



PAPER

Longitudinal links between childhood peer acceptance and the neural correlates of sharing

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Abstract

Childhood peer acceptance is associated with high levels of prosocial behavior and advanced perspective taking skills. Yet, the neurobiological mechanisms underlying these associations have not been studied. This functional magnetic resonance imaging study examined the neural correlates of sharing decisions in a group of adolescents who had a stable accepted status ($n = 27$) and a group who had a chronic rejected status ($n = 19$) across six elementary school grades. Both groups of adolescents played three allocation games in which they could share money with strangers with varying costs and profits to them and the other person. Stably accepted adolescents were more likely to share their money with unknown others than chronically rejected adolescents when sharing was not costly. Neuroimaging analyses showed that stably accepted adolescents, compared to chronically rejected adolescents, exhibited higher levels of activation in the temporo-parietal junction, posterior superior temporal sulcus, temporal pole, pre-supplementary motor area, and anterior insula during costly sharing decisions. These findings demonstrate that stable peer acceptance across childhood is associated with heightened activity in brain regions previously linked to perspective taking and the detection of social norm violations during adolescence, and thereby provide insight into processes underlying the widely established links between peer acceptance and prosocial behavior.

Research highlights

- Adolescents with a history of stable acceptance among peers more often choose to share valuable resources with strangers than adolescents with a history of chronic peer rejection, but only when sharing incurs no costs.
- Chronically rejected adolescents who report higher levels of perspective taking more often share with strangers than chronically rejected adolescents who report lower levels of perspective taking.
- Compared to chronically rejected adolescents, stably accepted adolescents exhibit higher levels of activity in brain regions supporting social cognition (e.g. pSTS/TPJ and temporal pole) and the detection of

norm violations (pre-SMA and AI) during costly sharing decisions.

- These findings provide insights into the neural and socio-cognitive processes underlying the widely established bidirectional links between peer acceptance and prosocial behavior.

Introduction

Acceptance among peers during childhood has strong positive associations with both concurrent and future mental health (Ladd & Troop-Gordon, 2003; Sturaro, van Lier, Cuijpers & Koot, 2011) and academic success (DeRosier, Kupersmidt & Patterson, 1994; Ladd,

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Kochenderfer & Coleman, 1997). Relationships with peers provide a socialization context in which children acquire key social skills (e.g. prosocial behaviors such as sharing) and socio-cognitive abilities (e.g. the ability to understand other people's perspective) needed for successful functioning in a complex social environment (Bukowski, Buhrmester & Underwood, 2011; Ladd, 1999; Rubin, Bukowski & Parker, 2006). Indeed, prosocial behaviors and perspective taking skills are instrumental in gaining and maintaining peer acceptance (Fink, Begeer, Hunt & Rosnay, 2014; Slaughter, Imuta, Peterson & Henry, 2015). Yet, the neural processes underlying the widely established links between long-term peer acceptance and prosocial behavior remain unexplored. To fill this gap in the literature, we examined the neural correlates of prosocial behavior in the form of sharing valuable resources in adolescents with a history of long-term stable peer acceptance and compared them to adolescents with a history of chronic peer rejection.

Neuroimaging studies have identified two distinct, but interacting, neural networks involved in (strategic) sharing decisions by combining functional magnetic resonance imaging (fMRI) with economic exchange games in which one person is given a set of valuable rewards and can then decide how much he/she would like to share with another person (Rilling & Sanfey, 2011). First, a 'salience network' consisting of the pre-SMA/ACC and insula has been found to be important for detecting norm violations (e.g. violations of fairness norms) in social decisions. For example, heightened pre-SMA/ACC and insula activity has been observed in people when they are treated unfairly (Sanfey, Rilling, Aronson, Nystrom & Cohen, 2003), when they see somebody else being treated unfairly (Corradi-Dell'Acqua, Civai, Rumiati & Fink, 2013) and also when they divide resources in an unfair manner themselves (Güroğlu, Will & Crone, 2014b). Second, a 'mentalizing network' consisting of regions in the medial prefrontal cortex (MPFC), temporal-parietal junction (TPJ), posterior superior temporal sulcus (pSTS), and temporal poles has been shown to be involved in switching attention to other people's perspective in social exchange (Gunther Moor, Güroğlu, Op de Macks, Rombouts, Van der Molen *et al.*, 2012; Güroğlu, van den Bos, van Dijk, Rombouts & Crone, 2011; van den Bos, van Dijk, Westenberg, Rombouts & Crone, 2011a). This mentalizing network is consistently identified in tasks that probe reasoning about other people's mental states (e.g. emotions, intentions and desires) (Blakemore, den Ouden, Choudhury & Frith, 2007; Saxe, Whitfield-Gabrieli, Scholz & Pelphrey, 2009) and in tasks in which participants are asked to take other people's perspective (Denny, Kober, Wager & Ochsner, 2012; Pfeifer, Masten, Borofsky, Dapretto, Fuligni *et al.*,

2009) or where they do this spontaneously (Wagner, Kelley & Heatherton, 2011).

Crucially, these two networks are differentially sensitive to developmental change (Güroğlu *et al.*, 2011; van den Bos, van Dijk, Westenberg, Rombouts & Crone, 2011b). That is, pre-SMA/ACC and insula responses to fairness violations do not differ in various phases of adolescent development. In contrast, activity in mentalizing regions (e.g. TPJ) continues to increase with age across adolescence and has been associated with age-related increases in prosocial behavior in situations that require higher levels of perspective taking (Güroğlu *et al.*, 2011; van den Bos *et al.*, 2011a). The current study addressed the question whether activity in these neural networks is sensitive to long-term exposure to developmentally relevant socialization experiences in the peer context, that is, stable high or low levels of acceptance among peers.

