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

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CHAPTER 4

NEURAL CORRELATES OF PUNISHING AND FORGIVING SOCIAL EXCLUSION IN ADOLESCENTS WITH A HISTORY OF CHRONIC PEER REJECTION

This chapter is submitted as:

Will, G.-J., Crone, E. A., van Lier, P. A. C., & Güroğlu, B. (submitted). Neural correlates of punishing and forgiving social exclusion in adolescents with a history of chronic peer rejection.

ABSTRACT

Social exclusion is a distressing experience and can lead to both retaliatory and prosocial behaviors toward the sources of exclusion. However, no study has examined how retaliatory and prosocial reactions to social exclusion and their neural correlates vary as a function of chronic peer group rejection. This functional Magnetic Resonance Imaging (fMRI) study examined the neural correlates of punishment and forgiveness of social exclusion in adolescents (age 14) who either had a chronic rejected status among peers (*n* = 19) or a stable accepted status (*n* = 27) across six elementary school grades. Participants played an economic game in which they distributed money between themselves and unknown peers who previously either included or excluded them in a virtual ball-tossing game (Cyberball). Decreasing the excluders' monetary profits (i.e., punishment) was associated with increased activity in the ventral striatum, dorsolateral prefrontal cortex (PFC) and parietal cortex in both groups. Refraining from punishment through equally sharing with the excluders (i.e., forgiveness) was associated with increased activity in dorsomedial PFC in both groups. Compared to stably accepted adolescents, chronically rejected adolescents showed higher activity in the dorsal striatum and lateral PFC when they forgave the excluders. These findings demonstrate that a history of chronic peer rejection is associated with differential neural activity during prosocial, but not during retaliatory, reactions to social exclusion in adolescence.

4.1 INTRODUCTION

Humans have a fundamental need to form and maintain lasting positive relationships with others. Social exclusion and rejection frustrate this need and lead to retaliation toward the sources of exclusion (Twenge, Baumeister, Tice, & Stucke, 2001) and decreases in prosocial behavior (Maner et al., 2007). Yet, people differ considerably in their reactions to acute rejection experiences. For example, children who have been chronically rejected by peers develop anxious and angry expectations about being rejected, which in turn predict greater difficulties in interactions with peers over time (London et al., 2007). A potential mechanism through which chronically rejected children may come to experience more difficulties in their peer group is through their reactions to everyday rejection experiences. Children who react to exclusion with retaliatory vengeance might be more likely to elicit further rejection than those who show behavior aimed at reconnecting after exclusion (Sandstrom, 2004). Therefore, we examined the neural and psychological processes involved in retaliatory (i.e. punishing) and prosocial (i.e. forgiving) reactions to social exclusion among adolescents with a history of chronic peer rejection and tested how their reactions differed from adolescents with a history of stable peer acceptance.

Social exclusion is a distressing experience and coincides with increased activity in brain regions involved in generating and regulating negative emotions, including the anterior cingulate cortex (ACC), the anterior insula (AI), and ventromedial- and ventrolateral regions of the prefrontal cortex (PFC) (Eisenberger, 2012). Moreover, ACC activation during social exclusion is enhanced in people who are more distressed by exclusion (Eisenberger et al., 2003), people who have anxious or angry expectations about interpersonal rejection (DeWall et al., 2012; Masten et al., 2009), who perceive lower levels of social support in their relationships (Eisenberger et al., 2007), and those who were chronically rejected by peers during childhood (Will, van Lier, Crone, & Güroğlu, 2015). Together, these studies demonstrate that a history of peer rejection and accompanying hypersensitivity to rejection are associated with enhanced neural responses to social exclusion, but how such a history might affect neural processes underlying retaliatory and prosocial reactions to exclusion remains to be investigated.

Neural processes underlying retaliatory and prosocial reactions have proven to be a reliably examined by giving participants the opportunity to distribute money between themselves and the people who previously included (i.e. includers) or excluded (i.e. excluders) them. Using this approach, studies have shown that people selectively punish the excluders by decreasing their monetary outcomes while treating the includers fairly (Gunther Moor et al., 2012; Will et al., 2014). This form of punishment has been associated with increased activity in the pre-supplementary motor area (pre-SMA)/ACC and AI. Refraining from punishment and sharing a sum of money equally with the excluders (i.e. forgiveness) has been associated with increased activation in brain regions important for perspective taking (i.e., the temporo-parietal junction [TPJ] and the dorsomedial prefrontal cortex [dmPFC]) and executive control (i.e., lateral prefrontal cortex (lPFC) (Gunther Moor et al., 2012; Will et al., 2014).

