Acceptance, rejection, and the social brain in adolescence : toward a neuroscience of peer relations

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CHAPTER 8

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, little is known about the neurobiological mechanisms underlying these associations. To address this question, 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 equally or unequally with varying costs and profits to them and unknown others. 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 the stably accepted group, compared to the chronically rejected group, showed higher levels of activation in the temporo-parietal junction, temporal pole, pre-supplementary motor area and anterior insula during costly compared to non-costly sharing decisions. These findings demonstrate that a stable accepted status across childhood is associated with heightened activity in brain regions previously linked to perspective taking and the detection of social norm-violations when making decisions about fairness, and thereby provide insight in the interconnections between peer acceptance and the neural processes underlying prosocial behavior.

8.1 INTRODUCTION

A basic prosocial tendency to share resources with another person is present early in human development (Blake, McAuliffe, & Warneken, 2014; Brownell, Svetlova, & Nichols, 2009; Svetlova et al., 2010), but prosocial behavior continues to grow in complexity across childhood and adolescence (Banerjee, Watling, & Caputi, 2011; Brownell, Ramani, & Zerwas, 2006). This increasing complexity of prosocial behavior is accompanied by developmental changes in the ability to take other people's perspective (Eisenberg et al., 1995; Eisenberg et al., 1991). Crucially, prosocial behavior and perspective-taking ability have important consequences for acceptance among peers and psychosocial adjustment. That is to say, children who show more prosocial behavior and who have better perspective taking skills are more accepted by their peers (Fink et al., 2014; Slaughter et al., 2002). Given that 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), it is important to gain a mechanistic understanding of links between acceptance among peers and the development of prosocial behavior.

Developmental changes in prosocial behavior have been linked to developmental changes in activity in brain regions implicated in perspective taking and 'theory of mind' in the medial frontal and temporo-parietal cortex (Fett et al., 2013; Güroğlu et al., 2011; van den Bos et al., 2011), suggesting that more advanced forms of prosocial behavior are associated with increased activity in brain regions supporting social cognition. Yet, how neural processes involved in prosocial behavior and perspective-taking relate to individual differences in exposure to peer acceptance remains an open question. Therefore, we examined how sustained exposure to either high or low levels of peer acceptance across childhood is associated with prosocial behavior when sharing valuable resources and its neural correlates in adolescence.

Prosocial behavior has strong developmental roots, which is evident from displays of helping and sharing behavior in infancy (Schmidt & Sommerville, 2011; Warneken & Tomasello, 2006). However, infants are much more reluctant to display prosocial behavior when it is costly, that is, when they have to give up some of their own possessions to act prosocial (Svetlova et al., 2010). Costly prosocial behavior has often been studied using economic exchange games in which one person (i.e., the allocator) is given a set of valuable rewards, such as money, candy or stickers and can then decide how much he/she would like to share with a second player (i.e., the recipient). Using economic games that we will refer to as 'equity games', prior studies have shown that the willingness to give up a reward to share equally differs in various phases of childhood and adolescence (Fehr et al., 2008; Fehr, Glätzle-Rützler, & Sutter, 2013; Meuwese et al., 2014; Steinbeis & Singer, 2013).

In these games, participants are given the opportunity to choose between either an equal split of resources (equity) or an alternative unequal distribution (inequity), which could benefit either themselves (advantageous inequity) or the other player (disadvantageous inequity). Between the ages of 3 and 8 years, children increasingly start to distribute resources in a way that ensures equal pay-offs for both players (Fehr et al., 2008). That is, whereas three-year olds are more likely to choose inequity that favors themselves, 7- and 8-year olds are more likely to choose the equity option, even when this requires them to give up a reward (i.e., they show advantageous inequity aversion). Eight year-olds are also more likely than 3-year-olds to choose the equity option when inequity results in a higher outcome for a peer (i.e., they show disadvantageous inequity aversion), even when this has no consequences for their own profits (Fehr et al., 2008). These findings show that although children are increasingly willing to pay a cost to distribute resources in a way that ensures equal pay-offs for everyone involved, their developing sense of fairness does not make them necessarily more generous or tolerant of higher outcomes for a peer. Between the ages 8 and 18, adolescents become less strict in choosing the equity option and they are progressively more likely to maximize other people's outcomes (by choosing a prosocial disadvantageous inequity option), but also to maximize their own outcomes (by choosing a self-maximizing advantageous inequity distribution) (Almås et al., 2010; Fehr et al., 2013; Meuwese et al., 2014). Taken together, these findings show that strict adherence to a fairness norm of equality first increases across childhood and then declines across adolescence. However, how such sharing decisions might differ as a function of peer acceptance or individual differences in perspective-taking abilities has not been studied yet.

Neuroimaging studies that combined economic exchange games with functional Magnetic Resonance Imaging (fMRI), two distinct, but interacting, networks of brain regions involved in decisions about fairness have been identified (Rilling & sanfey, 2011). First, a 'salience network' consisting of the pre-supplementary motor area/anterior cingulate cortex (pre-SMA/ACC) and anterior insula (AI) 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 AI activity has been observed in people when they are treated unfairly (Sanfey et al., 2003), when they see somebody else being treated unfairly (Corradi-Dell'Acqua et al., 2013) and also when they divide resources in an unfair manner themselves (Güroğlu, Will, & Crone, 2014).

