

EMPIRICAL ARTICLE

Longitudinal neural and behavioral trajectories of charity contributions across adolescence

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Abstract

This study examined the development of prosocial charity donations and neural activity in the ventral striatum when gaining rewards for self and for charity. Participants 10–22 years (95% European heritage) participated in three annual behavioral-fMRI waves (T1: $n = 160$, T2: $n = 167$, T3: $n = 175$). Behaviorally, donations to charity as measured with an economic Dictator Game increased with age. Perspective taking also increased with age. In contrast, self-gain and charity-gain enjoyment decreased with age. Ventral striatum activity was higher for rewards for self than for charity, but this difference decreased during adolescence. Latent growth curve models revealed that higher donations were associated with a smaller difference between ventral striatum activation for self and charity. These findings show longitudinal brain–donations associations in adolescence.

KEYWORDS

adolescence, fMRI, prosocial

INTRODUCTION

One of the hallmarks of human social interactions is prosocial behavior, which refers to behavior that benefits others (Carlo & Padilla-Walker, 2020). Prosocial behavior allows us to build close and reciprocal relationships, which is an important social skill during adolescence (Padilla-Walker & Carlo, 2014; Telzer, 2016). Adolescence is the formative period between childhood and adulthood during which young individuals extend their social environment outside the family context and acquire mature social goals (Blakemore & Mills, 2014; Telzer, 2016). Whereas much research has examined the development of prosocial behavior toward friends and family (Guroglu et al., 2014; Padilla-Walker et al., 2018; Telzer et al., 2010), much less is known about distant targets such as charity. Charity donation is costly for self

but beneficial for unknown others (Chierchia et al., 2020). Relational giving is often motivated by maintaining relationship status or reciprocity and may therefore be more tuned toward family and friends compared to unknown others (Brandner et al., 2021; Carlo & Padilla-Walker, 2020). Charitable giving, however, is characterized by an actual or perceived need of the recipient (Harbaugh et al., 2007). Although giving to charity does not result in direct reciprocal social connections, it may contribute to the need to be kind toward others, which is associated with several psychological, social, and health benefits (Fuligni, 2019).

Prosocial behavior is a multifaceted construct that is dependent on the relationship (e.g., known vs. unknown recipient) with the target and the need of the recipient (Carlo & Padilla-Walker, 2020). To study prosocial giving, prior studies made use of the Dictator Game, an economic game in

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which a participant divides valuable goods between self and another target, such that the other target has no influence on the distribution (Gummerum et al., 2008; Thielmann et al., 2020). When the other target is unknown, individuals give away approximately 20%–30% of valuable goods, suggesting some level of prosociality to unknown others. Giving to unknown others is relatively stable across adolescent development (Guroglu et al., 2009; van de Groep, Zanolie, & Crone, 2020).

Dictator Game giving is significantly higher when the target is a friend or family member, in which case participants donate at least half of their resources, possibly indicating equity norms in reciprocal relations (Telzer et al., 2010; van de Groep, Zanolie, & Crone, 2020). Differentiation between targets emerges during adolescence. Adolescents show age-related increases in prosocial behaviors directed toward friends (Blankenstein et al., 2019; Carlo & Padilla-Walker, 2020) but stable or decreases in prosocial behavior to unfamiliar or disliked peers (Guroglu et al., 2014; Van de Groep et al., 2022). Also, within an unknown peer group, adolescents are more prosocial to peers that are part of the in-group compared to the out-group (Do & Telzer, 2019).

These findings lead to the question how giving to charity develops in adolescence. Contrary to giving to unknown strangers, giving to charity often approaches equity norms (Spaans et al., 2020). Giving behavior sometimes exceeds equity norms, such as when the target is an individual who is in need, because of a poor immune system or COVID-19 symptoms during the COVID-19 pandemic (van de Groep, Zanolie, Green, et al., 2020). Even though prosocial giving has mostly been studied in the context of familiar others versus unknown strangers (Carlo & Padilla-Walker, 2020), it is not yet well understood how giving to charity develops across adolescence. This is an important question given that adolescents expand their social world and develop needs to more broadly contribute to society (Chierchia et al., 2020; Fuligni, 2019).

Pleasure when gaining for self and pleasure when gaining for others, also referred to as vicarious gains, can be an important driver for prosocial giving. This vicarious joy can be approximated by examining neural activity in response to rewards for self or others. Several functional Magnetic Resonance Imaging (fMRI) studies have demonstrated that the ventral striatum responds to gaining monetary or social rewards (Berridge & Kringelbach, 2015). This neural activity is dependent on several participant- and target characteristics, the first of which is age. Specifically, ventral striatum response to gaining rewards for self was found to be higher for adolescents than adults in a meta-analysis (Silverman et al., 2015). Some studies reported neural activity peaks in mid-adolescence (Schreuders, et al., 2018), but other studies reported a linear age-related decrease during adolescence (Chein et al., 2011). Finally, there are also studies reporting no age differences, but correlations with individual differences in reward seeking, possibly because these studies covered a relatively narrow age range (van Duijvenvoorde et al., 2014).

Furthermore, neural activity in the ventral striatum is higher when gaining for self than when gaining vicariously for others (Morelli et al., 2018), and these vicarious responses are dependent on the relationship strength with the vicarious target (Braams et al., 2014). Prior studies showed that developmental differences depend on the relationship with the target, such that neural responses to rewards for mothers (Braams & Crone, 2017) and stable, but not unstable best friends, peaked in mid-adolescence (Schreuders et al., 2021). Instead, for unstable best friends, vicarious gains correlated with friendship quality (Schreuders et al., 2021). Together, these findings show that ventral striatum activity is robustly related to rewards for self, but activity for vicarious rewards depends on factors including the strength of the relationship with the target. In a prior cross-sectional study that used data of the first wave of the current study, vicarious neural reward activity for charity in the scanner correlated with donations to charity outside of the scanner (Spaans et al., 2020). However, the age-related changes are not yet well understood.

Finally, prosocial behavior is dependent on individual personality factors such as empathy and social-cognitive perspective taking (Carlo & Padilla-Walker, 2020). Empathy refers to the affective and cognitive aspects of sharing emotional states, whereas social-cognitive perspective taking refers to the ability to take the perspective of others (Hawk et al., 2013). Prior studies showed that social-cognitive perspective-taking increases across adolescence (Dumontheil et al., 2010; Hawk et al., 2013). It has been suggested that perspective-taking is an important developmental process that mediates the relationship between age and giving in an Ultimatum Game, a strategic economic game in which the target can reject an offer (Guroglu et al., 2011). Although studies remain inconclusive on the developmental trajectory of empathy (Overgaaauw et al., 2017), multiple studies revealed empathy to be an important correlate of prosocial behavior (Van der Graaff et al., 2018). Other factors that may motivate charitable donations are the self-reported enjoyment associated with gains for self and charity (Braams et al., 2014; Spaans et al., 2020), as well as the subjective importance one assigns to charity (Carlo & Padilla-Walker, 2020), but it remains elusive how these factors change within individuals over time and how this relates to longitudinal changes in reward-related neural activation and charitable donations.

Taken together, giving to charity can be considered an altruistic form of giving because it has no direct personal benefit (Carlo & Padilla-Walker, 2020), but how prosocial behavior toward charity develops from childhood to adulthood remains inconclusive. In previous longitudinal neuroimaging studies, self-reported prosocial behaviors peaked in late adolescence (Blankenstein et al., 2019). Therefore, in this study, we used a three-wave accelerated longitudinal brain-behavior design to examine whether gains for self and vicarious gains for charity show separable neurodevelopmental patterns and whether these predict donating to charity outside of the scanner.

