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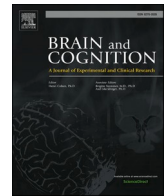
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# The relationship between structural properties of frontal cortical regions and response inhibition in 6–14-year-old children

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## ABSTRACT

Development of attentional skills and inhibitory control rely on maturational changes in the brain across childhood and youth. However, both brain anatomy and different components of attention and inhibition show notable individual variation. Research on ADHD and inhibitory training and control have shown that variations in the thickness and surface area of particularly inferior cortical structures are associated with attentional control. However, the intricacies of how the development of inhibitory control is associated with the anatomical variations beyond the general age- and gender-dependent differences have not been resolved. Here, we sought to address these questions by quantifying the cortical thickness and surface area in frontal cortical regions and inhibitory control using the stop signal task performance in 6–14-year-old children. Our results showed that the thickness of the left medial orbitofrontal cortex and the surface area of the left caudal anterior cingulate were associated with the inhibitory performance, beyond the variance that could be explained by the subjects' age and gender. The results highlight the importance of factoring in anatomical variations when following attentional development and the importance of evaluating multiple anatomical measures when aiming to link the properties of cortical structures with variations in cognitive performance.

## 1. Introduction

Brain development features polymorphic changes in the thickness, volume, and surface area of the cortex (Amlien et al., 2016; Koolschijn & Crone, 2013; Paus, 2005; Wierenga et al., 2014). In addition to linking with age-related maturation, cortical thickness, volume, and surface as a whole and across a range of brain regions are thought to associate with the cognitive skill level of children (Amlien et al., 2016; Curley et al., 2018; Estrada et al., 2019; Menary et al., 2013; Paus, 2005; Schnack et al., 2015). For example, 10-year-old children with a higher IQ were reported have a thinner cortex than those with a lower IQ, whereas the cortical surface area was shown to be larger in children with a higher IQ (Schnack et al., 2015). On the other hand, it is difficult to make causal inferences as also growth environment and socioeconomic status have been shown to correlate with brain structural measures (Parker et al., 2017). Especially for the developing brain, it is difficult to tease apart, even conceptually, the changes reflecting age-related development, and the variation in (age-independent) skill-level. Determining neural measures that specifically link with cognitive skills would be important

to identify potentially atypical developmental trajectories, and to find optimal support for individuals who would benefit from early interventions in neurocognitive development. However, to track atypical trajectories, the correct indicators need to be defined that can reveal individual variance in specific cognitive skills. Here, we explored whether two of the most frequently used structural measures of brain development, thickness and surface area, contribute to the between-individual variance in one of the core factors of psychological development, namely inhibitory control, beyond that of age-related maturation.

Attention and especially inhibitory control are key processes in human cognitive development. Their development contributes to increasing competence in many other cognitive and academic domains (e.g. reading, memory, arithmetic, emotion regulation). Moreover, many of the neurodevelopmental disorders feature deviances in typical development of attentional capacity or inhibitory control. In some cases, such as attention-deficit/hyperactivity disorder (ADHD), deficits in engaging needed attention for age-appropriate task performance, or inability to inhibit reactions to task unrelated stimuli or drives, is the

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core symptom. In other cases, problems in inhibitory control are occasionally observed, and it has been proposed that neural activation patterns could be used to help distinguish, e.g., ADHD from autism spectrum disorder (Albajara Sáenz et al., 2020). The most straightforward and robust approach to study the relationship between structural brain measures and attention and inhibitory control has been to examine subject populations with aberrant development (Almeida et al., 2010; Batty et al., 2010; Silk et al., 2016; Wolosin et al., 2009). It has been shown, for example, that the total cortical volume, total surface area, and mean cortical thickness differ between individuals with ADHD and typically developing age-matched individuals, and that these differences are most prominent in the frontal and parietal lobes (Silk et al., 2016; Wolosin et al., 2009). Although studies with different structural measures, thickness vs. surfaces area, give, in general, a similar picture in these group comparisons, there are also some differences. Within the frontal cortex, cortical thickness has been shown to be lower in ADHD children compared to healthy controls in pars opercularis (Batty et al., 2010; Liu et al., 2017), pars triangularis (Liu et al., 2017), superior frontal cortex (Almeida et al., 2010; Liu et al., 2017; Yang et al., 2015) and medial frontal cortex (Liu et al., 2017; Silk et al., 2016). For cortical surface area, ADHD related reductions have been observed, e.g., in the dorsolateral, inferior lateral and medial prefrontal cortex as well the orbitofrontal cortex and anterior cingulate, with considerable gender-specific variations (Dirlikov et al., 2015). These imaging findings in ADHD, especially concerning thickness, evidencing thinner cortex in some of the core areas for attention and inhibitory control, are somewhat contradictory with the notion of general developmental reduction in cortical thickness and association between low thickness and higher IQ. This highlights the need to account for the age-related changes in the association between brain measures and cognition. It may well be that there is an optimal developmental stage for cortical changes, associated with decrease/increase of thickness or surface area, which would lead to opposite correlation with skill level depending on age.