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 et al., 2012; Güroğlu et al., 2011; van den Bos et al., 2011). This mentalizing network is consistently identified in tasks that probe reasoning about other people's mental states (e.g. feelings, intentions and desires) (Blakemore et al., 2007; Saxe et al., 2009) and in tasks in which participants are asked to take other people's perspective (Denny, Kober, Wager, & Ochsner, 2012; Pfeifer et al., 2009) or where they do this spontaneously (Wagner, Kelley, & Heatherton, 2011). Prior work has demonstrated that these two networks are differentially sensitive to developmental change (Güroğlu et al., 2011;

van den Bos et al., 2011). 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 continues to increase across adolescence (Blakemore & Mills, 2014; Burnett, Sebastian, Cohen Kadosh, & Blakemore, 2011). That is, developmental increases in the recruitment of the TPJ have been associated with developmental increases in prosocial behavior, predominantly in situations that require higher levels of perspective taking (Güroğlu et al., 2011; van den Bos et al., 2011). The current study addressed the question whether activity in these circuits varies with individual histories of socialization experiences in the peer context (i.e. stable histories of peer acceptance or rejection).

For the present study 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 acceptance and rejection by peers 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). In an MRI scanner, both groups played three equity games (Fehr et al., 2008; Güroğlu, Will, & Crone, 2014) 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 'advantageous competitive inequity' game), could be costly for the participants themselves (costly sharing in the 'advantageous self-maximizing inequity' game), or could decrease the outcomes of the recipient (envious sharing in the 'disadvantageous prosocial inequity' game).

Based on widely established links between an accepted peer status and higher levels of prosocial behavior (Newcomb et al., 1993), we expected that the stably accepted group would more often choose the prosocial option in the equity games than the chronically rejected group (i.e. choosing the option that maximized the other person's profits). We hypothesized that stably accepted adolescents would report higher levels of perspective taking than chronically rejected adolescents (Fink et al., 2014; Slaughter et al., 2002) and we predicted that individual differences in perspective taking would correlate with higher levels of prosocial behavior (Eisenberg et al., 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 poles). We expected this to be most pronounced in decisions in which self-interest conflicts the most with the other person's interest (i.e. when sharing was costly), given that such decisions require higher levels of perspective taking (Güroğlu, van den Bos, & Crone, 2014).

8.2 METHOD

Participants and recruitment procedure

Participants were recruited from a longitudinal study (N = 1,189), 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. 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. 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 to be 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; SD = .77; 14 male) and 19 had a history of chronic peer rejection (M age = 14.0; SD = 0.61; 13 male). Stably accepted and chronically rejected adolescents did not differ in age, pubertal status, gender, age, pubertal status, ethnicity, or IQ (all ps > .15; see Supplementary ***Table S8.1***; see 8.5). 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: Equity games

Participants played three economic games, which have previously been used to assess equity preferences in children and adolescents (Fehr et al., 2008; Güroğlu, van den Bos, & Crone, 2014; Meuwese et al., 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 8.1***). In the advantageous competitive inequity game, the alternative distribution yielded the participants 1 coin, but left nothing for the recipient (1-0). Choosing the equity condition was therefore a non-costly sharing decision. In the advantageous self-maximizing inequity game participants, the alternative distribution yielded the participant 2 coins, but left nothing for the recipient (2-0). Choosing the equity condition was therefore a costly sharing decision, because participants had to forego one coin to share equally. In the disadvantageous prosocial inequity game the alternative distribution yielded the participant 1 coin and resulted in 2 coins for the recipient. Choosing the equity option would result in an outcome for the recipient that is lower than what he/she could have received (2 coins instead of 1) had the participant chosen for the alternative distribution. The equity option in the disadvantageous prosocial inequity game was therefore not the most prosocial option and choosing the equity option reflects disadvantageous inequity aversion. Instructions emphasized that the participants' decisions had consequences for both their own monetary profits and those of the recipients, who were told to be other participants in the study. The participants were told that after the experiment one choice would be randomly selected to be paid out to them as well as to the recipients. In reality, each participant received 2 Euros after completion of the task.

The neuroimaging task consisted of 60 trials (20 trials per game). 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 with 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 8.1***). Each trial was accompanied by a different name, indicating that each choice was for a different recipient. The position of the equal distribution (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.

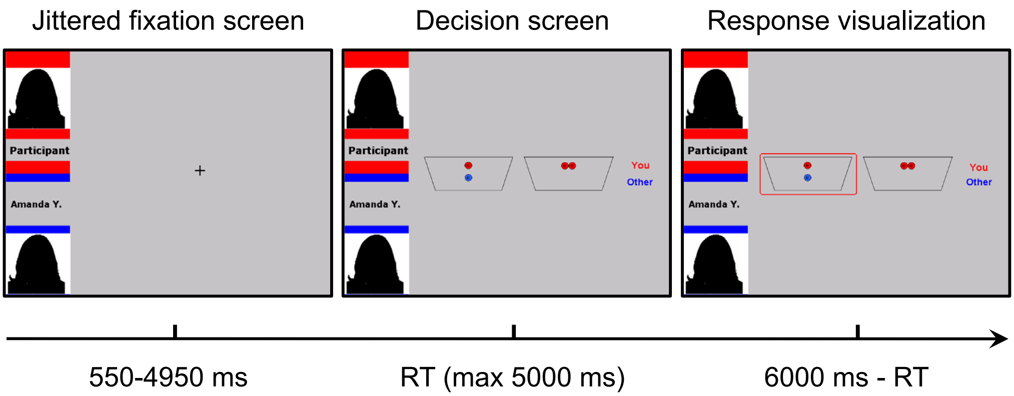

Figure 8.1 *Visual display of events presented in the one trial of the fMRI task. Each trial started with a fixation cross with a jittered duration (550–4950 ms). Subsequently, participants were presented a decision screen containing: the name of the participant in red, the name of the recipient in blue 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.*

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). 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)= 30ms, 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). Images were slice-time corrected, realigned, spatially smoothed using an 8-mm FWHM Gaussian filter, and spatially normalized to each participant's anatomical T1 scan. Translational movement parameters never exceeded 1 voxel (<3 mm) in any direction for any participant or scan. The normalization algorithm resampled the volumes to 3mm cubic voxels using a 12-parameter affine transformation and a nonlinear transformation involving cosine basic functions. All results are reported in MNI305 stereotactic space.

