

The neural development of prosocial behavior from childhood to adolescence

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Abstract

The transition from childhood to adolescence is marked by increasingly sophisticated social cognitive abilities that are paralleled by significant functional maturation of the brain. However, the role of social and neurobiological development in facilitating age differences in prosocial behavior remains unclear. Using a cross-sectional sample of children and adolescents ($n = 51$; 8–16 years), we examined the age-related correlates of prosocial behavior. Youth made costly and non-costly prosocial decisions to anonymous peers during a functional magnetic resonance imaging scan. Among a subsample of youth who made prosocial decisions ($n = 35$), we found quadratic age differences in neural activation that peaked in early adolescence relative to childhood and older adolescence. In particular, early adolescents showed heightened recruitment of the posterior superior temporal sulcus (pSTS), temporal pole and inferior frontal gyrus (IFG) when engaging in costly prosocial behavior at the expense of gaining a reward, whereas they evoked heightened pSTS and dorsolateral prefrontal cortex/IFG activation when engaging in costly vs non-costly forms of prosocial behavior. Given that we did not find age differences in prosocial behavior, this suggests that early adolescents show unique patterns of brain activation to inform similar levels of prosocial behavior.

Key words: prosocial behavior; pSTS; fMRI; childhood; adolescence

Introduction

Engagement in prosocial behavior, or voluntary actions intended to benefit others, is associated with a wide range of positive social and health outcomes during childhood and adolescence (e.g. Eisenberg et al., 2006). Mentalizing, or the ability to understand the mental states of oneself or others, is considered an important contributor to several types of prosocial behaviors, including giving and sharing (Eisenberg and Miller, 1987; McDonald and Messinger, 2011). Recent studies have begun to uncover the neurobiological mechanisms that promote prosocial behaviors across development (Telzer et al., 2011; van den Bos et al., 2011; Tusche et al., 2016). However, there is little convergence

from prior literature on whether the development of prosocial behavior from childhood to adolescence increases linearly (e.g. increasing from childhood to adolescence) or non-linearly (e.g. peaking in early adolescence). A better understanding of the neural correlates of prosocial decision-making may help resolve discrepancies in the behavioral research, especially given that there is significant structural (Mills et al., 2014) and functional (Burnett and Blakemore, 2009; Burnett et al., 2011; Klapwijk et al., 2013) maturation within neural circuits that support social cognition (e.g. mentalizing) and prosocial decision-making during this developmental window. Thus, the current study combined behavioral and neuroimaging methods to better interrogate age-related differences in the behavioral and neural correlates of

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prosocial behavior from childhood to adolescence. Delineating the specific age-related patterns is important in identifying potential sensitive periods in promoting other-oriented considerations and behaviors.

The developmental psychology and cognitive neuroscience literature converge on two possible patterns of prosocial development from childhood to adolescence: (i) linear increases in prosocial behavior from childhood to adolescence and (ii) non-linear differences, marked by peaks in prosocial behavior in early adolescence. One line of research has shown that early adolescents exhibit more prosocial behavior than children (Eisenberg and Fabes, 1998; Fabes et al., 1999), suggesting prosocial behavior may increase linearly with age. Linear age patterns of prosocial development suggest prosocial tendencies may develop and continue to increase from childhood to adulthood, likely due to improvements in social-cognitive skills that facilitate other-oriented considerations. Yet, another line of work has found differences even within the adolescent years, with greater prosocial tendencies observed in early adolescents compared to late adolescents (Carlo et al., 2007; Güroglu et al., 2014b; Meuwese et al., 2015; van Hoorn et al., 2016). These latter results provide initial evidence of non-linear (i.e. quadratic) age-related patterns in prosocial development, such that early adolescents engage more frequently in prosocial behaviors than children and mid-to-late adolescents. Non-linear age patterns of prosocial development suggest that early adolescence is a particularly sensitive window for prosocial development because of unique developmental processes that have yet to converge at earlier or later ages. Taken together, these data highlight the need to more clearly delineate between linear and non-linear age differences to better understand prosocial development from childhood to adolescence.

Emerging research has delineated the neural correlates involved in prosocial decision-making in youth. A network of the brain involved in mentalizing, comprising of the posterior superior temporal sulcus (pSTS), temporoparietal junction (TPJ), dorsomedial and medial prefrontal cortices (dmPFC, mPFC) and temporal pole, is correlated with youths' prosocial decisions (see Do et al., 2017 for a review; van Hoorn et al., 2016), as well as perspective taking and empathy abilities (Masten et al., 2010; Kral et al., 2017). A recent study reported age-related differences in the recruitment of the mentalizing network during prosocial decision-making (van Hoorn et al., 2016), such that early adolescents show greater dmPFC and pSTS activation when making prosocial decisions in the presence of anonymous peers compared to late adolescents (van Hoorn et al., 2016). These results support non-linear developmental patterns in the brain that peak during early adolescence, which is perhaps reflective of the ongoing maturation of social cognitive skills during this developmental window (Dumontheil et al., 2010; van den Bos et al., 2010; Overgaauw et al., 2014). Furthermore, prior work has shown that significant changes in perspective-taking abilities mediate the relation between age and prosocial behavior in children and adolescents (Güroglu et al., 2014a). Therefore, neural reactivity in regions that support social cognition may critically underlie other-focused, prosocial behavior, which changes across childhood and adolescence.