Based on well-established behavioral and cognitive signatures of a rejected (vs. an accepted) status, we hypothesized that the neural processes underlying prosocial reactions to exclusion would vary as a function of peer status history. In comparison with their accepted classmates, children with a rejected status are more likely to deal with interpersonal anger in aggressive ways that instigate further conflict (Fabes & Eisenberg, 1992; Rabiner, Lenhart, & Lochman, 1990) and they exhibit deficits in social cognition (e.g. less sophisticated 'theory of mind' skills) and executive control (e.g. problems in impulse control and emotion regulation) (Dodge et al., 2003; Eisenberg et al., 1997; Fink, Begeer, Hunt, & Rosnay, 2014). Based on these findings, we hypothesized that status-related differences in social cognition and executive control are likely to be associated with differential recruitment of neural circuitry supporting social cognition (e.g. dmPFC and TPJ) and executive control (e.g. lPFC) during prosocial reactions to exclusion.

To test this hypothesis, we recruited participants whose peer status (i.e., peer group acceptance and rejection) was assessed annually across six elementary school grades as part of a large-scale longitudinal study (van Lier & Koot, 2010). Using strict selection criteria, we invited participants who were either chronically rejected or had a stable accepted status among peers to participate in the current study. While undergoing functional Magnetic Resonance Imaging (fMRI), the participants were first included and then excluded by two unknown adolescents in a virtual ball-tossing game called Cyberball (Williams et al., 2000). Subsequently, they played an economic game, previously validated in adults, in which they could either punish or forgive the excluders (Will et al., 2014). Results on the neural correlates of exclusion in Cyberball are reported elsewhere (see: Will et al., 2015).

We anticipated that punishment of excluders would be associated with increased activity in the pre-SMA/ACC and AI (Sanfey et al., 2003; Strobel et al., 2011). In contrast, forgiveness was expected to be associated with increased activity in the dmPFC, TPJ and lPFC (Brüne et al., 2013; Will et al., 2014). With respect to individual differences, we expected that adolescents with a history of chronic peer rejection, relative to adolescents with a history of stable peer acceptance, would show: (i) lower levels of forgiveness toward excluders and (ii) enhanced recruitment of brain regions implicated in social cognition (e.g. dmPFC, TPJ) and executive control (e.g. lPFC) during forgiveness of excluders, consistent with findings demonstrating that adults who showed less forgiveness behavior activated these networks to a greater extent when they did forgive (Will et al., 2014). We also explored how individual differences in perspective taking and executive control were associated with punishment and forgiveness behavior and neural activity during forgiveness.

4.2 METHODS

Participants and recruitment procedure

Participants were recruited from a longitudinal study (*N* = 1,189) investigating the impact of social experiences on behavioral, emotional and academic outcomes between the ages of 6 and 12 (annually from first to sixth grade of elementary school) (van Lier & Koot, 2010). Each year, participants were asked to nominate the peers in their class whom 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 and adolescents from the lower (chronically rejected) and upper (stably accepted) 10th percentile were selected.

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. Seventeen adolescents were excluded because they were left-handed (*n* = 4), had an autism spectrum disorder (*n* = 1) or had braces (*n* = 12). Eight adolescents could not be reached. Of the remaining 106 candidate participants, 47 adolescents and their parents agreed to participate in the current fMRI study. Adolescents who chose not to participate in the fMRI study (*n* = 57) did not differ from those who did participant in terms of average social preference, age, or gender (all *p*s > .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, and one participant was excluded from the analyses due to an anomaly. Three participants were excluded from neuroimaging analyses because their head movement exceeded 1 voxel (3 mm) in at least one direction.

