Corticostriatal Connectivity during Prosocial Decision-making Relates to Giving Behavior during Adolescence

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Abstract

■ Prosocial behavior during adolescence becomes more differentiated based on the recipient of the action as well as the perceived value or benefit, relative to the cost to self, for the recipients. The current study investigated how functional connectivity of corticostriatal networks tracked the value of prosocial decisions as a function of target recipient (caregiver, friend, stranger) and age of the giver, and how they related to giving behavior. Two hundred sixty-one adolescents (9–15 and 19–20 years of age) completed a decision-making task in which they could give money to caregivers, friends, and strangers while undergoing fMRI. Results indicated that adolescents were more likely to give to others as the value of the prosocial decision (i.e., the difference between the benefit to other relative to the cost to self) increased; this effect was stronger for known (caregiver and friends) than unknown targets, and increased with age. Functional connectivity between the nucleus accumbens (NAcc) and OFC increased as the value of the prosocial decisions decreased for strangers, but not for known others, irrespective of choice. This differentiated NAcc-OFC functional connectivity during decision-making as a function of value and target also increased with age. Furthermore, regardless of age, individuals who evinced greater value-related NAcc-OFC functional connectivity when considering giving to strangers relative to known others showed smaller differentiated rates of giving between targets. These findings highlight the role of corticostriatal development in supporting the increasing complexity of prosocial development across adolescence. ■

INTRODUCTION

Prosocial behavior—voluntary acts with the intention of benefitting others—becomes increasingly complex across development. This complexity has been characterized by greater selectivity based on the recipients of the actions as well as the perceived value/benefit (relative to cost to self) for the recipients (Do & Telzer, 2019; Padilla-Walker, Carlo, & Memmott-Elison, 2018; Güroglu, van den Bos, & Crone, 2014). This age-related increase in complexity parallels significant neurobiological development during adolescence (Crone & Fuligni, 2020; Blakemore & Mills, 2014; Crone & Dahl, 2012). Although previous studies of prosocial behavior during adolescence focused on examining either the family (Telzer, Fuligni, Lieberman, & Galván, 2013, 2014; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011), hypothetical in-group versus out-group peers (Do & Telzer, 2019), or friends versus strangers (van de Groep et al., 2022; van de Groep, Zanolie, & Crone, 2020; Güroglu, van den Bos, et al., 2014) as the target recipients, it is less known how prosocial behavior and their neural correlates might be differentiated across development when all of these recipients (family, friends,

and strangers) are considered together. In addition, few studies have examined how functional connectivity between key regions implicated in prosocial behaviors (e.g., ventral striatum, PFC) relate to the increasing complexity in prosocial decision-making during adolescence. The current study investigated how functional connectivity of corticostriatal networks track the relative value of costly prosocial decisions (i.e., difference between benefit to other vs. cost to self) as a function of target recipient and age of the giver, and whether they predict individual differences in the amount of giving.

Although research on the development of prosocial behavior during adolescence is still in its nascent stages, two aspects of prosocial development have been found to be relatively consistent across studies: increased selectivity among target recipients and increased giving as the value/benefit of the prosocial behavior outweighs costs to self. Less known is how these two aspects interact to influence prosocial behaviors across adolescence. Increased selectivity among target recipients in prosocial behavior has been observed across adolescence, in particularly between known and unknown individuals (Karan et al., 2022; van de Groep et al., 2020, 2022; Padilla-Walker et al., 2018; Güroglu, van den Bos, et al., 2014). For example, Güroğlu, Will, and Crone (2014) found that whereas 9- and 12-year-old children gave equally to close friends

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and strangers, older adolescents (15 and 18 years old) increasingly gave more to their friends than strangers. In previous analyses from the same data set as the current article that additionally examined family/caregivers as a target recipient, we found that rates of giving to family and friends increased with age (through 20 years) whereas there were no age-related changes in rates of giving to strangers, which remained relatively low (Karan et al., 2022). In addition to greater selectivity between target recipients, research also demonstrates that individuals take into account the value of the prosocial decisions, typically behaving more prosocially as the value of the prosocial behavior to others increasingly outweighs the cost to oneself. Findings regarding whether this value-related giving differs by target, however, have been mixed. For example, Do and Telzer (2019) found that youth (8–16 years old) gave more to in-group peers than out-group peers, and that youth were more likely to give to others as the giving value increased. The effect of giving value, however, did not differ by target nor were there any detectable age differences in giving behavior. In contrast, van de Groep and colleagues (2022) found that older adolescents (relative to younger participants) gave more to friends than unfamiliar peers when the cost to self was small relative to when the cost was large (van de Groep et al., 2022). These findings are in line with economic models of prosocial decision-making that indicate that costly prosociality often emerges under conditions in which resources significantly favor the recipient more than oneself, outweighing individuals' selfish inclination to keep rewards for themselves (Güroglu, Will, et al., 2014; Williams & Moore, 2014; Fliessbach et al., 2012). In the context of this framework, prosocial offers with low giving value (i.e., when the net benefit to the recipient is small relative to cost to self) may indicate a more difficult decision, requiring greater cognitive (and supporting neurobiological) resources to override the selfish inclination and/or to increase the prosocial motivation to give to others. It is possible that the difficulty in determining when to be prosocial to others, especially when the cost to self is high and/or the benefit to the recipient is low, is modulated by social relationships, such that less effort may be required when deciding to be prosocial to close others than to strangers.

Burgeoning fMRI research on prosocial development suggests that these developmental differences in prosocial behavior may be supported by development in brain regions implicated in reward processing, mentalizing, and cognitive control during adolescence, but the precise mechanisms are not well understood. Neuroimaging studies of giving behavior during adolescence have found that adolescents engaged the ventral striatum (VS), the TPJ, and the dorsolateral prefrontal cortex (DLPFC) when giving to others (Karan et al., 2022; van de Groep et al., 2022; Schreuders, Klapwijk, Will, & Güroğlu, 2018), with some studies showing greater activation in these regions when giving to friends compared with unfamiliar peers

(van de Groep et al., 2022; Schreuders et al., 2018). When the value of prosocial behaviors was taken into consideration, van de Groep and colleagues (2022) found that, compared with younger participants, older adolescents engaged the left lateral and anterior PFC more strongly when giving small versus large amounts; this effect, however, did not differ by target despite there being behavioral differences based on target. Using a parametric modulator of giving value (difference in benefit for others relative to cost to self) in fMRI analyses, which allows examination of trial-to-trial variability in giving value within experimental conditions (e.g., in-group vs. out-group peers), Do and Telzer (2019) did not observe any differences in regional activation as a function of giving value, target, or age of giver.