Current study

Although prior research suggests there are developmental differences in the neural correlates of prosocial decision-making, these studies have focused exclusively on either adolescents (Telzer et al., 2013, 2014; van Hoorn et al., 2016; Will

et al., 2018) or adults (Telzer et al., 2015; van der Meulen et al., 2016) and have not included child participants nor a wider age range to test for age-related associations across childhood and adolescence. In the current study, we used a cross-sectional design to examine the behavioral and neural correlates of prosocial decision-making in youth from ages 8–16 years. While there are several types of prosocial behaviors, including sharing or group cooperation (Eisenberg et al., 2006; Padilla-Walker and Carlo, 2007), we operationalized prosocial behavior as the act of giving rewards to another individual. During functional magnetic resonance imaging (fMRI), participants made two types of prosocial decisions on an experimental task: (i) give points to anonymous peers at a cost to themselves (costly prosocial behavior) or (ii) give points to anonymous peers at no cost to themselves (non-costly prosocial behavior). The first goal was to delineate the neural correlates involved in engaging in costly prosocial behavior compared to receiving rewards for oneself (i.e. keeping points for oneself) or engaging in non-costly types of prosocial behavior. The second goal was to test for both linear and quadratic age associations with prosocial behavior at the behavioral and neural level, independent of the frequency of prosocial behavior. The third goal was to examine whether neural activation to prosocial behavior predicts individual differences in the frequency of prosocial behavior, independent of age.

Methods

Participants

Fifty-six healthy children and adolescents were recruited from community advertisements. All participants were right-handed and free of MRI contraindications (e.g. braces). Five participants were excluded [$n = 1$ due to excessive motion (>2 mm in any direction), $n = 3$ due to technical errors, $n = 1$ did not complete scan]. The final sample included 51 children and adolescents between ages 8–16 years ($M = 13.55$, s.d. = 2.72; 28 females). Parent reports of children's ethnicity or race were comprised of 76.50% European American, 3.90% African American, 3.90% Asian American, 3.90% Hispanic or Latino and 11.80% Multi-ethnic. Annual family income was categorized into five bins: 10.7%, $<\$14\,999$ – $\$29\,999$; 27.7%, $\$30\,000$ – $\$59\,999$; 10.7%, $\$60\,000$ – $\$89\,999$; 31.9%, $\$90\,000$ – $\$119\,999$; and 19.2%, $\$120\,000$ – $\$150\,000+$. Parent reports of maximum educational attainment (maternal | paternal) were comprised of 3.9% | 6.4% less than high school diploma, 6.1% | 12.8% high school diploma, 20.4% | 6.4% some college, 14.3% | 12.8% associate's degree, 32.7% | 27.7% bachelor's degree, 0% | 2.1% some graduate school, 18.4% | 27.7% master's degree (M.A., M.S.) and 4.1% | 4.3% professional degree (e.g. M.D., Ph.D.). As described below, a subsample was included in the fMRI analyses of prosocial behavior, which included 35 children and adolescents between 8–16 years ($M = 13.71$, s.d. = 2.65; 20 females). There were no significant differences between the included and excluded participants for age, gender, ethnicity, annual family income or parental education. Parents and youth provided written consent and assent, respectively, in accordance with the university's Institutional Review Board guidelines.

Costly giving fMRI task

We used a costly giving task from previous work on prosocial decision-making in adolescents (Telzer et al., 2013, 2014, 2015) that was modified to be more child-appropriate. Participants

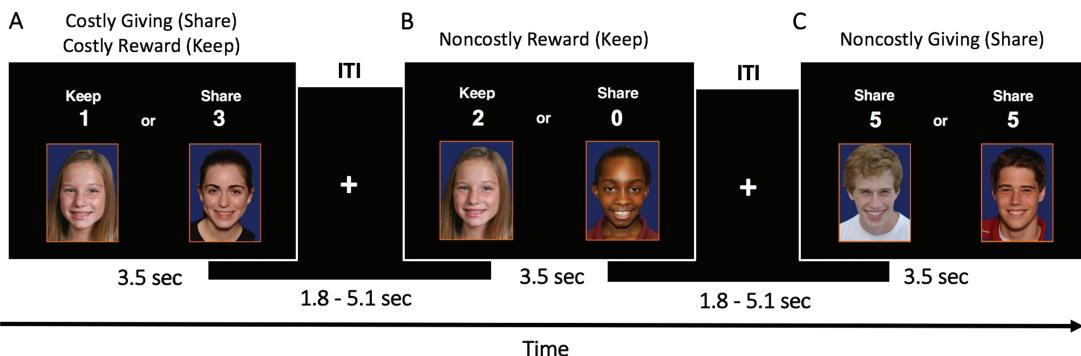


Fig. 1. Schematic representation of Costly Giving fMRI task. There were four trial types of interest based on the type of decision made on the Costly Giving fMRI task: Costly Giving, Costly Reward, Non-costly Reward and Non-costly Giving. The choice yoked to each trial type is indicated in parentheses. On Costly Giving trials, participants chose to forgo personal gains to give points to an unknown peer. On Costly Reward trials, participants chose to keep points for oneself at the expense of another peer gaining greater rewards. On Non-costly Reward trials, participants chose to keep points for oneself at no cost or benefit to another peer. On Non-costly Giving trials, participants chose between one of two unknown peers to give points to at no cost to their own gains (i.e. no option to keep points for oneself). ITI = inter-trial interval.

were informed that they would be playing a game in which their decisions would impact peers who previously participated in the study. In reality, the peers featured in the task were confederates. Participants saw pictures of the previous participants, whose pictures were from several databases (e.g. National Institute of Mental Health Child Emotional Faces Picture Set) (Egger et al., 2011) that were equally distributed by age (range: 7–17 years), gender and race (White, Black and Asian). On each trial, participants viewed two pictures of themselves and/or other peers and made decisions to 'keep' the points shown above one picture or 'share' (i.e. give) the points shown above the other picture by pressing their right or left index finger, respectively (Figure 1). To control for motor-related neural activation and heuristic responding, the location of the pictures and response options were counterbalanced on the left or right of the screen across trials. The point values associated with each decision (i.e. Keep or Share) ranged from 1–10 to create variability in responses and decrease heuristic responding. Participants were instructed that the total points kept for themselves or given to other peers during the task could be exchanged for non-monetary prizes (e.g. candy) in real life. Notably, participants were informed that the other players would not know what their decisions were. No information was provided on how the peers would receive points that were given to them during the task or if/how they would receive points that were ostensibly given to them from previous participants. Participants were not told that future participants would play the game, so reciprocity or anticipation of future earnings was not expected. Participants were not shown a running total of their own or peers' earned points.