We scanned two groups of adolescents who participated in an ongoing longitudinal study (Menting, Van Lier & Koot, 2011; Sturaro *et al.*, 2011; van Lier & Koot, 2010). Based on longitudinal assessments of peer acceptance and rejection across six elementary school grades, we selected participants who were highly liked by their peers and who were almost never disliked (i.e. adolescents with a history of *stable peer acceptance*) and participants who were highly disliked and were almost never liked (i.e. adolescents with a history of *chronic peer rejection*) (Bukowski, Sippola, Hoza & Newcomb, 2000; Coie, Dodge & Coppotelli, 1982; Jiang & Cillessen, 2005; Newcomb & Bukowski, 1983). In an MRI scanner, both groups played three allocation games (Fehr, Bernhard & Rockenbach, 2008; Güroğlu *et al.*, 2014b) in which they could choose to share money equally or unequally with unknown others over a sequence of trials. An equal distribution of money could bear no costs (i.e. non-costly sharing in the 'non-costly equity' game), could be costly for the participants themselves (costly sharing in the 'costly equity' game), or could decrease the outcomes of the recipient (envious sharing in the 'envious equity' game). By giving stably accepted and rejected adolescents the opportunity to share valuable resources with anonymous others who could not reciprocate or punish social decisions, this study is the first to examine how prosocial preferences – stripped away from strategic or reputational concerns and existing relationships with interaction partners – differed as a function of sustained exposure to either high or low levels of peer acceptance.

Based on widely established links between an accepted peer status and higher levels of prosocial behavior (Caputi, Lecce, Pagnin & Banerjee, 2012; Layous, Nelson, Oberle, Schonert-Reichl & Lyubomirsky, 2012; Newcomb, Bukowski & Pattee, 1993), we expected that

the stably accepted adolescents would more often choose the prosocial option in the allocation games (i.e. choosing the option that maximized the other person's profits) than the chronically rejected adolescents. Behavioral differences between accepted and rejected children are most pronounced when children act spontaneously, and diminish or even disappear when rejected children are given enough time to deliberate their social decisions (Rabiner, Lenhart & Lochman, 1990). Therefore, we hypothesized that behavioral differences between accepted and rejected children are most pronounced during the first trials of the allocation games, which is comparable to behavior in single-shot versions of economic games (van den Bos, van Dijk & Crone, 2012). We hypothesized that stably accepted adolescents would report higher levels of perspective taking than chronically rejected adolescents (Fink *et al.*, 2014; Slaughter *et al.*, 2015) and we predicted that individual differences in perspective taking would correlate with higher levels of prosocial behavior (Eisenberg, Carlo & Murphy, 1995). We further expected that stably accepted adolescents would show higher levels of activity in brain regions implicated in perspective taking in social decision-making (e.g. mPFC, pSTS, TPJ, temporal pole). We expected this to be most pronounced in decisions where self-interest conflicts most with the other person's interest (i.e. when sharing was costly for the participants), given that such decisions require higher levels of perspective taking (Güroğlu, van den Bos & Crone, 2014a).

Method

Participants and recruitment procedure

Participants were recruited from a longitudinal study ($N = 1189$), which investigated the impact of social experiences on behavioral, emotional and academic outcomes between age 6 and 12 years. From first to sixth grade of elementary school, participants annually nominated the classmates they liked most and liked least (unlimited nominations). Using those nominations, an average social preference score (liked most – liked least nominations) across the six waves was calculated to index stable histories of acceptance and rejection (Bukowski *et al.*, 2000; Coie *et al.*, 1982; Jiang & Cillessen, 2005; Newcomb & Bukowski, 1983). That is, adolescents from the lower (chronically rejected) and upper (stably accepted) 10th percentile of the average social preference score were selected for the fMRI study.

Based on these criteria, suitability for participation in an fMRI study and availability of recent contact

information, 131 adolescents were asked to participate in the fMRI study after the sixth wave of the large-scale longitudinal study (see also Will, Crone, van Lier & Güroğlu, 2016; Will, van Lier, Crone & Güroğlu, 2016). Twenty adolescents were excluded because they were left-handed ($n = 4$), had an autism spectrum disorder ($n = 1$) or had braces ($n = 15$). Seven adolescents could not be reached. Of the remaining 104 candidate participants, 47 adolescents and their parents agreed to participate in the current fMRI study. Those who chose not to participate in the fMRI study ($n = 57$) did not differ from those who were scanned with respect to average social preference, age, or gender (all $ps > .25$).

All participants indicated that they were healthy and reported no contraindications for MRI (e.g. no head injuries, no history of neurological or psychiatric disorders), except for four participants with a history of rejection who were diagnosed with Attention-Deficit Hyperactivity Disorder (ADHD). Of those, three participants with ADHD were on a stable dose of methylphenidates, but were medication-free on the day of scanning and the preceding day. A radiologist reviewed all anatomical scans after which one participant was excluded from the analyses due to an anomaly.

The final sample consisted of 46 adolescents of which 27 had a history of stable peer acceptance (M age = 14.0, range = 12–15, $SD = .77$, 14 male) and 19 had a history of chronic peer rejection (M age = 14.0, range = 12–15, $SD = 0.61$, 14 male). Stably accepted and chronically rejected adolescents did not differ in age, pubertal status (assessed using the Pubertal Development Scale; Petersen, Crockett, Richards & Boxer, 1988), gender, age, ethnicity, or IQ (assessed using the Similarities and Block Design subtests of the Wechsler Intelligence Scale for children; Wechsler, 1999), all $ps > .14$ (see Supplementary Table 1). All participants and their parents gave informed consent for the study. The recruitment procedure was blind, such that experimenters were not informed about individual participants' peer status history. Both the longitudinal study and the fMRI study were approved by the medical ethical committees of the respective universities.