It has been established that attention and inhibitory control develop prominently during childhood, but in general their development is considered to be a long-lasting complex process that continues until early adulthood (Boen et al., 2021; Williams et al., 1999). Posner and Petersen (Posner & Petersen, 1990) posited that attention is composed of distinct sub-components of alerting attention, orienting attention and executive attention, a notion which has been supported by subsequent studies (Mullane et al., 2016; Sobeh & Spijkers, 2012; Suades-González et al., 2017). A central function within executive attention is cognitive inhibition which allows the blocking of orienting attention towards stimuli that are irrelevant for one's own behavior (Rueda et al., 2015). Response inhibition is considered as one of the crucial building blocks for executive skills (Diamond, 2013). The most common approach to quantify the level of response inhibition has been to use the so-called stop signal task (Curley et al., 2018; Kenemans et al., 2023; Sender-ecka et al., 2012; Wang et al., 2019) that measures the inhibition of an already initiated response. However, the development of different cortical areas that underlie the type of inhibitory control in stop signal task has been studied less.

The developmental changes in cortical thickness mostly converge to show age-related cortical thinning, the rate of which varies across regions (Shaw et al., 2008). While a body of evidence suggests that the cortical thickness is maximal at early childhood, the findings have been somewhat inconsistent and it is unclear to which age the cortical thinning continues (Walhovd et al., 2017). Generally speaking, cortical thinning follows region-specific trajectories, and, e.g., reaches the maximum in sensorimotor cortices at an earlier age than in frontal areas or in the posterior temporal cortex (Gogtay et al., 2004). As for the cortical surface area, evidence shows that it substantially increases until 12 years of age with moderate further changes (Amlien et al., 2016). Notably, the changes in cortical surface area reflect complex interactions between changes related to brain size and changes in the degree of cortical gyrification, both of which vary by age (Raznahan et al., 2011).

Accordingly, cortical thinning and expansion of cortical surface area show different age-dependent profiles (Amlien et al., 2016; Schnack et al., 2015; Wierenga et al., 2014), suggesting that development of cortical surface area and thickness are at least partially driven by different underlying processes (Wierenga et al., 2014). Thus, the different anatomical measures of cortical development can show varying and individual trajectories (Bethlehem et al., 2022) and it is unclear how the co-development of cortical thickness and surface area are related to cognitive development. Clarifying their specific contribution, specifically to explain inter-individual variation in inhibitory control, would crucially help to define target measures for evaluating neurocognitive integrity in developing (and adult) brain.

In typically developing children, studies of the relationship between the anatomical cortical properties and inhibitory control have led to somewhat inconsistent findings. For example, Delalande and colleagues (Delalande et al., 2020) observed that the thickness of pars triangularis and orbitalis was associated with the level of inhibition, whereas Curley and colleagues (Curley et al., 2018) did not find evidence linking the thickness of pars opercularis with inhibitory performance. On the other hand, relatively larger cortical surface area of the bilateral opercular region and the right pars opercularis has been linked with better motor-inhibitory performance (Curley et al., 2018). Conversely, changes in both cortical thickness and surface area associated with training related to inhibitory control have been observed in several prefrontal cortical regions such as the pars opercularis, triangularis, and orbitalis of the inferior frontal gyri (Delalande et al., 2020). Overall, both in ADHD and typically developing children, development of inhibitory control has been associated with both cortical thickness and surface across a wide range of cortical regions, often encompassing the same inferior frontal cortical structures (Delalande et al., 2020; Liu et al., 2017). However, especially in the typically developing population, the specificity of the association between cortical and development of attentional and inhibitory control and the role of, e.g., age and gender in them, is still unclear.

Here, we combined anatomical magnetic resonance imaging (MRI) and stop signal task performance in 6–14-year-old children to address these questions. Specifically, we evaluated the relationship between stop-signal reaction-time (SSRT) that measures the inhibition of an already initiated response and cortical thickness and surface area across frontal cortical regions to determine whether the development of the anatomical properties within these regions would be associated with the development of inhibitory control. We hypothesized that SSRT would be associated with thickness and surface area in distinct regions, so that the region-specific structural measures would explain the variance in task performance beyond the age and gender of the children.