Four trials of interest were defined based on the type of decisions that participants made on the task: Costly Giving, Costly Reward, Non-costly Giving and Non-costly Reward. On Costly Giving trials, participants gave a higher amount of points to another peer at the expense of gaining fewer points for themselves (Figure 1A). On Costly Reward trials, participants kept a lower amount of points for themselves at the expense of another person gaining more points (Figure 1A). On Non-costly Reward trials, participants kept a higher amount of points for themselves over giving zero points to a peer, thereby measuring the receipt of a personal reward when there was no benefit or cost to others (Figure 1B). On Non-costly Giving trials, participants chose between one of two peers to give points to (i.e. there was no option to keep points for themselves) (Figure 1C). Across two functional runs, participants completed 60 Costly trials (which

for analyses are divided into Costly Giving and Costly Reward based on their decisions), 30 Non-costly Giving trials and 30 Non-costly Reward trials, which were presented in a randomized order. Following previous research (Telzer et al., 2011), more costly trials were administered since responses on non-costly trials are highly consistent (i.e. participants often choose to give on Non-costly Giving trials and keep on Non-costly Reward trials) relative to costly trials, which show greater response variability and are further divided into two trials types based on their decision. The stimulus event (i.e. faces and decisions) was presented for 3.5 s followed by a jittered inter-trial interval (ITI), which displayed a fixation cross for a range of 1.8–5.1 s.

Our primary interest was examining the unique psychological and neurobiological processes associated with Costly Giving decisions, which involve a conflict between gaining a personal reward and giving a reward to another individual and thus reflect prosocial behavior motivated by more other-focused concerns. Specifically, we conducted three comparisons to delineate how Costly Giving is unique from the receipt of personal rewards or engagement in non-costly types of prosocial behavior: (i) Costly Giving > Costly Reward, (ii) Costly Giving > Non-costly Reward and (iii) Costly Giving > Non-costly Giving. First, we examined differences between Costly Giving and Costly Reward decisions, as Costly Giving decisions tend to be more difficult and altruistic than Costly Reward decisions, which instead prioritize personal gains at the expense of potential gains for others. Second, we contrasted how Costly Giving decisions differ from gaining a personal reward at no cost to others' outcomes (i.e. Non-costly Reward), which is consistent with prior work examining differences between eudaimonic, prosocial choices and hedonic, personally rewarding choices (Moll et al., 2006; Telzer, Masten et al., 2010; Telzer et al., 2011; Telzer et al., 2014). Finally, we examined differences between costly and non-costly prosocial decisions in order to isolate psychological processes related to prosocial behavior with and without an autonomous, costly component, respectively. Compared to Costly Giving decisions, Non-costly Giving decisions involve involuntarily giving to others without the option to keep rewards for oneself, thereby eliciting prosocial behavior that is neither autonomous nor self-sacrificing because outcomes do not impact one's own gains.

fMRI data acquisition and analysis

Imaging data were collected with a 3 Tesla Siemens Trio MRI scanner. The task included T2*-weighted echoplanar images

[EPI; slice thickness = 3 mm, 38 slices, repetition time (TR) = 2 s]; [echo time (TE) = 25 ms, matrix = 92 × 92, field of view (FOV) = 230 mm, voxel size = 2.5 × 2.5 × 3 mm³]. A T1*-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) scan (TR = 2.3 s, TE = 2.1 ms, FOV = 256, matrix = 192 × 192, sagittal plane, slice thickness = 1 mm, 160 slices) and a T2-weighted, matched-bandwidth (MBW), high-resolution, anatomical scan (TR = 4 s, TE = 63 ms, FOV = 230, matrix = 256 × 256, sagittal plane, slice thickness = 1 mm, 187 slices) were acquired for registration purposes. EPI and MBW scans were acquired at an oblique axial orientation in order to maximize brain coverage and reduce signal dropout.

Neuroimaging data were pre-processed and analyzed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Pre-processing included spatial realignment to correct for head motion and co-registration of all images to the high-resolution MPRAGE structural scan, which was then segmented into gray matter, white matter and cerebrospinal fluid. The normalization transformation matrices were applied to the functional and MBW structural images to transform them into standard stereotactic space as defined by the Montreal Neurological Institute (MNI) and the International Consortium for Brain Mapping. The normalized functional data were smoothed using an 8 mm full-width-at-half maximum Gaussian kernel to increase the signal-to-noise ratio. Each trial was convolved with a canonical hemodynamic response function and filtered in the temporal domain using a non-linear high-pass filter (128 s cutoff) to remove low-frequency drift across the time series. A restricted maximum likelihood algorithm with an autoregressive model order of 1 was used to estimate serial autocorrelations.

