Nice traits or nasty states : dispositional and situational correlates of prosocial and antisocial behavior in childhood

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Chapter 5

Neuroanatomical correlates of donating behavior in middle childhood

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Abstract

The neurobiological correlates of prosocial behavior are largely unknown. We examined brain structure and functional connectivity correlates of donating to a charity, a specific, costly, form of prosocial behavior. In 163 children, donating was measured using a promotional clip for a charity including a call for donations. Children could decide privately whether and how much they wanted to donate from money they had received earlier. Whole brain structural MRI scans were obtained to study associations between cortical thickness and donating behavior. In addition, resting state functional MRI scans were obtained to study whole brain functional connectivity and to examine functional connectivity between regions identified using structural MRI. In the lateral orbitofrontal cortex/pars orbitalis and pre-/postcentral cortex, a thicker cortex was associated with higher donations. Functional connectivity with these regions was not associated with donating behavior. These results suggest that donating behavior is not only situationally driven, but is also related to brain morphology. The absence of functional connectivity between the clusters that was associated with donating behavior might imply that these cortical thickness clusters are involved in different underlying mechanisms of donating.

Introduction

Prosocial behavior is voluntary behavior intended to benefit another individual (Eisenberg, Fabes, & Spinrad, 2007), and can already be observed in young children (Warneken & Tomasello, 2006). While prosocial behavior is often assumed to be situationally driven (e.g. Van IJzendoorn, Bakermans-Kranenburg, Pannebakker, & Out, 2010), several studies showed an association between brain morphology and prosocial behavior (e.g. Thijssen et al., 2015), which may indicate that variation in prosocial behavior is also (partially) inherent to individuals. As distinct neurobiological mechanisms might underlie different types of prosocial behavior, differentiating between the various types of prosocial behavior is important (Paulus, 2014; Paulus, 2015). Therefore, the current study focuses on the neurobiological correlates of a specific, costly type of observed prosocial behavior: donating to a charity. We will focus on middle childhood, as children this age have a well-developed concept of the value of money (Berti & Bombi, 1981) and the neurobiological correlates underlying donating behavior in children are largely unknown.

Although prosocial behavior can be observed in children as young as 18 months old (Warneken & Tomasello, 2006), to our knowledge only two studies examined neurobiological correlates of prosocial behavior in children. A thicker cortex in the left superior frontal and rostral middle frontal cortex has been shown to be associated with more parent-reported prosocial behavior in typically developing 6-9-year-old children, whereas a smaller bifrontal diameter in preterm infants at term equivalent postmenstrual age (37-43 weeks) was related to lower levels of parent-reported prosocial behavior at age 5 (Rogers et al., 2012; Thijssen et al., 2015). These studies focused on parental reports of child prosocial behavior, covering the broad range of helpful, empathic, costly and non-costly prosocial behaviors. However, various types of child prosocial behavior can be distinguished, such as helping, sharing, donating, and comforting (e.g. Dunfield, Kuhlmeier, O'Connell, & Kelley, 2011; Warneken & Tomasello, 2009). It has been suggested that such distinct types of prosocial behavior have different underlying social-cognitive mechanisms which are reflected in distinct neurobiological correlates (Dunfield & Kuhlmeier, 2013; Paulus, 2014; Paulus, Kühn-Popp, Licate, Sodian, & Meinhardt, 2013). In the adult literature on the neurobiological correlates of prosocial behavior, an important distinction has been made between non-costly types of prosocial behavior (e.g. Masten, Eisenberger, Pfeifer, & Dapretto, 2010; Masten, Morelli, & Eisenberger, 2011) and costly prosocial behavior (e.g. Moll et al., 2006). Costly prosocial behavior is thought to be a predictor of consistent altruistic behavior, whereas non-costly donations are not (Gneezy, Imas, Brown, Nelson, & Norton, 2012). Donating to a charity represents a costly type of prosocial behavior. While prosocial behavior can be self-serving (Batson & Shaw, 1991), donating to a charity can be considered altruistic, since no compensation or benefit in return is expected (Van IJzendoorn et al., 2010). It is thought to result from higher levels of perspective taking, empathic concern, and moral reasoning (Brehm, Powell, & Coke, 1984; Eisenberg & Shell, 1986; Fishman, 2006; Verhaert & Van den Poel, 2011).