Preregistered hypotheses

All of the hypotheses included in the current study were preregistered here: <https://osf.io/8gc6x/>, see <https://osf.io/h7u46/> for the project page. Deviations from the preregistration are described in Appendix S1. For the current study, we split our preregistered hypotheses into three separate aims. The first aim was to examine the developmental neural pattern of vicariously gaining for self and charity. We expected that activation for self-gain within the Nucleus Accumbens (NAcc; defined as a priori region-of-interest [ROI] within the ventral striatum) would peak in mid-adolescence (Braams et al., 2015). A prior study using a vicarious gain paradigm showed NAcc activity for gains relative to no-gains for parents, but no vicarious NAcc activity for gains relative to no-gains for strangers (Brandner et al., 2021). Here, we test the vicarious reward activity in NAcc for charity as these recipients are more distant than family members (Brandner et al., 2021) or friends (Braams & Crone, 2017), but remain personally meaningful (Carlo & Padilla-Walker, 2020). Concerning the developmental patterns, two prior studies reported adolescents-specific peaks in neural activity in NAcc for vicarious gains for mothers (Braams & Crone, 2017) and stable best friends (Schreuders et al., 2021). However, there is currently no empirical evidence concerning the developmental trajectory for more distant, but personally relevant charity targets. Therefore, we explored the developmental trajectory for neural responses to vicarious charity gains in addition to the developmental trajectory of gains for self and gains for both parties.

The second aim was to investigate the development of behavioral patterns of prosociality over the course of adolescence outside of the scanner (i.e., charitable giving, perspective taking, empathic concern, enjoyment, and charity importance). We expected that prosocial donations in a Dictator Game and self-perceived enjoyment of gaining money for self and charity would show a peak in mid-to-late-adolescence (Blankenstein et al., 2019). We expected that age-related changes in perspective taking across adolescence would increase with age (Blankenstein et al., 2019). We expected empathic concern to show no age related changes (Gruhn et al., 2008).

The third aim was to study the associations between initial levels and change rates of neural activity for self versus charity gains, and associations between initial levels and change rates interrelations with perspective taking, charity donations and pleasure of self-gain (other preregistered variables of aim 2 are described in Appendix S2). We focused specifically on these variables based on cross-sectional results at the first time-point, showing less neural differentiation between self-gain and charity-gain for individuals who scored higher on perspective taking and those who donated more to charity, while the reversed relation was found for self-reported pleasure of self-gain (Spaans et al., 2020). We hypothesized that individual differences in the level (i.e., intercept) and change (i.e., linear slope) of perspective taking, donation behavior and pleasure of self-gain would be

related to individual differences in the level (i.e., intercept) and change (i.e., linear slope) in striatal activity when contrasting self-gains with charity-gains.

METHODS

Participants and procedure

This study used an accelerated longitudinal design with three time points, separated by approximately 13 months between waves. The full sample consisted of 160 participants between the ages of 11 and 21 (86 females) at the first time point, 167 participants between ages 10 and 22 (84 females) at the second time point, and 175 participants between ages 11 and 24 (90 females) at the third time point (see Table 1 for demographics, Figure 1 for an overview across ages and genders, and Figure S1: Appendix S2 for a flow chart for inclusion and attrition). To increase sample size at the edges of our age distribution, at timepoint 2, 15 young adolescents were newly recruited (10–12 years, $M = 11.7$, $SD = .48$). At timepoint 3, 14 young adults were newly recruited (21–24 years, $M = 22.85$, $SD = .59$).

The majority of participants ($N = 180$; 95.2%) were born in the Netherlands, and participants born elsewhere reported European heritage. There were 41 participants where one ($N = 34$) or both ($N = 7$) parents were born abroad, of which 58% in other European countries. Parents of participants reported gross annual family income (11.6% declined to disclose), with 15 families reporting an annual income lower than €31,000 (7.9%), whereas 65 families reported an annual income greater than €76,000 (34.4%) (Table 1). Table 1 presents the number of participants included in the study, the number of participants who completed the MRI scan, and the number of participants included in the MRI analyses (after data quality check; see MRI procedures).

During each data collection wave, informed consent was obtained from participants (and their parents in case of minors). All newly recruited participants were right-handed and had normal or corrected-to-normal vision. Participants were screened with questionnaires on three separate occasions (once by phone-call, once by e-mail and once on the testing-day) for MRI contraindications and for (history of) neurological and/or psychiatric disorders. All anatomical MRI scans were reviewed by a radiologist at the first and second time point. Due to procedural changes at the imaging facility, scans collected at the third time point were not reviewed. No anomalous findings were reported for scans reviewed by the radiologist. The study and all of its procedures were approved by the ethical commission board of Leiden University Medical Center.

For their participation in the full experiment (that includes tasks that are part of a larger project), minors (10–17 years old) were paid 40 euros and adults (18 years and older) were paid 50 euros. At the end of the research day, participants and charity received extra money for the completion of the COSY task and the One-Shot Charity Dictator

TABLE 1 Sample characteristics.

(sub)group	N	N behavior	N MRI-inclusion	Gender	Mean age	Age range	Family income	Country of birth
T1	160	160	157	86 female (45.5%)	15.96	11.03–21.21		
T2	167	152	140	84 female (44.4%)	16.66	10.74–22.39		
T3	175	145	135	90 female (47.6%)	18.14	11.83–24.11		
Full longitudinal sample	189	189	184	96 female (50.8%)	17.08	11.03–24.11	7.9% < €31.000 7.4% €31.000–€46.000 17.4% €46.000–€61.000 21.1% €61.000–€76.000 34.4% > €76.000 11.6% did not report	95% Netherlands, 5% other ^a

^aAmerica, Brunei, China, Germany, Dutch Antilles, Saudi-Arabia, Spain, Turkey, South-Africa (all $N = 1$). N refers to all participants who were included in the study at each time point and completed online assessments (IRI: perspective-taking and empathy; two participants at T2 and one participant at T3 had incomplete IRI data). N behavior refers to all valid data of participants who completed the MRI task, enjoyment ratings and charity donations (enjoyment ratings; at T2 1 participant had invalid data), N MRI refers to all participants who were included in the MRI analyses after quality control (see methods section). For fMRI, 99 participants had valid data at three scans, 50 participants had valid data at two scans and 35 participants had valid data at one scan, leading to 184 unique participants. In [Figure S1](#): Appendix S2 we present the flow chart for inclusion and attrition at all time points for all measures.

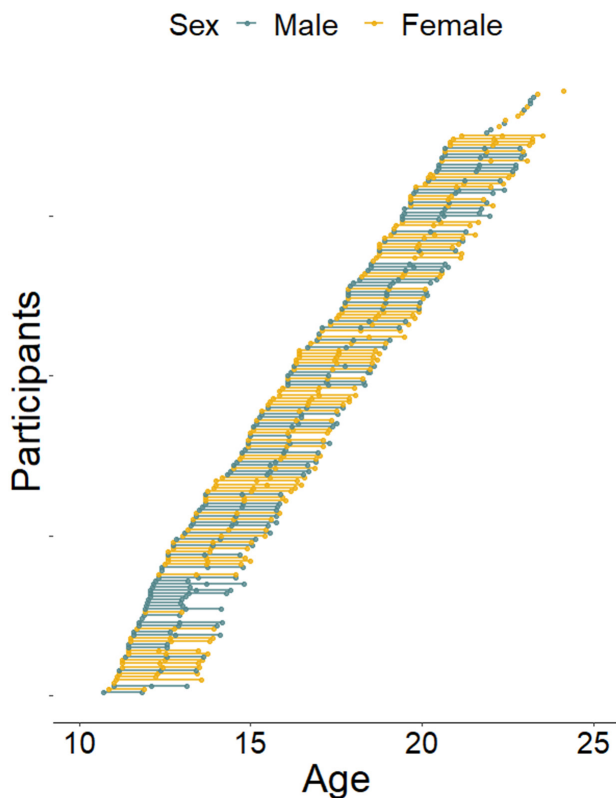


FIGURE 1 This figure shows the inclusion of participants in the study organized by age and gender, where each dot represents a time point and each line a longitudinal measurement. More information about the sample can be found in [Table 1](#) and the flow chart for inclusion in [Figure S1](#): Appendix S2.