Individual level, fixed-effects analyses were conducted using the general linear model (GLM) in SPM8. The task was modeled as an event-related design, with each trial's onset defined as the presentation of the face stimuli and duration defined as the reaction time of the decision. The events of interest included (i) giving at the expense of gaining a reward (Costly Giving), (ii) gaining a reward at the expense of giving to another individual (Costly Reward), (iii) gaining a reward at no cost to another individual's gains (Non-costly Reward) and (iv) giving at no expense to one's gains (Non-costly Giving). All events were modeled with a parametric regressor [i.e. parametric modulation (PM)] to control for the magnitude of the points that could be given/kept across trials, which may reflect decisions motivated by a desire to maximize the total points awarded to whoever stood to gain the most (participant or peer confederate; i.e. utility maximization) instead of truly prosocial considerations. Thus, neural responses observed in the event of interest (e.g. Costly Giving) controlled for neural responses that tracked linear increases in utility maximization. The PM was the trial-level difference between the amount of points that could be given vs kept on Costly Giving and Costly Reward trials (range: 1–5 point difference), the amount of points that were given to another peer on Non-costly Giving trials (as points that could be given were equal between the two decisions) and the amount of points that were kept for oneself on Non-costly Reward trials (as points that could be given were always zero). Point values were mean centered within each event type for each individual. Decisions to give points when there was no benefit to a peer on Non-costly Reward trials were modeled separately as covariates of no interest and were excluded from further analyses. The rest periods and jittered ITIs were not explicitly modeled and therefore

served as an implicit baseline. Six motion parameters were modeled as regressors of no interest. Using the parameter estimates from the GLM, linear contrast images comparing each of the conditions of interest were calculated for each individual.

Individual subject contrasts were then submitted to random-effects, group-level analyses in GLMflex, which corrects for variance-covariance inequality, partitions error terms, removes outliers and sudden activation changes in the brain and analyzes all voxels containing data (http://mrtools.mgh.harvard.edu/index.php/GLM_Flex). To correct for multiple comparisons, we conducted a Monte Carlo simulation using the updated version (April 2016) of 3dFWHMx and 3dClustSim programs from the AFNI software package (Ward, 2000). We submitted the group residuals generated from GLMflex's random-effects, group-level analysis to the 3dFWHMx program to calculate the spatial group smoothness, assuming an auto-correlation function (-acf). This approach is notably similar to cluster correction methods used in SPM and FMRIB Software Library (FSL) and thus deviates from Analysis of Functional Neuroimaging (AFNI's) default method of estimating the group smoothness using the residuals from first-level analyses. We entered the estimated group smoothness parameters into the 3dClustSim program, which conducted 10,000 Monte Carlo simulations on each contrast's group-level brain mask using a voxel-wise threshold of $P < 0.001$, corresponding to $P < 0.05$, Family-Wise Error corrected, to determine the minimum cluster size for the whole brain (range: 20–23 contiguous voxels).

To investigate the neural correlates of prosocial behavior, group-level analyses were constrained to participants who had sufficient rates of prosocial decisions on the Costly Giving condition ($n = 35$). To ensure we had adequate statistical power in the individual subject GLM, 16 participants were excluded from fMRI analyses due to low rates of costly giving decisions ($n = 8$ never made a costly giving decision and $n = 8$ made <4 costly giving decisions in a single run of the task). Given that there were no demographic differences between the two sets of participants, we used this conservative exclusion criterion to ensure that there were enough trials per condition to appropriately examine the neural correlates of prosocial decision-making among youth who actually engaged in these behaviors. Subject-specific data on the frequency of prosocial decisions in the full ($n = 51$) and reduced ($n = 35$) samples are reported in [Supplementary Figure 1](#).

At the group level, the first aim was to contrast neural responses to costly prosocial behavior relative to other types of reward- or prosocial-related decisions, controlling for utility maximization. Whole-brain t-tests were conducted to examine the main effects of Costly Giving decisions against the main effects of (i) gaining a personal reward over engaging in prosocial behavior (Costly Giving > Costly Reward), (ii) gaining a personal reward at no cost or benefit to another individual (Costly Giving > Non-costly Reward) and (iii) engaging in involuntary non-costly prosocial behavior (Costly Giving > Non-costly Giving). The second aim was to delineate age-related associations in neural activation during prosocial decision-making, controlling for differences in utility maximization and the frequency of prosocial behavior. We conducted whole-brain regression analyses correlating linear and quadratic age regressors with neural activation during the Costly Giving > Costly Reward, Costly Giving > Non-costly Reward and Costly Giving > Non-costly Giving contrasts, controlling for utility maximization and frequency of Costly Giving. The linear age predictor was a linear age variable used to detect differences with increasing

Table 1. Summary of whole-brain activation during costly prosocial behavior

Anatomical region	BA	x	y	z	t	k
Costly Giving > Costly Reward^a						
None						
Costly Giving > Non-costly Reward						
None						
Costly Giving > Non-costly Giving						
L inferior temporal gyrus	37	-51	-58	-23	-4.08	32
L precuneus		0	-58	22	-4.25	26

L and R refer to left and right hemispheres; BA refers to Brodmann area of peak voxel; k refers to the number of voxels in each significant cluster; t refers to peak activation level in each cluster, such that positive values indicate greater activation to Condition A > Condition B and negative values indicate less activation to Condition A > Condition B (or greater activation to Condition B > Condition A); and x, y and z refer to MNI coordinates. fMRI results are reported at $P < 0.001$, with a corrected cluster size ranging from 20–23 contiguous voxels. ^aGiven $n = 1$ made <4 costly reward decisions in a single run of the task, group-level comparisons with Costly Reward trials were conducted in $n = 34$ from the subsample of youth who had sufficient rates of prosocial behavior on the task.

age, and the quadratic age predictor was calculated by squaring age in order to detect non-linear age differences. All regression analyses using the quadratic age predictor controlled for the linear age predictor. Finally, the third aim was to investigate whether neural activation during costly prosocial decision-making covaried with the frequency of costly prosocial behavior, above and beyond differences in utility maximization and age. We conducted whole-brain regression analyses correlating the frequency of Costly Giving with neural activation during Costly Giving > Costly Reward decisions, controlling for utility maximization and linear and quadratic age. Given the participants' highly consistent responses on non-costly trials ('Give' on Non-costly Giving trials: $M = 100\%$, s.d. = 0%; 'Keep' on Non-costly Reward trials: $M = 88.54\%$, s.d. = 21.05%), associations between the frequency of costly giving and the Costly Giving > Non-costly Giving and Costly Giving > Non-costly Reward contrasts were not expected to be of interest and thus were not analyzed. All reported fMRI results can be found on Neurovault: <https://neurovault.org/collections/ZUSAPCBB/>.