One potential explanation for the inconsistencies in the neuroimaging findings could be because of the focus on regional activation as opposed to examining functional coupling between disparate brain regions—especially between those implicated in processes such as reward, mentalizing, social cognition, and cognitive control—which have been shown to undergo significant development during adolescence (Casey, Galván, & Somerville, 2016; Casey, 2015). Indeed, although Do and Telzer (2019) did not observe differences in regional activation as a function of giving value, target, or age of giver, differences in giving value and target emerged when they examined functional connectivity. Specifically, they found that youth exhibited greater functional coupling between the VS and the posterior superior temporal sulcus (pSTS) when considering decisions with greater value for out-group members than in-group members. Greater value-related VS-pSTS functional coupling when making decisions for out-group relative to in-group members was associated with a reduction in intergroup biases in prosocial behaviors (i.e., less selectivity between out-group and in-group; Do & Telzer, 2019). Given that the VS and pSTS have been implicated in reward processing and mentalizing/perspective-taking, respectively, greater VS-pSTS functional coupling when making decisions for out-group relative to in-group peers might suggest that greater cortical resources, especially in regions involved in cognitive control, reward, and social cognition, and greater strength in connectivity between these regions, are engaged when deciding to give to strangers and out-group members than in-group/known others. Taken together, these findings suggest that adolescents consider both the value of the prosocial decision and the intended target (particularly between in-group vs. out-group peers) when making prosocial decisions and that these processes may be supported by developing corticostriatal networks. In addition, these findings highlight the added value of investigating functional connectivity in addition to regional activation to elucidate neurobiological mechanisms of prosocial development.

Whereas these studies focused on comparing adolescents' prosocial behavior between friends/in-group and unfamiliar/out-group peers, it is unknown how the family

fits into the social dynamics of prosocial behaviors. Studies that examined giving to the family during development have only considered the family as the target recipient. These studies have found that giving money to one's family at a cost to oneself was associated with increased activation in reward-related regions (e.g., VS and ventral tegmental area) and regions implicated in mentalizing and self-control (e.g., DLPFC, TPJ, pSTS, dorsomedial prefrontal cortex; Telzer et al., 2011, 2013). In one of the first studies to investigate the role of the family within prosocial decision-making among peers, Karan and colleagues (2022) found that, whereas individuals were more likely to give to known others (caregivers and friends) than to strangers across adolescence, giving behavior did not, on average, differ between caregivers and friends. Whether behavioral differences between caregivers and friends might emerge when the value of the prosocial behavior is also considered is unknown. Karan and colleagues (2022) also did not find differences in brain activation between targets when giving, which could be because of the focus on regional activation of disparate regions rather than their interactions as discussed above. Hence, it remains an open question whether family and friends are indeed represented similarly in the adolescent brain regarding prosocial decision-making and behavior. Investigating the role of the family in influencing prosocial behavior during adolescence would provide insight into the complex social development during adolescence.

The current study investigated how functional connectivity of corticostriatal networks tracked the relative value of prosocial decisions (i.e., difference between benefit to other vs. cost to self) as a function of target recipient and giver age, and whether they predicted individual differences in giving behavior (both giving rate and RT). We have previously reported results on rates of giving as a function of target (caregivers, friends, and strangers) and age of giver as well as the neural regions involved in giving to others, primarily focusing on the VS, pSTS, TPJ, and medial and lateral PFC regions as a priori ROIs (Karan et al., 2022). The current study extends and differs from this prior study in the following ways: (1) Instead of averaging giving rate across trials, the current study used multilevel logistic regression analyses to model trial-by-trial variability in giving behavior as a function of the value of prosocial decisions, and (2) instead of examining regional activation among trials where participants chose to give, we utilized a parametric modulator to model the value of all of the giving trials, regardless of choice, and used functional connectivity approaches to delineate how interactions between regions implicated in prosocial behavior might differ as a function of value and recipient, and how these relations differ across adolescence and contribute to giving behavior. Regarding behavior, we hypothesized that individuals will be more likely to give to others as the value of the prosocial decision (difference between benefit to other relative to cost to self) increases, and that this effect would be stronger for known others (family and

friends) than strangers. Greater differentiation in giving behavior as a function of value and target would increase with age. Whether giving behavior differs between family and friends will be explored. Regarding the brain, based on findings from Do and Telzer (2019), we hypothesized that stronger functional connectivity between corticostriatal regions during decision-making would track with the giving value of the decisions, and that the strength of this value-based functional connectivity would be stronger for unknown compared with known others and gets stronger across age. In addition, we also hypothesized that value- and target-related differences in corticostriatal functional connectivity will be associated with value- and target-related differences in giving behavior, over and above effects of age.

METHODS

Participants

Data from 261 participants (ages 9–15 years [$n = 222$] and 19–20 years [$n = 39$]) who completed all three runs of the task were included in the current study. Of the 261 participants, $n = 194$ were included in fMRI analyses (scans were excluded if > 20% of frames exceeded a 0.9-mm framewise displacement and only participants who have good quality scans for all three runs were included). Participants came from one of two parent studies: Approximately half of the participants ($n = 127$, 47.9% female) participated in a cross-sectional study (Study 1), and 140 participants (47.5% female) completed the present measures as part of the first wave of a longitudinal study (Study 2). Study 2 utilizes an accelerated longitudinal design with plans to fill in gaps in the age range (i.e., between 16 and 18 years) in subsequent waves; hence, there exists a gap in the age range between 16 and 18 years. With the exception of slightly different scanning parameters for the structural MRI image (detailed below), the study protocol and task procedures for these two studies were identical. A statistical power analysis performed with an alpha = .05 and power = 0.80 indicated that a sample of at least 120 participants is needed to detect a medium to large effect, estimated from previous studies (van de Groep et al., 2020, 2022). Hence, our sample of 194–261 participants is sufficient.

The reported self-identified racial/ethnic breakdown of our sample was diverse: 28.7% White, 18.9% Hispanic or Latino, 11.4% Asian American, 6.9% African American, 0.9% Native American, 18.9% Multi-ethnic (reported more than one ethnicity), and 11.4% Other. Parents reported a wide range of household incomes (ranging from $15 K to $3 M per year, M = $176,300 per year) with 16% reporting up to $50 K per year, 21% reporting between $50 K and $100 K, 29% reporting between $100 K and $200 K, and 33% reporting over $200 K per year; income data were missing for 1% of the sample.

Adolescents between the ages of 9–15 years were recruited via flyers, advertisements, and through class

presentations to schools within the Los Angeles Unified School District. Participants were also recruited from the Clinical and Translational Science Institute database of families in the University of California Los Angeles (UCLA) and affiliated medical systems. Finally, participants aged 19–20 years were recruited from undergraduate classes at UCLA to include older adolescents in the estimates of age differences in behavior and neural activation. All participants were right-handed, fluent in English, free of MRI contraindications, had no previous psychiatric diagnoses, and were not pregnant or trying to become pregnant at the time of the study session. Parents and youth provided written consent and assent in accordance with UCLA's Office of the Human Research Protection Program and institutional review board.

Procedure

While undergoing fMRI scans, participants completed a costly giving task (described in the Giving Task section) that has been adapted from previous research to assess prosocial decision-making (Telzer et al., 2011, 2013, 2014). Before learning about the task, participants were asked to select a (nonromantic, nonrelated) friend and a caregiver without being told that they would later earn money for them. Participants then completed measures assessing their relationship quality with these individuals (described in Measures section).

Measures

Inclusion of Other in the Self Scale

Participants completed the Inclusion of Other in the Self (IOS) Scale (Aron, Aron, & Smollan, 1992) for their caregiver and friend. The IOS Scale assesses how close participants feel with another person or group. On this scale, participants are shown seven pairs of circles that range from just touching to almost completely overlapping. One circle in each pair is labeled "self," and the second circle is labeled with the target (i.e., caregiver or friend). Participants were asked to choose one of the seven pairs that best describes their relationship with each target. Greater overlap in the circles suggests a closer relationship. We did not administer the IOS for the stranger, but we presumed the perceived closeness to be 0 or no overlap.