The final sample consisted of 43 adolescents, including 25 adolescents with a history of stable peer acceptance (*M* age = 14.0; *SD* = 0.78; 13 male) and 18 adolescents with a history of chronic peer rejection (*M* age = 14.1; *SD* = 0.57; 13 male). Stably accepted and chronically rejected adolescents did not differ in age, pubertal status, gender, race or IQ (all *p*s > .16; see Supplementary ***Table S4.1***). This study was conducted in accordance with the ethical standards of the American Psychological Association as expressed in the Declaration of Helsinki. 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 the scanner environment with a mock scanner. After receiving instructions, participants carried out the following tasks in the scanner: (i) Cyberball inclusion with two anonymous peers, (ii) Cyberball exclusion by two novel anonymous peers, and (iii) A Dictator game in which participants distributed money between themselves and one of the players from the previous Cyberball games (i.e., one of the includers or the excluders; see ***Figure 4.1A***). Participants could see the stimuli on a screen located at the head of the scanner bore via a mirror mounted on the head coil. Head movement was restricted through the use of foam inserts inside the coil. After scanning, participants filled out a battery of questionnaires and were debriefed. Participants received a monetary compensation for participation and small gifts.

fMRI tasks

Cyberball

Participants played two rounds of a virtual ball-tossing game called Cyberball (Williams et al., 2000). Participants were told that the other players in the game with were other participants in the experiment who were connected with them via the Internet. First, participants played Cyberball with two unfamiliar peers (i.e. the includers; two cartoon figures accompanied by a girl's and a boy's name) who included them in a game where each player received the ball an equal amount of times (10/30 throws). Subsequently, they played another round of Cyberball with two novel unfamiliar players (i.e. the excluders; with a new boy's and a new girl's name) who threw the ball once to the participants at the start of the game, but further excluded the participants by not throwing the ball to them for the remainder of the game (28/30 throws).

Dictator Game

Following Cyberball, participants played a modified Dictator Game in which they could distribute coins between themselves and a recipient (Will et al., 2014). The recipient was one of the players from either the first or the second Cyberball game (i.e., Team 1 and Team 2, respectively). Participants were told that the coins represented real money and that their decisions determined how much money they and the recipients would receive at the end of the experiment. In reality, each participant received the same fixed amount of money as compensation.

Participants were given a dichotomous choice to either share an amount of money equally or unequally (see ***Figure 4.1B***). The equal distribution (which always took the form of 5 coins for self/5 for the recipient) was pitted against an unequal alternative, which varied across three conditions: (i) beneficial inequality (8 coins for the participant /2 for the recipient), (ii) non-costly inequality (5 coins for the participant /2 for the recipient), (iii) prosocial inequality (4 coins for the participant /6 for the recipient, which was a filler condition that was added to the fMRI design but not analyzed separately. Decision-making in the prosocial inequality condition was only included in the behavioral analyses and not in the fMRI analyses examining the neural correlates of punishment and forgiveness.

The Dictator Game consisted of 120 trials (20 trials per condition; 3 inequality conditions × 2 recipients) and was administered in 2 runs of 207 volumes each, lasting about 15 minutes in total. After a screen with fixation cross which had a jittered duration (*M* = 1540 ms; *SD* = 1083 ms; min = 550 ms; max = 4950 ms; optimized with Opt-Seq2, Dale, 1999; surfer.nmr.mgh.harvard.edu/optseq/), participants were presented with a decision screen that showed: (i) the two distributions they could choose from and (ii) whether the recipient was a player from Team 1 (i.e. an includer) or Team 2 (i.e. an excluder) (see ***Figure 4.1A***). Participants could choose one of two distributions of money by pressing a button with the index or middle finger of their right hand. After a button was pressed, a red rectangle appeared around the chosen distribution until 6 seconds after trial onset. Failing to respond within 5 seconds resulted in the presentation of a screen with "Too late!" with the duration of 1 second. Trials without a response consisted of less than 1% of all trials and were excluded from further analyses.