Results

Behavioral results

Descriptive statistics, including correlations between all study variables, are reported in *Supplementary Table 1*. Given participants' highly consistent responses on non-costly trials, behavioral analyses of prosocial behavior were constrained to Costly Giving and Costly Reward trials (60 total); mean-level differences in the frequency and reaction time (RT) of the other trial types are reported in the Supplementary Materials. A series of generalized linear mixed models were estimated in SAS 9.4 to investigate the relation between RT, age and gender on youths' propensity to give in the full sample ($n = 51$). Trials (Level 1; mean centered within participants) were nested within participants (Level 2; mean centered across participants), with the outcome variable defined as the binary decision to give vs keep on each trial (1 = give, 0 = keep). Likelihood ratio tests were conducted to determine whether the addition of trial- and person-level variables significantly improved the model fit (Raudenbush, 2004). All models included a random intercept and controlled for the main effect of gender (1 = female, 0 = male) and $RT \times$ gender interaction. For interpretation, unstandardized model estimates have been converted from logits to odds ratio (OR).

In Model 1, we tested the within- and between-person effect of RT on youths' propensity to give on Costly Giving and Costly Reward trials. The RT of each trial's decision (Level 1) significantly predicted youths' propensity to give ($b = 1.181$, SE = 0.103, 95% confidence intervals [CI] [0.979, 1.382]; OR = 3.257, 95% CI [2.662, 3.984]), such that slower RT on a costly trial was associated with a greater likelihood of giving. The mean RT (MRT) of each participant (Level 2) also significantly predicted youths' propensity to give ($b = 2.400$, SE = 0.798, 95% CI [0.796, 4.003]; OR = 11.023, 95% CI [2.217, 54.796]), such that an average participant with a slower average RT on costly trials showed a greater likelihood of giving. A log likelihood ratio test confirmed that the inclusion of the within- and between-person effects of RT significantly improved model fit from the null model (i.e. random intercept with no predictors), $\chi^2(2) = 151.02$, $P < 0.000$.

Next, we added the main and interaction effects of linear age (Model 2) and quadratic age (Model 3) to the generalized linear mixed model to examine whether age explained additional variance in the propensity to give above RT differences, controlling for gender. The linear and quadratic terms of age did not significantly predict the propensity to give, nor did their respective interactions with trial-level RT. There were also no main or interaction effects of gender on the propensity to give. A log likelihood ratio test indicated that the inclusion of age (linear, quadratic) and gender did not improve model fit, thus Model 1 was retained.

fMRI results

Neural activation to Costly Giving > Costly Reward decisions

Main effects. No regions showed significant differences to the Costly Giving > Costly Reward or the inverse contrast.

Age effects. There was no significant linear age effect on neural activation to Costly Giving > Costly Reward decisions or the inverse contrast (*Table 2*). There was a negative correlation between the quadratic regressor of age and several regions implicated in social processing, including the bilateral pSTS, left temporal pole, right inferior frontal gyrus (IFG) and right cuneus (*Table 2*). For descriptive purposes, we extracted parameter estimates of signal intensity from the regions that showed a quadratic age effect and plotted the patterns of activation against age. Neural activation in the pSTS, temporal pole, IFG and cuneus show an inverted U-shaped curve (*Figure 2*), such that early adolescents, compared to children and mid-adolescents, showed relatively heightened activation in these brain regions when making costly prosocial decisions vs making costly reward decisions.

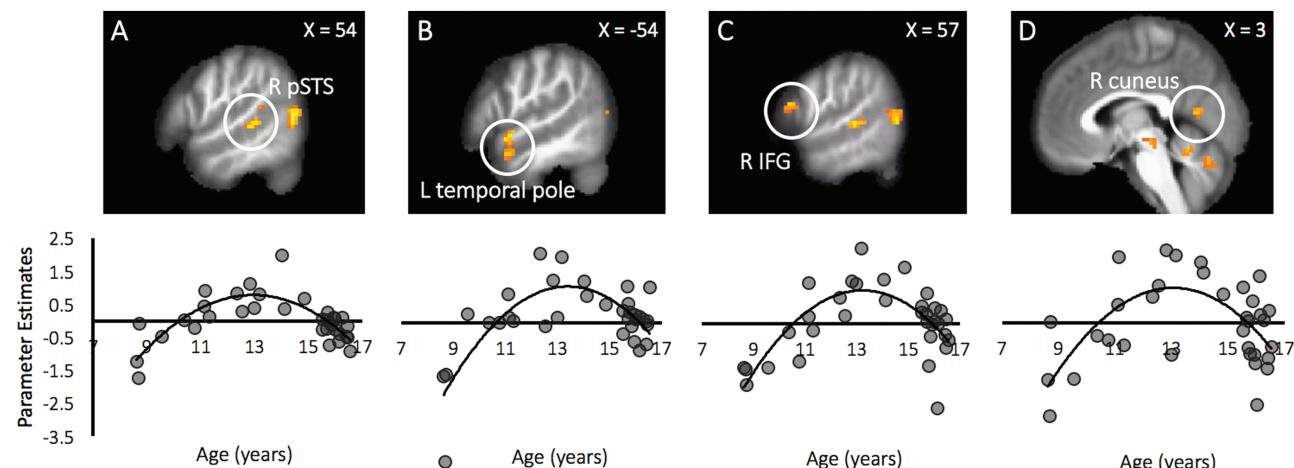


Fig. 2. Age differences in neural responses to costly giving vs costly reward decisions. There were quadratic age differences in the brain regions supporting decisions to forgo personal rewards to be prosocial to another peer from childhood to adolescence (Costly Giving > Costly Reward). Compared to children and mid-adolescents, early adolescents exhibited relatively greater activation in the (A) pSTS, (B) temporal pole, (C) IFG and (D) cuneus during costly prosocial behavior.