Game, which ranged from €1–5 extra. Amounts to be paid out to the participant were paid out directly, amounts paid out to charity were tallied and donated to the charity at the end of the study.

Experimental paradigms

COSY fMRI-task

To investigate neural responses to vicarious gains for charity independent of behavior, we used a false-choice fMRI-task called the COSY (Charity or Self Yield) task, which has previously been reported in a separate adult sample (Spaans et al., 2019) and in a separate report of the cross-sectional findings of the first time point of the current study (Spaans et al., 2020). Participants could choose their preferred charity from a list of 10 options of charities in the Netherlands. Participants were informed that they could earn money for themselves and the self-chosen charity by selecting one of two options.

On each trial, participants were presented with two curtains. Participants could choose which of the curtains to open with an index or middle finger button press. Participants had 2000 ms response time. Following response, an onscreen hand indicated which option was selected. Next, the chosen curtain opened in a fluid animation (14 frames presented for 50 ms each), with the outcomes fully visible from the seventh frame onwards. The outcomes were either a division of 4 euro stakes between parties, or a division of 2 euro stakes between parties. In case of a division of 4 euros (high magnitude), this could result in the following outcomes: Self High [€ 4 self, € 0 charity]; Charity High [€ 0 self, € 4 charity], or Both High [both € 2]. In case of a division of 2 Euros (low magnitude), this could result in the following outcomes: Self Low [€ 2 self, € 0 charity]; Charity Low [€ 0 self, € 2 charity]; or Both Low [both € 1]. In addition to these gain trials, we included a zero gain baseline condition Both No Gain [both € 0:]. A black jitter screen (0–880 ms) was presented after the outcome presentation, marking the end of a trial. [Figure 2](#) shows a graphical presentation of the trial sequence.



FIGURE 2 This figure shows the basic trial flow of the zero-sum COSY task. At trial onset, a black screen was presented with a jittered duration between 0 and 8800 ms. subsequently, a fixation cross was shown for 500 ms, followed by the response selection screen for 2000 ms. After a response was made, an animation was shown onscreen for the remainder of the 2000 ms. Then, the next 14 screens showed a fluid animation of the hand pulling the curtain open and revealing the outcome (shown here; self € 2, charity € 2). The feedback remained onscreen for 2300 ms. In case participants failed to respond within the timeframe of the response selection, no animation occurred and a screen with the phrase “Too Late!” was shown for 3000 ms. Outcome conditions are displayed in the table below the trial flow.

The task consisted of 105 trials in total, with 15 presentations of each outcome condition. The order of trials was optimized for our design using the program Optseq2 (Dale, 1999). The task was presented in two separate 6-min blocks with a short break in between. The blocks consisted of 55 and 50 trials. At the end of the session, money earned was paid out to participants and charity. Participants were explained that they would receive the average of the outcome of three randomly selected trials in the task. In reality, the selection was pseudo-randomized to ensure that participants received pay-out for both parties, with amounts for both self as well as for charity, of € 1–€ 2 in steps of € 0.50. The exact amounts were counterbalanced across participants.

Pleasure ratings

After the fMRI session and completion of the COSY-task, participants rated their subjective enjoyment on a 1–7 scale when gaining for self and charity for all outcome options (€ 0, € 1, € 2, and € 4). Averages for each time point are presented in Table 2.

Perceived importance and knowledge charity

Participants rated the perceived importance of chosen charities on a scale from 1 to 7, as well as knowledge of the charity on a scale from 1 to 7. Averages for each time point are presented in Table 2.

Empathic concern and perspective taking

Empathic concern and perspective taking were assessed online 1 week prior to the day of the MRI scan using the empathic concern and perspective taking subscales of the Interpersonal Reactivity Index (IRI) questionnaire (Hawk et al., 2013). The perspective-taking scale consisted of six items. A typical item from this scale is “I sometimes try to understand my friends better by imagining how things look from their perspective.” The empathic concern scale consisted of six items. A typical item from this scale is “I often have tender, concerned feelings for people less fortunate than me.” Items were rated using a 5-point Likert scale from 0 (does not at all apply to me) to 4 (completely applies to me). For each subscale, the mean of the six items was computed for analyses. Chronbach's alpha values ranged between .718 and .770 for the empathic concern subscale and between .749 and .825 for the perspective taking subscale across waves.

Behavioral donating task

Finally, at the end of the full session, participants played a One-shot Dictator game for the charity of their choice. Participants could distribute 600 valuable coins between themselves and the charity by selecting one of seven possible divisions on a scale of 1–7 (1 = 600 for self, 0 for charity; 2 = 500 for self, 100 for charity; 3 = 400 for self, 200 for charity; 4 = 300 for self, 300 for charity; 5 = 200 for self; 400 for charity; 6 = 100 for self; 500 for charity; 7 = 0 for self; 600 for

TABLE 2 Averages of enjoyment ratings for self and charity for 0, 1, 2, and 4 Euros for all three time points.

	Self € 0	Self € 1	Self € 2	Self € 4	Charity € 0	Charity € 1	Charity € 2	Charity € 4	Importance charity	Knowledge charity
T1	2.97	4.74	5.32	6.01	2.54	5.10	5.63	6.13	5.83	4.59
T2	3.05	4.36	5.09	5.86	2.65	4.87	5.45	6.05	5.55	4.36
T3	3.02	4.29	4.94	5.66	2.54	4.79	5.35	5.99	5.51	4.32

charity). Participants were not informed about the value of the coins before their choice, but afterwards the payout was 100 coins = € 0.50, resulting in a total payout ranging from € 0 to 3. Participants were informed that the pay-out was given to the charities; there was no deception in this study. In order to prevent socially desirable behavior, it was stressed that their chosen distribution would remain completely anonymous. To ensure anonymity, and to prevent participants adapting their behavior based on the monetary outcomes on the fMRI task, the sum of both the fMRI task and the behavioral One-Shot Charity Dictator Game was paid out at the very end of the experiment. Only the total sum of the money earned in the COSY-game (€1–€2), counterbalanced and the Dictator Game (€0–€3) together was displayed on the screen. Thus, in total, participants could earn a range of €1–€5 for themselves and charity at each timepoint.

MRI data acquisition

MRI data was acquired using a Philips 3.0 Tesla scanner with a standard whole-head coil attached. For functional MRI scans, we used T2*-weighted Echo-Planar Imaging (TR = 2.2 s, TE = 30 ms, FOV: 220 × 220 × 111.65 mm, voxel size = 2.75 × 2.75 × 2.75). Functional scans consisted of two runs with 175 and 169 volumes, respectively. The task was displayed on a screen placed behind the scanner, which participants were able to see through a mirror that was attached to the head coil. The functional task lasted for about 13 minutes in total. In addition to fMRI sequences, we collected structural images for anatomical reference (high-resolution 3D T1), TR = 9.751 ms, TE = 4.59 ms, FOV = 224 × 177 × 168 mm. Participants' head movements were restricted by using foam triangles to limit available space in the coil.

MRI data analyses

Preprocessing

We used the software package SPM12 (Wellcome Trust Centre for Neuroimaging, London) to preprocess and analyze all MRI-data. At T1 160 participants were included in the MRI session, at T2 152 participants and at T3 145 participants (Table 1). For fMRI analyses, three participants at T1, 12 participants at T2 and 10 participants at T3 were excluded for framewise displacement motion higher than 3 mm (T1: 2; T2: 10; T3: 10) or because of technical problems and/or artifacts during data collection (T1: 1; T2:

2; T3: 0). The final sample for fMRI analyses was therefore 157 participants at T1, 140 participants at T2 and 135 participants at T3. In total, 99 participants had valid data for all three scans, 50 participants had valid data for two scans, and 35 participants had valid data for one scan (184 participants in total).