A first-level GLM was defined for each participant's functional run that included regressors for each decision in each game separately (equity game [3] × choice [2]). The fMRI time series were modeled by a series of events with zero duration at the onset of stimulus presentation and were convolved with a canonical hemodynamic response function (HRF). The GLM also contained a basic set of cosine functions that high-pass-filtered the data, a regressor indicating missed trials, and a covariate to control for run effects. The participant-specific contrast images were obtained at the subject level and were then submitted to group level analyses at the second level, where participants served as a random effect in a full factorial analysis of variance (ANOVA) with equity game as a within-subjects factor and peer status history as a between-subjects factor. Given that choice-patterns showed little variation within subjects, but varied considerably between subjects, modeling the data based on the participants' choices would result in an unbalanced design with varying amounts of trials per cell (see Güroğlu, Will, & Crone, 2014). Because our hypotheses focused on the individual differences in neural processes associated with varying costs associated with fairness, we collapsed across choices and focused on the main effect of equity game and the equity game × peer status history interaction consistent with prior work (Gunther Moor et al., 2012; Steinbeis et al., 2012). Consequently, our analyses were based on a balanced design with the same amount of trials for each participant (20 per game; 60 in total).

For group analyses, contrast maps of each decision in each game relative to a low-level visual baseline (i.e. fixation cross) were entered in a factorial 3 × 2 ANOVA with equity game (advantageous self-maximizing inequity-fixation, advantageous competitive inequity-fixation and disadvantageous prosocial inequity-fixation) as a within-subjects factor and peer status history (stably accepted vs. chronically rejected adolescents) as a between-subjects factor. We examined the main effect of equity game and the equity game × peer status history interaction; 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 followed up the main effect of game and the equity game × peer status history interaction by planned *t*-contrasts to examine differences between the games and groups. We used the MarsBaR toolbox (Brett et al., 2002; http://marsbar.sourceforce.net/) to extract activity in functional regions of interest. For each ROI, the blood oxygenation level dependent (BOLD) signal across functional clusters of voxels was averaged and the center of mass is reported.

8.3 RESULTS

Behavioral results

Equity choices and peer status history

To examine associations between peer status history and equity choices in the three equity games, 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 equity game, trial number, peer status history × equity game and equity game × trial number two-way interactions, and a equity game × trial × peer status history three-way interaction term as predictor variables. We included trial number as a predictor to explore the possibility that prosocial behavior could change as a function of time given that it was assessed through repeated exposure to multiple one-shot games. The logistic regression model yielded a main effect of advantageous self-maximizing inequity game (ß = -1.28, *SE* = 0.33, Wald = -3.92, $p < .001$), a two-way interaction between advantageous competitive inequity game and status (ß = -1.32, *SE* = 0.48, Wald = -2.72, $p = .006$), and a three-way interaction between advantageous competitive inequity game, status and trial number (ß = 0.06, *SE* = 0.03, Wald = 2.12, $p = .034$).

Follow-up contrasts showed that both stably accepted and chronically rejected participants chose the equity distribution less often in the advantageous self-maximizing inequity Game (*M* = 45%) than in the disadvantageous prosocial inequity Game (*M* = 70%; $p < .001$) and the advantageous competitive inequity Game (*M* = 70%; $p < .001$), indicating that participants were less likely to share equally when this was costly. Equity choices in the latter two games did not differ significantly from each other ($p = 1$). In the advantageous competitive inequity game, stably accepted adolescents chose the equity distribution more often (*M* = 76%) than the chronically rejected adolescents (*M* = 62%; ß = -2.83, *SE* = 1.08, Wald = -2.16, $p = .009$), demonstrating that the stably accepted adolescents were more likely to share equally than the chronically rejected adolescents, but only when this was non-costly. The three-way interaction showed that the difference between the two peer status history groups in the advantageous competitive inequity game diminished as the scanning session progressed (see

Figure 8.2). There were no group differences in the advantageous self-maximizing inequity game (chronically rejected adolescents: *M* = 40%; stably accepted adolescents: *M* = 49%, p = .75) or the disadvantageous prosocial inequity game (chronically rejected adolescents: M = 70%; stably accepted adolescents: M = 70%; p = .67). Reaction times (RTs) were slower in the disadvantageous prosocial inequity game (*M* = 1394 ms; *SD* = 21 ms) than in the advantageous self-maximizing inequity game (*M* = 1245 ms; *SD* = 21 ms) and advantageous competitive inequity game (*M* = 1265 ms; *SD* = 22 ms). Reaction times did not differ between the two groups (main effect and interactions between game and peer status history, all *p*s > .09).

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 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), self-reported perspective-taking, and a status × perspective taking (mean-centered) two-way interaction term as predictor variables. These regression analyses showed that self-reported perspective taking interacted with peer status history to predict equity choices in the advantageous self-maximizing inequity game (ß = 3.61, *SE* = 1.38, Wald = 2.62, p = .009), but not in the disadvantageous prosocial inequity game (ß = -0.92, *SE* = 1.04, Wald = -0.88, p = .377). The interaction between peer status history and perspective taking was a marginally significant predictor in the advantageous competitive inequity game (ß = 2.22, *SE* = 1.26, Wald = 1.76, p = .079). Follow-up correlations between percentage of equity choices and perspective taking in each group separately showed that in the chronically rejected group, self-reported perspective-taking correlated with equity choices in the advantageous competitive inequity game (r = .62, p = .004) and the advantageous self-maximizing inequity game (r = .74, p < .001; see ***Figure 8.3***). In the stably accepted group perspective taking did not correlate with equity choices (all *p*s > .23; see ***Figure 8.3***). Taken together, these findings demonstrate that chronically rejected adolescents who reported higher levels of perspective taking were more likely to share equally when this was costly (advantageous self-maximizing inequity game) and when equity carried no costs (advantageous competitive inequity game). However, they were not more likely to allocate more money to unknown peers than to themselves in the disadvantageous prosocial inequity game.