## 2. Materials and methods

### 2.1. Subjects

Originally, 78 children were recruited to participate in the study. Out of these subjects, 9 were excluded from the analyses because of observed structural abnormalities in the MRI data (2 cases), overt number of mistakes in stop-signal task (1 case) or lacking MRI data (6 cases) due to failed recordings, magnetic interference, or refusal to undergo the recording. The MRI and stop-signal task data were successfully collected from 69 children (31 females) aged 6–14 years (average age 10.12, SD 1.45). None of the children had any neurological diseases or medication that would have affected their central nervous system. All participants had a normal hearing as determined with an audiometer (0–20 dB). In addition to the MRI and behavioral data analyzed in this study, the subjects participated also in and magnetoencephalography (MEG) experiment, the results of which have been reported earlier (van Bijnen et al., 2022; van Bijnen et al., 2023). The study was carried out in accordance with the Declaration of Helsinki and it was approved by the Human Sciences Ethics Committee of the University of Jyväskylä (21/

04/2016, ref.: 4/2016). An informed consent was obtained from all participants and their guardians.

## 2.2. Behavioral data

The inhibitory performance of the subjects was measured using the stop-signal task (SST) from the Cambridge Neuropsychological Test Automated Battery (J. Fray et al., 1996). In the stop-signal task, the subjects were shown arrows that were pointed either to left or right. They were instructed to press, as quickly as possible, the button corresponding to the direction of the arrows. The task consisted of 5 blocks of 64 trials each. Before performing the task, subjects were presented 16 trials to practice the task. In the task, 25 % of the trials included an auditory stop-signal which indicated that the subjects should withhold their response and not press a button. Each block comprised four sub-blocks with 16 trials of which 12 were go trials and four stop trials presented in a random order. The stop-signal delay (SSD) was adapted individually following a staircase design. Here, the time delay between the visual stimulus and auditory sound (stop signal) was varied so that successful inhibition of the response led to an increase of the delay by 50 ms and unsuccessful inhibition to its decrease by 50 ms. The amount of delay was determined such that the subject could withhold his/her response successfully 50 % of the times. The stop-signal reaction time (SSRT), in turn, was calculated by subtracting the SSD from the median reaction time of the trials without the auditory stop-signal. A greater time interval between the auditory signal and the median reaction time indicates lower inhibitory performance. In addition, the verbal and non-verbal reasoning skills of the subjects were measured using the Wechsler Intelligence Scale for Children (WISC-III) similarities and block design subtests (Wechsler, 1991). In the similarities test, the subjects were asked to describe how two words are alike. Higher points indicate better skills in forming concepts and associations as well as logical linguistic reasoning at the abstract level. In the block design, the subjects were required to copy a pattern from a figure using colored blocks. Each trial was scored based on the accuracy of the performance as well as the time it takes to complete the task. The test measures the subjects' nonverbal reasoning and ability to understand complex visual information, with higher scores indicating better task performance. The similarities and block design tests were used to ensure that the subjects' verbal and non-verbal reasoning were within the range of the standard population. In the analyses of the present study, we focus only on the SSRT data. Table 1 shows the demographic and behavioral data for the whole subject sample as well as separately for the females and males.

There were no significant differences in the age of the subjects or in any of their behavioral characteristics between females and males (Age,  $p = 0.96$ ; SSRT,  $p = 0.08$ ; Block design,  $p = 0.19$ ; Similarities,  $p = 0.54$ ).

## 2.3. Magnetic resonance imaging data and analysis

T1 and T2 weighted 3D-SE anatomical magnetic resonance images were collected using a 1.5 T GE scanner (GoldSeal Signa HDxt) at Synlab

**Table 1**  
Summary of demographic and behavioral data.

Demographics	Total	Female	Male
Number of participants	69	31	38
Age (years)	10.12 (1.45)	10.20 (1.54)	10.06 (1.39)
SSRT (ms)	212.98 (61.83)	197.42 (57.02)	225.67 (63.41)
Block design	38.68 (11.36)	37.06 (12.52)	40.00 (10.31)
Similarities	22.67 (5.07)	22.68 (5.62)	22.66 (4.65)

Mean and standard deviation of the demographic and behavioral data. For SSRT, lower time values indicate better inhibitory performance, whereas for the block design and similarities tests higher scores indicate better skills in non-verbal and verbal reasoning, respectively. SSRT correlated significantly with age ( $r = -0.48$ ,  $p = 0.00033$ ) but not with block design ( $r = -0.15$ ,  $p = 0.23$ ) or similarities tests ( $r = -0.19$ ,  $p = 0.12$ ).