Experimental procedure

Participants were first familiarized with imaging procedures using an MRI mock scanner. Next, they received instructions about the games they would be playing in the scanner and practiced 10 trials of the task before entering the scanner. Participants were informed that during practice trials their decisions had no consequences for their earnings and there was no recipient. After scanning, participants first filled out a

battery of questionnaires before being debriefed and receiving financial compensation for participating in the study.

Neuroimaging task: allocation games

Participants played three allocation games previously used to assess fairness preferences in children and adolescents (Fehr *et al.*, 2008; Güroğlu *et al.*, 2014a; Meuwese, Crone, de Rooij & Güroğlu, 2014; Steinbeis & Singer, 2013). They were asked to distribute valuable coins between themselves and a recipient. They could choose between an equal distribution of coins (1 for self; 1 for the recipient) and an unequal distribution, which varied in each game (see Figure 1). In the non-costly equity game, the alternative distribution yielded the participants 1 coin, but left nothing for the recipient (1–0). Choosing the equity option was therefore a *non-costly* sharing decision. In the costly equity game participants, the alternative distribution yielded the participant 2 coins, but left nothing for the recipient (2–0). Choosing the equity option was therefore a *costly* sharing decision, because participants had to forego one coin to share equally. In the envious equity game the alternative distribution yielded

the participant 1 coin and resulted in 2 coins for the recipient. Choosing the equity option in this game decreases the recipient’s potential earnings (2 coins instead of 1). Choosing the equity in the envious equity game was therefore an *envious* sharing decision.

Prior to the experiment participants were told that their decisions had consequences for both their own monetary profits and those of the recipients. The recipients were said to be other adolescents of the same age as the participants, who agreed to take part in the experiment on a future testing day. The instructions emphasized that: (1) these recipients were not present at the testing site, (2) they were not former classmates who participated in the longitudinal study, (3) the participants had not met these children before, and (4) the participants would not meet the recipients at a later time. The participants were told that after the experiment one chosen distribution would be randomly selected to be paid out to them and the recipient. In reality, each participant received 2 euros after completion of the task.

Neuroimaging data were collected in a single functional run of 210 volumes (lasting 7.7 minutes). The neuroimaging task consisted of 60 trials (20 for each of the three allocation games), which were presented in a

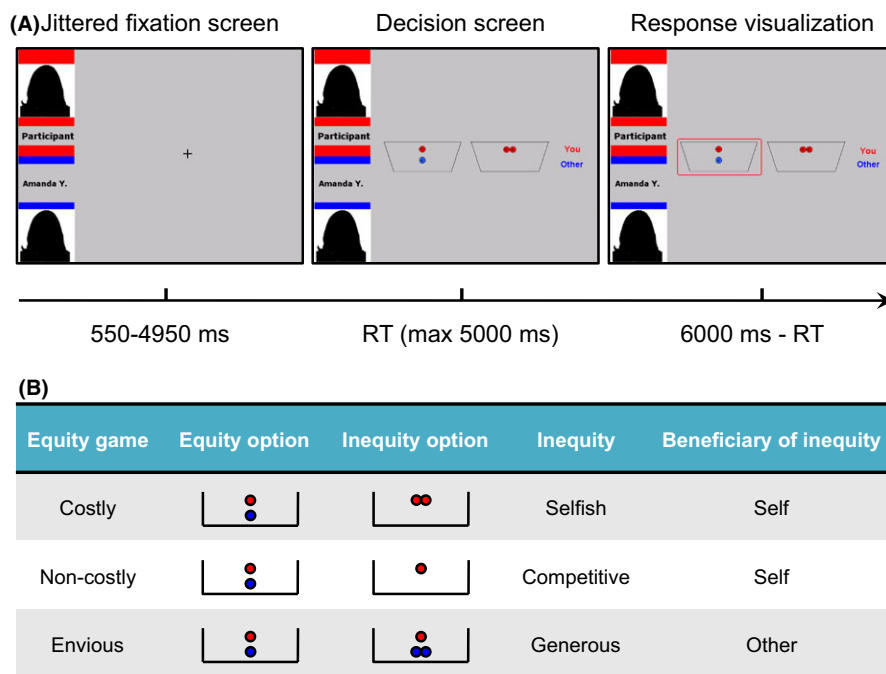


Figure 1 (A) Visual display of events presented in the one trial of the fMRI task. Each trial started with a fixation cross with a jittered duration (550–4950 ms). Subsequently, participants were presented a decision screen containing: the name of the participant in red, the name of the recipient in blue and the two distributions of coins the participant could choose from. Coins for the participant were displayed in red and coins for the recipient were displayed in blue. Participants were given 5000 ms to respond. After responding, a red rectangle appeared around the distribution of their choice until 6000 ms after trial onset. (B) Properties of the three allocation games.

randomized fashion. Each trial started with a jittered fixation cross (mean = 1540 ms, min = 550 ms, max = 4950 ms; optimized with Opt-Seq2, Dale, 1999; surfer.nmr.mgh.harvard.edu/optseq/). Subsequently, participants were presented with a screen containing the two distributions of coins they could choose from and the name (first name with first letter of last name) of a same-gender peer who was the recipient on that particular trial (see Figure 1). Each trial was accompanied by a different name, indicating that each choice was for a different recipient. The position of the equal distribution on the screen (left or right) was counterbalanced. Responses could be made by a button press with the index finger (left side alternative) or middle finger (right side alternative) of the right hand. At the moment that the participants made their choice a red rectangle appeared around the distribution of their choice until 6 s after trial onset. If participants had not responded within 5 s a screen was presented with 'Too late!' for the duration of 1 s. Trials without a response consisted of less than 1% of all trials and were excluded from further analyses.