To examine associations between RTs, peer status history and perspective taking, we ran three similar random effects regression models with RT as the dependent variable and peer status history (0: stably accepted; 1: chronically rejected), self-reported perspective-taking a and two-way interaction terms as predictor variables. Self-reported perspective-taking correlated negatively with RTs when deciding to share equally in each equity game (advantageous

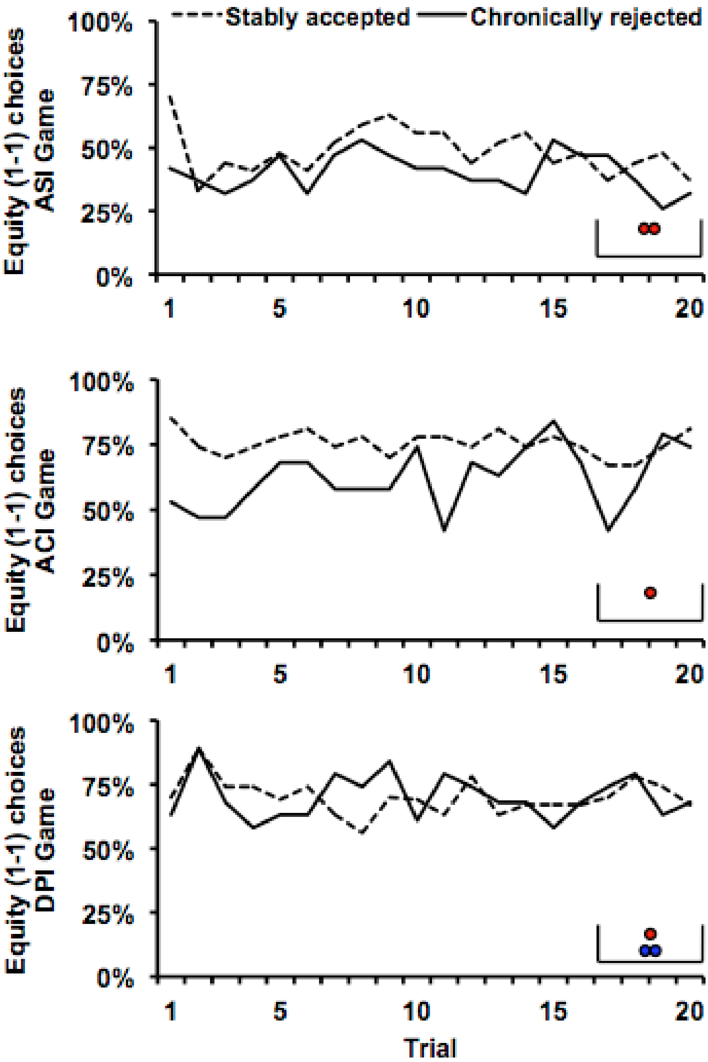

Figure 8.2 *Percentage of equity offers chosen by stably accepted and chronically rejected adolescents in each of the three equity games plotted as a function of trial number. The equity offer (which was always 1 coin for the participant and 1 coin for the recipient) was pitted against an alternative 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).*

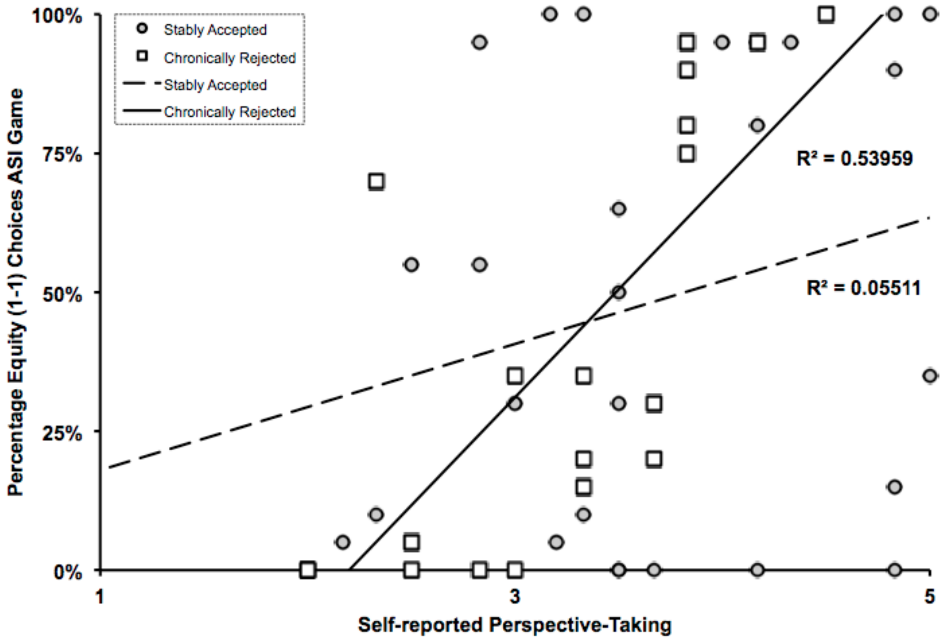

Figure 8.3 *Chronically rejected participants who reported higher levels of perspective taking were more likely to give up a reward to share equally (choosing 1-1 instead of 2-0 in the advantageous self-maximizing inequity Game). In the stably accepted group, no relation between perspective taking and prosocial behavior was observed.*