Neural activation to Costly Giving > Non-costly Reward decisions.

Main effects. No regions showed differences in activation during Costly Giving relative to Non-costly Reward decisions or vice versa.

Age effects. There were no linear or quadratic age differences on the neural correlates of costly giving relative to non-costly reward decisions (Table 2).

Neural activation to Costly Giving > Non-costly Giving decisions.

Main effects. Youth exhibited greater activation in the inferior temporal gyrus and precuneus during costly prosocial behavior relative to non-costly prosocial behavior (Table 1). No regions showed differences during non-costly relative to costly prosocial behavior.

Age effects. Linear age was negatively associated with activation in the dmPFC during Costly Giving > Non-costly Giving decisions (Table 2), such that there were age-related decreases in the dmPFC from childhood to adolescence during costly giving vs non-costly giving. Quadratic age was negatively correlated with activation in the bilateral pSTS and left IFG/dorsolateral prefrontal cortex (dlPFC; Table 2). For descriptive purposes, we extracted parameter estimates of signal intensity from significant brain regions during Costly Giving > Non-costly Giving and plotted the patterns of activation against age (Figure 3). Early adolescents exhibited relatively heightened activation in the pSTS and IFG/dlPFC when engaging in costly prosocial behavior compared to non-costly prosocial behavior.

Associations between neural activation to prosocial decisions and frequency of prosocial behavior.

Finally, we tested whether neural activation during costly prosocial decisions was associated with individual differences in the frequency of costly giving, independent of age or utility maximization. Greater frequency of costly giving was negatively correlated with dorsal anterior cingulate cortex (dACC) activation ($xyz = 0, 35, 19, t = -5.036, k = 45; P < 0.001$: 21 contiguous voxels) during Costly Giving > Costly Reward decisions, controlling for linear and quadratic age. For descriptive purposes, we extracted parameter estimates of signal intensity from the dACC in response to Costly Giving > Costly Reward and plotted the patterns of activation against the frequency of costly giving. Controlling for age, youth who exhibited less dACC activation

when choosing to forgo gaining personal rewards to give rewards to another individual engaged in more costly prosocial behavior on the task (Figure 4).

Discussion

The present study addressed three aims: (i) examine neurobiological differences when youth engaged in costly and non-costly forms of prosocial behaviors, (ii) elucidate the age-related correlates of prosocial decision-making from childhood to adolescence and (iii) examine associations between neural responses and the frequency of prosocial behavior, independent of age. Although there were largely no differences in neural reactivity to costly giving relative to the other decision types at the main effect level, we found quadratic age differences in the neural correlates of costly prosocial behavior, with relative peaks in activation during early adolescence compared to childhood and mid-adolescence. Not only did early adolescents exhibit greater activation in social-cognitive regions (pSTS, temporal pole, IFG) when engaging in costly prosocial behaviors over

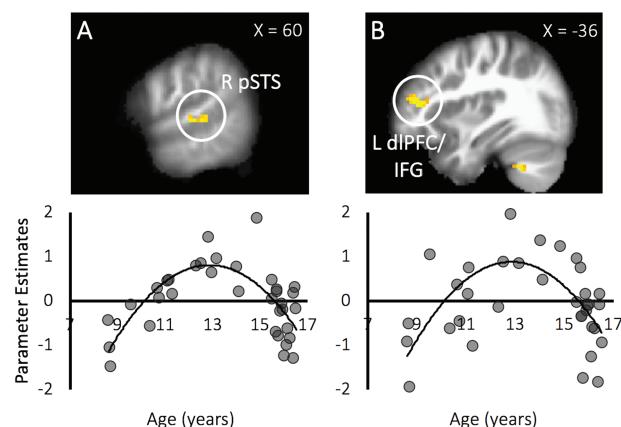


Fig. 3. Age differences in neural responses to costly vs non-costly giving decisions. There were quadratic age associations in neural reactivity to costly vs non-costly prosocial behavior that peaked during early adolescence, such that early adolescents recruited relatively greater activation in the (A) pSTS and (B) dlPFC/IFG than children and mid-adolescents.

Table 2. Linear and quadratic effects of age on the neural correlates of costly prosocial behavior

Anatomical region	BA	x	y	z	t	k
<u>Age (Linear)</u>						
Costly Giving > Costly Reward^a						
None						
Costly Giving > Non-costly Reward						
None						
Costly Giving > Non-costly Giving						
R dMPFC	9	21	56	34	-5.75	192
<u>Age² (Quadratic)</u>						
Costly Giving > Costly Reward^a						
R pSTS	21	54	-37	4	-4.97	223
L temporal pole	22	-54	5	-8	-4.97	58
R cuneus	18	3	-64	10	-4.22	27
L pSTS	39	-63	-49	10	-4.51	23
R IFG	44	57	20	16	-3.81	21
Costly Giving > Non-costly Reward						
None						
Costly Giving > Non-costly Giving						
R pSTS	21/22	63	-28	4	-4.35	51
L dlPFC/IFG	46	-36	35	13	-4.33	42
L pSTS	21/22	-51	-37	10	-4.75	32

L and R refer to left and right hemispheres; BA refers to Brodmann area of peak voxel; k refers to the number of voxels in each significant cluster; t refers to peak activation level in each cluster, such that positive values indicate a positive association between age and neural activation to Condition A > Condition B and negative values indicate a negative association between age and neural activation to Condition A > Condition B; and x, y and z refer to MNI coordinates. fMRI results are reported at $P < 0.001$, with a corrected cluster size ranging from 20–23 contiguous voxels. ^aGiven $n = 1$ made <4 costly reward decisions in a single run of the task, group-level comparisons with Costly Reward trials were conducted in $n = 34$ from the subsample of youth who had sufficient rates of prosocial behavior on the task ($n = 35$).