Perspective taking questionnaire

The tendency to take other people's perspective was assessed using the perspective taking subscale of the Interpersonal Reactivity Index (IRI; Davis, 1983), which included items such as 'I sometimes try to understand my friends better by imagining how things look from their perspective'. All items were rated on a scale of 1 (*not at all*) to 5 (*very much*) and averaged to a mean score. The questionnaire was administered after the scanning session and took approximately 5 minutes to complete.

fMRI data acquisition

Scans were acquired using a 3T Philips Achieva MRI system at the University Medical Center with a standard whole-head coil. After obtaining a localizer scan, we obtained T2*-weighted Echo-Planar Images (EPI) (repetition time (TR) = 2.2 sec, echo time (TE) = 30 ms, slice matrix = 80 × 80 matrix, slice thickness = 2.75 mm, slice gap = 0.28 mm gap, field of view (FOV) = 220 mm) during a single functional run of 210 volumes (lasting 7.7 minutes). The first two volumes of the functional run were discarded from further analysis to allow for equilibration of T1 saturation effects. After the functional images, we obtained a high-resolution 3D T1-Fast Field Echo scan for anatomical reference (TR = 9.760 ms; TE = 4.59 ms, flip angle = 8 degrees, 140 slices, 0.875 × 0.875 × 1.2 mm³ voxels, field of view = 224 × 168 × 177 mm³). Stimuli were presented using E-Prime software onto a screen in the magnet bore,

which participants could see through a mirror attached to the head coil. Participants could give their responses by using a fiber optic response box. During scanning foam inserts restricted head motion.

fMRI data analysis

Preprocessing and analysis of the MRI data was carried out using SPM8 statistical parametric mapping image analysis software (Wellcome Trust Centre for Neuroimaging, University College London). Functional images were slice-time corrected, realigned, co-registered to individual structural T1 scans, normalized to a T1 template, and spatially smoothed using an 8 mm, full-width at half-maximum isotropic Gaussian kernel. The normalization algorithm resampled the volumes to 3 mm cubic voxels using a 12-parameter affine transformation and a nonlinear transformation involving cosine basic functions. Translational movement parameters never exceeded 1 voxel (< 3 mm) in any direction for any participant or scan. All results are reported in MNI305 stereotactic space.

A first-level General Linear Model (GLM) was defined for each participant that included six decision regressors, a regressor indicating missed trials, and a basic set of cosine functions that high-pass-filtered the data. Given that our experiment employed a fast event-related design and average reaction times were nearly a second faster than the TR (*M* reaction times = 1307 ms; *SD* = 421 ms), the fMRI time series were modeled as a series of zero-duration events (time-locked at the onset of the decision-screen) and convolved with a canonical hemodynamic response function.

The participant-specific contrast images were subsequently submitted to group-level analyses at the second level where participants served as a random effect in a full factorial 3 × 2 analysis of variance (ANOVA) with allocation game as a within-subjects factor (3 levels: costly equity game, non-costly equity game, envious equity game) and peer status history (2 levels: stably accepted vs. chronically rejected adolescents) as a between-subjects factor. Consistent with prior work (Gunther Moor *et al.*, 2012; Steinbeis, Bernhardt & Singer, 2012), we collapsed across equity and inequity choices within each game. This approach ascertains that all analyses are based on a balanced design with the same number of trials for each participant (20 per game; 60 in total) instead of an unbalanced design with varying numbers of trials per cell (see Güroğlu *et al.*, 2014b).

We examined the main effect of allocation game and the allocation game × peer status history interaction as *F*-contrasts in the ANOVA. We followed up these *F*-contrasts with planned *t*-contrasts to examine differences

between the games and groups. Results were considered significant at an uncorrected threshold of $p < .001$ with a minimum cluster size of 10 contiguous voxels to balance between Type 1 and Type 2 errors (Lieberman & Cunningham, 2009). We also report which clusters are significant using Family-wise Error (FWE) cluster-correction at $p < .05$ with a cluster-forming threshold of $p < .001$. We used the Marsbar toolbox (Brett, Anton, Valabregue & Poline, 2002; <http://marsbar.sourceforge.net/>) to extract subject-level contrast values in clusters of activity derived from our whole-brain analyses. For each cluster the center of mass is reported.

Results

Behavioral results

Equity choices and peer status history

To examine differences in equity choices between the chronically rejected and stably accepted group, we performed a random effects logistic regression model with equity as the dependent variable (0: inequity offer; 1: equity offer) and peer status history (0: stably accepted; 1: chronically rejected), dummy-coded variables for each allocation game, trial number, and all two-way and three-way interactions as predictor variables. The logistic regression yielded a main effect of costly equity game ($\beta = -1.23$, $SE = 0.30$, $Wald = -4.13$, $p < .001$), a two-way interaction between non-costly equity game and status history ($\beta = -1.44$, $SE = 0.38$, $Wald = -3.81$, $p < .001$), and a three-way interaction between non-costly equity game, status and trial number ($\beta = 0.06$, $SE = 0.03$, $Wald = 2.12$, $p = .034$). To test whether these results are robust to the exclusion of trial number as a covariate, we ran a separate logistic regression without trial number as a predictor (and without two-way and three-way interactions between trial number and the other variables). This random effects logistic regression also yielded a main effect of costly equity game ($\beta = -1.36$, $SE = 0.16$, $Wald = -8.43$, $p < .001$) and a two-way interaction between non-costly equity game and peer status history ($\beta = -0.81$, $SE = 0.23$, $Wald = -3.94$, $p < .001$) on equity choices.

Follow-up contrasts showed that both stably accepted and chronically rejected participants chose the equity distribution less often when fairness was costly. That is, both groups of adolescents chose the equity offer less often in the costly equity game compared to the envious equity game ($p < .001$) and the non-costly equity game ($p < .001$). Stably accepted adolescents displayed more non-costly sharing ($M = 76\%$) than the chronically

rejected adolescents ($M = 62\%$; $\beta = -2.83$, $SE = 1.08$, $Wald = -2.16$, $p = .009$). There were no group differences in costly sharing ($p = .75$) or envious sharing ($p = .67$; see Figure 2). The three-way interaction showed that the difference between the groups in non-costly sharing was most pronounced during the first trials (see Figure 2).