Giving Task

Participants were shown a series of financial offers in which they could earn money for themselves, their chosen caregiver and friend, and a future participant who was unknown to the participant (stranger). Participants completed three runs of this task, one for each target recipient (caregiver, friend, or stranger), with the order of target counterbalanced across participants.

On each run, participants saw four different types of offers: (1) costly giving (40 trials per target), in which the target would receive money at a cost to the participant; (2) non-costly reward (16 trials per target), in which participants earned money without a cost to the other person; (3) non-costly giving (five trials per target), in which the other person earned money without a cost to the participant; and (4) control trials (16 trials per target), in which neither the participant nor the other person gained or lost any money. Trials, regardless of type, were presented in a randomized order. Fewer non-costly reward trials were presented because previous research and pilot data have shown consistently high acceptance rates for those trials (Telzer et al., 2011). In addition, although we were not interested in examining non-costly giving trials, those trials were presented to participants to provide experiential variation in decision-making and to keep participants engaged throughout the task.

On each offer, participants saw the words YOU at the top left of the screen and the name of the target at the top right of the screen (e.g., MOM). The amount that each recipient could respectively gain or lose for that offer was displayed beneath the names. For example, on a costly giving trial, participants would see a negative dollar amount (e.g., −$1.25) underneath YOU and a positive dollar amount (e.g., +$3.00) underneath the target's name, indicating that the participant would essentially give up $1.25 for the target to receive $3.00. The giving value represents the difference in the amount that the target would gain relative to how much the participant would give. In this example, the giving value of the trial is $1.75 (the difference between $3.00 and $1.25). Participants were instructed to either accept or reject each offer using a handheld button box.

The current study focused on participants' behavior and functional connectivity on costly giving trials. The costs to participants ranged from $1.00 to $3.75, and the gain for recipients ranged from $2.50 to $7.00. On each costly giving offer, the amount that recipients could gain was always greater than the cost to the participants. The giving values (benefit to the recipient vs. cost to self) ranged from $1.00 to $5.00 and increased by 0.25 intervals. Costs and rewards were combined such that the differences/giving values would be distributed approximately evenly across $1–$2, $2–$3, $3–$4, and more than $4. Each offer was presented for 3 sec, during which participants made their responses to accept or reject the offer, followed by a jittered fixation (500–4000 msec; Figure 1).

To encourage independent decision-making on each trial (i.e., that the current decision does not depend on prior choices), participants were told before starting the task that a few trials would be randomly selected at the end of the task to determine how much money the participant and each recipient had earned. As such, earnings for each recipient were not cumulative, but was only cumulative across the selected trials. Specifically, a random set of trials were selected upon the completion of each run to

Figure 1. Schematic representation of the giving task and examples of costly giving trials. Each trial is presented for 3 sec, followed by a jittered fixation (500–4000 msec). The name of the relevant target was indicated in the top right of the stimuli. The giving value represents the difference in the amount that the target would gain relative to how much the participant would give. For example, the giving value of the trial on the left is $1.50 (the difference between $2.50 and $1.00) and the giving value of the trial on the right is $4.50 (the difference between $7.00 and $2.50).
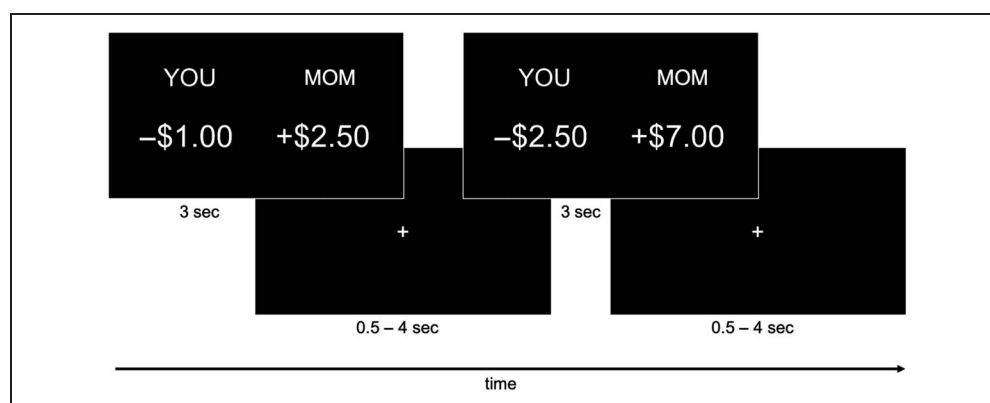
determine how much money the participant and each target/recipient earned. Payouts for the participant included their earnings on the task for themselves as well as how much the previous participant in the study earned for their stranger (i.e., the current participant). Payouts for the caregiver and the friend were placed in separate envelopes, with a letter from the investigators of the study explaining the contents of the envelope attached. These envelopes were given to the participants to give to the targets (participants did not know ahead of time how the targets were going to receive the payouts). Earnings for the stranger were included in the payout for the next participant.

fMRI Data Acquisition

Neuroimaging data were acquired on a Siemens Prisma 3-Tesla MRI scanner. Foam padding was placed around each participant's head for comfort and to constrain head movement. The task was presented via a projector, which participants viewed through a mirror attached to the head coil.

For each participant, an initial set of three (one in each plane: coronal, sagittal, axial) 2-D structural scout (localizer) gradient-echo images (repetition time [TR] = 3.15 msec, echo time [TE] = 1.37 msec, matrix size = 160 × 160, field of view [FOV] = 260 mm, 128 slices, flip angle = 8°, 1.6-mm thick, 1.6-mm inplane resolution, 0.32-mm gap) was acquired to enable prescription of slices obtained in structural and functional scans. A T1-weighted magnetization prepared rapid gradient echo structural scan (parameters for participants from Study 1: TR = 1900 msec, TE = 2.26 msec, matrix size = 256 × 256, FOV = 250 mm, 176 slices, flip angle = 9°, 1 mm thick, 1-mm inplane resolution, 0.5-mm gap; parameters for participants from Study 2: TR = 2000 msec, TE = 2.52 msec, matrix size = 256 × 256, FOV = 256 mm, 192 slices, flip angle = 12°, 1 mm thick, 1-mm inplane resolution, 0.5-mm gap), coplanar with the functional scans, was collected for all participants.

The giving task consisted of three functional (echo planar T2*-weighted gradient-echo) MRI scans. Each functional run (TR = 2000 msec, TE = 30 msec, matrix size = 64 × 64, FOV = 192 mm, 34 slices, flip angle = 90°, 4 mm thick, 3-mm inplane resolution, no gap) lasted 6 min 40 sec.

fMRI Data Preprocessing and Analysis

fMRI data were preprocessed and analyzed using the FMRIB Software Library. Preprocessing for each run included skull-stripping, motion correction, slice timing correction, nonlinear high-pass temporal filtering (128 sec), and spatial smoothing (6-mm FWHM). Functional images were registered to the high-resolution magnetization prepared rapid gradient echo (6 degrees of freedom) and then to standard Montreal Neurological Institute space (12 degrees of freedom).