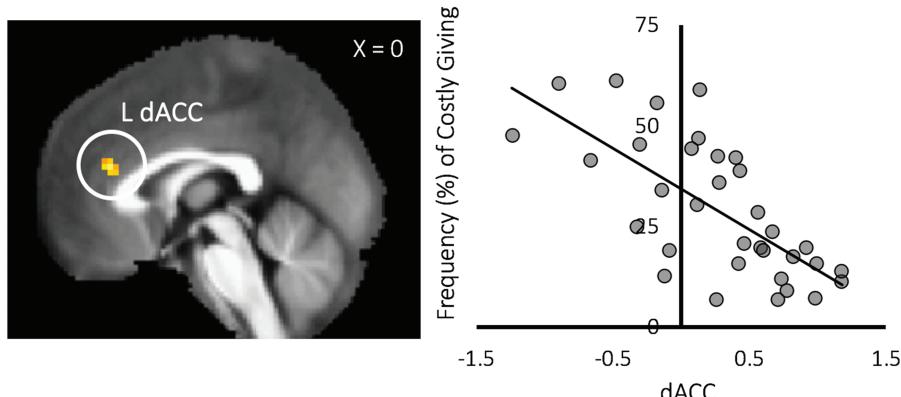


Fig. 4. Relation between frequency of costly giving and dACC activation to costly giving vs costly reward decisions. Controlling for age, participants who exhibited less activation in the dACC engaged in higher rates of costly prosocial behavior.

the receipt of costly rewards, but they also exhibited greater activation in social-cognitive (pSTS) and regulatory (IFG/dlPFC) regions when making costly relative to non-costly prosocial decisions. To our knowledge, this is the first study to investigate age-related differences in the neural correlates of prosocial decision-making across a wide developmental period spanning childhood and adolescence, providing converging evidence for quadratic age-related differences in the brain. Moreover, regardless of age, youth who exhibited less dACC reactivity during costly prosocial behaviors engaged in higher rates of costly giving, suggesting that brain regions involved in affective processing or conflict monitoring may be critically involved in youths' overall propensity to give.

Age-related correlates of prosocial behavior

Although there were no age-related differences in behavior, we found quadratic age associations in the neural correlates under-

lying costly prosocial decisions, which peaked in early adolescence relative to childhood and mid-adolescence. The frequency and MRT of costly prosocial decisions did not differ by age in the current study, which is consistent with prior experimental research on costly vs non-costly prosocial behavior in youth (Gummerum et al., 2008; Güroğlu et al., 2009; Güroğlu et al., 2014a). Despite similar rates of costly prosocial behavior across age, early adolescents make prosocial decisions differently than children and late adolescents, as evidenced by greater recruitment of the pSTS, temporal pole and IFG when engaging in costly prosocial behavior. In other words, when engaging in the same rate of prosocial behavior as their younger and older peers (and controlling for utility maximization), early adolescents demonstrate uniquely heightened activation in brain regions involved in social-cognitive and regulatory processing.

Developmental changes in social relationships and social cognition that are thought to converge during early adolescence

may contribute to non-linear patterns of sociocognitive brain responses during prosocial decision-making. Relative to childhood and mid-adolescence, early adolescence is characterized by a significant shift in the importance and amount of time spent with family members to peers, which is associated with greater sensitivity to peer evaluation and increasingly advanced social-cognitive abilities (Steinberg and Morris, 2001; Brown, 2004; Somerville et al., 2013; Blakemore and Mills, 2014). Prosocial behaviors and other-oriented social skills (e.g. mentalizing) are instrumental for establishing positive peer relationships and maintaining peer acceptance from an early age (Lejuez et al., 2003; Fink et al., 2014; Slaughter et al., 2015; Will et al., 2018). Heightened recruitment of regions involved in social-cognitive and regulatory processing to prosocial behavior could provide a mechanism by which positive, prosocial behaviors are impacted by implicit peer influences (Somerville et al., 2018). Specifically, developmental shifts in the desire to establish or maintain peer acceptance may be related to increases in neural responses during prosocial decision-making from childhood to early adolescence but declines after this transition, when youth establish more independence from peers (and family) and become more autonomous decision-makers.

Costly Giving > Costly Reward decisions.

At the neural level, we found quadratic age differences in the pSTS, temporal pole, IFG and cuneus during costly prosocial behavior relative to gaining a personal reward (Costly Giving > Costly Reward), which peaked in early adolescence relative to childhood and mid-adolescence. Decisions to engage in costly prosocial behavior are often complex and difficult because they require individuals to weigh other-oriented concerns against more selfish inclinations. Although we did not have a priori expectations about the role of the cuneus, previous research has implicated brain regions associated with social cognition, including the pSTS, temporal pole and IFG, in prosocial decision-making (van Hoorn et al., 2016; Will et al., 2018). In particular, the pSTS and temporal pole are involved in mentalizing about others' intentions, emotions and beliefs (Saxe et al., 2004; Blakemore et al., 2007; Pfeifer et al., 2009; Blakemore and Mills, 2014) and empathic processing (Lamm and Singer, 2010; Morelli et al., 2014). Relative to other regions in the social brain network, the pSTS uniquely serves as a central hub for social information processing, which includes social perception, action observation and theory of mind (Yang et al., 2015) and has been associated with greater self-reported altruism in adults (Tankersley et al., 2007). Thus, the pSTS may be crucially activated when integrating the multiple social cognitive processes (e.g. mentalizing) inherent in costly prosocial behavior, a process that might be exaggerated during early adolescence due to developmental peaks in self-conscious emotions and sensitivity to peer evaluation (Somerville et al., 2013).