Behavioral results: equity choices and perspective taking

Stably accepted adolescents ($M = 3.70$; $SD = 0.84$) reported marginally higher levels of perspective taking than chronically rejected adolescents ($M = 3.24$; $SD = 0.73$), $t(44) = 1.97$, $p = .056$. To examine

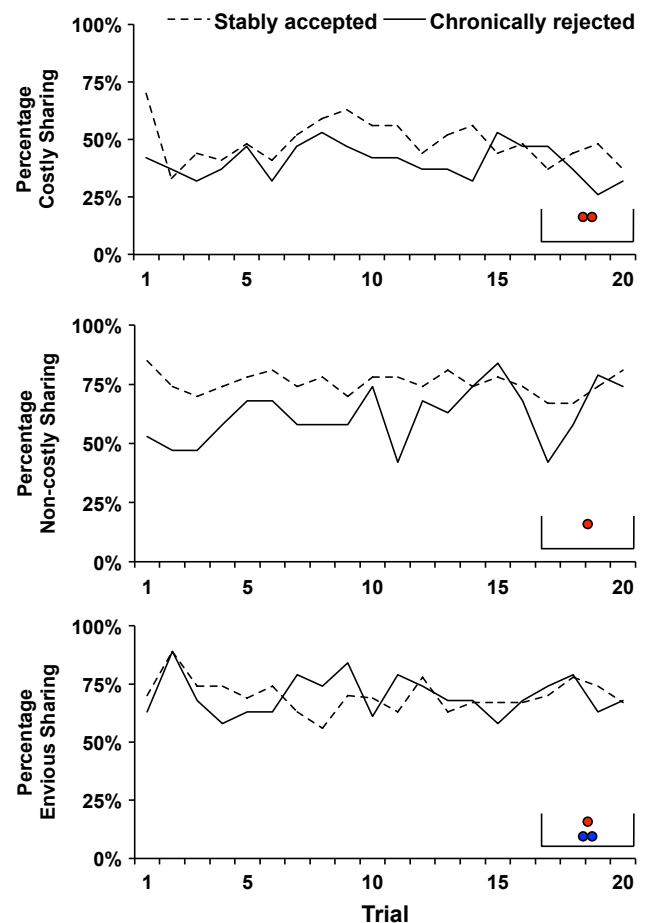


Figure 2 Percentage of equity offers chosen by stably accepted and chronically rejected adolescents in each of the three allocation games plotted as a function of trial number. The equity offer (which was always 1 coin for the participant and 1 coin for the recipient) was pitted against an alternative offer, which is graphically depicted in the right bottom corner of each graph (red coins represent coins for the participant and blue coins those for the recipient).

associations between equity choices, peer status history and perspective taking, we ran three random effects logistic regression models with equity as the dependent variable (0: inequity offer; 1: equity offer) and peer status history (0: stably accepted; 1: chronically rejected), perspective taking, and a status \times perspective taking (mean-centered) interaction term as predictor variables. Perspective taking interacted with status history to predict costly sharing choices in the costly equity game ($\beta = 3.61$, $SE = 1.38$, $Wald = 2.62$, $p = .009$), but not non-costly sharing in the envious equity game ($\beta = -0.92$, $SE = 1.04$, $Wald = -0.88$, $p = .377$) and non-costly equity game ($\beta = 2.22$, $SE = 1.26$, $Wald = 1.76$, $p = .079$). Follow-up correlations in each group separately showed that this interaction effect was qualified by a correlation between perspective taking and costly sharing choices in the chronically rejected adolescents ($r = .74$, $p < .001$; see Figure 3), but not in the stably accepted adolescents ($p = .235$).

Neuroimaging results

Whole-brain ANOVA results

To identify brain regions that were differentially involved in the allocation games and interactions with peer status history, we first conducted a whole-brain ANOVA with allocation game as within-subject factor (three levels:

costly, non-costly, envious equity) and peer status history as a between-subjects factor (two levels: stably accepted vs. chronically rejected). The ANOVA revealed a main effect of allocation game in bilateral striatum (peaks at 9, 14, 7 and -6 , 17, 4), pre-SMA (peak at 12, 20, 58) and right TPJ (peak at 60, -55 , 16) and an interaction effect between allocation game and peer status history in left pSTS/TPJ (peak at -45 , -52 , 7), right inferior frontal gyrus (IFG)/AI (peak at 27, 23, -14) and right Temporal pole (peak at 45, 17, -17) (see Supplementary Table 2 for a complete list of activations).

Follow-up whole-brain t -contrasts

To further examine the nature of the main effect of game and the game \times peer status history interaction, we followed these F -contrasts up with planned t -contrasts. First, to investigate the main effect of game, we contrasted each game with the other two games. The contrast examining heightened activity in the costly equity game relative to the two other games (Costly equity game $>$ [Non-costly equity + envious equity games]) resulted in activation in bilateral striatum (peaks at 9, 14, 7 and -6 , 17, 4), vmPFC (peak at -6 , 44, -2), Pre-SMA (peak at 6, 20, 58), dACC (peak at 9, 29, 19) and rTPJ (peak at 63, -49 , 13; see Figure 4). The contrast examining heightened activity in the non-costly equity game relative to the two other

