for age, sex, and image quality in all the models. None of the associations survived FDR multiple comparison corrections.

3.3.2 | Destrieux atlas

At the uncorrected $p < .05$ level, significant positive associations were found at the rostral ACC (gyrus and sulcus), superior frontal gyrus, and the rostral middle frontal gyrus in the left hemisphere. In the right hemisphere, significant uncorrected effects were found in the interior frontal orbital gyrus, orbital gyrus, and sylvian fissure areas. Two ROIs survived FDR multiple comparison corrections: at the sylvian fissure and the inferior frontal orbital gyrus.

4 | DISCUSSION

The present study investigated the association between cortical morphology and parasympathetic cardiac control during middle childhood. Prior studies have found positive

associations between measures of parasympathetic regulation of heart rate and cortical thickness in frontal and prefrontal cortical areas during adulthood. Our findings extend prior work by showing that cross-level integration is established during middle childhood and the cortical location and direction of the associations are comparable to those seen during adulthood.

The cortical regions where we found significant positive associations between cortical thickness and RSA include frontal and parietal areas (e.g., lateral OFC, superior frontal gyrus, inferior frontal orbital gyrus, and superior parietal cortex) that are key nodes of the central autonomic and the fronto-parietal control network. The frontal cortical areas are reciprocally connected with the central nucleus of the amygdala, hypothalamus, periaqueductal gray, and ventrolateral medulla, among others, to allow for flexible information flow between top-down and bottom-up emotion regulation systems (Banks et al., 2007). As Thayer et al. (2012) noted, this brain–body mechanism may serve a vertical integration function that allows for flexible control and appraisal of excitatory activity following sympathetic nervous system activation. In the context of our findings, this may mean that the vertical integration between resting RSA and cortical thickness in prefrontal and frontal cortices is established or is in the process of fine-tuning during middle childhood. Furthermore, the superior parietal cortex is a key node of the fronto-parietal network that has distributed connections with diverse brain networks and plays a central role in integrating higher-order cognitive, sensory, attentional, visuomotor, and working memory functions (Marek & Dosenbach, 2018). Moreover, the parietal cortex function has been associated with cardiac health and, if damaged, may predict long-term adverse cardiac outcomes (Rincon et al., 2008). Our findings suggest that the superior parietal cortex may be involved in the regulation of the peripheral nervous system by integrating cognitive, emotional, and/or motor response to support rapid and flexible control over the excitatory input. These findings are in line with prior work examining autonomic processing networks using structural tractography that showed rich pathways between frontal, parietal, and temporal cortical areas within the central autonomic and fronto-parietal networks (Reisert et al., 2021). Our findings have important implications for understanding how this putative brain–body mechanism may support effective regulatory functioning, and possibly resilience to emotional disorders, externalizing behaviors, or poor health outcomes prior to adolescence.

Our findings may also have important clinical implications. Prior work has shown that cortical thickening in the left OFC and superior frontal cortex from pre- to post-intervention was associated with positive change in high-frequency heart rate variability (which, similar to RSA, is an indicator of parasympathetic cardiac control) and reduction in depressive symptoms in adolescents (Koenig et al., 2018b). Notably, this study implemented a medication-based treatment for depression for adolescents; thus, it is yet to be established whether similar patterns of change would emerge in non-medication-based, evidence-based interventions for emotional disorders. For example, interventions that rely on the regular practice of paced breathing exercises have a potential to mechanistically shape RSA and therefore cortical thickness via the vagus nerve. Importantly, it has been shown in adults that several weeks of mindfulness intervention can lead to cortical thickening in prefrontal regions (Dwivedi et al., 2021; Kang et al., 2013; Lazar et al., 2005), possibly due to the effects of mindful breathing on changes in RSA. Given that children with elevated anxiety and depressive symptoms can benefit from mindfulness-based interventions (Hofmann et al., 2010), future randomized clinical trials are encouraged to examine the effect of mindful breathing exercises on salutary changes in the mechanistic association between cortical thickness and RSA during middle childhood and the extent to which such interventions can prevent the onset or mitigate the burden of emotional disorders later in development.

One strength of our study is that we examined the association between resting RSA and cortical thickness using three methodological approaches: a whole-brain approach and two exploratory atlas-based approaches. The whole-brain analyses yielded support for the presence of a positive brain–body association during middle childhood and the exploratory analyses, using the Des-A but not the DK-A, extended these findings showing similar positive associations at two ROIs (i.e., sylvian fissure, inferior frontal orbital gyrus). These results also suggest that the Des-A may be more sensitive to capturing RSA–cortical thickness co-variation than DK-A during middle childhood.

Our findings also extend previous work showing that the methodological decisions researchers make may have meaningful influence on the conclusions that are drawn. Although our ROI analyses were exploratory and only two ROIs survived multiple comparison correction, comparing multiple methodological approaches when examining associations between brain morphology and autonomic nervous system functioning is important for integrating scientific knowledge across various analytical approaches used by different research groups. We also show that brain atlases with fine anatomic resolution (Des-A) may provide a more detailed understanding of the hemispheric localization of resting RSA–cortical thickness associations than those with less granular resolution (DK-A).

The present study has other strengths and limitations that are important to note. One strength is that we measured cortical thickness and RSA during middle

childhood—a developmental period that is relatively understudied but is key to the study of regulatory independence from caregivers and early markers of emotional disorders. Moreover, we examined these biological processes in a diverse and vulnerable group of children at risk for experiencing chronic stress. Although our sample size is comparable to other studies (e.g., Winkelmann et al., 2017; Woodward et al., 2008; Yoo et al., 2018), a larger participant pool would make our analyses more robust. Also, during the physiological data collection, children engaged in a paced breathing exercise in the presence of their parents. Given that parents can function as co-regulators to their children (Gunnar et al., 2015), it is possible that the presence of the parents may have had a buffering effect on children's RSA outcomes. Future studies may examine associations between cortical thickness and resting RSA measured in different contexts. Finally, multiple timepoints would also allow us to make more detailed inferences about resting RSA–cortical thickness associations during middle childhood.

5 | CONCLUSIONS

We examined the association between two biological measures of regulatory functioning, resting RSA and cortical thickness, using three analytical approaches (whole-brain and two exploratory, atlas-based analyses). Our findings suggest that adult-like, positive associations between cortical thickness and RSA are already established or are in the process of forming during middle childhood in frontal and parietal cortical areas. Frontal areas may support effective top-down control of excitatory input, whereas parietal regions may support flexible allocation of cognitive resources at times of distress. Considering that children can benefit from the availability of this hypothesized brain–body mechanism for effective emotion regulation during middle childhood, our findings may have important implications for prevention and intervention for emotional disorders, especially the ones that rely on breathing exercises to reduce the stress response and regain emotional equilibrium.

AUTHOR CONTRIBUTIONS

Marta Korom: Conceptualization; data curation; formal analysis; methodology; software; visualization; writing – original draft. **Alexandra Tabachnick:** Conceptualization; data curation; formal analysis; methodology; project administration; writing – review and editing. **Tabitha Sellers:** Conceptualization; writing – original draft. **Emilio A. Valadez:** Data curation; project administration; writing – review and editing. **Nim Tottenham:** Conceptualization; writing – review and editing. **Mary Dozier:** Conceptualization; funding acquisition; investigation; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data/code that support the findings of this study are available from the first author (initials MK), upon reasonable request.

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