competitive inequity game: $r = -.45$, $p = .002$; advantageous self-maximizing inequity game: $r = -.44$, $p = .008$; disadvantageous prosocial inequity game: $r = -.43$, $p = .004$) and with sharing unequally (choosing 1-2) in the disadvantageous prosocial inequity game ($r = -.45$, $p = .006$). PT did not correlate with RT when deciding to share unequally in the advantageous competitive inequity and advantageous self-maximizing inequity game (both *p*s > .28). Self-reported perspective-taking did not interact with status to predict RTs. Thus, individual differences in perspective taking predicted higher RTs (i.e., slower reactions) for equity choices in all games and for maximizing the other person's outcomes in the disadvantageous prosocial inequity game, but not for selfish choices.

Neuroimaging results

Whole-brain ANOVA results

To identify brain regions that were differentially involved in the equity games and interactions with peer status history, we first conducted a whole-brain ANOVA with equity game as within-subject factor (three levels: advantageous self-maximizing inequity, advantageous competitive inequity game, disadvantageous prosocial inequity) and peer status history as a between-subject factor (two levels: stably accepted vs. chronically rejected). The ANOVA revealed a main effect of equity 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 equity game and peer status history in left 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 S8.2*** for a complete list of activations; 8.5).

Follow-up whole-brain t*-contrasts*

To further examine the nature of the main effect of game and the game × 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 advantageous self-maximizing inequity game relative to the two other games (Advantageous self-maximizing inequity > [Advantageous competitive inequity + disadvantageous prosocial inequity]) 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 8.4***). The contrast examining heightened activity in the advantageous competitive inequity game relative to the two other games (Advantageous competitive inequity > [Advantageous self-maximizing inequity + disadvantageous prosocial inequity]) resulted in no significant clusters of activation. The contrast examining heightened activity in the disadvantageous prosocial inequity game relative to the other two games (Disadvantageous prosocial inequity > [Advantageous self-maximizing inequity + advantageous competitive inequity]), resulted in heightened activity in bilateral middle occipital gyrus (peaks at -24, -94, 4 and 27, -91, 7) (see Supplementary ***Table S8.3*** for a complete list of activations; 8.5).

To further examine the equity game × peer status history interaction, we followed the *F*-contrasts reported above up 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 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 advantageous self-maximizing inequity game relative to the other two games Stably accepted adolescents > Chronically rejected adolescents (Advantageous self-maximizing inequity game > [Advantageous competitive inequity game + disadvantageous prosocial inequity game]). No brain regions showed higher

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[1] *Although the current paper focused on the question how neural processes during sharing decisions vary as a function of peer status history, we also tested whether our prior findings on the neural correlates of inequity choices replicated (Güroğlu, Will, & Crone, 2014). The results of this analyses are reported in the Supplementary material and show that our prior findings partially replicate (see 8.5).*

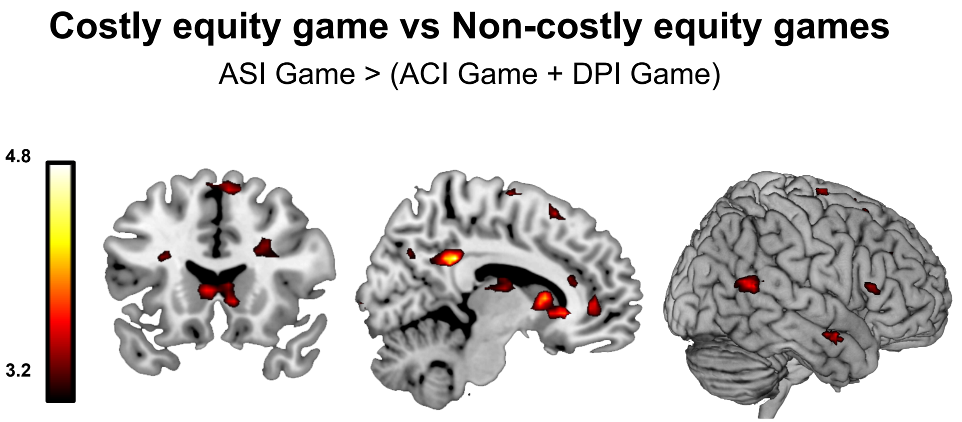

Figure 8.4 *Both groups of adolescents showed increased activity in bilateral striatum (peaks at 9, 14, 7 and -6, 17, 4), vmPFC (peak at -6, 44, -2), Pre-SMA (peak at 6, 20, 58), dACC (peak at 9, 29, 19) and rTPJ (peak at 63, -49, 13) when making decisions in the advantageous self-maximizing inequity game in which fairness was costly relative to the other games where fairness could be established without costs (Advantageous self-maximizing inequity > [Advantageous competitive inequity + disadvantageous prosocial inequity]).*

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 S8.4*** for a complete list of activations; 8.5).