For each run (target), costly giving trials were modeled with a parametric modulator to determine whether and how the brain tracks changes in the magnitude of the giving value, irrespective of the actual decisions. This approach is similar to the brain-as-predictor approach used by Do and Telzer (2019), whereby neural responses during the decision phase was used to predict individual differences in behavior (Berkman & Falk, 2013). The parametric modulator reflected the difference in the amount that the target would gain relative to how much the participant would give, with greater values reflecting greater differences (range: $1.00–$5.00, mean = $2.70, SD = $1.06). For example, on a trial where the participant would give up $1.00 for the target to gain $2.50, the giving value of the trial is $1.50 (the difference between $2.50 and $1.00). On a different trial where the participant would give up $2.50 for the target to gain $7.00, the giving value of this trial is $4.50 (the difference between $7.00 and $2.50). All values in the parametric modulator were mean-centered within each run.

To examine whether corticostriatal connectivity differs as a function of giving value, target, and age, we conducted

psychophysiological interaction analyses. We chose an anatomically defined bilateral nucleus accumbens (NAcc) seed because previous research has shown that the ventral striatum, in which the NAcc is located, is associated with prosocial decisions (Telzer et al., 2011, 2013, 2014). The NAcc seed was derived from the Harvard-Oxford atlas, thresholded at 50%.

For each run, we extracted the deconvolved time-series from the NAcc seed region (physiological regressor), convolved the parametric modulator for costly giving trials with the canonical double-gamma hemodynamic response function (psychological regressor), and multiplied the time-series of the physiological regressor by the psychological regressor (psychophysiological interaction term), which identifies brain regions that co-varied with the NAcc as a function of giving value. Other explanatory variables were modeled using stick functions convolved with a canonical double-gamma hemodynamic response function: non-costly reward, non-costly giving, and control trials. For each participant, each run/target was combined using fixed-effects analyses, generating the following contrasts: known others versus strangers, family versus friend. These contrasts were selected to parallel contrasts used for behavioral data analysis (detailed below). At the group level, we conducted a whole-brain general linear model with linear and quadratic age regressors (mean-centered) for each of the target contrasts using FLAME 1, cluster-corrected at $Z > 3.1, p < .05$.

We supplemented the connectivity analyses with whole-brain parametric analyses to examine regions that track with the magnitude of costly giving value, regardless of decision, and whether parametrically modulated activation to costly giving value differ by target (known others vs. strangers, family vs. friend) and age (modeling both linear and quadratic effects).

T-statistic maps of analyses have been uploaded to NeuroVault (https://identifiers.org/neurovault .collection:14342).

Analysis Plan

Giving Decision

Multilevel logistic regression analyses were conducted in R using the *lme4* package to estimate the likelihood of giving as a function of giving value, target, and age. Decision (1 = accept, 0 = reject or no response) for each trial was modeled as a function of the Giving Value (mean-centered at 2.7), target (using Helmert Effect Codes: Known Others vs. Stranger [Stranger = −.666, Family = .333, Friend = .333], Family vs. Friend [Friend = −.5, Stranger = 0, Family = .5]), and Age (mean-centered at 13.1 years). Fixed effects included Giving Value × Target × Age interactions and all lower-order interactions. Random effects included random intercepts and slopes for all within-subject variables (i.e., giving value, target, and their interactions).

Response Time

Multilevel logistic regression analyses were conducted in R using the *lme4* package to estimate RT to give as a function of Giving Value, Target, and Age. RT in seconds for each trial was modeled as a function of the Choice (0 = accept, 1 = reject or no response), Giving Value (mean-centered at 2.7), Target (using Helmert Effect Codes: Known Others vs. Stranger [Stranger = −.666, Family = .333, Friend = .333], Family vs. Friend [Friend = −.5, Stranger = 0, Family = .5]), and Age (mean-centered at 13.1 years). Fixed effects included Choice × Giving Value × Target × Age interactions and all lower-level interactions. Random effects included random intercepts and slopes for all within-subject variables (i.e., giving value, target, and their interactions).

RESULTS

Means and standard errors (*SE*s) representing relationship closeness as assessed by the IOS for caregiver and friend are shown in Figure 2. Repeated-measures analyses indicated a main effect of Age, such that closeness to caregiver and friend decreased with age ($B = −0.22, SE = 0.022, t(4940) = −9.50, p < .001$); a main effect of Target, characterized by greater closeness to their caregiver than friend ($B = −2.54, SE = 0.37, t(278) = −6.90, p < .001$); and a Target × Age interaction, such that the difference in closeness between caregiver and friend was largest during childhood and decreased with age ($B = 0.145, SE = 0.028, t(278) = 5.15, p < .001$). In other words, children reported being closer to their caregiver than to their friend; this difference in closeness between caregiver and friend gets smaller across development.

Behavioral Results

Results from the multilevel logistic regression analysis estimating likelihood of giving as a function of Giving Value, Target, and Age are presented in Table 1. Analyses revealed
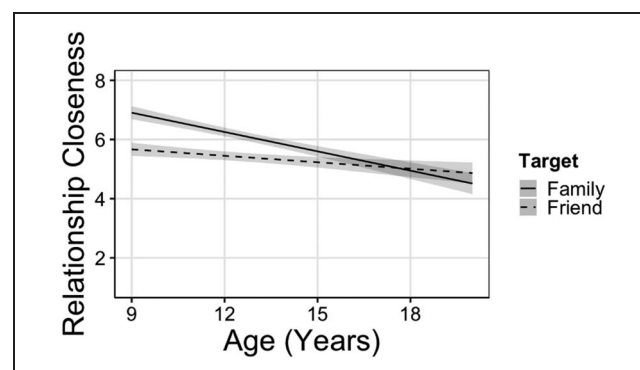

Figure 2. Children reported having a closer relationship to their caregiver than to their friend. This difference decreased across development.

Table 1. Results from Multilevel Logistic Regression Analysis Estimating Likelihood of Giving Behavior as a Function of Giving Value, Target, and Age

Variable	Estimate	SE	Odds Ratio	Z	p
Intercept	−0.343	0.090	0.71	−3.79	**< .001**
Giving Value	0.425	0.035	1.53	12.05	**< .001**
Target (Stranger vs. Known Others)	0.768	0.079	2.16	9.71	**< .001**
Target (Family vs. Friend)	0.456	0.084	1.58	5.41	**< .001**
Age	0.050	0.027	1.05	1.82	.068
Giving Value × Target (Stranger vs. Known Others)	0.075	0.036	1.08	2.12	**.034**
Giving Value × Target (Family vs. Friend)	0.055	0.046	1.08	1.19	.234
Giving Value × Age	0.060	0.011	1.06	5.57	**< .001**
Target (Stranger vs. Known Others) × Age	0.088	0.024	1.09	3.63	**< .001**
Target (Family vs. Friend) × Age	0.040	0.026	1.06	1.53	.125
Giving Value × Target (Stranger vs. Known Others) × Age	0.028	0.011	1.03	2.50	**.013**
Giving Value × Target (Family vs. Friend) × Age	−0.003	0.015	1.00	−0.22	.826

Acceptance of costly giving trials (1 = accept, 0 = reject or no response) for each trial was modeled as a function of the Giving Value (mean-centered at 2.7), Target (using Helmert Effect Codes: Known Others vs. Stranger [Stranger = −.666, Family = .333, Friend = .333], Family vs. Friend [Friend = −.5, Stranger = 0, Family = .5]), and Age (mean-centered at 13.1 years). Significant effects are denoted in **bold**.