Research on the neurobiological correlates of donating behavior has mainly focused on functional magnetic resonance imaging (fMRI) studies in adults, and to date have mainly shown associations with increased activity in prefrontal brain regions. For example, a monetary donation to a family member was associated with increased brain activity in the dorsolateral prefrontal cortex (DLPFC) and dorsomedial prefrontal cortex (DMPFC) (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011). Others found a positive association between activation of the DMPFC during a social judgment task and later donating (Wyatz, Zaki, & Mitchell, 2012). Activity in the anterior prefrontal cortex during costly donating was associated with engagement in real-life charitable activities (Moll et al., 2006). Increased activity during donating was also found in reward areas of the brain such as the ventral striatum and the nucleus accumbens (Harbaugh, Mayr, & Burghart, 2007; Kuss et al., 2013; Moll et al., 2006).

While studies on brain activity patterns during donating are informative on the function of certain brain areas, studies on brain morphology may help to understand the long-term neurobiological associations of donating behavior. Studies on brain morphology are especially interesting since prosocial behavior is thought to be at least partly situationally determined (e.g. Van IJzendoorn et al., 2010). While differences in brain activity associated with donating do not exclude the possibility of situational morality, differences in brain morphology might indicate that donating behavior is not only situationally determined but also (partially) inherent to the child itself. Several studies indeed show that brain structure is associated with donating behavior in adults. For example, grey matter volume in the temporo-parietal junction was positively associated with the amount of money given to another person, whereas lesions in the ventromedial prefrontal cortex were negatively associated with monetary donations (Krajbich, Adolphs, Tranel, Denburg, & Camerer, 2009; Morishima, Schunk, Bruhin, Ruff, & Fehr, 2012).

To the best of our knowledge, no study to date has examined the neurobiological correlates of costly prosocial behavior such as donating in children. To study whether variance in donating behavior is not only situationally driven, but also has a neuroanatomical component, we examined brain morphology, more specifically cortical thickness, in relation to donating behavior in middle childhood. Furthermore, we utilized resting state fMRI to examine whether functional connectivity with clusters identified using structural MRI was associated with donating behavior and whether the structural clusters share a functional organization related to donating behavior. Such analysis might shed light on a network of brain areas involved in donating behavior and might also provide more insight into whether brain areas identified in the structural analyses work in cooperation when it involves donating behavior. We conducted a hypothesis-free whole-brain analysis of structural MRI data, and we used the resulting clusters for the resting state fMRI analyses. Gender differences in prosocial behavior (Ladd & Profilet, 1996), cortical thickness (Luders et al., 2006), and functional connectivity (Tomasi & Volkow, 2012) have been reported. Therefore, we test a priori whether results are similar for boys and girls.

Methods

Setting

The current study is embedded within the Generation R Study, a population-based prospective cohort from early fetal life onwards in Rotterdam, the Netherlands (Jaddoe et al., 2012; Tiemeier et al., 2012). All mothers who had a delivery date between April 2002 and January 2006 and who were resident in Rotterdam were invited to participate. At age 8, a subsample participated in detailed measures on (f)MRI, neuropsychological, and behavioral functioning. The study was approved by the Medical Ethics Committee of the Erasmus Medical Centre in Rotterdam. Written informed consent was obtained from all adult participants.

Study population

In order to ensure the sample contained sufficient variation in prosocial behavior, three groups of children were recruited from the larger Generation R cohort: highly aggressive, highly prosocial, and typical children. These selections were based on parental reports on the aggressive behavior scale of the Child Behavior Checklist/1½–5 (CBCL, Achenbach & Rescorla, 2000) and the prosocial scale of the Strengths and Difficulties Questionnaire (SDQ, Goodman, 1997). Trajectories of aggressive behavior were distinguished for children of Dutch origin who had at least two CBCL aggression scores available at 1.5, 3, and/or 6 years of age. A three-trajectory solution was selected as optimal, comprising a high, intermediate, and low aggression trajectory (Wildeboer et al., 2015). Children in the high aggression trajectory were eligible for the highly aggressive group. Children in the lowest aggression trajectory with high prosocial SDQ scores (14 or 15, potential range 5-15) were eligible for the high prosocial group. Children in either the low aggression trajectory with a prosocial score < 14 or in the intermediate aggression trajectory were considered eligible for the typical group. This resulted in a total sample of 291 children who were invited to take part in the current study.