8.4 DISCUSSION

The present study examined links between peer acceptance during childhood and perspective taking, sharing decisions and the neural correlates of sharing decisions 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 (i.e. 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 resources could be shared equally without costs to the decision-maker. Second, when considering a choice option where equal sharing was costly, stably accepted adolescents showed greater activation in left TPJ/pSTS, right temporal pole, right IFG/AI, and pre-SMA than chronically rejected adolescents. These findings have several

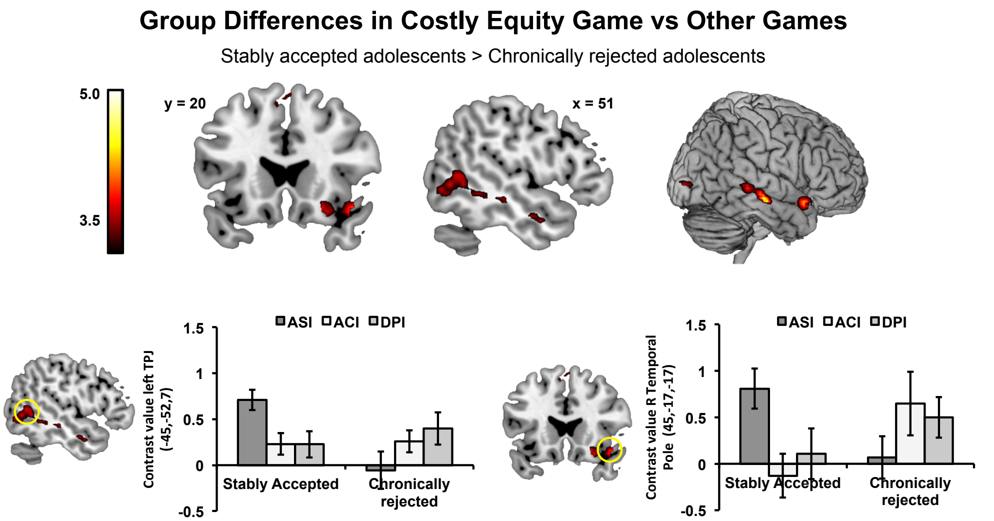

Figure 8.5 *Stably accepted adolescents exhibited heightened activity in left pSTS/TPJ (peak at -45, -52, 7), right IFG/AI (peak at 27, 23, -14), right Temporal pole (peak at 45, 17, -17) and pre-SMA (peak at -3, 23, 55) compared to chronically rejected adolescents in the advantageous self-maximizing inequity game relative to the other two games (Stably accepted adolescents > Chronically rejected adolescents [Advantageous self-maximizing inequity game > {Advantageous competitive inequity game + disadvantageous prosocial inequity 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. ACI = advantageous competitive inequity game; DPI = disadvantageous prosocial inequity game; ASI = advantageous self-maximizing inequity game.*

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

The current findings add to a growing body of work examining the role of aversion to advantageous inequity (i.e. receiving more than another person) and disadvantageous inequity (i.e. receiving less than the other person) in the development of sharing. Behaviors reflecting both advantageous and disadvantageous inequity aversion seems to peak around age 8 (Blake & McAuliffe, 2011; Fehr et al., 2008; McAuliffe, Blake, Kim, Wrangham, & Warneken, 2013) and decline progressively across adolescence (Meuwese et al., 2014). The current findings show that advantageous inequity aversion does not only vary with age, but also with adolescents' peer status history. Adolescents with a history of stable peer acceptance were more likely to avoid advantageous inequity through sharing equally than adolescents with a history of chronic peer rejection, but only when equity could be established without costs. Differences between the two groups were most pronounced during the first trials of the game.

Furthermore, perspective-taking skills moderated associations between childhood peer status and (costly) sharing behavior. It has been widely established that children who are more accepted by their peers have more advanced theory of mind skills (Fink et al., 2014; Slaughter et al., 2002), and exhibit higher levels of prosocial behavior than children who are rejected by their peers according to their parents, peers, teachers and trained observers (Eisenberg et al., 1993; Ladd, Price, & Hart, 1988; Newcomb et al., 1993). Our results showed no relations between perspective taking and prosocial choice in the stably accepted group. However, chronically rejected adolescents who reported higher levels of perspective taking equally shared more often with the recipients than chronically rejected adolescents who reported lower levels of perspective-taking; both when this was costly and when this was non-costly. Prosocial choices that maximized the recipient's profits, but at the same time resulted disadvantageous inequity (choosing 1-2 in the disadvantageous prosocial inequity game), were neither associated with perspective taking nor with peer status history.

Taken together, our findings indicate 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. These results suggest that advantageous inequity aversion is modulated by individual differences in peer acceptance during childhood and individual differences in perspective taking, whereas disadvantageous inequity aversion does not vary with either of these variables.

Individual differences in perspective taking also predicted slower reaction times for prosocial choices (equity choices in the advantageous competitive inequity game and advantageous self-maximizing inequity game and maximizing the other person's outcomes in the disadvantageous prosocial inequity game), but not for selfish choices, across all participants. These findings suggest that perspective taking in the context of fairness decisions is a deliberative process, which could reflect several mechanisms. For example, the longer reaction times might reflect increased levels of attention allocated to the perspective of the recipient or a greater switching between the perspective of the self and the perspective of the recipient. They could also reflect increased conflict between several competing motivations, e.g. increased conflict between a selfish motivation to maximize personal outcomes and an other-oriented motivation. Perspective taking as deliberative process could also explain why group differences in non-costly prosocial behavior were most pronounced at the start of the scanning session. Speculatively, repeated exposure to the same decisions allowed for more time to overthink decisions. This is consistent with prior work that demonstrated that behavioral differences between children with an accepted and a rejected status are most pronounced when children are required to act spontaneously, but that the differences become less pronounced or even disappear, when rejected children are given enough time to think about their decisions (Rabiner et al., 1990).