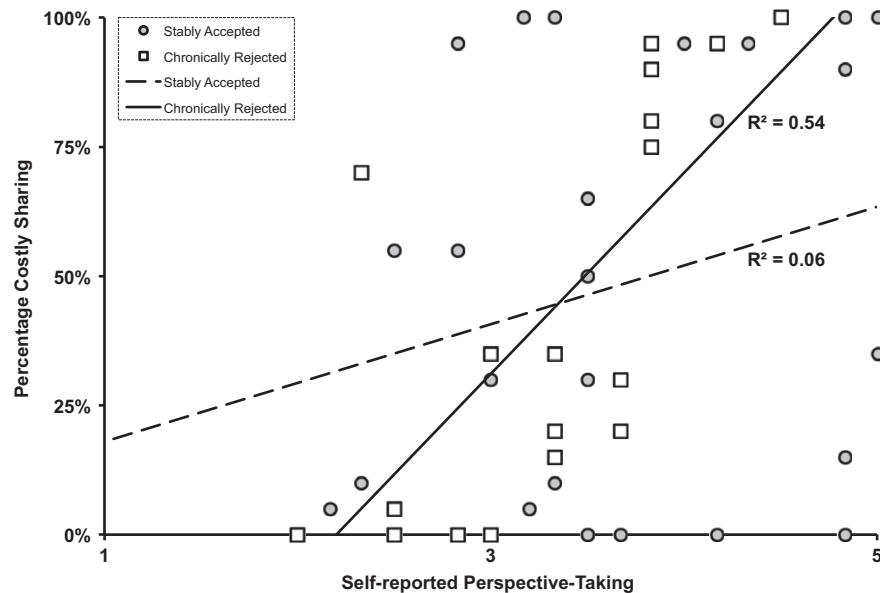


Figure 3 Chronically rejected participants who reported higher levels of perspective taking were more likely to give up a reward to share equally (choosing 1–1 instead of 2–0 in the costly equity game). In the stably accepted group, no relation between perspective taking and costly sharing was observed.

games (Non-costly equity game > [Costly equity + envious equity games]) resulted in no significant clusters of activation. The contrast examining heightened activity in the envious equity game relative to the other two games (Envious equity > [Costly equity + non-costly equity]) resulted in heightened activity in bilateral middle occipital gyrus (peaks at $-24, -94, 4$ and $27, -91, 7$) (see Supplementary Table 3 for a complete list of activations).

To further examine the allocation game \times peer status history interaction, we followed up the F -contrasts reported above with whole-brain t -contrasts comparing the two peer status history groups on all three contrasts outlined above. These analyses showed that stably accepted adolescents exhibited heightened activity in left pSTS/TPJ (peak at $-45, -52, 7$), right temporal pole (peak at $45, 17, -17$), pre-SMA (peak at $-3, 23, 55$), and right IFG/AI (peak at $27, 23, -14$) compared to chronically rejected adolescents in the costly equity game relative to the other two games Stably accepted adolescents > Chronically rejected adolescents (Costly equity game > [Non-costly equity game + envious equity games]; see Figure 5). No brain regions showed higher levels of activity in the stably accepted adolescents in the other two contrasts. Furthermore, no brain regions showed higher levels of activity in the chronically rejected adolescents compared to stably accepted adolescents in any of the three equity games (see Supplementary Table 4 for a complete list of activations). Behavioral and neuroimaging results remained unchanged after including gender as a covariate in our analyses. Results of neuroimaging analyses focusing on replicating prior findings on the neural correlates of inequity choices (Güroğlu *et al.*, 2014b) are reported in the supplementary material.

Discussion

The present study examined links between long-term peer acceptance during childhood and perspective taking, sharing decisions and their neural correlates in adolescence. Adolescents with a history of stable peer acceptance and adolescents with a history of chronic peer rejection made a series of anonymous sharing choices that differed in the extent to which an equal distribution of money incurred no costs (non-costly sharing), was costly for the participants themselves (costly sharing), or decreased the recipient's potential earnings (envious sharing). Two main findings distinguished the stably accepted group from the chronically rejected group. First, stably accepted adolescents were more likely to share equally than chronically rejected adolescents when sharing was non-costly. Second, when considering costly sharing of resources, stably accepted adolescents showed greater activation in left pSTS/TPJ, right temporal pole, right IFG/AI, and pre-SMA than chronically rejected adolescents. These findings have several implications for understanding the mechanisms underlying longitudinal links between peer acceptance and the development of prosocial behavior.

Associations between peer status history, sharing, and perspective taking

Adolescents with a history of stable peer acceptance were more likely to share equally with anonymous peers than adolescents with a history of chronic peer rejection, but only when fairness could be established without costs. This finding corroborates a large body of work showing that children who are rejected by peers show low levels of prosocial behavior (Caprara, Barbaranelli, Pastorelli,

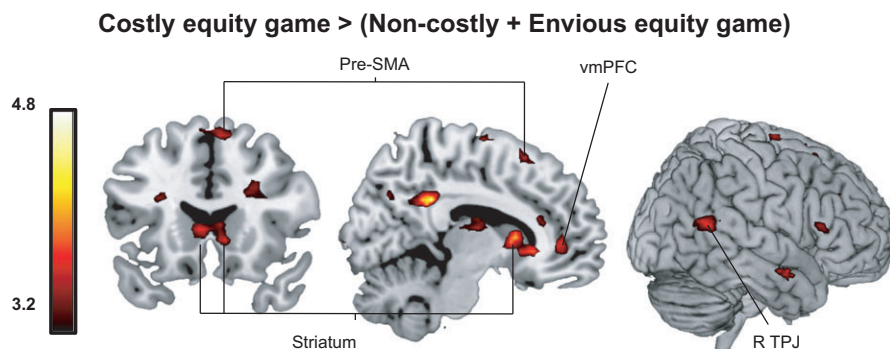


Figure 4 Both groups of adolescents showed increased activity in bilateral striatum (peaks at $9, 14, 7$ and $-6, 17, 4$), vmPFC (peak at $-6, 44, -2$), Pre-SMA (peak at $6, 20, 58$), dACC (peak at $9, 29, 19$) and rTPJ (peak at $63, -49, 13$) when making decisions in the game in which sharing was costly relative to the other games where sharing was not costly (Costly equity > [Non-costly equity + envious equity]).