Fifty-nine children and/or their parents refused to participate. Two hundred thirty-two children visited our research center, 43 of whom had no (f)MRI data because of time constraints, because they did not feel at ease to go into the scanner, or due to technical problems with the scanner. For the remaining 189 children, an MRI T_1-weighted scan was obtained. For 18 children, data quality was insufficient. Another seven children had missing data on the donating task, because the child was still busy donating when the researcher entered the room (*n* = 3), due to technical difficulties (*n* = 2), misunderstanding of the task (*n* = 1), or because their parent did not want a financial reward for the child (*n* = 1). One child had an IQ score < 70 (IQ = 56) and was therefore excluded. This resulted in a final sample of 163 children, with 58 children in the aggressive, 50 in the prosocial and 55 children in the typical group. See **TABLE 5.1** for sample characteristics. Children who were included in the structural analyses (*n* =163) did not differ from the eligible but non-participating or excluded children (*n* = 128) on gender, age, IQ, maternal education, family income, parity, or handedness. Data on resting state fMRI was missing for 14 children, five children were excluded because of excessive movement (described below) and 14 children were excluded because of registration (spatial normalization) problems. This resulted in a sample of 130 children who were eligible for the resting state fMRI analyses.

TABLE 5.1
Sample characteristics

Child characteristics	*M*(*SD*/range) / No. (%)	Family characteristics	*M*(*SD*/category) / No. (%)
Gender, no. girls (%)	87 (53)	Education mother, no. (%) higher	128 (79)
Age MRI, *M*(*SD*)	8.62 (0.75)	Income, *M* category, €	4,000-4,800
No. donated €0.20 coins, *M*(*SD*)		Parity, *M*(*SD*)	1.13 (0.66)
Without probe	7.07 (6.55)		
With probe	9.60 (7.01)		
Trajectory group			
Prosocial, no. (%)	50 (31)		
Aggressive, no. (%)	58 (36)		
Typical, no. (%)	55 (34)		
IQ, *M*(range)	106.13 (70-135)		
Handedness, no. right (%)	146 (90)		

N = 163

Measures

Donating behavior. Donating behavior was measured using an adapted version of the donating task by Van IJzendoorn et al. (2010) when the children were on average 8.59 years of age (*SD* = 0.75). Children received 20 coins of 20 eurocents (€4.00) prior to the start of the task and in the absence of their parent. It was made explicit that they received the money because of their participation in previous tasks. Subsequently they were left alone and watched a short UNICEF movie about a girl in Bangladesh who had to work in a stone pit and therefore could not go to school. The movie was presented as a means to raise money to help the girl go to school. When the movie ended, the children were asked by a voice-over and by a text on the computer screen whether they wanted to donate money to the charity via a money box that was placed in front of them. The money box contained several other coins, to enhance the credibility. Though not the focus of the current study, for a random half of the children a video-fragment followed after the movie that showed a probe of a same-sex peer in the same research setting donating money to the charity. Children were left alone for the duration of the movie and for the 30 seconds immediately following the movie.

The amount of donated money was counted by the experimenter after the session, in absence of the child. At the end of the study, the total amount of donated money was transferred to UNICEF.

Money donations were not normally distributed, but showed multiple peaks in the distribution. Therefore we distinguished four categories: donated nothing (0 coins; $n = 27$), donated less than half (1-9 coins; $n = 76$), donated half or more than half (10-19 coins; $n = 34$), donated everything (20 coins; $n = 26$).

Covariates. Gender, age at MRI scanning, version of the donating task and IQ were included in all analyses as covariates. IQ was assessed at age 6 using Mosaics and Categories, two subtests from the Snijders-Oomen Non-verbal Intelligence Test – Revised (Tellegen, Winkel, Wijnberg-Williams, & Laros, 2005). Other covariates (educational level of the mother, income, parity, total brain volume, and handedness) were included when they generated a 5% change in predictor effect estimate. Data on educational level of the mother was assessed when the children were 6 years of age using a questionnaire, and missing data were replaced by data from an earlier assessment. Educational level was divided into the categories only secondary and higher education. Income and parity were assessed using a questionnaire at age 6. In 11 cases, data on income was missing. For four children, missing values could be replaced by an earlier measure of income (at birth). In the remaining seven children, missing values were replaced by the mean income category (€4,000-4,800 per month). Due to moderate skewness, this variable was square root transformed and reflected to approach normality (Tabachnik & Fidell, 2007). Data on parity was missing for six children. Missing values were replaced by an earlier measure of parity (at birth). Total brain volume (TBV) was measured at the same time as cortical thickness, using a T_1-weighted scan (see below). Handedness was measured after the scanning session using the Edinburgh Handedness Inventory (Oldfield, 1971).