Questionnaires

Executive functioning

To assess executive functioning the participants' parents filled out the 'Behavioral regulation index' scale of the 'Behavior Rating Inventory of Executive Function' questionnaire (BRIEF; Gioia, Isquith, Guy, & Kenworthy, 2000; Huizinga & Smidts, 2011). The Behavioral regulation index represents the ability to shift cognitive sets and to modulate behavior and emotions. The scale comprises of three subscales: inhibition (the capacity to suppress impulses, e.g. "Blurts things out"), shifting (the capacity to flexibly adjust behavior to changing demands of a given situation, e.g. "Becomes upset by new situations", and emotional control (the ability to regulate emotional responses, e.g. "Has explosive, angry outbursts". All items were rated on a scale consisting of 1 (*never*), 2 (*sometimes*) to 3 (*often*) and summed. Higher scores on the Behavioral regulation index reflect increased difficulty with behavioral regulation.

Perspective taking

To assess the capacity to adopt another person's point of view participants filled out the perspective-taking subscale of the Interpersonal Reactivity Index (IRI; Davis, 1983) (e.g., "Before criticizing somebody, I try to imagine how I would feel if I were in their place."). All items were rated on a scale from 1 (*not at all*) to 5 (*very much*) and averaged to a mean score of trait perspective-taking.

fMRI data acquisition

Scans were acquired using a 3T Philips Achieva MRI system at the Leiden University

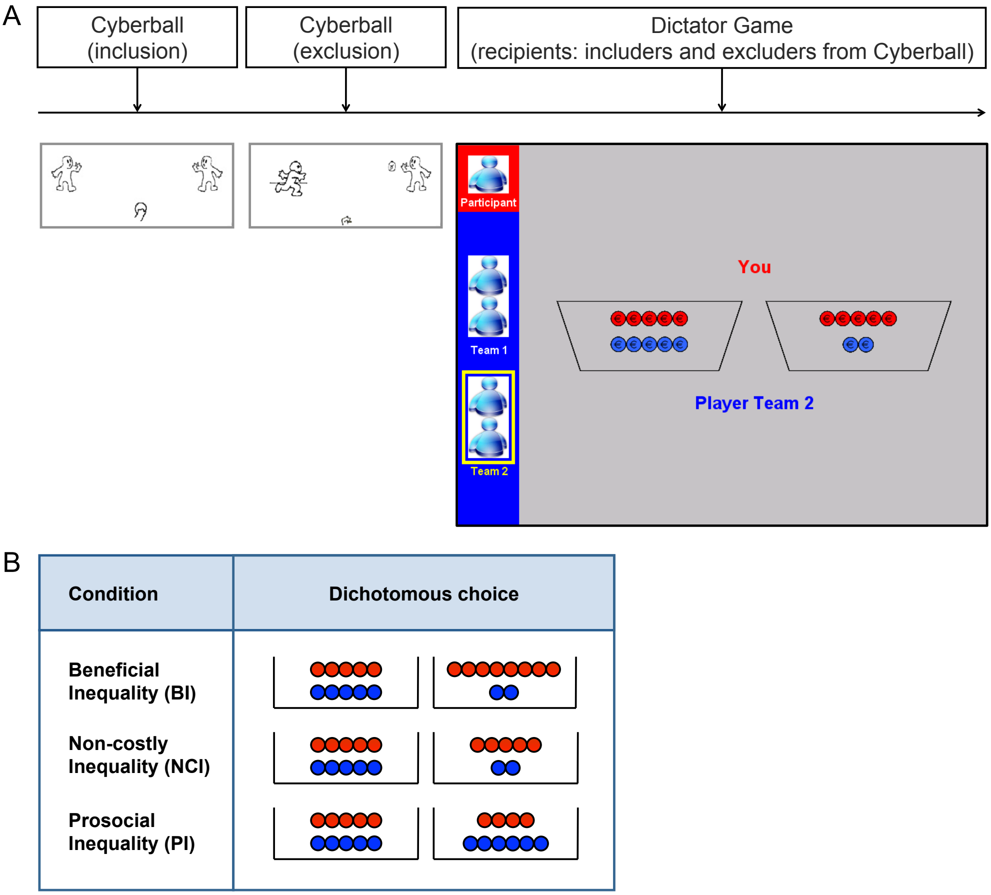

Figure 4.1 *(A) Experimental procedure: Participants carried out the following tasks in the scanner: (i) Cyberball inclusion with two anonymous peers (includers), (ii) Cyberball exclusion by two novel anonymous peers (excluders), and (iii) Dictator game in which participants distributed money between themselves (depicted with red coins) and the players from the Cyberball games (i.e., includers and excluders; depicted with blue coins). (B) In every trial, participants were given a dichotomous choice between either an equal distribution of money and an unequal distribution, of which the latter varied depending on the inequality condition.*