a significant Giving Value × Target (Known Others vs. Strangers) × Age interaction on giving decisions ($b = 0.0278$, $SE = 0.011$, $Z = 2.497$, $p = .0125$). Follow-up analyses were conducted to investigate the Giving Value × Target interaction at younger ($−1\ SD = 9.78$ years) and older ($+1\ SD = 16.42$ years) ages. Among younger participants, although there was a main effect of Giving Value such that children were more likely to give as the giving value increased ($b = 0.224$, $SE = 0.049$, $Z = 4.542$, $p < .001$), this effect did not differ by target ($b = −0.0173$, $SE = 0.049$, $Z = −0.351$, $p = .726$). Among older participants, as giving value increased, the likelihood of giving (i.e., accepting offer) increased ($b = 0.526$, $SE = 0.051$, $Z = 12.159$, $p < .001$); this effect of Giving Value was stronger for known others than for strangers ($b = 0.168$, $SE = 0.053$, $Z = 3.153$, $p = .00162$; Figure 3). The effect of Giving Value did not differ between family and friends (Value × Target: $b = 0.055$, $SE = 0.046$, $Z = 1.190$, $p = .234$; Value × Target × Age: $b = −0.0032$, $SE = 0.0147$, $Z = −0.219$, $p = .827$). However, participants at average age (i.e., 13.1 years) were more likely to give to family than friends at average giving value (i.e., 2.7; $b = 0.456$, $SE = 0.084$, $Z = 5.416$, $p < .001$).

Results from the multilevel logistic regression analyses estimating RT to give as a function of Giving Value, Target, and Age are presented in Table 2. There was a Choice ×
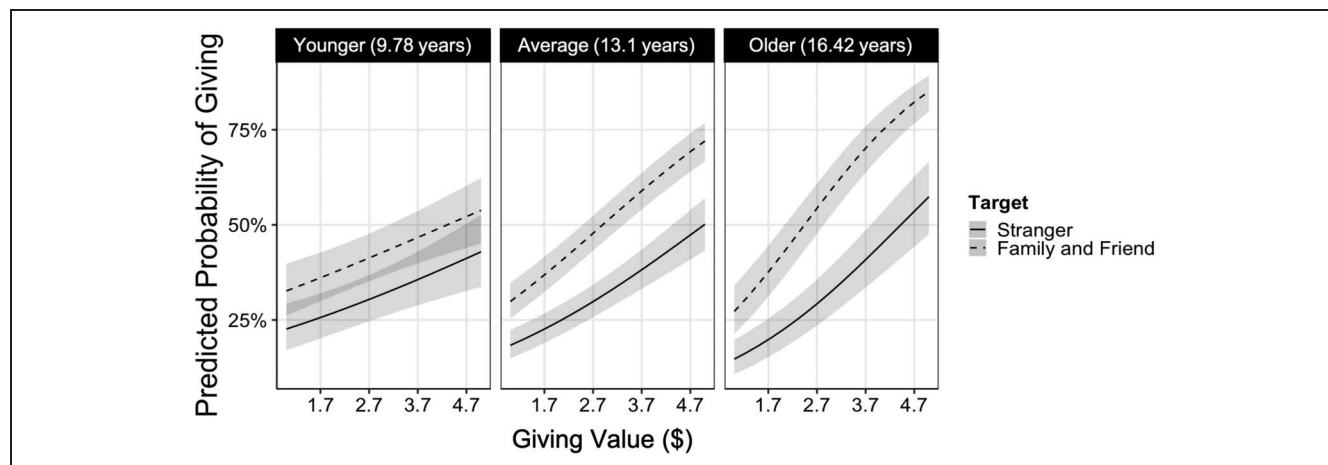

Figure 3. Younger individuals were more likely to give to others as giving value increased; this effect did not differ by target. Although older individuals were also likely to give more to others as giving valued increased, the effect was stronger for known others (family/caregiver and friends) than for strangers.

Table 2. Results from the Multilevel Logistic Regression Analyses Estimating RT to Give as a Function of Giving Value, Target, and Age

| Variable	Estimate	SE	t	p
Intercept	1.4980	0.015	98.62	**< .001**
Choice	0.0007	0.006	0.11	.909
Giving Value	−0.0116	0.004	−2.95	**.003**
Target (Stranger vs. Known Others)	−0.0280	0.015	−1.81	.071
Target (Family vs. Friend)	−0.0562	0.019	−3.01	**.003**
Age	−0.0136	0.005	−2.94	**.004**
Choice × Giving Value	0.0083	0.005	1.61	.107
Choice × Target (Stranger vs. Known Others)	0.0335	0.013	2.66	**.008**
Choice × Target (Family vs. Friend)	0.0236	0.015	1.61	.107
Choice × Age	−0.0010	0.002	−0.53	.599
Giving Value × Target (Stranger vs. Known Others)	0.0020	0.008	0.25	.801
Giving Value × Target (Family vs. Friend)	−0.0065	0.008	−0.79	.430
Giving Value × Age	−0.0037	0.001	−3.12	**.002**
Target (Stranger vs. Known Others) × Age	−0.0038	0.005	−0.81	.421
Target (Family vs. Friend) × Age	0.0047	0.006	0.83	.409
Giving Value × Target (Stranger vs. Known Others) × Age	−0.0025	0.002	−1.05	.295
Giving Value × Target (Family vs. Friend) × Age	−0.0022	0.002	−0.90	.370
Choice × Giving Value × Target (Stranger vs. Known Others)	−0.0027	0.011	−0.26	.799
Choice × Giving Value × Target (Family vs. Friend)	0.0027	0.012	0.22	.825
Choice × Giving Value × Age	0.0049	0.002	3.08	**.002**
Choice × Target (Stranger vs. Known Others) × Age	0.0043	0.004	1.10	.270
Choice × Target (Family vs. Friend) × Age	0.0008	0.005	0.17	.868
Choice × Giving Value × Target (Stranger vs. Known Others) × Age	0.0016	0.003	0.50	.615
Choice × Giving Value × Target (Family vs. Friend) × Age	0.0021	0.004	0.57	.571

RT in seconds for each trial was modeled as a function of the Choice (0 = accept, 1 = reject or no response), Giving Value (mean-centered at 2.7), target (using Helmert Effect Codes: Known Others vs. Stranger [Stranger = −.666, Family = .333, Friend = .333], Family vs. Friend [Friend = −.5, Stranger = 0, Family = .5]), and Age (mean-centered at 13.1 years).

Giving Value × Age interaction ($b = 0.00489$, $SE = 0.00159$, $t(608) = 3.077$, $p = .002$) such that older participants were faster than younger participants to accept trials as the giving value increased ($b = −0.00367$, $SE = 0.00118$, $t(654) = −3.121$, $p = .00188$). In contrast, although older participants were faster to reject trials ($b = −0.0146$, $SE = 0.00461$, $t(285) = −3.158$, $p = .0018$), no differences in RT were observed as a function of giving value for rejected trials ($p = .340$). There was also a Choice × Target (Known Others vs. Stranger) interaction ($b = 0.0335$, $SE = 0.0126$, $t(244) = 2.660$, $p = .0078$) such that participants were trending faster to accept offers for known others than strangers ($b = −0.028$, $SE = 0.0155$, $t(402) = −1.808$, $p = .071$), but showed no differences in RT by target when rejecting offers ($p = .706$).