Stably accepted adolescents > Chronically rejected adolescents

[Costly equity game > (Non-costly + Envious equity game)]

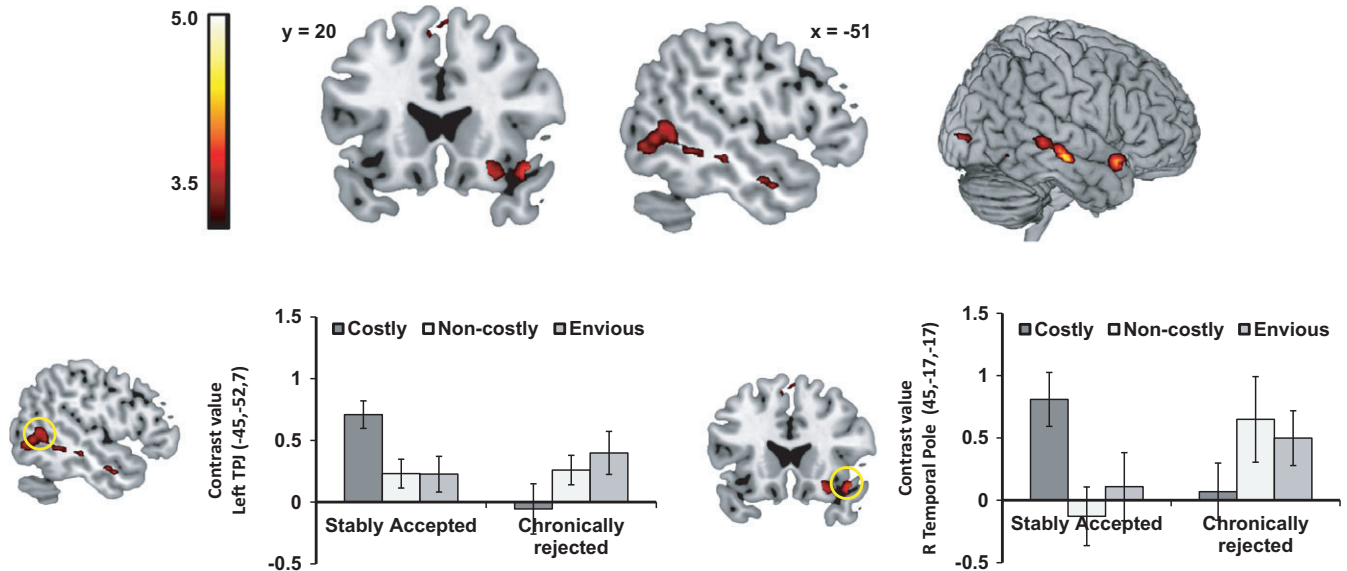


Figure 5 Stably accepted adolescents exhibited heightened activity in left pSTS/TPJ (peak at $-45, -52, 7$), right IFG/Al (peak at $27, 23, -14$), right Temporal pole (peak at $45, 17, -17$) and pre-SMA (peak at $-3, 23, 55$) compared to chronically rejected adolescents in the costly equity game relative to the other two games (Stably accepted adolescents > Chronically rejected adolescents [Costly equity game > {Non-costly equity + envious equity game}]). Subject-level contrast values in left pSTS/TPJ and right temporal pole were extracted for decisions in each game separately and plotted to facilitate interpretation.

Bandura & Zimbardo, 2000; Veenstra, Lindenberg, Oldehinkel, De Winter, Verhulst *et al.*, 2008; Zimmer-Gembeck, Geiger & Crick, 2005) and extends it by showing that chronically rejected children act less generously towards others even when they can do so without expending any efforts or costs. When fairness was costly, the link between peer status history and prosocial behavior was moderated by individual differences in perspective taking. Together these findings partly confirm the hypothesis that stably accepted adolescents show more prosocial behavior than chronically rejected adolescents, but also nuance this oversimplified notion in three important ways.

First, we found no evidence of generally elevated levels of prosocial behavior in stably accepted adolescents relative to their chronically rejected counterparts. Findings suggesting that accepted children show more prosocial behavior than rejected children are predominantly based on interactions with familiar peers with whom children interact repeatedly (e.g. classmates) (Caprara *et al.*, 2000; Veenstra *et al.*, 2008; Zimmer-Gembeck *et al.*, 2005). Our results suggest that stably accepted adolescents are just as likely to maximize self-interest as chronically rejected adolescents when they can

do this anonymously in economic games with no consequences for their reputation. Future studies could critically test for the role of pre-existing relationships or reputation in prosocial behavior by coupling stably accepted and chronically rejected children with known others (e.g. friends vs. non-friends) or with unknown others with whom they either interact repeatedly or only once.

Second, not all chronically rejected adolescents show lower levels of prosocial behavior than their accepted counterparts. In fact, chronically rejected adolescents who reported higher levels of perspective taking shared more often with the recipients than those who reported lower levels of perspective taking when this was costly. This moderation of the link between a history of peer rejection and prosocial behavior by perspective taking suggests that individual differences in social cognition may have important consequences for the developmental pathways associated with chronic peer rejection. Better-developed social cognitive skills, such as perspective taking, may not only carry benefits for peer acceptance (Fink *et al.*, 2014; Slaughter *et al.*, 2015), but also disadvantages, such as making children more vulnerable to negative feedback (Cutting & Dunn, 2002). Rejected

children and adolescents form a heterogeneous group consisting of aggressive/externalizing and withdrawn/internalizing subtypes (Ladd, 2006). Future research with larger samples could test whether individual differences in social cognition can help dissociate between a developmental pathway where peer rejection in combination with underdeveloped social skills leads to more aggression and externalizing behavior over time and one involving better-developed social skills, which may lead to more withdrawal and more internalizing problems over time.