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 involved in social decision-making. The pre-SMA/ACC and insula have a domain general role in encoding representations of the physiological state of the body and affective signals that guide decision-making (Chang et al., 2013; Singer et al., 2009). Heightened pre-SMA/ACC and insula activity has been repeatedly associated with detecting violations of social norms, including fairness in social decision-making (Corradi-Dell'Acqua et al., 2013; Güroğlu et al., 2010; Güroğlu, Will, & Crone, 2014). Heightened pre-SMA and insula activity might thus 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 decisions-making in economic games (Gunther Moor et al., 2012; Güroğlu et al., 2011; van den Bos et al., 2011). Possibly, heightened activity in mentalizing-regions during costly sharing decisions, reflects higher levels of orienting toward the other person's outcomes or an increased switching 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., 2002). 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., 2011), but also that these circuits are differentially sensitive 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 in the advantageous self-maximizing inequity game relative to the other games 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. A fundamental issue in developmental cognitive neuroscience centers on the question how trajectories of neural, cognitive and behavioral development are shaped by complex interactions between genetically determined maturational processes, and (social) environmental factors (Crone & Dahl, 2012; Will & Güroğlu, in press). This study provides evidence of variation in neural processes underlying social decision-making that can be attributed to environmental factors (i.e. childhood socialization experiences). Consequently, the current findings lay the foundations for future longitudinal neuroimaging studies that can disentangle how internal (e.g. genetic; Avinun et al., 2011) and external (e.g. peer status) factors act separately, and jointly, on brain development and the development of prosocial behavior.

Furthermore, the results advance our understanding of the mechanisms that might underlie the established links between peer acceptance and development of prosocial behavior. Crucially, longitudinal studies have shown that displays of prosocial behavior are the strongest predictor of 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.

8.5 SUPPLEMENTARY MATERIAL

Table S8.1 *Participant characteristics.*

Characteristics and Questionnaires	Group, Mean (*SD*) Chronically Rejected (n = 19)	Stably Accepted (n = 27)	p-value[a]
Mean Social Preference[b] (selection variable)	-1.60 (0.52)	1.16 (0.18)	< .001
Gender (% Male)	74.6	51.9	.14
Age	14.0 (0.61)	14.0 (0.77)	.91
Pubertal status (PDS)			
o Males	2.34 (0.77)	2.19 (0.59)	.58
o Females	3.17 (0.26)	2.72 (0.63)	.15
Race/Ethnicity (% Caucasian)	100%	96.3%	.40
IQ (WISC Similarities and Block Design)	96 (12.45)	100 (10.25)	.20
Current social competence (parent reported)	4.56 (0.61)	5.40 (0.57)	< .001
Anxiety during elementary school (teacher reported)[b]	0.40 (0.84)	-0.31 (1.01)	< .05
Conduct problems during elementary school (teacher reported)[b]	0.71 (1.33)	-0.67 (0.52)	< .001

[a]*All p-values obtained using t tests except for race and gender (Chi-square tests).*

[b]*Average across 6 years of elementary school, Z-standardized*

Table S8.2 *Brain regions revealed by whole-brain analyses full factorial 3 × 2 ANOVA with equity game as a within-subjects factor and peer status history as a between-subjects factor testing for peer status history differences in the equity games (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Main effect of Equity game						
Middle Occipital gyrus	R	42	4.52	30	-94	4
Posterior Cingulate gyrus	R	54	4.30	9	40	31
Middle Occipital gyrus	L	15	4.22	-24	-94	4
pSTS/TPJ	R	25	3.76	60	-55	16
Pre-supplementary motor area	R	19	3.74	12	20	58
Striatum	R/L	31	3.61	9	14	7
			3.40	-6	17	4
			3.35	-9	11	-2
Thalamus	L	26	3.57	-3	-7	10
Interaction effect Equity game × Peer status history						
Middle Temporal gyrus	R	33	4.39	54	-19	-11
Inferior Frontal gyrus/Anterior Insula	R	12	4.01	27	23	-14
Temporal Pole	R	21	3.89	45	17	-17
pSTS/TPJ	L	10	3.56	-45	-52	7

Note. L/R=Left/Right; k=cluster size in 3×3×3mm voxels; *z*=*z*-score; MNI coordinates =xyz voxel coordinates in MNI space of the peak voxel. pSTS = Posterior Superior Temporal Sulcus; TPJ = Temporo-parietal junction

Table S8.3 *Brain regions revealed by planned whole-brain follow-up t contrasts comparing each equity game with the other two equity games (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Advantageous self-maximizing inequity game > (Advantageous competitive inequity game + Disadvantageous prosocial inequity game)						
Posterior Cingulate gyrus	R	310	4.67	9	-40	31*
Striatum	R/L	344	4.14	9	14	7*
			4.01	-3	-16	13*
			3.95	-6	17	4*
Pre-supplementary motor area	R/L	47	3.94	6	20	58*
			3.49	-6	14	64*
Ventromedial prefrontal cortex	L/R	57	3.89	-6	44	-2*
			3.87	6	44	1*
Fusiform gyrus	R	38	3.77	33	-61	14*
pSTS/TPJ	L	44	3.75	63	-49	13*
Calcarine gyrus	L	18	3.73	0	-94	13*
Middle Temporal gyrus	L	18	3.65	57	2	-17*
Supplementary motor area	L	16	3.50	15	-4	70*
Inferior Frontal gyrus	L	11	3.46	48	23	13*
Anterior Cingulate cortex	L	10	3.39	9	29	19*
Advantageous competitive inequity game > (Advantageous self-maximizing inequity game + Disadvantageous prosocial inequity game)						
No significant clusters of activation						
Disadvantageous prosocial inequity game > (Advantageous self-maximizing inequity +Advantageous competitive inequity game)						
Middle Occipital gyrus	L	26	4.15	-24	-94	4
Middle Occipital gyrus	R	39	4.10	27	-91	7

Note. L/R=Left/Right; k=cluster size in 3×3×3mm voxels; *z*=*z*-score; MNI coordinates =xyz voxel coordinates in MNI space of the peak voxel. pSTS = posterior Superior Temporal Sulcus; TPJ = Temporo-parietal junction. * = also significant using FDR correction, $p < .05$, > 10 voxels).