MR-Image acquisition. An extensive description of the (f)MRI data collection procedure is given elsewhere (White et al., 2013). In brief, before being scanned, children were familiarized with the scan environment in a mock scanning session. MRI data collection took place on a 3 Tesla scanner (General Electric Discovery MR750, Milwaukee, MI, USA) using an 8-channel head coil for signal reception. T_1-weighted inversion recovery fast spoiled gradient recalled (IR-FSPGR) sequence was obtained with the following parameters:

TR = 10.3 ms, TE = 4.2 ms, TI = 350 ms, NEX = 1, flip angle = 16°, readout bandwidth = 20.8 kHz, matrix 256 × 256, imaging acceleration factor of 2, and an isotropic resolution of 0.9 × 0.9 × 0.9 mm^3.

Echo planar imaging was used for the resting state fMRI session with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 85°, matrix = 64 x 64, FOV = 230 mm x 230 mm, slice thickness = 4 mm. A total of 160 volumes (acquisition time = 5min 20 seconds) were collected for the functional connectivity analyses, which has been shown to have adequate time to provide stable resting-state networks (White et al., 2014). During the structural MRI acquisition, children were allowed to watch a movie or listen to music. For the resting state fMRI scan, children were asked to keep their eyes closed and not to think about anything in particular.

Image processing

Preprocessing structural data. *Cortical reconstruction and volumetric segmentation was* performed with the Freesurfer image analysis suite (http://surfer.nmr.mgh.harvard.edu/). The technical details of these procedures are described in prior publications (Dale, Fischl, & Sereno, 1999; Jovichich et al., 2006; Reuter, Schmansky, Rosas, & Fischl, 2012). Briefly, this process included the removal of non-brain tissue, automated Talairach transformation into standard space, intensity normalization, tessellation of the gray/white matter boundary, automated topology correction, and surface deformation. Once the cortical models were complete, the images underwent surface inflation (Fischl, Sereno, & Dale, 1999), registration to a spherical atlas (Fischl, Sereno, Tootell, & Dale, 1999), and the parcellation of the cerebral cortex into units based on gyral and sulcal structure (Desikan et al., 2006). Cortical thickness was calculated as the closest distance from the gray/white boundary to the gray/CSF boundary at each vertex on the tessellated surface (Fischl & Dale, 2000). The thickness map was smoothed with a 10 mm full-width half-maximum Gaussian kernel prior to the surface based analyses. Several studies using Freesurfer in typical and atypical developing school-age children are available (El Marroun et al., 2014; Juuhl-Langseth et al., 2012). Cortical segmentation of the anterior part of the temporal lobes in Freesurfer can be unreliable where small regions of grey matter are excluded from the cortical thickness measure. This is a problem that has been previously reported by a number of users of the software. As the cortical thickness in this region is unreliable, any findings in this region of the brain will be ignored.

Preprocessing resting state fMRI data. Resting state fMRI data were preprocessed using a combination of tools from the Analysis of Functional NeuroImages package (AFNI) (Cox, 1996), the Functional MRI of the Brain Software Library (FSL) (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012), and in-house software written in Python. Preprocessing of the resting state fMRI included slice-timing correction, motion correction, removing the first four volumes, and applying a high-pass temporal filter at a frequency of 0.01Hz. Next, the six motion correction parameters, the mean white matter signal, and mean cerebral spinal fluid (CSF) signal were regressed out of each voxel's time course (Fox, Zhang, Snyder, & Raichle, 2009). Finally, in order to further ameliorate the impact of motion, the FSL motion outlier tool was used to compute the "DVARS" metric (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012).

Volumes which were flagged as having increased motion were scrubbed from the time series data (Power et al., 2012). Even with the scrubbing procedure, data severely corrupted by motion are not suitable for analysis and thus any subjects with greater than 0.5 mm relative root mean square motion were excluded altogether. Using a two-step approach, resting state fMRI datasets were then aligned to a study specific child template created according to the method described by (Muetzel et al., *in press*). For registration to the template, the resting state fMRI datasets were first aligned to their respective T_1-weighted image, using a 6 degrees of freedom linear transformation. Then, the T_1-weighted image was aligned to the child template using a 12 degrees of freedom affine transformation.

Image quality

The rating of the structural MR-image quality involved two steps. First, raw images were visually checked at the scan site for movement or other artifacts. Image quality was rated on a 6-point scale (usable, poor, fair, good, very good, excellent). Second, after the image was processed through the Freesurfer pipeline, a visual inspection of the segmentation quality took place and all images were rated on a 7-point scale (not reconstructed, poor, fair, sufficient, good, very good, excellent). Images rated as unusable or poor at the scan site, images that could not be processed by Freesurfer, and images with a poor segmentation quality were excluded from the analyses. For the resting state fMRI images, the subjects with major registration problems, excessive motion, or incomplete data were excluded.