fMRI Results

Functional connectivity analyses of costly giving trials, irrespective of actual decisions, revealed a Giving Value × Target (Known Others vs. Strangers) × Age interaction in NAcc connectivity with the inferior frontal gyrus (IFG; $x = 58$, $y = 26$, $z = 8$, $Z = 4.1$) and OFC ($x = 44$, $y = 34$, $z = −4$, $Z = 3.76$; Figure 4A). To probe the nature of the interaction, parametrically modulated NAcc-IFG and NAcc-OFC connectivity values were extracted for each target and then connectivity values for the family and friend runs were averaged and compared against the connectivity values for strangers as a function of age. As illustrated in Figure 4B, as age increased, there was stronger NAcc-OFC connectivity when considering giving to

Figure 4. (A) Functional connectivity analyses of costly giving trials, irrespective of actual decisions, revealed a Giving Value × Target (Known Others vs. Strangers) × Age interaction in the NAcc connectivity with the IFG ($x = 58$, $y = 26$, $z = 8$, $Z = 4.1$) and OFC ($x = 44$, $y = 34$, $z = -4$, $Z = 3.76$). (B) Visual depiction of Giving Value × Target × Age interaction in NAcc-OFC functional connectivity. As giving value decreased (denoted by more negative values on the y axis), older individuals showed stronger NAcc-OFC connectivity when considering giving to strangers (solid line) compared with known others (dashed line); NAcc-OFC connectivity did not differ as a function of giving value or target for younger individuals.
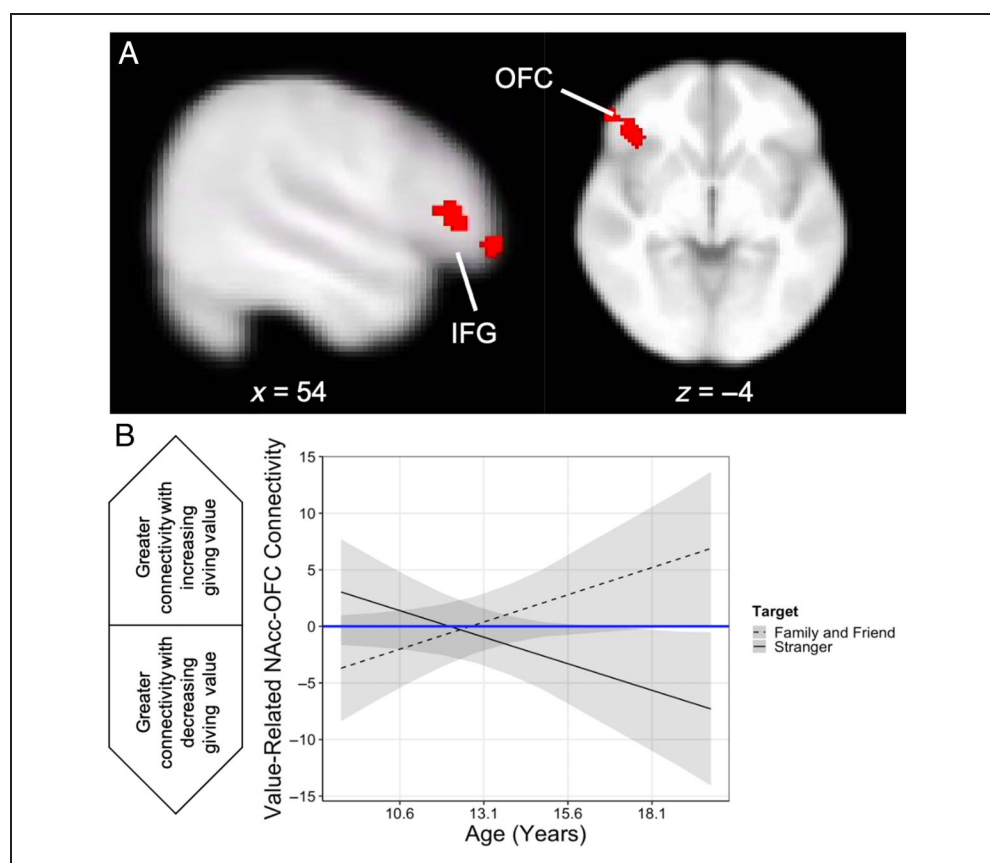
strangers (compared with known others) as giving value decreased (denoted by more negative values on y axis). Similar patterns were observed for NAcc-IFG connectivity.

There was also a positive quadratic effect of age for the family versus friend contrast in functional connectivity between the NAcc and lingual gyrus ($x = 12$, $y = -72$, $z = -6$, $Z = 4.85$) and lateral occipital cortex ($x = 42$, $y = -62$, $z = 12$, $Z = 3.88$).

Supplemental whole-brain parametric modulation analyses revealed a positive association between costly giving value and left DLPFC ($x = -44$, $y = 22$, $z = 32$, Z statistic = 4.13), left superior frontal gyrus ($x = -24$, $y = 30$, $z = 56$, Z statistic = 4.21), bilateral ACC (left: $x = -12$, $y = 38$, $z = 14$, Z statistic = 4.67; right: $x = 6$, $y = 44$, $z = 6$, Z statistic = 4.60), left posterior cingulate cortex ($x = -4$, $y = -32$, $z = 34$, Z statistic = 5.07), and left lateral occipital cortex ($x = -40$, $y = -76$, $z = -12$, Z statistic = 4.71; Figure 5). There was also a negative association between costly giving value and left postcentral gyrus ($x = -46$, $y = -30$, $z = 62$, Z statistic = 3.96). These associations did not differ as a function of Target, Age, or Target × Age.

Relating Functional Connectivity to Giving Behavior

To determine whether age-related differences in parametrically modulated NAcc-IFG and NAcc-OFC functional connectivity as a function of target (known others vs. strangers) might relate to age-related differences in decisions to give, difference values in parametrically
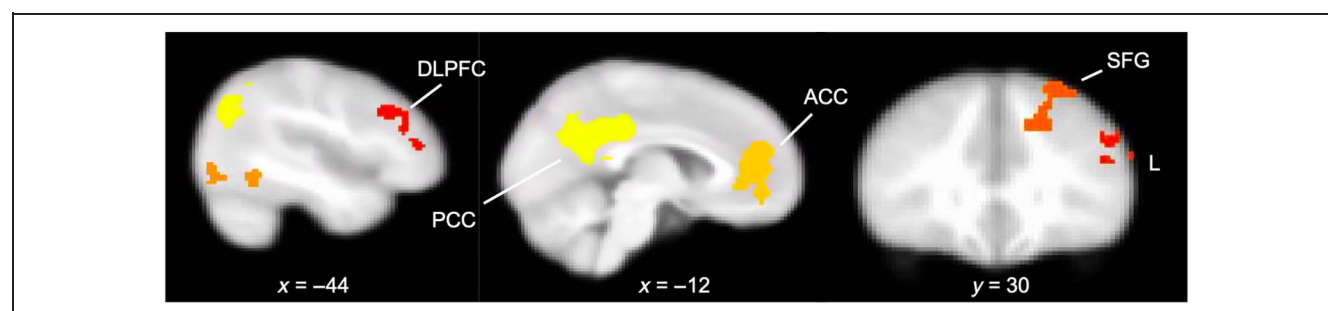

Figure 5. Whole-brain parametric modulation analyses revealed a positive correlation between giving value and activation in left DLPFC, superior frontal gyrus, bilateral ACC, left posterior cingulate cortex, and left lateral occipital cortex.

modulated NAcc-IFG and NAcc-OFC functional connectivity between known others and strangers were extracted for each participant and entered (along with their interactions with giving value and the two target contrasts) into the multilevel logistic regression model used for behavioral analyses. Separate analyses were conducted for NAcc-IFG and NAcc-OFC functional connectivity (Table 3).