Jyväskylä with the following parameters: TR of 540, TE of 10 ms, flip angle of 90°, matrix size of 512 x 512 at 0.5 mm x 0.5 mm in-plane resolution and 0.6 mm slice thickness. The MRI data were analyzed using the automatic cortical segmentation and parcellation process in Freesurfer 5.3 (Fischl, 2012). In the analysis, the cortical gray matter was first segmented from the MRI data and the data were morphed into isotropic 1 mm voxels (256 x 256 x 256). In the analyses we used the automatically generated Desikan-Killiany anatomical parcellation (Desikan et al., 2006) and selected seven bilateral cortical regions (superior frontal cortex, medial orbitofrontal cortex, caudal anterior cingulate, rostral anterior cingulate, pars opercularis, pars triangularis and pars orbitalis) as the regions of interest (ROI) for subsequent analyses. The regions were selected as their thickness, surface area or volume has been linked with attentional development, variations in levels of attentional control or reactivity to inhibitory training (e.g., Curley et al., 2018; Delalande et al., 2020; Liu et al., 2017; Silk et al., 2016). Fig. 1 shows the selected ROIs. For these ROIs, we extracted the surface area and cortical thickness values yielded by the Freesurfer MRI parcellation statistics. As the surface area value, we used the ROI values normalized by the total surface area across both hemispheres whereas for cortical thickness we used the original value for each ROI.

## 2.4. Statistical analysis

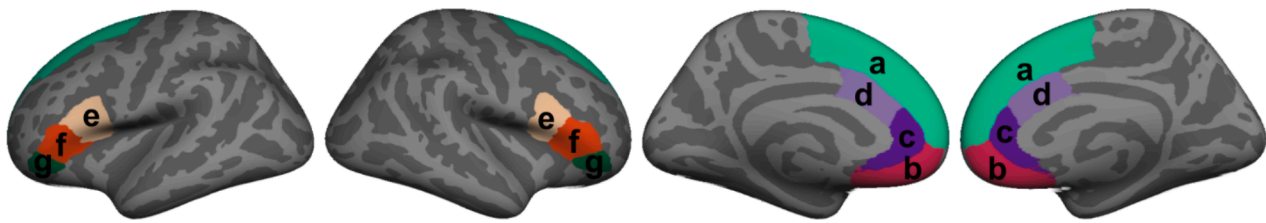
The effects of the age, gender, and cortical measures (ROI thickness and surface area) on SSRT were examined using multiple linear stepwise backward regression in SPSS 28.0 (IBM). The analyses were conducted separately for each ROI and cortical measure. In the analysis, we applied the default parameters (e.g.,  $p \geq 0.1$  removal criterion) within the stepwise backward regression. The regression analysis was conducted in the whole group of subjects as well as separately in the males and the females. In addition to the regression analysis, we examined with Pearson's linear correlation whether the age of the subjects or SSRT would be correlated with the cortical thickness or normalized surface area within the ROIs, or the mean cortical thickness or total surface area across the whole cortex.

To obtain a more comprehensive view on the relationship between cortical development, age and inhibitory control, we further applied factor analysis to explore whether the variability across the different measures would reflect distinct underlying (latent) variables and whether these variables would explain the variability in SSRT. Here, we conducted two different analyses in SPSS. First, we examined across all cortical measures, age and SSRT the loadings of the different variables across the factors. Secondly, we conducted factor analysis separately for the cortical thickness and surface area measures across the ROIs and evaluated the effects of the factor scores obtained from these analyses, age and gender on SSRT via using multiple linear stepwise backward regression. The details of the factor analyses are reported in Supplementary material.

## 3. Results

Across the seven ROIs, in three cases either the thickness or surface area remained in the model after the backward regression. For all these three cases, both other independent variables (age, gender) remained in the model as well, with age influencing the SSRT performance significantly ( $p < 0.0005$ ) in all these regions. Table 2 shows the B, Standard error, t, and significance values for these three cases, and Table 3 shows the p-values for cortical thickness/surface area for all ROIs for the full model comprising age, gender, and the cortical measures. In the *left medial orbitofrontal cortex*, cortical thickness had a significant effect on SSRT ( $p = 0.040$ ) and in the *right pars triangularis* the effect approached significance ( $p = 0.094$ ). In both regions, the thinner the cortex was, the lower the SSRT. In the *left caudal anterior cingulate*, the normalized surface area had a significant effect on SSRT ( $p = 0.036$ ) with a larger surface area leading to lower SSRT. For all other ROIs, the cortical





**Fig. 1.** ROIs selected for the analyses. Bilateral superior frontal cortex (a), medial orbitofrontal cortex (b), caudal anterior cingulate (c), rostral anterior cingulate (d), pars opercularis (e), pars triangularis (f) and pars orbitalis (g).