Data analysis

Chi-square tests, *t*-tests, and analysis of variance were used for non-response analyses and analyses on demographic characteristics of the sample. A data-driven vertex-wise GLM analysis of cortical thickness and donatingbehavior was performed across the entire cortex using Freesurfer's Qdec (www.surfer.nmr.mgh.harvard.edu). Age, gender, IQ, and version of the donating task were used as covariates in this whole-brain surface-based analysis. Monte Carlo Null-Z Simulation analyses using 10,000 iterations ($p < .05$) was used to correct for the effect of multiple comparisons. In addition, a moderation effect of gender on the relation between cortical thickness and donating was tested in Qdec. For significant clusters, mean cortical thickness was extracted for each participant and exported to SPSS 21.0. Then, linear regression models including additional covariates were run to further investigate the association between donating behavior and cortical thickness.

To co-register cortical thickness clusters with the resting state data and obtain region-specific time-series of the clusters, the surface-based cluster from Freesurfer was first converted into a 3D nifti volume for each individual. The Freesurfer template brain was aligned to the study specific child template. The resulting transformation matrix was applied to the cluster volume, resulting in the morphologically defined clusters being coregistred to all functional datasets. Whole brain functional connectivity of the cluster was assessed with FSL FEAT (FMRI Expert Analysis Tool) in FSL (FMRIB's Software Libray; Smith et al., 2004), using general linear model (GLM) at the single-subject level. The time-series of the cluster (obtained using the FSL tool fslmeants) was used as the design matrix without convolution with a HRF. This resulted in subject-level, whole-brain maps representing the connectivity between the morphological clusters and the rest of the brain. These whole-brain, subject-level maps were then supplied to higher-level analyses to test for group differences in connectivity using FSL's FLAME I module (FMRIB's local analysis of mixed effects). In a similar fashion we tested whether there is any evidence for a gender specific association between donating behavior and whole brain functional connectivity per cluster. The statistical maps were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p < .05$. An ANCOVA design was utilized, with donating behavior as the independent variable and analyses were adjusted for age, gender, IQ, and version of the donating task. All variables were centered.

In case we observed associations between donating and several cortical thickness clusters, functional connectivity between these clusters was computed using the average correlation between the time-series of one of the clusters (the seed cluster) and the voxels of the other cluster(s) in FSL's Featquery. The resulting mean z-scores were used as a predictor of donating behavior in linear regression models including age, gender, IQ, and version of the donating task as covariates. We tested the change in predictor effect estimate for the same covariates as selected for the structural analyses (except TBV) and included those covariates that caused ≥ 5% change.

Results

Univariate associations

We tested whether the amount of donated money was dependent on (prosocial, antisocial, or typical) group membership and version of the task (with or without probe). The three groups did not differ on the amount of donated coins, $F(2, 160) = 0.39$, $p = .676$, partial $\eta^2 = .01$. Therefore, group membership was not taken into account in further analyses. However, children who saw a same-sex peer donating money to the charity donated more coins than children who did not watch the probe, $t(161) = -2.50$, $p = .013$, Cohen's $d = -0.39$. To control for this difference, we included the version of the donating task as a confounder in further analyses.

Association between cortical thicknessand donating behavior

Analyses in Qdec revealed three significant clusters in the right hemisphere after Monte Carlo correction for multiple testing (***FIGURE* 5.1**). The first cluster was located in regions overlapping with the lateral orbitofrontal cortex (lOFC) and pars orbitalis. The second cluster covered parts of the precentral and postcentral cortex. For cluster statistics and coordinates see **TABLE 5.2**. An additional cluster was found in the anterior part of the temporal lobe. The results of this cluster are however not reported, because of concerns with the reliability in the measurement (see Image processing). Gender did not moderate the relation between cortical thickness and donating behavior. Correlations between all variables in the models, including both clusters, are reported in **TABLE 5.3**.