Third, by manipulating benefits for the other person while keeping costs to the decision-maker constant, we showed that prosocial choices that maximized the recipient's profits (but resulted in having less than the other person) were neither associated with perspective taking nor with peer status history. Taken together, these results show that stably accepted adolescents and chronically rejected adolescents who report higher levels of perspective taking are more likely to share equally, but they are not more tolerant of higher outcomes in a peer.

Neuroimaging results: links between childhood peer status and activation of the saliency and mentalizing network

When deciding whether or not to pay a cost to share equally, stably accepted adolescents showed more activity in left pSTS/TPJ, right temporal pole, pre-SMA, and right IFG/AI than chronically rejected adolescents. These regions have previously been implicated in separate processes in social decision-making. The pre-SMA/ACC and AI have a domain general role in encoding representations of the physiological state of the body and affective signals that guide decision-making (Chang, Yarkoni, Khaw & Sanfey, 2013; Singer, Critchley & Preuschoff, 2009). Heightened pre-SMA/ACC and insula activity has been repeatedly associated with detecting violations of social norms, including fairness norms in social decision-making (Corradi-Dell'Acqua *et al.*, 2013; Güroğlu, van den Bos, Rombouts & Crone, 2010; Güroğlu *et al.*, 2014b). Heightened pre-SMA and insula activity might reflect a greater degree of conflict or emotional processing associated with violating the equity norm in situations in which fairness is costly, compared to situations in which fairness is not costly.

The pSTS/TPJ and temporal pole have been shown to be involved in mentalizing, i.e. thinking about other people's mental states (Denny *et al.*, 2012; Gweon, Dodell-Feder, Bedny & Saxe, 2012), and social decision-making in economic games (Gunther Moor *et al.*, 2012; Güroğlu *et al.*, 2011; van den Bos *et al.*, 2011a).

Possibly, heightened activity in mentalizing regions during costly sharing decisions reflects greater allocation of attention to the other person's outcomes or increased switching between perspectives of the self and the other (Koster-Hale & Saxe, 2013; Mitchell, 2008; Van Overwalle, 2009). Together, these heightened neural responses in the stably accepted adolescents might indicate that they experience greater conflict and allocate greater levels of attention to the other person's outcomes than the chronically rejected adolescents. This is in line with studies reporting that children with an accepted status engage in more other-oriented thought than children with a rejected status (Fink *et al.*, 2014; Slaughter *et al.*, 2015). Together these findings extend prior work by showing that separable networks involved in social decision-making are not only differentially sensitive to developmental change (Güroğlu *et al.*, 2011; Steinbeis *et al.*, 2012; van den Bos *et al.*, 2011a), but also to individual differences in peer acceptance during childhood.

Limitations and future directions

A couple of limitations warrant consideration. First, our fMRI paradigm was not optimal for dissociating neural processes involved in equity vs. inequity choices. Participants were consistent in their choices, which proves that they were not choosing randomly and made meaningful choices. However, contrasting equity choices with inequity choices within games would have resulted in unbalanced analyses (i.e. comparisons based on varying amounts of trials) or in a severe loss of power (e.g. through exclusion of participants who consistently chose equity or inequity in a certain game). A strength of the current analyses is that they are based on a balanced design in which contrasts were based on a sufficient amount of trials that did not vary between participants. Nonetheless, it remains a limitation that heightened neural responses when confronted with costly sharing decisions relative to non-costly sharing decisions could not be attributed to either the selfish (inequity: 2–0) or the prosocial (equity: 1–1) choice.

Second, our data do not speak to the question whether higher neural responses in the stably accepted group (relative to the chronically rejected group) were *caused* by their stable high status, or whether they reflect a propensity that was already present before stably accepted adolescents attained their accepted peer status in childhood. Future longitudinal studies should investigate whether children who show heightened mentalizing-related activity early in childhood are more likely to become accepted by peers when they enter formal schooling. Furthermore, it would be interesting to test

whether perspective taking instructions or instructions to allocate more attention to the other person's earnings can increase mentalizing-related activity. Similarly, it would be interesting to test whether experimentally heightened activity in the mentalizing network translates into more frequent displays of prosocial behavior and whether this could have positive consequences for acceptance among peers.

Conclusions

The current study demonstrates that neural responses during sharing decisions in adolescence vary as a function of sustained peer acceptance during childhood. The results provide insights into the neural and socio-cognitive processes that underlie the widely established links between peer acceptance and development of prosocial behavior. Crucially, longitudinal studies have shown that prosocial behaviors are among the strongest predictors of concurrent and future peer acceptance across childhood and adolescence (Asher & Coie, 1990; Caprara *et al.*, 2000). In turn, peer acceptance is an important predictor of later mental health and academic success (DeRosier *et al.*, 1994; Ladd & Troop-Gordon, 2003; Sturaro *et al.*, 2011). A mechanistic understanding of bidirectional associations between peer acceptance and the development of prosocial behavior can provide valuable insights for designing interventions that can help children and adolescents who suffer from mental health or academic problems due to a lack of acceptance among peers.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Participant characteristics.

Table S2. Brain regions revealed by whole-brain analyses full factorial 3×2 ANOVA with 'allocation game' as a within-subjects factor and 'peer status history' as a between-subjects factor testing (all thresholded $p < .001$ uncorrected, > 10 voxels).

Table S3. Brain regions revealed by planned whole-brain follow-up t contrasts comparing each allocation game with the other two allocation games (all thresholded $p < .001$ uncorrected, > 10 voxels).

Table S4. Brain regions revealed by planned whole-brain follow-up t contrasts comparing the two peer status history groups on the comparison of each allocation game with the other two allocation games (all thresholded $p < .001$ uncorrected, > 10 voxels).

Data S1. Supplementary analyses