**Table 2**  
The role of age, gender and cortical measures on SSRT.

<i>Left medial orbitofrontal cortex, cortical thickness</i>				
	B	SE	t	p
Age	-17.89	4.48	-3.99	0.00017
Gender	27.52	12.71	2.17	0.034
Thickness	81.03	38.64	2.10	0.040
<i>Right pars triangularis, cortical thickness</i>				
	B	SE	t	p
Age	-20.62	4.44	-4.64	0.000017
Gender	28.61	12.94	2.21	0.031
Thickness	69.56	40.95	1.70	0.094
<i>Left caudal anterior cingulate, surface area</i>				
	B	SE	t	p
Age	-20.09	4.37	-4.60	0.000020
Gender	22.90	12.70	1.80	0.076
Surface area	-2.31	1.08	-2.14	0.036

Results from the multiple linear stepwise backward regression examining the influence of age, gender and cortical measures on SSRT for cases where a cortical measure remained in the model.

**Table 3**  
Effects of cortical thickness and surface area on SSRT.

<i>Cortical region</i>	<i>Thickness</i>	<i>Surface area</i>
superior frontal cortex (L)	0.65	0.47
superior frontal cortex (R)	0.62	0.96
medial orbitofrontal cortex (L)	<b>0.040</b>	0.96
medial orbitofrontal cortex (R)	0.312	0.19
caudal anterior cingulate (L)	0.701	<b>0.036</b>
caudal anterior cingulate (R)	0.75	0.31
rostral anterior cingulate (L)	0.79	0.42
rostral anterior cingulate (R)	0.89	0.63
pars opercularis (L)	0.77	0.48
pars opercularis (R)	0.82	0.37
pars triangularis (L)	0.74	0.69
pars triangularis (R)	0.094	0.173
pars orbitalis (L)	0.192	0.80
pars orbitalis (R)	0.62	0.12

Effects (p-values) of cortical thickness and surface area on SSRT for the full model comprising age, gender and thickness or surface area.

measures were removed from the model during the backward regression. In these cases, age had a significant effect on SSRT ( $B=-19.931$ ,  $p = 0.000035$ ) and the effect of gender approached significance ( $B=25.432$ ,  $p = 0.054$ ). For the cases where cortical thickness had remained in the model, the effect of gender on SSRT was significant (left medial orbitofrontal cortex,  $p = 0.034$ ; right pars triangularis,  $p = 0.031$ ), whereas for Left caudal anterior cingulate where the surface areas remained in the model the effect of gender was not significant ( $p = 0.076$ ). In the structures showing the involvement of cortical thickness or surface area (left medial orbitofrontal cortex, right pars triangularis and left caudal anterior cingulate) we also tested with mediation analysis whether the cortical properties would mediate the effects of age and gender on SSRT. No significant effects were observed ( $p > 0.19$  for all tests).

We also evaluated separately for females and males with multiple

linear stepwise backward regression whether the age of the subjects and cortical thickness and surfaces area would affect SSRT. For all models, the cortical measures proved to be non-significant, whereas the influence of age on SSRT was significant for both groups ( $p = 0.027$  for females,  $p = 0.00032$  for males). We then tested whether the age or SSRT of the subjects would be correlated with any of the cortical measures (cortical thickness and surface area in the ROIs, mean cortical thickness or total surface area). In the bilateral rostral anterior cingulate, age was positively correlated with the ROI surface area (left,  $r = 0.27$ ,  $p = 0.024$ ; right,  $r = 0.31$ ,  $p = 0.0086$ ). In the left medial orbitofrontal cortex, SSRT was positively correlated with the ROI thickness ( $r = 0.30$ ,  $p = 0.014$ ). Fig. 2 shows the scatterplots and linear trendlines for these ROIs. The full set of scatterplots and linear trendlines for all correlation tests are shown in Supplementary figures 1 and 2. In addition to the above significant findings, the tests showed that in the left medial orbitofrontal cortex, the correlation between age and cortical thickness approached significance ( $r = -0.21$ ,  $p = 0.078$ ) and that the correlation between SSRT and the normalized surface area approach significance in the right pars triangularis ( $r = 0.21$ ,  $p = 0.079$ ), medial orbitofrontal cortex ( $r = 0.21$ ,  $p = 0.089$ ), caudal anterior cingulate ( $r = -0.23$ ,  $p = 0.056$ ) and rostral anterior cingulate ( $r = -0.23$ ,  $p = 0.061$ ). For all other tests no significant or marginally significant effects were detected ( $abs(r) < 0.2$ ,  $p > 0.1$ ).