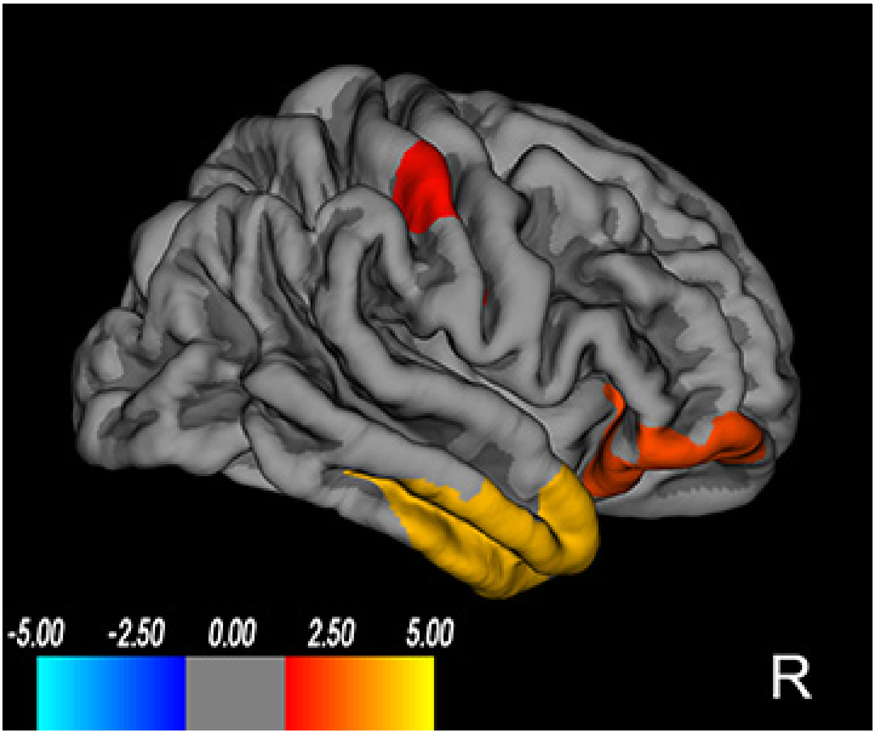

FIGURE 5.1
Cortical thickness clusters in the right hemisphere associated with donating, corrected for age, gender, IQ, and version of the donating task and Monte Carlo correction for multiple testing ($p < .05$)*. Colors represent – log10 p-value.* R = *right hemisphere.* N = 163.

TABLE 5.2
Cortical Thickness Clusters Related to Donating Behavior

Cluster	Cluster size (mm2)	Talairach coordinates			No. of vertices within cluster	Clusterwise *p*-value
		TalX	TalY	TalZ		
lOFC/pars orbitalis (RH)	1229.08	33.2	51.0	-11.6	1976	.0040
Pre-/postcentral (RH)	913.78	46.3	-14.1	32.0	2252	.0313

N = 163
Note. Analyses were corrected for age, gender, IQ, and version of the donating task. An additional cluster was found in the anterior part of the temporal lobe. The results of this cluster are however not reported due to reasons mentioned in the Methods section.

To control for the effect of potential confounding covariates and to estimate the effect size of each cluster, we performed linear regression analyses in SPSS 21.0, predicting donating behavior from the two clusters in separate models. The baseline adjusted analysis (adjusted for age, gender, IQ, version of the donating task) revealed an association between cortical thickness in the lOFC/pars orbitalis cluster and donating,

TABLE 5.3
Correlations Between Variables in the Cortical Thickness Model

	1.[a]	2.	3.	4.	5.	6.
1. Donating[a]	-					
2. lOFC/pars orbitalis	.28***					
3. Pre-/postcentral	.34***	.32***				
4. Age	.14	-.06	-.05			
5. Gender[b]	.04	.03	.10	-.03		
6. IQ	.04	-.08	.04	-.07	-.04	
7. Total brain volume	.14	.27**	.09	.07	-.37***	.20*

$N = 163$
Note. Pearson and point-biseral correlations were used in case of two continuous or one continuous and one dichotomous variable respectively. lOFC = lateral orbitofrontal cortex.
[a] Partial correlations: controlled for version of the donating task
[b] Gender is coded as 0 (boy) and 1 (girl).
$^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

$B = 1.14$ (95% CI 0.57-1.71), $\beta = .30$, $p < .001$. The association between cortical thickness in the lOFC/pars orbitalis cluster and donating remained comparable in size, $B = 1.07$ (95% CI 0.47-1.68), $\beta = .34$, $p = .001$, after additionally including total brain volume as a covariate (no other covariate caused an effect estimate change ≥ 5%). The baseline adjusted analysis (adjusted for age, gender, IQ, version of the donating task) also revealed an association between cortical thickness in the pre-/postcentral cluster and donating, $B = 1.65$ (95% CI 0.95-2.36), $\beta = .34$, $p < .001$. None of the covariates accounted for a 5% change in the predictor effect estimate. Version of the donating task did not moderate the relation between donating and cortical thickness of the two clusters.

Association between resting state, functional connectivity and donating behavior

Due to more pronounced susceptibility artifacts in some of the children, the lOFC/pars orbitalis cluster extracted from the cortical thickness analysis did not completely overlap with the resting state image. Therefore, we excluded all children with < 90% overlapping data between the FreeSurfer based cluster and their mean resting state fMRI image ($n = 4$), resulting in a final sample of 126 children for the resting state analysis. To correct for differences in the amount of overlap, we included the percentage of overlap (range 90%-100%) as a covariate in all models.