Table S8.4 *Brain regions revealed by planned whole-brain follow-up t contrasts comparing the two peer status history groups on the comparison of each equity game with the other two equity games (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Stably accepted adolescents > Chronically rejected adolescents (Advantageous self-maximizing inequity game > [Advantageous competitive inequity game + disadvantageous prosocial inequity game])						
Middle Temporal gyrus	R	135	4.83	54	-19	-11*
Inferior Frontal gyrus/Anterior Insula	R	71	4.29	27	23	-14*
Temporal Pole			4.23	45	17	-14
pSTS/TPJ	L	179	4.13	-45	-52	7
Middle Temporal gyrus	L	10	3.92	-48	-1	20
Calcarine gyrus	R	26	3.86	21	-91	1
Superior Occipital gyrus	L	41	3.74	-18	-91	1
Precentral gyrus	L	38	3.67	-39	-1	58
Pre-supplementary motor area	L/R	15	3.44	-3	23	55
Stably accepted adolescents > Chronically rejected adolescents (Advantageous competitive inequity game > [Advantageous self-maximizing inequity game + disadvantageous prosocial inequity game])						
No significant clusters of activation						
Stably accepted adolescents > Chronically rejected adolescents (Disadvantageous prosocial inequity game > [Advantageous self-maximizing inequity +advantageous competitive inequity game])						
No significant clusters of activation						

Note. L/R=Left/Right; k=cluster size in 3×3×3mm voxels; *z*=*z*-score; MNI coordinates =xyz voxel coordinates in MNI space of the peak voxel. pSTS = Posterior Superior Temporal Sulcus; TPJ = Temporo-parietal junction. * = also significant using FDR correction, $p < .05$, > 10 voxels).

Supplementary analysis

To test whether our prior findings on the neural correlates of advantageous and disadvantageous inequity choices replicated, we ran the 2 main whole-brain analyses reported in our prior paper (see Güroğlu, Will, & Crone, 2014; **Chapter 7**). The 'Inequity > Equity choice' contrast (collapsed across equity games and across peer status history groups) resulted in activity in the bilateral inferior frontal gyrus, bilateral AI, pre-SMA, and dorsal ACC, which replicates our findings in young adults (see Supplementary ***Figure S8.1*** and Supplementary ***Table S8.5***). The 'Inequity > Equity' contrast within the disadvantageous prosocial inequity game (prosocial inequity [1-2] vs. envious equity [1-1]) did not result in significant clusters of activation at our chosen threshold. In young adults this contrast resulted in heightened activity in the ventral striatum and ventromedial PFC activity.

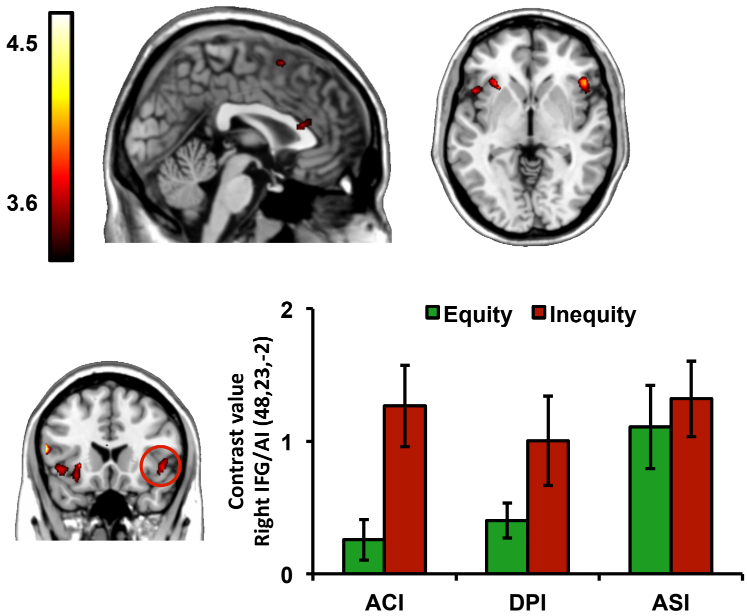

Figure S8.1 *Network of brain regions from the 'Inequity > Equity' contrast collapsed across equity games and across peer status history groups; p < .001, 10 voxel threshold. Bar graph displays contrast estimates obtained from ROI analysis in right AI (MNI 48, 23, -2) for inequity and equity choices in the three equity games. Error bars indicate standard error of the mean. ACI = advantageous competitive inequity game; DPI = disadvantageous prosocial inequity game; ASI = advantageous self-maximizing inequity game.*

Table S8.5 *Brain regions revealed by planned whole-brain follow-up t contrasts comparing each equity game with the other two equity games (all thresholded* p < *.001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Inequity > Equity (all equity games)						
Inferior frontal gyrus (vlPFC)	L	14	4.18	-57	20	13
Inferior frontal gyrus	R	45	3.83	48	23	-2
Anterior Insula	L	32	3.74	-27	20	-2
Pre-supplementary motor area	L/R	61	3.65	-9	8	64
Inferior frontal gyrus/Anterior Insula	L	31	3.60	-45	17	-5
Dorsal anterior cingulate cortex		19	3.48	0	26	16

Note. L/R=Left/Right; k=cluster size in 3×3×3mm voxels; *z*=*z*-score; MNI coordinates =xyz voxel coordinates in MNI space of the peak voxel. vlPFC = ventrolateral prefrontal cortex.