We also investigated via two different types of factor analyses whether the variability across the different measures would reflect latent underlying variables and whether these variables would explain the variability in SSRT (see Supplementary material, Supplementary Figures 3, 4 and 5, and Supplementary tables 1, 2 and 3). In the first analysis, we evaluated simultaneously across all cortical measures (thickness and surface area of all ROIs), age and SSRT the main factors of the data and their loadings. The analysis revealed that only one factor had non-zero loadings for both age (0.81) and SSRT (-0.76). This factor had non-zero loadings for the thickness of the left medial orbitofrontal cortex (-0.44) and the surface area of the bilateral rostral anterior cingulate (left, 0.40; right, 0.34) and right medial orbitofrontal cortex (-0.31). In the second analysis, we conducted the factor analysis across all thickness and surface area measures (separately for thickness and surface area) and applied linear regression to evaluate whether the factors would explain SSRT beyond the age and gender of the subjects. No significant findings were detected, but for one thickness factor the factor remained in the regression model ( $p = 0.080$ ). This factor had non-zero loadings for the thickness of the bilateral medial orbitofrontal cortex (left, 0.77; right, 0.76), the right rostral anterior cingulate (0.39) and the left pars orbitalis (0.31). For all other factors, the cortical factors were eliminated from the regression model.

#### 4. Discussion

We clarified whether cortical thickness and surface area across different frontal cortical regions contribute to the performance level in a response inhibition task, namely the stop signal task, in 6–14 years-old-children. In particular, we examined whether the cortical measures would bring additional explanatory value on the variance in task performance across individuals above age and gender that are known to

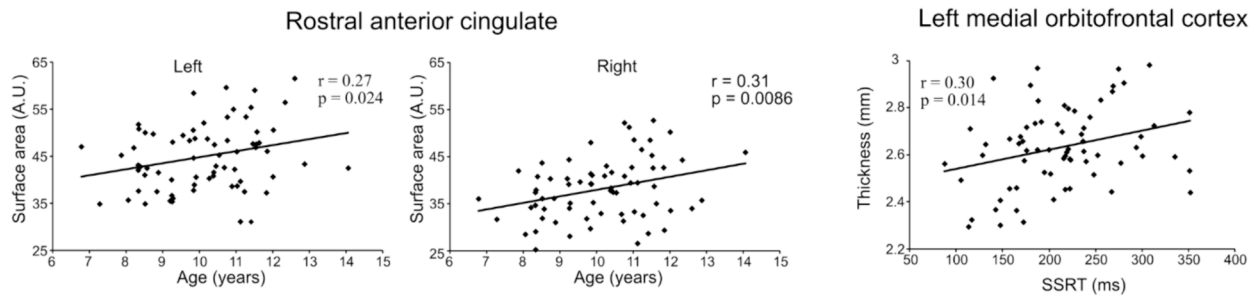


Fig. 2. Correlation between the age of the subjects and normalized surface area in the bilateral rostral anterior cingulate (left) and between SSRT and cortical thickness in the left medial orbitofrontal cortex (right).

influence both cognitive performance and cortical thickness/surface area. Our results show that the thickness and surface area of distinct brain regions were associated with the development of inhibitory control. We observed, using multiple linear regression, that inhibitory control as quantified by the SSRT is associated with the thickness of the left medial orbitofrontal cortex and the surface area of the left caudal anterior cingulate beyond the variation that could be explained by the subjects' age and gender. The observed effects in thickness and surface area were opposite, with better inhibitory performance being linked with a thinner cortex and larger surface area. The findings align with previous studies that have shown similar opposing associations for IQ differences (Schnack et al., 2015) as well as positive correlation between level of inhibitory control and cortical surface area (Curley et al., 2018). Our results highlight the importance of factoring in anatomical variations for following attentional development as well as the importance of considering different measures when aiming to link the properties of cortical structures with variations in cognitive performance (Silk et al., 2016).

While our results align with the opposing relationships between IQ and cortical thickness and surface area (Schnack et al., 2015), there were two obvious discrepancies with previous literature related to the link between cortical thickness and surface area in ADHD as well as the effects of inhibitory training on cortical thickness. As regards the first discrepancy, earlier studies related to inhibitory control that have indicated that children with ADHD show both reduced cortical thickness and surface area compared to typically developing children (Dirlikov et al., 2015; Liu et al., 2017). The observed association between improved performance and thinner cortex in the present study thus somewhat deviates from earlier studies on ADHD. There are several factors that can explain this apparent discrepancy. First, it is possible the changes related to aberrant development and variation within the typically developing population do not fully align. For example, the atypical neurotransmission in ADHD is associated with complex, compensatory changes (Tripp & Wickens, 2009), leading potentially to anatomical properties that would be unexpected considering the variations that are observed within healthy population. Specifically, in typically developing individuals both increased attentional skills and increasing age are commonly linked with a thinner cortex and larger surface area (Curley et al., 2018; Delalande et al., 2020), a notion that seems to contradict with the observed cortical thinning in ADHD (Batty et al., 2010; Liu et al., 2017; Silk et al., 2016). However, in ADHD, the cortical structures showing atypical thinning are likely to be different from the structures that show thinning related to improved inhibitory control within typically developing children, as was the case in our study. We observed that a thinner left medial orbitofrontal cortex was associated with better inhibitory performance whereas previous studies have demonstrated atypically thin cortex in ADHD, e.g., in the pars opercularis, orbitalis and triangularis, superior frontal cortex, lateral orbitofrontal cortex and right medial orbitofrontal cortex (Almeida et al., 2010; Batty et al., 2010; Liu et al., 2017).