Analyses revealed that differences in parametrically modulated NAcc-OFC functional connectivity between known others versus strangers were associated with the difference in the probability of giving to known others versus strangers, averaged across giving value and over and above any effects of age (Target × NAcc-OFC interaction:

$b = -0.0037$, $SE = 0.0019$, $Z = -1.992$, $p = .046$). Simple effects tests of target at low ($-1\,SD$), average, and high ($+1\,SD$) levels of NAcc-OFC functional connectivity differences indicated that the disparity in giving more to known others than strangers decreased as the difference in parametrically modulated NAcc-OFC functional connectivity between known others and strangers increased (effect of Target for low connectivity difference: $b = 0.901$, $SE = 0.128$, $Z = 7.028$, $p < .001$; effect of Target for average connectivity difference: $b = 0.741$, $SE = 0.088$, $Z = 8.381$, $p < .001$; effect of Target for high connectivity difference: $b = 0.56$, $SE = 0.122$, $Z = 4.589$, $p < .001$). In other words, individuals who evinced greater NAcc-OFC functional connectivity when considering giving to strangers (vs. known

Table 3. Results from the Multilevel Logistic Regression Analyses Estimating Likelihood to Give as a Function of Giving Value, Target, and Connectivity Difference (Difference in Value-related Connectivity between Strangers and Known Others), over and above Effects of Age

Probability of Giving	NAcc-IFG Connectivity				NAcc-OFC Connectivity			
	Estimate	SE	Z	p	Estimate	SE	Z	p
Intercept	−0.361	0.100	−3.601	**< .001**	−0.367	0.100	−3.662	**< .001**
Giving Value	0.438	0.042	10.416	**< .001**	0.437	0.042	10.341	**< .001**
Target (Stranger vs. Known Others)	0.736	0.089	8.28	**< .001**	0.741	0.088	8.381	**< .001**
Target (Family vs. Friend)	0.436	0.091	4.77	**< .001**	0.435	0.092	4.747	**< .001**
Age	0.083	0.031	2.683	**.007**	0.087	0.031	2.843	**.004**
Connectivity Difference	0.0005	0.002	−0.243	.808	−0.003	0.002	−1.240	.215
Giving Value × Target (Stranger vs. Known Others)	0.058	0.042	1.392	.164	0.060	0.042	1.422	.155
Giving Value × Age	0.063	0.013	4.875	**< .001**	0.065	0.013	5.007	**< .001**
Target (Stranger vs. Known Others) × Age	0.124	0.027	4.506	**< .001**	0.128	0.027	4.709	**< .001**
Giving Value × Target (Family vs. Friend)	0.029	0.055	0.53	.596	0.026	0.055	0.475	.635
Target (Family vs. Friend) × Age	0.025	0.029	0.876	.381	0.027	0.029	0.956	.339
Giving Value × Connectivity Difference	0.001	0.001	1.779	.075	0.001	0.001	0.926	.355
Target (Stranger vs. Known Others) × Connectivity Difference	−0.001	0.002	−0.825	.409	−0.004	0.002	−1.991	**.046**
Target (Family vs. Friend) × Connectivity Difference	0.003	0.002	1.559	.119	0.002	0.002	1.075	.282
Giving Value × Target (Stranger vs. Known Others) × Age	0.024	0.013	1.834	.067	0.024	0.013	1.773	.076
Giving Value × Target (Family vs. Friend) × Age	−0.021	0.018	−1.203	.229	−0.021	0.018	−1.169	.242
Giving Value × Target (Stranger vs. Known Others) × Connectivity Difference	−0.001	0.001	−1.211	.226	−0.001	0.001	−1.142	.254
Giving Value × Target (Family vs. Friend) × Connectivity Difference	0.001	0.001	1.175	.240	0.001	0.001	1.018	.309

Separate analyses were conducted for NAcc-IFG and NAcc-OFC connectivity differences. Acceptance of costly giving trials (1 = accept, 0 = reject or no response) for each trial was modeled as a function of Giving Value (mean-centered at 2.7), Target (using Helmert Effect Codes: Known Others vs. Stranger [Stranger = −.666, Family = .333, Friend = .333], Family vs. Friend [Friend = −.5, Stranger = 0, Family = .5]), and Age (mean-centered at 13.1 years).

Figure 6. Disparity in giving more to known others (dashed line) than strangers (solid line) decreased as the difference in value-related NAcc-OFC functional connectivity between strangers and known others increased (small, average, and large differences indicated by panels).

Difference in Value-Related NAcc-OFC Connectivity Between Strangers and Known Others (Family and Friend)
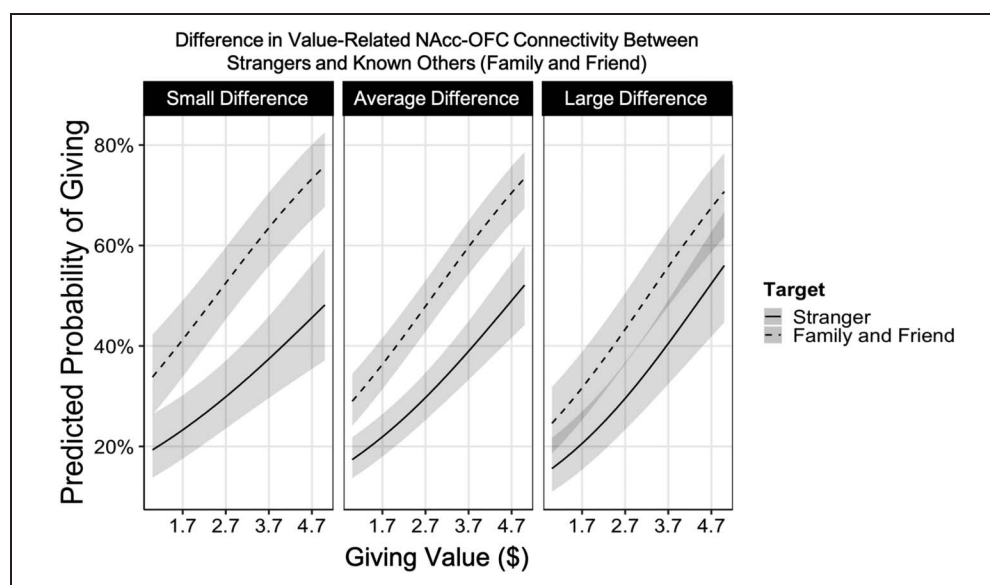
others) as giving value decreased showed smaller differentiated rates of giving based on target (i.e., more impartial giving; Figure 6).

NAcc-OFC functional connectivity was not related to RT to accept offers as a function of giving value or target, over and above any effects of age. NAcc-IFG functional connectivity was not related to giving behavior or RT, over and above any effects of age.