In addition to the pSTS and temporal pole, the IFG showed early adolescent peaks during costly prosocial relative to costly reward decisions. The IFG is important for both the representation of others' actions (Iacoboni, 2009) and cognitive control (Aron et al., 2004). Our results suggest that the extent to which the IFG is activated when making costly prosocial decisions differentially motivates youth toward prosocial actions, with early adolescents more likely to recruit this region during prosocial decisions compared to children and mid-adolescents. Indeed, IFG reactivity to emotional faces explains the link between empathic concern in late childhood and subsequent prosocial behavior in early adolescence (Flournoy

et al., 2016), underscoring the importance of engaging the IFG early in life in order to sustain or increase prosocial behaviors across development. Taken together, these results build on prior research showing regions implicated in social cognitive processing differentially support costly prosocial engagement from childhood to adolescence.

Costly Giving > Non-costly Giving decisions.

Similar quadratic age-related differences were found in the pSTS and IFG/dlPFC during costly prosocial behavior compared to non-costly prosocial behavior, with peaks in early adolescence relative to childhood and mid-adolescence. Prosocial behaviors involving a personal cost (e.g. loss of potential gains) evoked greater activation in brain regions that support social-affective processing (pSTS) and cognitive regulation (IFG/dlPFC) compared to engaging in non-costly prosocial behaviors that have little effect on one's self-interests. Given the need to voluntarily sacrifice one's self-interests to help another individual, costly prosocial behaviors may require that early adolescents—more so than children or mid-adolescents—regulate their self-interests and consider others' interests to a greater extent than when engaging in non-costly prosocial behaviors (e.g. sharing public goods). There was only one linear age effect, such that dmPFC showed age-related decreases during costly giving vs non-costly giving from childhood to adolescence. Given all but one analysis showed quadratic age associations, these findings collectively suggest that social-affective and regulatory brain systems are important for the deliberation of more autonomous and costly forms of prosocial behavior, with exaggerated effects during early adolescence compared to childhood and mid-adolescence.

dACC activation predicts frequency of giving

Independent of age, the frequency of costly giving behavior was negatively correlated with dACC activation during Costly Giving > Costly Reward decisions among youth who made costly prosocial decisions. Youth who engaged in higher rates of costly giving behavior exhibited less dACC activation when forgoing personal gains in order to be prosocial to another individual. Previous research has implicated the dACC in conflict monitoring (Carter et al., 1998) and the social pain that results from rejection or empathy for negative emotions (Morelli et al., 2014; Rotge et al., 2015). Thus, neural regions associated with conflict monitoring or unpleasant social emotions can moderate youths' proclivity toward prosocial engagement. Perhaps having less conflicting emotions about the discrepancy between self-other rewards facilitates engagement in costly prosocial behavior, though future research should test this hypothesis.

Limitations

A few limitations should be noted. First, we used a cross-sectional design in order to examine the behavioral and neural development of prosocial behavior from childhood through adolescence. While testing for non-linear age associations in cross-sectional data can start to address inconsistencies in prosocial development found in prior research (Do et al., 2016), longitudinal designs are particularly advantageous for investigating more complex growth trajectories (beyond linear and quadratic age associations) or diverging developmental trends based on gender (van der Graaff et al., 2014) or pubertal status (Braams et al., 2015) that may better characterize youths' prosocial behavior. While the current results suggest that we should potentially capitalize on early adolescents' heightened recruitment of social-cognitive regions to promote other-focused behaviors, an

alternative possibility is that childhood and mid-adolescence are instead the sensitive periods for encouraging prosocial behavior because less recruitment of social-cognitive regions is needed to engage in the same rates of prosocial behavior. Longitudinal methods can provide a more comprehensive understanding of these age-related differences (see Kraemer et al., 2000), as well as explore how within-person individual differences can influence prosocial decision-making over time. Future longitudinal studies that utilize at least three time points should unpack the specific role of age-related changes in brain development that promotes prosocial behavior.

The subsample used in fMRI analyses of prosocial behavior was relatively small, thus limiting the generalizability of some of the current findings beyond youth who are inclined toward costly prosocial decision-making. While this approach allowed us to characterize age-related associations in the neural correlates of prosocial decision-making among youth who actually engaged in costly prosocial behaviors, we are limited in understanding prosocial development in youth who do not engage in the behavior. Youth likely engage in higher or more variable rates of prosocial behavior, which binary assessments of prosocial behavior are less sensitive at capturing than continuous measurement of prosocial behavior (e.g. van Hoorn et al., 2016). The experimental design may also be underpowered to detect true effects or retain true null effects due to our small sample size. Reported null results (e.g. between age and the frequency of prosocial decisions) may thus arise erroneously from a lack of statistical power. Future studies should address these study limitations by using continuous measurement of prosocial behavior and larger sample sizes, thereby increasing the statistical power necessary to probe age and possible gender differences in costly prosocial behavior among youth. Nonetheless, these results provide compelling evidence that ongoing neurobiological changes during childhood and adolescence differentially influence prosocial development.

Conclusion

The current study addresses an important gap in the literature on whether developmental differences in prosocial decision-making at the neural level follow linear or non-linear (e.g. quadratic) associations with age from childhood to mid-adolescence. Neural evidence supports quadratic age differences, such that early adolescents who engaged in prosocial decision-making show greater recruitment of social-cognitive and regulatory regions compared to children and mid-adolescents. Given that we did not find age differences in prosocial behavior, this suggests that early adolescents show unique patterns of brain activation to inform similar levels of prosocial behavior. Future research should examine how age-related differences in youths' neural sensitivity to prosocial decision-making can foster other-oriented abilities and prosocial behaviors over time.

Supplementary data

Supplementary data are available at SCAN online.

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