There was no association between donating behavior and resting state functional connectivity of the lOFC/pars orbitalis cluster to any region of the brain, corrected for age, gender, IQ, version of the donating task, and percentage overlap for the lOFC/pars orbitalis cluster. Also, the pre-/postcentral cluster did not show resting state functional connectivity to any region of the brain associated with donating behavior, corrected for age, gender, IQ, and version of the donating task. Gender did not moderate these results. The partial correlation between the connectivity of the two clusters and donating was $R = .06$, $p = .503$, corrected for version of the donating task. In the baseline adjusted hierarchical regression analysis (adjusted for age, gender, IQ, version of the donating task, and percentage overlap lOFC/pars orbitalis cluster) connectivity between the two clusters and donating behavior were not associated, $B = 0.03$ (95% CI -0.06 – 0.12), $\beta = .05$, $p = .554$. Education of the mother, income, and handedness affected the effect estimate ≥ 5% and were therefore included in the model. Again, no effect of connectivity between the two clusters on donating behavior emerged, $B = 0.03$ (95% CI -0.06 – 0.12), $\beta = .06$, $p = .496$. Gender did not moderate the relation between connectivity of the two clusters and donating.

Discussion

The current study examined the neurobiological correlates of donating behavior in middle childhood. A thicker cortex in a cluster covering regions of the right lateral orbitofrontal cortex and pars orbitalis and in a cluster comprising parts of the right pre- and postcentral cortex was related to higher donations. No gender differences in the association between cortical thickness and donating behavior were found. Whole brain resting state functional connectivity with the lOFC/pars orbitalis and the pre-/postcentral cluster was not associated with donating behavior. Furthermore, resting state functional connectivity between these two clusters was not associated with donating behavior. Lastly, there was no moderating effect of gender.

The current study focused on donating behavior, an altruistic type of prosocial behavior as one has to give up something without expecting anything in return. While several studies examined the association between brain function and donating, we are the first to show that variance in children's donating behavior is associated to a measure of brain morphology, namely cortical thickness. Several studies report donating behavior to be largely influenced by situational factors (e.g. Van IJzendoorn et al., 2010; Van IJzendoorn & Bakermans-Kranenburg, 2014), the current results however suggest that part of the variance in donating behavior can be explained by characteristics inherent to the child. This is in line with the finding that there is consistency to costly prosocial behavior (Gneezy et al., 2012).

The presence of neuroanatomical correlates of donating behavior is in line with a study on a partly overlapping sample, showing an association between cortical thickness and the broad construct of prosocial behavior as measured by parent-reports. In a frontal cluster covering parts of the left superior frontal and rostral middle frontal cortex, a thicker cortex was associated with higher levels of prosocial behavior (Thijssen et al., 2015). As this cluster does not overlap with the current results, the findings suggest that different types of prosocial behavior might have distinct neurobiological correlates. This is consistent with a study in infants showing distinct neural activation patterns for specific types of prosocial behaviors (helping and comforting) (Paulus et al., 2013).

In the current study we found no association in resting state functional connectivity between the two morphological clusters and donating behavior, suggesting that these clusters do not share a functional organization related to donating behavior. Independent mechanisms seem to play a role in donating to a charity. Further, we did not find an association between donating behavior and resting state functional connectivity of the two clusters with the rest of the brain. As donating to a charity is a complex task, possibly involving multiple cognitive and affective abilities (e.g. Aguilar-Pardo, Martínez-Arias, & Colmenares, 2013; Krevans & Gibbs, 1996), the lack of an association between our task and resting state functional connectivity between these clusters might suggest that these clusters represent different underlying mechanisms of donating behavior, which do not work in close cooperation when it involves donating. The lack of connectivity related to donating behavior could also be due to the fact that we had to limit our resting state fMRI analyses to the clusters emerging in our structural analyses, due to limited statistical power. As a result, we may have missed connections between brain regions for which connectivity might play a role in donating behavior.

Previous studies, mainly on task-based brain activity, reported on the lOFC/ pars orbitalis and the pre-/postcentral to be involved in several types of emotional and social behavior and cognition, which might reflect the different mechanisms underlying donating behavior. Prior work has shown that activity in the lOFC was associated with participants withholding donations because they felt the cause was unjust (Moll et al., 2006). Furthermore, the (l)OFC has been implicated in the processing of rewards, such as money (Izuma, Saito, & Sadato, 2008; Kringelbach, 2005; Sescousse, Redouté, & Dreher, 2010) and processing threats of punishment (Kringelbach & Rolls, 2004; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). Such activity is suggested to lead to changes in emotional and social behavior (O'Doherty et al., 2001). Activity in the lOFC was also found to prevent involvement in inappropriate behavior (Berthoz, Armony, Blair & Dolan, 2002), and adults with damage to the OFC lack the awareness of social norm violation (Beer, John, Scabini, & Knight, 2006).