For preprocessing, all images were corrected them for slice timing acquisition and differences in rigid body motion. Structural and functional volumes were spatially normalized to T1 templates by an algorithm using a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. Then, all volumes were resampled to voxels of 3 × 3 × 3 mm. We based our templates on the MNI305 stereotaxic space (Cocosco et al., 1997). Finally, we used an isotropic Gaussian Kernel (6 mm FWHM) to spatially smooth the data.

fMRI-analysis

To calculate the relevant contrasts, we modeled the fMRI time series convolved with the hemodynamic response function with events that corresponded to the outcome phase of a trial. Specifically, the events of interest that we modeled were the outcome conditions “Self High,” “Self Low,” “Charity High,” “Charity Low,” “Both High,” “Both Low,” and “Both No Gain.” These events were time-locked to the frame on which participants could observe the outcome (seventh frame of the curtain-opening animation) with zero-duration. Trials with no response from the participants were coded as “Missing” and modeled separately as invalid trials, and were not included in further analyses. The modeled events were added as regressors in a general linear model, along with six motion regressors and a basic set of cosine functions that high-pass filtered the data and a covariate for session effects. The least squares parameter estimates of height of the best-fitting canonical HRF for each condition were used in pairwise contrasts. The resulting contrast images, computed on a subject-by-subject basis, were submitted to random-effects group analyses. Contrast analyses for each Beneficiary (Self, Both, Charity) relative to Both No Gain were performed using *t*-tests. For the whole brain fMRI analyses, we collapsed high- and low-magnitude trials to focus the comparisons specifically on gains in the three conditions (Self, Both, Charity) relative to Both No gain trials.

All images were thresholded by using a False Discovery Rate (FDR) cluster correction (initial threshold at $p < .001$).

fMRI region-of-interest analysis

Consistent with the preregistration, we extracted the NAcc region of interest for vicarious gaining for self, charity and both beneficiaries and conducted our follow-up analyses on this region. We used an anatomical mask of the left and right NAcc extracted from the Harvard–Oxford subcortical atlas, thresholded at 40%. The coordinates were $x = -9.57$, $y = 11.70$, $z = -7.10$ (left NAcc, 28 voxels) and $x = 9.45$, $y = 12.60$, $z = -6.69$ (right NAcc, 26 voxels). We performed the ROI analyses using the Marsbar toolbox (Brett et al., 2002). We specifically focused on the NAcc because prior studies indicated this part of the ventral striatum as a key region in reward processing (Braams et al., 2015).

General condition effects

General condition effects were examined in a repeated measures ANOVA for the NAcc ROI. The Condition (Self, Both, Charity) \times Magnitude (high/low) \times Time (3) repeated measures ANOVA was performed on the structurally defined NAcc-ROI activation. All six conditions were referenced to the Both-No-Gain baseline.

Statistical analyses univariate and multivariate growth curve models

For our first and second aim we conducted a series of univariate latent growth curve models (LGMs) in Mplus version 8 (Muthén & Muthén, 1998) to determine the developmental shape of neural activity of self gain and vicarious gain for charity (aim 1) and the development of donations to charity, empathic concern, perspective taking, enjoyment ratings and participants' perceived importance of the charity (aim 2).

To account for the large age heterogeneity at each wave (which is inherent to the accelerated longitudinal design of this study), we applied the TSCORES option in Mplus to scale the factor loading of each participant based on his/her actual age at each measurement (for more information see Mehta & West, 2000; Appendix S2).

For our third aim, we conducted a series of multivariate LGMs to test the longitudinal associations between intercept and slopes of striatal activation and behavioral development. Specifically, we tested whether the intercept and linear slopes of the behavioral measures (i.e., charitable donations, perspective taking, empathic concern, importance of charity, enjoyment ratings for self) correlated with the intercept and linear slope of a difference score of the Self Gain > Charity Gain fMRI contrast. Additionally, we examined whether the intercept of behavioral measures (charity donations, perspective taking, empathic concern, importance of charity, enjoyment ratings for self), predicted change in activation in the Self Gain – Charity Gain contrast, and vice versa,

whether the intercept of activation in the Self Gain – Charity Gain contrast predicted change in behavioral measures. We were interested in both mean level intercepts and slopes to capture the mean level development across the entire sample (i.e., modeled with fixed effects). In addition, we allowed the intercept and slopes to vary between people (i.e., modeled with random effects for intercept and slopes) to examine whether individual differences in self-report measures predicted individual differences in NAcc activity for Self-Gain > Charity Gain.

We focused on Self Gain > Charity Gain contrast because it most clearly captures the balance between valuing outcomes for self to valuing outcomes for others, similar to behavior in the Dictator Game where outcomes for self are weighed against outcomes for others (Gummerum et al., 2008; Thielmann et al., 2020). Higher similarity between Self-gain and Charity-Gain reflects stronger similarity in valuing outcomes for self and charity.

RESULTS

The results are organized in three sections. First, we show neural responses for Self-Gain > Both-No-Gain, Both-Gain > Both-No-Gain and Charity-Gain > Both-No-Gain using whole brain analyses at three time points averaged across all participants. Second, for each developmental measure we describe whether the dependent variables are best explained by null (i.e., intercept only), linear, or quadratic age models. Third, we report the results of the multivariate LGMs to test the intercept–slope associations using LGMs.

Neural responses for Self Gain, Charity Gain and Both Gain

We computed whole brain analyses for the contrasts Self-Gain > Both-No-Gain, Both-Gain > Both-No-Gain, and Charity-Gain > Both-No-Gain, separately for each time point. Results of the first time point were previously described in Spaans et al. (2020). As can be seen in Figure 3a, Self-Gain > Both-No-Gain resulted in activity in the ventral striatum, including the NAcc, at all timepoints. Both-Gain > Both-No-Gain resulted in activity in the ventral striatum at Time points 1 and 2. At each time point, the whole brain contrast for Charity-Gain > Both-No-Gain did not result in consistent activity in the ventral striatum.

A full list of all other activations is reported in Tables S1–S3 for waves 1, 2, and 3 respectively, and in Neurovault (see <https://neurovault.org/collections/9665/>).

Repeated-measures ANOVA for task effects

To examine the general effects of conditions on NAcc activity, an initial Condition (Self, Both, Charity) \times Magnitude

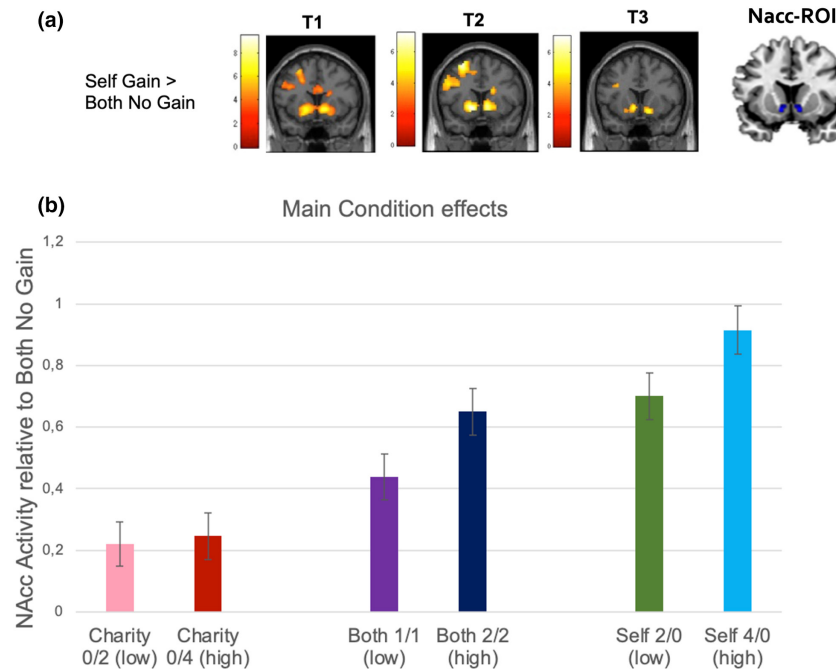


FIGURE 3 (a) From left to right: Activation patterns in the NAcc for Self-Gain > Both-No-Gain at each of the three time-points. Coronal view at coordinates, $y = 12$. Activation displayed is FDR cluster corrected. NAcc-ROI is derived from the Harvard-Oxford subcortical atlas (b). Average activity across all time points for each condition relative to the no-gain baseline. The first number in the horizontal labels indicates gain for self and the second number gains for charity.