The second conceptual discrepancy is related to training induced

improvements in inhibitory control that Delalande et al. found to be associated with *increased* cortical thickness in, e.g., the right pars opercularis (Delalande et al., 2020). While the specific area was not the same as within the present study showing a relationship between inhibitory control and cortical thickness, the opposite direction of the effect is interesting. It is possible that training-related, quickly occurring changes may be different from slowly accumulating differences influenced by genetic and environmental factors. These results are in line with the interpretation that cognitive processes, including inhibitory control, are supported by a network of cortical areas, the development of which follow specific trajectories. In this framework, a compromised performance level may result from an atypical developmental trajectory, which may feature also accelerated maturation in specific cortical areas. Indeed, recent theoretical accounts advocate the idea of neurodevelopmental disorders as phenotypes arising from cellular-level dysfunctions in 'randomly' distributed cortical areas (Astle et al., 2023). However, it may not be possible to associate the coarse-level measures such as thickness and surface area of the cortex and their variations with single micro-level characteristic as these measures reflect, e.g., the number of synapses, level of myelination, blood circulation etc. Further, as stated above, it is possible that the results from studies of ADHD relate to compensatory processes in the brain – not the core dysfunction. To understand how the development of these different frontal areas contributes to variation in inhibitory control, neuroimaging studies would need to be accompanied, e.g., with functional studies with pharmacological or neuromodulatory manipulation that allow also causal inference.

Notably, we observed that children with better inhibitory control had a larger surface area in the left caudal anterior cingulate, an area where decreased cortical surface area has been associated with ADHD (Dirlikov et al., 2015). Considering also the commonly observed reduction in cortical surface area in ADHD (Silk et al., 2016; Wolosin et al., 2009) and the association between better motor-inhibitory performance and larger surface area in pars opercularis (Curley et al., 2018), this finding aligns well with the previous literature, and lends further support for the significance of this area and its intact development for attentional control. Our findings specifically indicate that the development of left caudal anterior cingulate has an important role for successful response inhibition, in line with earlier literature (Botvinick et al., 2004; Chambers et al., 2009; Falkenstein et al., 1999; Huster et al., 2010; Nieuwenhuis et al., 2003; Smith et al., 2007). It should also be noted that Delalande et al. found opposing effects linking surface area with inhibition within their own study across cortical regions (Delalande et al., 2020). They observed that the inhibitory control training was associated with surface area decreases in the right superior frontal pars opercularis and increases in the left inferior frontal and in right orbital sulcus. These earlier findings thus both align and misalign with the present observation of improved attentional control being related with increased surface area. Altogether, these findings highlight the complexity of relating anatomical differences and variation to cognitive performance and its changes. This may be a particularly important

consideration in developmental studies as attention and its different components, cortical thickness and cortical surface area follows region-specific trajectories with age- and gender-dependent profiles (Amlien et al., 2016; Gogtay et al., 2004; Raznahan et al., 2011; Schnack et al., 2015; Wierenga et al., 2014). Thus, factoring in the multiple sources of influences on inhibitory control and cortical measures remains a challenging task.

It is also important to acknowledge the specific attentional task when interpreting our results and linking them with earlier findings. Here, we applied the SST to determine the level of one component of executive functions, namely response inhibition. While we are used to grouping together different subprocesses of attention and inhibitory control to represent 'executive control', the specific task used may critically influence which neural networks are linked with executive control. Moreover, the findings from comparing ADHD vs. typically developing individuals are likely to reflect the most apparent contrast between the groups in general, and they do not necessarily capture the areas that are critical for specific attentional skills. Thus, studies correlating cortical measures with behavioral performance (either in typical or atypically developing brain) are more likely to pinpoint the areas that directly contribute to the task performance.