The pars orbitalis, also part of the prefrontal cluster, has been associated with empathy. Intentionally and passively empathizing increased brain activity in this region, as compared to a control (cognitive load) condition (Rameson, Morelli, & Lieberman, 2012). Further, the pars orbitalis is part of a network associated with empathy for pain experienced by others (Lamm, Decety, & Singer, 2011). Moreover, the pars orbitalis is involved in decisions about moral dilemmas, and in interpersonal guilt after causing harm to another person (Majdandžić et al., 2012; Yu, Hu, Hu, & Zhou, 2014).

An association between brain activity and empathy, as well as mentalizing, was also found for the regions comprising our second cluster, the pre- and postcentral cortex (Decety, Michalska, & Akitsuki, 2008; Lombardo et al., 2009). More specifically, the precentral cortex was found to be associated with affective empathy, such as feeling sympathy, and the postcentral cortex to cognitive empathy, such as perspective taking (Hooker, Verosky, Germine, Knight, & D'Esposito, 2010). The pre- and postcentral cortex are also involved in emotion processing and self-reported social skills (Ferri et al., 2013; Lawrence et al., 2006; Ruby & Decety, 2004). The involvement of these brain areas in social behaviors and cognitions is thought to be related to the presence of the mirror neuron system in these regions (e.g. Beyer, Münte, & Krämer, 2014). Mirror neurons, involved in the understanding of actions of others, are found in the pre- and postcentral region (Dushanova & Donoghue, 2010; Rizzolatti & Craighero, 2004). Lastly, the precentral gyrus was found to be active during costly donations in adults (Telzer, Fuligni, Lieberman, & Galván, 2013).

We found cortical thickness clusters in the right hemisphere related to donating behavior. The fact that we did not find clusters in the left hemisphere does not imply that similar regions on the left side are not involved in donating behavior. For example, for the OFC it was not the hemispheric distinction, but rather the lateral and medial areas of the OFC that showed differential effects in a study on reward and punishment (O'Doherty et al., 2001). In larger samples, similar brain areas in the left hemisphere might be identified. Furthermore, we did not find an effect of gender on the association between cortical thickness and donating behavior, whereas gender moderated the association between cortical thickness and parent-reported prosocial behavior (Thijssen et al., 2015). This discrepancy might be due to the different measures and types of prosocial behavior involved, or to the smaller sample size of the present study. Moreover, there was no association between gender and donating behavior (partial $R = .04$, $p = .601$) in the current study.

Several limitations should be mentioned. As we studied donating behavior and structural brain measures at the same time, we cannot infer any causal relation between these constructs and the direction of effects remains uncertain. While we suggest that brain morphology might influence donating behavior of the child, the reverse effect cannot be excluded. However, the current results provide important information in light of the paucity of studies exploring the neurobiological correlates of donating behavior in children. Furthermore, we based the functional interpretation of our structural findings mostly on studies involving brain *activity* related to several behavioral and cognitive constructs. As the relation between brain function and structure is only rarely studied (Sui, Huster, Yu, Segall, & Calhoun, 2014), such interpretations remain speculative. Besides, the cortical clusters found in the current study have been associated to a variety of cognitive and behavioral outcomes and reverse inference cannot be excluded. Lastly, we identified a third cluster in the right temporal lobe for which a thicker cortex was related to higher donations, but we could not interpret this finding due to concerns about the accuracy of surface segmentation in this area. Future studies with different MRI approaches are needed to assess this region in relation to donating behavior.

In sum, we identified two clusters, covering parts of the lOFC/pars orbitalis and the pre-/postcentral cortex, in which a thicker cortex was related to children's willingness to share or even give up their well-deserved monetary resources. This indicates that donating to a charity is not only dependent upon the specifics of the situation, but also on child characteristics. The pertinent effect was found in regions that have previously been associated with social norm compliance and the processing of threats of punishment. The locations of these clusters have also been implicated in several forms of empathy and being able to understand the actions of others. As donating behavior was not associated with resting state functional connectivity between the lOFC/pars orbitalis and the pre-/postcentral cluster, these two clusters might indicate distinct underlying mechanisms of donating behavior.

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