(high/low) \times Time (3) repeated-measures ANOVA was performed on the structurally defined NAcc-ROI activation. This ANOVA showed a main effect of Condition, $F(2, 392) = 24.60$, $p < .001$, confirming higher NAcc activation for Self-Gain relative to Both-Gain, $F(1, 98) = 8.78$, $p < .001$, and Self-Gain relative to Charity-Gain, $F(1, 98) = 43.33$, $p < .001$. NAcc activation for Both-Gain was also significantly higher than for Charity-Gain, $F(1, 98) = 18.86$, $p < .001$. There was also a main effect of Magnitude, $F(1, 98) = 7.01$, $p = .009$, confirming higher NAcc activation for high-magnitude compared to low-magnitude trials. There was no significant Condition \times Magnitude interaction, $F(1, 196) = 1.23$, $p = .30$ (Figure 3b).

Univariate latent growth curve models

Next, we tested developmental change patterns using LGMs for each of the six Condition and Magnitude conditions, referenced to the Both-No-Gain baseline. Tables 3 and 4 show the ICC value and the AIC/BIC outcomes for the activation contrasts and behavioral variables, respectively.

Developmental patterns of neural self and vicarious gains

We tested null (including a fixed and random intercept only model), linear (including a fixed and random linear slope model), and quadratic (including a fixed and random quadratic slope model) for all six task conditions on the NAcc-ROI

activation to provide a comprehensive overview of developmental patterns reference to the both no gain condition (Table 3; Figure 4). To provide a full overview for all conditions, we present the results from all conditions separately. Results revealed that NAcc activity for Self-Gain-High-Magnitude, Self-Gain-Low-Magnitude, Both-Gain-High-Magnitude and Both-Gain-Low-Magnitude all showed a linear decrease over time, based on the lowest AIC/BIC values. The relationships between striatal activity for Charity-Gain-Low-Magnitude and age, and Charity-Gain-High-Magnitude and age were best explained by a null model, suggesting no age-related changes. There were no significant quadratic age models.

Developmental patterns self-report variables

In addition to the contrast conditions during vicarious gains, we tested the null, linear, and quadratic age relations for self-report variables (Table 4; Figure 5). First, the relation between donation behavior in the Dictator game and age was best described by a linear increasing model. Second, the relationship between perspective taking and age was best described by an increasing linear model, whereas the relationship between empathic concern and age was best described by the null model.

Third, both perceived enjoyment for self-gains and age, and perceived enjoyment for charity-gains and age were best described by a linear decreasing model. The relationship between the perceived enjoyment for gains for both self and charity was best described by the null model.

TABLE 3 ICC values, N values, and fit parameters for intercept only, linear and quadratic models for all activation contrasts in NAcc.

Measure	ICC ^a	N (T1, T2, T3)	Age model								
			Intercept only			Linear			Quadratic		
			AIC	BIC	SSABIC	AIC	BIC	SSABIC	AIC	BIC	SSABIC
SelfGainHigh – BothNoGain	.049	159, 140, 135	1702.169	1712.231	1702.729	1720.546	1701.322	1720.546	1965.387	1987.816	1965.646
SelfGainLow – BothNoGain	.099	159, 140, 135	1629.697	1637.309	1627.808	1636.652	1617.428	1636.652	1617.826	1640.255	1618.085
CharityGainHigh – BothNoGain	.079	159, 140, 135	1635.327	1644.939	1635.438	1656.115	1636.891	1656.115	1687.206	1709.634	1687.464
CharityGainLow – BothNoGain	.004	159, 140, 135	1600.914	1610.526	1601.025	1623.895	1604.671	1623.895	1823.870	1846.298	1824.128
BothGainHigh – BothNoGain	.221	159, 140, 135	1647.587	1657.199	1647.698	1662.542	1643.318	1662.542	1645.098	1667.536	1645.356
BothGainLow – BothNoGain	.138	159, 140, 135	1618.713	1628.325	1618.824	1633.218	1613.994	1633.218	1638.157	1660.585	1638.416
SelfGain – CharityGain	.333	159, 140, 135	1461.086	1470.698	1461.197	1477.791	1458.567	1477.791	1465.001	1497.041	1465.369

Note: Values in bold indicate the best fitting model. In case AIC and BIC were not consistently different between models, SSA/BIC was inspected to determine the best model fit.

^aICCs were computed in SPSS.

TABLE 4 ICC values, N values, and fit parameters for intercept only, linear and quadratic models for all variables.

Measure	ICC ^a	N (T1, T2, T3)	Age model								
			Intercept only			Linear			Quadratic		
			AIC	BIC	SSABIC	AIC	BIC	SSABIC	AIC	BIC	SSABIC
Perspective Taking	.846	160, 165, 174	828.015	837.740	838.232	818.281	798.830	818.281	1109.767	1132.460	1110.287
Empathic Concern	.830	160, 165, 174	805.789	815.514	806.011	826.773	807.322	826.773	809.140	831.832	809.659
Charity Donations	.771	160, 151, 145	1025.806	1035.457	1025.965	1028.122	1008.799	1028.122	1087.505	1110.047	1087.876
Importance of Charity	.744	160, 151, 145	1289.644	1299.305	1289.803	1290.062	1270.740	1290.062	1617.448	1639.990	1617.819
Self Gain Enjoyment	.639	160, 151, 145	1339.320	1348.981	1339.479	1353.085	1333.763	1353.085	1335.450	1357.993	1335.822
Charity Gain Enjoyment	.713	160, 151, 145	1220.660	1230.321	1220.819	1238.551	1219.228	1238.551	1320.288	1342.830	1320.569
Both Gain Enjoyment	.561	160, 151, 145	1367.810	1377.471	1367.969	1387.770	1368.448	1387.770	1368.380	1390.923	1368.752

Note: Bold values indicate the best fitting model. In case AIC and BIC were not consistently different between models, SSA/BIC was inspected to determine the best model fit.

^aICCs were computed in SPSS.

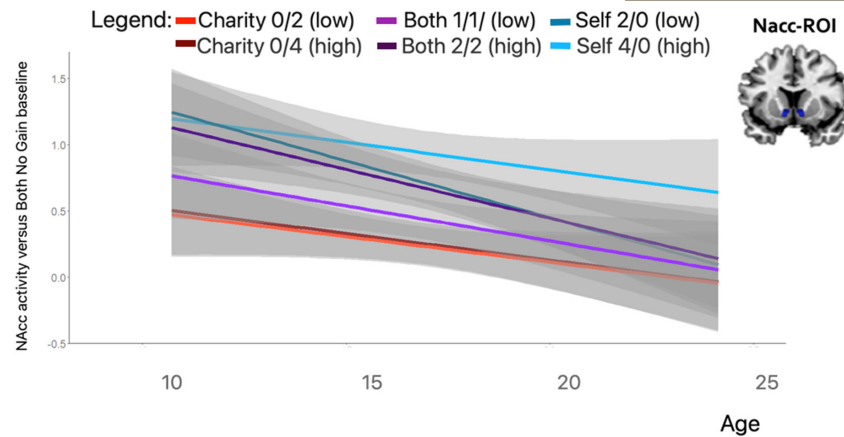


FIGURE 4 This figure shows the six condition lines with age on the x-axis, plus an image of the ROI in the ventral striatum (the NAcc, specifically). All conditions are presented relative to the Both-No-Gain Condition. Developmental decreases were observed for Self-gain High, Self-Gain Low, Both-Gain High, and Both-Gain Low. The conditions Charity-Gain High and Charity Gain Low showed no developmental effects.