In the present study, we observed that the thickness of the left medial orbitofrontal cortex and the surface area of the left caudal anterior cingulate explained a portion of the variance within the inhibitory performance in typically developing 6–14-year-old children. While it is interesting that the inhibitory performance was explained by distinct anatomical measures across the two regions, it is difficult to assign a deeper meaning for this observation as a multitude of possible explanations exist. First, as the development of cortical thickness and surface area follow region-specific trajectories with complex origins (Amlien et al., 2016; Gogtay et al., 2004; Raznahan et al., 2011), it is very possible that within the present sample of children the variance in inhibitory control is somewhat randomly explained by different anatomical measures across cortical regions. This line of thought is conceptually supported by the findings showing that the two regions continue developing from childhood until adulthood, as indicated by the age-dependent linear changes in functional connectivity from the anterior cingulate (Kelly et al., 2009) and differences in orbitofrontal activity between children and adults as well as adolescents and adults (Loh & Rosenkranz, 2022; Pfeifer et al., 2007). Naturally, it is also possible that the distinct linkage between inhibitory control and cortical anatomy across the two regions is related to more fundamental differences in the structure of the anterior cingulate and orbitofrontal cortex such as their different cytoarchitectures or myeloarchitectures (Amunts & Zilles, 2015). That is, the role of the cortical thickness and surface area in influencing inhibitory performance may vary across regions with distinct patterns of cell bodies and types or myelinated nerve connections.

It is also possible that the difference between the left caudal anterior cingulate and medial orbitofrontal cortex is related to specifics of the measured inhibitory control property and its development within the 6–14-year-old age-group. In general, it has been shown that inhibitory control develops earlier than other aspects executive control (Davidson et al., 2006; Rueda et al., 2004). Here, we used SSRT to determine the performance within one component of inhibition, namely the inhibition of an already initiated response. For the stop signal task, it has been shown that the rate of improvement within the task is not linear as a function of age and that the improvement for the different trial types within the task (e.g., stop-respond and stop-inhibit) plateaus at different ages (Dupuis et al., 2019). Thus, it is also possible that the improvements within inhibitory control as measured by SSRT are differentially influenced by age-dependent changes of cortical thickness and surface area across cortical regions, with one aspect being critical at an earlier age (e.g., 6–10 years) while the other would continue to be relevant for inhibitory development throughout adolescence into adulthood. Future studies with larger sample sizes than that of the present study could try

to tease apart such possible effects across younger and older children.

With our experimental paradigm we were not able to fully resolve the mechanism through which the observed effects took place. We found that the age and gender of the subjects influenced the inhibitory performance, with the effects becoming occasionally more significant when the anatomical information was included in the regression model. We thus evaluated whether the cortical thickness or surface area would mediate the effects of age or gender on inhibitory control. No significant findings were detected, but some weak trends were present in the data. Thus, while no evidence of such mediation was observed, suggesting a more independent role of the cortical thickness and surface area on inhibitory control, it is also possible that the lack of evidence is due to too small a sample size. It is also conceivable that the parcellation used in the analyses that merges functionally and anatomically distinct regions together was too coarse, both regarding the linear regression and the mediation analysis; using a more fine-grained parcellation could have revealed more effects in one or both analyses. However, the use of the parcellation was motivated by the statistical power within the study, and a larger subject cohort would be needed to probe these aspects.

In addition to the regression analysis, we also applied exploratory factor analysis to examine whether the variability across both types of cortical measures, age and SSRT would reflect latent underlying variables and whether factors across the thickness and surface area measures would explain the variability in SSRT. Interestingly, both age and SSRT had non-zero loadings for the same single factor that involved the thickness of the left medial orbitofrontal cortex and the surface area of the bilateral rostral anterior cingulate and right medial orbitofrontal cortex. Moreover, when examining separately the latent thickness and surface area variables, the cortical thickness factor comprising the bilateral medial orbitofrontal cortex, right rostral anterior cingulate and left pars orbitalis explained marginally significantly the variance in SSRT beyond the age and the gender of the subjects. The results from these analyses further highlight the importance of the medial orbitofrontal cortex and rostral anterior cingulate in the inhibition of an already initiated response for 6–14 year-old children. However, the findings from the factor analyses should be replicated in a larger cohort to support these interpretations.

## 5. Conclusions

Here, we studied the contribution of the thickness and surface area of frontal cortical regions on inhibitory control as determined using the stop signal task performance in 6–14-year-old children. Our results showed that better inhibitory performance was associated with a thinner cortex in the left medial orbitofrontal cortex and larger surface area in the left caudal anterior cingulate, beyond what could be explained by age and gender alone. These findings demonstrate that the anatomical variability within the developing brain crucially influences the behavioral performance within inhibitory control and that it is critical to consider different anatomical measures when aiming to understand the role of this variability in human development.

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### CRediT authorship contribution statement

**Jan Kujala:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Formal analysis, Conceptualization. **Sanna-mari Matveinen:** Writing – review & editing, Formal analysis, Conceptualization. **Sam van Bijnen:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Tiina Parviainen:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.



## Data availability

Data will be made available on request.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandc.2024.106220>.

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