DISCUSSION

In the current study, we investigated how functional connectivity of corticostriatal networks track the value of prosocial decisions as a function of target recipient (caregiver, friend, stranger), how they differ across giver age, and whether they predict individual differences in giving behavior. Behaviorally, we found that individuals were more likely (and faster) to give to others as the value of the prosocial decision—the difference between the benefit to other versus cost to self—increased. The effect of this value-based giving behavior was stronger when the recipients were known (i.e., family and friends) than unknown (i.e., strangers). That is, the value threshold at which individuals decided to give was lower for known others than for stranger. Moreover, this differentiation in giving behavior as a function of value and target increased with age. These findings are consistent with existing work demonstrating that youth consider both the value and recipient of prosocial decisions (van de Groep et al., 2022; Do & Telzer, 2019). We did not find differences in value-based giving behavior between family and friends, highlighting the continued importance of close others during adolescence.

Our functional connectivity findings paralleled our behavioral findings. We found that functional connectivity between the NAcc and OFC and between the NAcc and IFG tracked the value of the giving decisions for strangers,

but not for known others, such that greater NAcc-OFC and NAcc-IFG connectivity was associated with decreasing giving value (i.e., as the difference between the benefit to others relative to cost to self gets smaller) when considering whether to give to strangers, irrespective of choice. This Value × Target effect in NAcc-OFC and NAcc-IFG functional connectivity during decision-making increased with age. In other words, when presented with an offer where the relative benefit-to-cost ratio is low, older individuals evinced stronger NAcc-OFC and NAcc-IFG functional connectivity when evaluating these decisions for strangers than for known others. In younger individuals, NAcc-OFC and NAcc-IFG functional connectivity did not track the value of giving decisions nor did it differ by target. Furthermore, regardless of age, individuals who evinced greater NAcc-OFC functional connectivity when considering giving to strangers (relative to known others) among prosocial decisions with lower value showed smaller differentiated rates of giving based on target (i.e., more impartial giving). Value-related NAcc-IFG functional connectivity was not associated with giving behavior, over and above any effects of age. It is possible that the association between NAcc-IFG connectivity and behavior may be driven by age differences and was attenuated when we controlled for age.

The NAcc, within the ventral striatum, plays a role in risk and reward processing (Braams, van Duijvenvoorde, Peper, & Crone, 2015) and is also involved in prosocial allocation of rewards to others, especially to close/known others relative to strangers (van de Groep et al., 2022; Schreuders et al., 2018; Telzer et al., 2011, 2013, 2014). The OFC has also been associated with risk and reward processing (Braams et al., 2015; Padmanabhan, Geier, Ordaz, Teslovich, & Luna, 2011; van Leijenhorst, Moor, et al., 2010; van Leijenhorst, Zanolie, et al., 2010; Galván et al., 2006) and structural connectivity between these two regions (i.e., the accumbofrontal tract) has been implicated in

value-based decision-making regarding rewards to self (Uy & Galván, 2020). Our findings suggest that this NAcc-OFC circuit is also involved in evaluating the value of prosocial decisions for others—in particular, strangers—and may play a role in mitigating biases in giving between strangers and known others, especially when the relative benefit to other versus cost to self is low. Importantly, we found that this value-based NAcc-OFC connectivity when making prosocial decisions for strangers increased with age, which is in line with research showing a protracted developmental trajectory of the accumbofrontal tract (Karlsgodt et al., 2015) and further demonstrates the increasing complexity of prosocial development. The IFG has been implicated in impulse control and its co-activation with the NAcc when evaluating giving decisions of lower value to strangers might suggest increasing engagement in regulatory processes to inhibit self-maximizing impulses during prosocial decision-making (Bellucci, Camilleri, Eickhoff, & Krueger, 2020; Crone & Fuligni, 2020). That this value- and target-related NAcc-IFG functional connectivity increased with age underscores the importance of the PFC and its connectivity with the NAcc in the development of prosocial behavior during adolescence. These findings support the formulation that prosocial offers with low giving value, especially to out-group/unknown others may reflect a more difficult decision and thus require greater cognitive and neurobiological resources to override the selfish inclination to keep rewards for oneself and/or to increase the prosocial motivation to give to others. Moreover, these findings suggest that this difficulty is compounded by who the recipient is, requiring even greater cortical resources when the recipient is unknown compared with known.

In contrast to other studies (e.g., Do & Telzer, 2019), we did not find associations between giving value or target and functional connectivity between the NAcc and regions implicated in mentalizing or social cognition (e.g., TPJ, pSTS, dorsomedial prefrontal cortex) during prosocial decision-making. This could be because of methodological differences in task design and/or differences in social cognitive demands between tasks. For example, in Do and Telzer (2019), on each trial, participants were given the choice to either keep a certain amount or to share/give a certain amount to their peers; hence, the same offer can be categorized as a self-reward or a costly give. In the current study, self-reward trials are distinct from costly giving trials, and on costly giving trials, participants could only decide between giving or not giving without an option to gain money for themselves. Therefore, on our task, the value of the costly giving offers might be more salient than other social cognitive aspects.

There are several limitations that should be considered when interpreting the results. First, our fMRI analyses focused on the decision-making process of prosocial opportunities rather than on functional connectivity differences between individuals' actual choices. This decision was motivated by the generally low rates of giving toward strangers as well as on offers with lower value, which would not only limit statistical power to detect effects, but would also limit our sample to only those who chose to give to others. Second, although the simplicity of our task facilitated the inclusion of younger individuals, it limited our ability to investigate more complex features of prosocial behavior, such as the need of the recipients, which may involve greater mentalizing or social cognition. Third, because both costs to self and gains to others were integrated in the costly giving trials, we are unable to disentangle the potential differential impact of costs versus benefits on participants' giving behavior. Fourth, although our analyses revealed age differences in giving behavior and functional connectivity in corticostriatal networks during prosocial decision-making, the cross-sectional nature of the study precludes conclusions regarding developmental change. Moreover, we did not have data on individuals between 16 and 18 years of age, so our age effects are only interpolated for this age group. Finally, although we consider this a reasonably diverse sample both ethnically and economically, the sample is skewed toward higher socioeconomic status (SES), on average, which may limit the representativeness of the sample. Future studies with samples representing a greater variety of racial/ethnic/cultural groups from a range of socioeconomic backgrounds would provide insight into potential differences and other processes in prosocial behavior as a function of culture or SES.

In conclusion, the current study contributes novel evidence for increased consideration of both the value (i.e., benefit to others relative to cost to self) and the recipients (family/caregiver, friends, and strangers) when making prosocial decisions across adolescence. Specifically, we showed that although younger individuals appeared to consider only the value of the prosocial offer when deciding to give, older individuals also considered who the recipients of the prosocial offers were and ultimately chose to give more often to known others than to strangers. These behavioral differences were paralleled by value-, target- and age-related differences in corticostriatal functional connectivity (specifically, between the NAcc and OFC/IFG) when making prosocial decisions, providing evidence that protracted development in corticostriatal regions supports the increasing complexity of prosocial development across adolescence.

Data Availability Statement

Data will be made available upon request. T-statistic maps of analyses have been uploaded to NeuroVault (https://identifiers.org/neurovault.collection:14342). Script for

behavioral analysis is available on GitHub (https://github .com/jessicauy/GIV_connectivity).

Author Contributions

Jessica P. Uy: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Visualization; Writing—Original draft; Writing—Review & editing. Andrew J. Fuligni: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing—Original draft; Writing—Review & editing. Naomi I. Eisenberger: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing— Review & editing. Eveline Crone: Writing—Review & editing. Eva H. Telzer: Writing—Review & editing. Adriana Galván: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing—Original draft; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .12; W/M = .24; M/W = .08; W/W = .56.

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