Finally, the relationship between the perceived importance of charity and age was best described by a linear decreasing model.

Multivariate growth curve models

Following the preregistered hypotheses, we conducted a series of multivariate growth curve models to examine how self-report measures and donation intercepts and slopes were related to intercepts and slopes of the NAcc-ROI difference scores: Self-Gain > Charity-Gain.

For the interpretation of the intercept–slope and slope–slope associations between self-reported measures and NAcc-ROI activity the sign of the linear slope (increasing or decreasing) of both variables (e.g., Self-Gain > Charity-Gain and behavioral measures) is important. In all cases, the linear slope of the NAcc difference scores was negative. This indicates that, on average, the difference between activation for Self-Gain > Charity-Gain decreased within individuals over time, showing more similarity between valuing outcomes for self and charity. The linear slopes of charity donations, perspective taking and empathy were positive (i.e., increasing over time). The linear slopes of self-gain enjoyment, charity-gain enjoyment and charity-importance were negative (i.e., decreasing over time). The fit indices of null, linear and quadratic LGMs are presented in Table 4. Table 5 shows all coefficients and significance values.

Charity donations and self-gain versus charity gain

The LGMs tested for relations between behavior and behavior at the start (intercept) and the change over time (slopes). First, we tested for the relation between donations and NAcc activity for Self-gain > Charity-Gain. As can be seen in Table 5 and Figure 6, the analysis for charity donation and NAcc activity for Self-gain > Charity-Gain resulted in

a significant intercept–intercept relation: Participants who showed higher charity donations, showed more similarity in the Self Gain > Charity Gain contrast ($b = -1.069, p = .038$). As can be seen in Figure 6a, specifically individuals who donated less showed stronger Self-relative to Charity-Gain NAcc activity. Next, we addressed the question whether intercept donating behavior was associated with neural activity changes over time. There was indeed a significant intercept–donation and slope–NAcc activity relation. Figure 6b shows that there was an inverse relation: those adolescents who started with higher charity donations (i.e., the intercept) showed a relative increase (i.e., linear slope) in similarity in NAcc Self Gain > Charity Gain over time, $b = 0.644, p < .001$. Finally, there was a significant positive slope–slope association ($b = 0.388, p = .011$), showing that increases in donation over time were associated with increases in NAcc Self Gain > Charity Gain over time. These findings show that participants who started with more extreme scores became more similar to the general group over time.

Perspective taking and self-gain versus charity gain

We addressed whether NAcc activity for Self-Gain > Charity-Gain showed similar relations with other preregistered behavioral measures. The results for perspective taking were partly similar to the patterns observed for donation behavior. As can be seen in Table 5, the analysis for perspective taking and NAcc activity for Self-Gain > Charity-Gain resulted in a significant intercept–perspective taking and slope–NAcc activity relation. Participants who started with lower perspective taking showed relatively more similarity in the Self Gain – Charity Gain contrast over time relative to adolescents with higher perspective taking ($b = 0.541, p < .001$). Again, these findings showed that participants who started with more extreme scores became more similar to the general group over time.

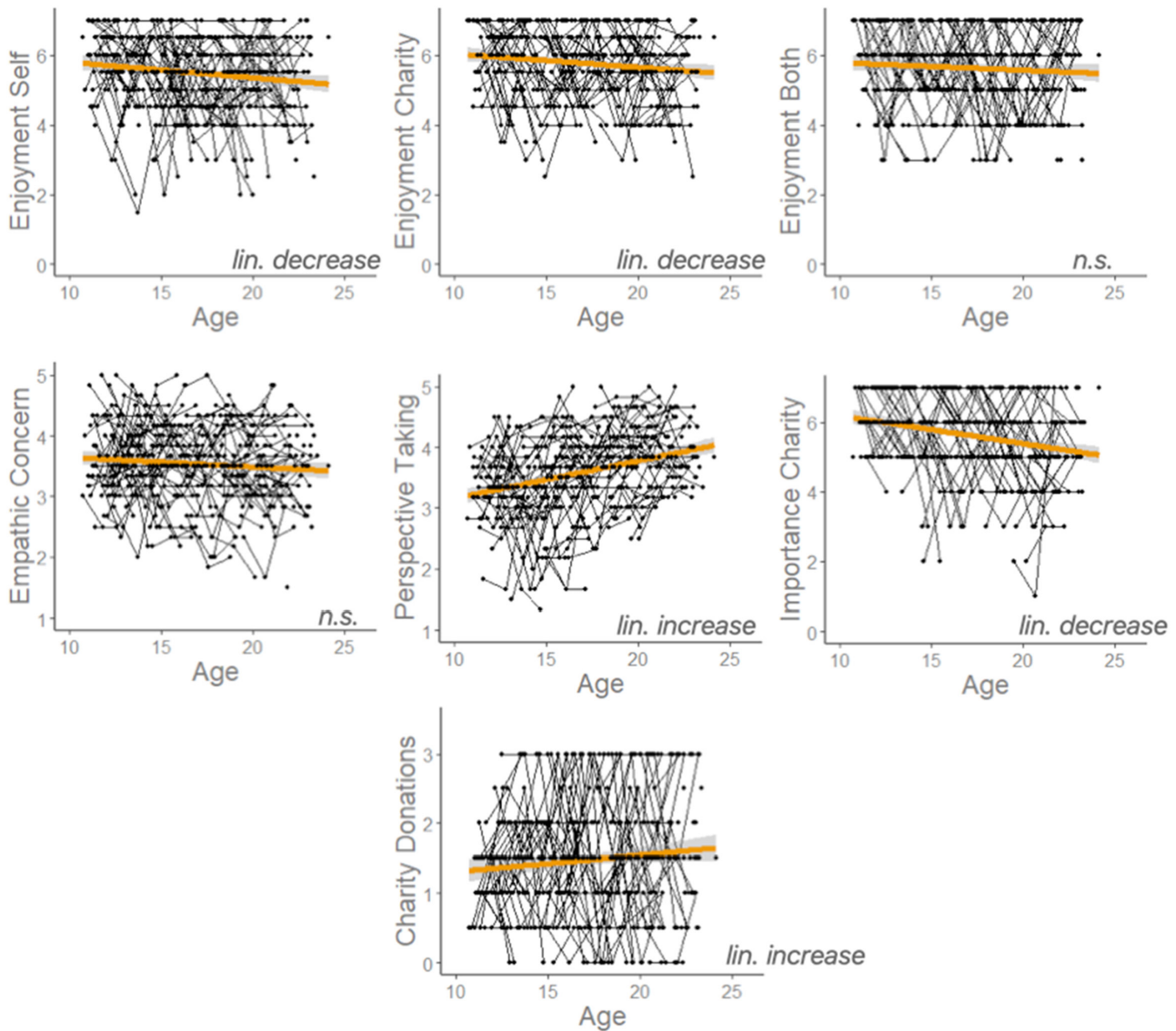


FIGURE 5 From left to right, first row: developmental patterns of perceived enjoyment for self gains, charity gains and both gains; second row: developmental patterns of IRI empathic concern, IRI perspective taking, and perceived importance of the chosen charity; third row: Charity donations in Euro's (note that the scale is adjusted to equivalents of Euro's relative to Spaans et al., 2020). Trend line shows the mean, gray outline shows the 95% confidence interval of the mean. IRI perspective taking and charity donations increased with age. Self enjoyment, charity enjoyment and charity importance decreased with age. Both gain importance and IRI empathy showed no developmental effects.

The intercepts and slopes of perspective taking and activation in the Self-Gain > Charity-Gain contrast were not significantly associated (all p 's > .281).

Self-enjoyment and self-gain versus charity gain

Finally, we addressed whether results for subjective self-gain enjoyment would show an opposite effect to donations and perspective taking. Indeed, as can be seen in Table 5, the analysis for self-enjoyment and NAcc activity for Self-Gain > Charity-Gain resulted in a significant positive intercept–intercept relation. This relation showed that adolescents who reported a higher perceived enjoyment for self gains showed a larger difference in activation in the

Self-Gain > Charity-Gain contrast ($b = 2.141, p = .027$), consistent with the notion that subjective pleasure for gaining for self is related to higher Self-Gain NAcc activity. There was a significant opposite intercept–self enjoyment and slope–NAcc activity relation: Those adolescents with a relatively lower intercept of perceived enjoyment for self gains showed more differentiation in the Self-Gain > Charity-Gain contrast over time compared to adolescents who reported relatively higher intercepts for perceived enjoyment for self gains ($b = -.532, p < .001$). The reverse was also true; a higher activation (intercept) difference in the Self Gain > Charity Gain contrast was associated with a stronger decrease in perceived self-enjoyment ($b = -.211, p < .008$). These findings showed that participants who started with more extreme scores became more similar to the general group over time.

The slopes of perceived enjoyment for self gains and Self-Gain > Charity-Gain contrast were not significantly associated ($p = .076$).

The preregistered relations between NAcc activity for Self-Gain > Charity-Gain and charity enjoyment, charity importance and empathic concern are reported in Appendix S2.

TABLE 5 Intercept-slope associations for Self Gain – Charity Gain.

Self report measures	Self Gain – Charity Gain difference score	
	INT	LS
Charity donations		
INT	-1.069*	.644***
LS	.067	.388*
Perspective taking		
INT	-.548	.541***
LS	.039	.061
Self enjoyment		
INT	2.141*	-.532***
LS	-.211**	-.382
Charity enjoyment ^a		
INT	.64	.459**
LS	.004	.113*
Charity importance ^a		
INT	1.345	-1.426***
LS	-.130	-.248
Empathic concern ^a		
INT	-.836	.785***
LS	.075	.167

Abbreviations: INT, intercept; LS, linear slope.

* $p < .05$, ** $p < .01$, *** $p < .001$.

^aDescribed in the supplement.

Exploratory analyses

This study design also allowed up to examine which variables may explain variance in the developmental trajectory of charity donation behavior. In five additional analyses, we explored the relations between the intercepts and linear slopes of donation behavior on the one hand, and the respective intercepts and slopes of perspective taking, empathic concern, self- and charity- enjoyment, and importance of charity. Table 6 shows all coefficients and significance values.

Results revealed no significant relations between donation behavior and either perspective taking or empathic concern (all $ps > .128$). With respect to reported enjoyment, those adolescents with a higher intercept on enjoyment for self gains increased more in charity donations ($b = 0.367$, $p < .001$), and those adolescents who started higher on charity donations decreased less in enjoyment for self gains ($b = .330$, $p < .001$). Additionally, those adolescents who started higher on charity enjoyment increased less in charity donations ($b = -.398$, $p < .001$). Finally, with respect to importance of charity, results revealed that those adolescents who started higher on perceived importance of charity increased less in charity donations ($b = -.727$, $p < .001$). These findings show that participants who started with more extreme scores became more similar to the general group over time.

DISCUSSION

The aims of the current study were threefold. First, we aimed to test the developmental patterns of ventral striatum activity during (vicariously) gaining rewards for self and charity. Second, we tested the developmental trajectories of behavioral variables that have previously been related to vicarious gains, specifically enjoyment of gains, perspective taking, empathy, and donation behavior outside the fMRI scanner.

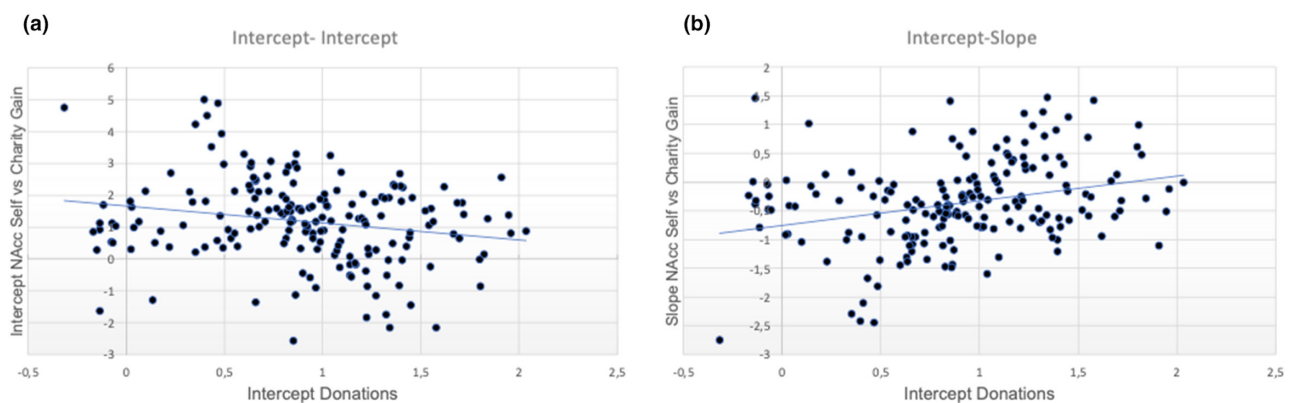


FIGURE 6 LGM for donations behavior and NAcc activity for Self Gain–Charity Gain relations. (a) (intercept–intercept relation) shows that adolescents who donate less show higher activity in NAcc for self compared to charity, and vice versa: adolescents who donate more show more similarity in NAcc for self and charity. (b) (intercept–slope relation) shows that individuals who show higher donation behavior at the starting point differentiate more between NAcc for self and charity over time, and vice versa, individuals who show lower donation behavior differentiate less between NAcc for self and charity over time, possibly reflecting regression to the mean. Note that intercepts and slopes are estimated in a full model including age, and values are nonscaled estimations and can therefore be negative for intercept donations (see text for explanation).

TABLE 6 Intercept–slope associations for charity donations.

Self report measures	Charity donations	
	INT	LS
Perspective taking		
INT	.223	-.168
LS	-.102	-.043
Empathic concern		
INT	.026	.089
LS	-.002	.017
Self enjoyment		
INT	-1.135	.367***
LS	.330***	.194
Charity enjoyment		
INT	.184	-.398***
LS	-.177	-.024
Charity importance		
INT	.467	-.727***
LS	-.357	-.017

Abbreviations: INT, intercept; LS, linear slope.

* $p < .05$, ** $p < .01$, *** $p < .001$.

Third, we investigated whether the developmental patterns found for three behavioral variables (perspective taking, charity donations and pleasure of self-gain) were related to developmental trajectories of the neural activities for self reward versus vicarious charity reward using multivariate LGMs.

The results supported the hypothesis that gains for self resulted in strongest ventral striatum activity (self gain), followed by gains that were shared between self and charity (both gain), whereas gains for only charity (charity gain) resulted in the lowest activity in the ventral striatum, consistent with our prior findings in adults Spaans et al. (2019). Furthermore, whereas neural activity for self gain, enjoyment of self gain, and enjoyment of charity gain decreased during adolescence, perspective taking and donations to charity increased during adolescence. Finally, neural responses to vicarious gains for charity were positively associated with donations to charity. Specifically, those adolescents with less neural differentiation between gains for self and charity showed relatively higher donating behavior.

In the next section, we will describe and discuss all pre-registered hypotheses.

Preregistered hypotheses

The first main aim of the study was to examine the development of self-related and vicarious neural activity when gaining rewards for charity relative to rewards for self. The study made use of a novel paradigm examining rewards only for self, rewards only for charity and rewards for both.

Consistent with prior studies, rewards for self resulted in increased activity in the ventral striatum, including the NAcc (Sescousse et al., 2013) and this NAcc activity was higher for younger adolescents and decreased during adolescence and early adulthood. This developmental pattern is consistent with a prior meta-analysis showing higher ventral striatum activity for adolescents compared to adults to rewarding stimuli (Silverman et al., 2015).

We first examined developmental trajectories for rewards for self. The current accelerated three-wave longitudinal study supported the hypothesis of a general decrease in neural activation in the ventral striatum. The decrease was observed for self-gains (high and low) and for conditions where both parties gained rewards (both high and both low), in line with prior studies reporting an age-related decrease in ventral striatum activity to rewards for self (Silverman et al., 2015; Smith et al., 2015).

Contrary to expectations, activity in the ventral striatum for rewards for self showed a linearly decreasing, not a quadratic pattern, despite prior studies showing a peak in activity in mid-adolescence (Braams et al., 2015). A possible explanation is that the current study represented outcomes for two beneficiaries (self and charity) rather than a single beneficiary (self). In addition, the current study used a “no gain” baseline, whereas prior studies used a loss baseline. It has been shown that adolescent-specific changes are not limited to rewarding stimuli but also to aversive stimuli (Galvan & McGlennen, 2013), so possibly the quadratic pattern is more strongly observed when comparing two opposite values (reward and loss). Finally, the participants enrolled in this study were between ages 10 and 24, and possible quadratic age patterns might only be revealed when also including younger and older age groups. For example, the estimated trajectory in a three-wave longitudinal study comparing participants in the age range 8–29 years showed a larger late adolescent drop compared to early adolescent increase in ventral striatum activity (Schreuders, et al., 2018).

Second, we examined development of neural activity for vicarious rewards for charity. Consistent with a prior study in adults using the same design Spaans et al. (2019), ventral striatum activity for charity was significantly lower than ventral striatum activity for both gains and self gains. A prior meta-analysis also demonstrated that ventral striatum activity is higher for personal than vicarious gains (Morelli et al., 2015). Vicarious charity reward did not result in elevated neural activity in mid adolescence, despite previous studies showing an adolescent-specific reward response for vicarious rewards for mothers (Braams & Crone, 2017) and stable friends (Schreuders et al., 2021). The general age comparison for vicarious charity rewards resulted in a null model. Individual differences, independent of age, were a stronger predictor of neural activity to vicarious charity rewards. Consistent with expectations, ventral striatum activity was higher for participants who were more willing to donate to charity, similar to what was observed in the cross-sectional study that included the first time point of this study (Spaans et al., 2020). A prior study using a reinforcement

learning paradigm also revealed that ventral striatum activity for charity-related prediction errors was higher in participants who were more willing to donate (Kuss et al., 2013).

To unravel the developmental time course of potential factors that could influence charity-related neural activity (aim 2), we examined the developmental patterns of perspective taking, empathy, enjoyment of winning and importance of the charity, in additions to Dictator Game donations. As predicted, perspective taking and donations to charity increased with age (Hawk et al., 2013). Consistent with prior studies, empathy showed no developmental changes (Hawk et al., 2013; Overgaauw et al., 2017). Subjective enjoyment of gaining reward for self and charity decreased with age, similar to prior research reporting that subjective pleasure of gaining rewards decreased with age (Schreuders, et al., 2018). Finally, the importance assigned to the charity also decreased with age, similar to what was previously observed in the cross-sectional subsample of this study (Spaans et al., 2020). We used multivariate LGMs to understand the dynamic longitudinal relations between activity in the ventral striatum when gaining for self versus charity, and the developmental patterns of donation behavior, perspective taking, and pleasure of self gain (aim 3). These analyses revealed that perspective taking and donations to charity covaried with neural activity for self versus charity, suggesting an important interplay between neural affective and developmental cognitive processes in predicting prosocial behavior.

Our findings suggest a developmental pattern of individual differences in development toward a normative endpoint of more similar neural activation in the NAcc with winning both for self and others over time. For instance, those adolescents who donated more in general showed less differentiation between winning for self versus charity in the ventral striatum. However, over time, these individual differences in activity in self vs charity contrasts became less pronounced such that adolescents who started with relatively higher donations also showed a less pronounced decrease in activity differences of self and charity reward activation over time compared to adolescents who started with lower donations. In sum, these findings suggest individual differences in development toward more similar neural activation for self gains and charity gains that may depend on the baseline levels of charity donations.

Explorative analyses

Explorative analyses further allowed us to examine the relation between individual difference factors and donation behavior. First, we showed that donation behavior to charity, as indicated through giving behavior, increased with age in adolescence. This finding showed that increases in giving are not limited to family members (Brandner et al., 2021) and friends (Blankenstein et al., 2019; Guroglu et al., 2014), but can also be observed for unknown others in need (Carlo & Padilla-Walker, 2020). These findings are consistent with a prior study which also showed generous giving in

adolescence to others in need in relation to the COVID-19 pandemic, such as patients or medical doctors (van de Groep, Zanolie, Green, et al., 2020).

Donation behavior toward charity, however, was not related to perspective taking and empathic concern, suggesting that other individual difference factors may play a larger role in explaining donation behavior (Carlo & Padilla-Walker, 2020). Longitudinal analyses revealed that higher starting levels of enjoyment for self-gains, as well as lower starting levels of enjoyment for charity-gains and perceived importance for charity, predicted stronger increases in donation behavior. Given the negative correlation between enjoyment for self-gains and donation behavior, possibly, those adolescents who start higher on self-enjoyment, show a catch-up effect associated with an increase in donation behavior over time. In addition, those who started higher on donation behavior may show an overcompensation effect, with a relatively less steep decline in enjoyment for self-gains.

Such an overcompensation effect could also possibly explain why those who started higher on charity enjoyment showed a less strong increase in charity donations over time. However, this finding needs to be interpreted with caution, as results showed only one significant intercept/slope association. Other factors that were not examined in this study that may influence giving behavior are environmental support factors, such as peer relations (Schreuders, et al., 2018) or family support (Wong et al., 2020). Future studies should incorporate this broader context when examining predictors for donation behavior in adolescence (Carlo & Padilla-Walker, 2020).

Limitations and future directions

This study had several strengths as well as limitations that should be addressed in future research. Strengths are the longitudinal neuroimaging design which contributed to methodological robustness and allowed us to examine individual differences in intra-individual change measures and interrelations with neural activity changes. A second strength was the combination of self-report with experimental measures to assess donation behavior and neural activity using fMRI, which together provides a richer assessment of the development of prosocial motivations.

Limitations are the relatively homogenous group in terms of socio-economic background and diversity: a wider variation would allow us to generalize the results more broadly. Future research should also provide a more detailed index of family structure and relations as these may impact general prosocial motivations (Yoo et al., 2013). Second, the assessments spanned a period of approximately 4 years in total, and therefore we could not examine how these measures predicted longer term outcomes. Third, the explorative analyses examined five additional relations on top of the preregistered hypotheses; these relations should be considered preliminary and confirmed in future research. Fourth,

each part of the design disentangled specific components of prosocial motivations, but we could not examine neural activity during actual donations. Fifth, the repeated exposure to the same task over multiple sessions may have influenced the anticipated gains over time. Therefore, future research can build upon this study with more complex donation designs in combination with functional neuroimaging.

CONCLUSION

Taken together, this rich longitudinal behavioral-neuroimaging study allowed us to examine several components of prosocial motivation, neural responses, and behavior directed toward charity. We found support for the hypothesis that adolescents, with increasing age, show an increase in perspective taking and donations to charity, although we did not observe a plateau after mid-adolescence as was initially predicted (Padilla-Walker et al., 2018). Using functional neuroimaging, we demonstrated that a decrease in hedonic reward experiences for self relative to vicarious charity reward was associated with a developmental increase in prosocial donations toward charity. Prior studies examining developmental responses to vicarious rewards suggested an adolescent specific peak in vicarious gains for mothers (Braams & Crone, 2017) and stable friends (Schreuders et al., 2021). We found no evidence for a peak in neural activity to vicarious gains for charity. Instead, neural responses were dependent on individual differences in perspective taking and charity donations. Together, these findings indicate that motivations to act prosocially toward charity might be the result of an interplay between increasing levels of perspective taking, decreasing hedonic pleasures, and affective responses to high personal rewards (Thielmann et al., 2020).

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