Medical Center. After obtaining a localizer scan, T2*-weighted Echo-Planar Images (EPI) were acquired (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 × 220 × 114.68 mm) during two functional runs of 207 volumes each. The first two volumes in each functional run were discarded to allow for equilibration of T1 saturation effects. High-resolution T1-weighted and T2-weighted anatomical scans (TR = 9.760 ms; TE = 4.59 ms, 140 slices, 0.875 × 0.875 × 1.2 mm voxels, field of view =224 × 168 × 177 mm) were acquired for anatomical reference.

fMRI data analysis

MRI data were preprocessed and analyzed 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. 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. All results are reported in MNI305 stereotactic space.

A first-level general linear model was defined for each participant's functional run that included a boxcar regressor for each epoch of interest (e.g., decision phase) and convolved with a canonical hemodynamic response function (HRF). The duration of epochs in which participants submitted a response was modeled using the participant's reaction time. Regressors were defined separately for equality and inequality choices made in each of the three inequality conditions and analyzed separately for includers and excluders. This model consisted of 12 decision-related regressors (i.e., inequality condition [3] × recipient [2] × choice [2]), a regressor indicating missed trials, and a covariate for each run to control for run effects (3), resulting in a General Linear Model (GLM) with a total of 16 predictors and contained a basic set of cosine functions that high-pass-filtered the data. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each condition separately were used in pair-wise contrasts at the subject level. The resulting contrast images were submitted to group analyses where participants were treated as a random effect. Subsequently, we performed one-tailed t-tests of which 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). Consistent with prior work (Will et al., 2014), punishment was operationalized as the average of beneficial and non-costly unequal distributions chosen for the excluders minus those chosen for includers (Excluders inequality > Includers inequality). Forgiveness was operationalized as the average of equality offers for excluders minus equality towards includes in the beneficial and non-costly inequality conditions (Excluders equality > Includers equality). For group comparisons, contrast images were entered into separate second-level analyses for each contrast of interest, where peer status history (chronically rejected vs. stably accepted) was the between-subjects variable in independent samples t-tests. We used the MarsBaR toolbox (Brett et al., 2002; http://marsbar.sourceforce.net/) to extract activity in functional regions of interest.

4.3 RESULTS

To investigate punishment and forgiveness behavior toward excluders, we performed a repeated measures ANOVA with recipient (2 levels: includers vs. excluders) and inequality condition (3 levels: beneficial inequality, non-costly inequality and prosocial inequality) as within-subjects factors and peer status history (2 levels: chronically rejected vs. stably accepted) as a between-subjects factor for the percentage of unequal offers in the Dictator Game. This analysis yielded main effects of recipient, $F(1, 41) = 30.37$, $p < .001$, $\eta_p^2 = .43$, inequality condition, $F(2, 82) = 35.90$, $p < .001$, $\eta_p^2 = .47$, and a recipient × inequality condition interaction, $F(2, 82) = 34.62$, $p < .001$, $\eta_p^2 = .46$. Participants chose the inequality distribution more often for the excluders than for the includers in the beneficial and non-costly inequality conditions (both *p*s < .001; see ***Figure 4.2***). In contrast, they chose the inequality distribution more often for the includers than for excluders in the prosocial inequality condition ($p = .031$). Neither interaction effects with peer status history, nor a main effect of peer status history were found. Thus, both stably accepted and chronically rejected adolescents punished the excluders by choosing unequal distributions of money for the excluders and they did this to a similar extent.

Reaction times were faster in the beneficial inequality condition (*M* = 1591 ms; *SD* = 69 ms) than in non-costly inequality (*M* = 1744 ms; *SD* = 76) and prosocial inequality (*M* = 1798 ms; *SD* = 74) conditions, but did not differ between recipients and the two groups, all *p*s > .09. Chronically rejected adolescents (*M* = 44.8) had more parent-reported behavioral regulation difficulties than stably accepted adolescents (*M* = 34.8), $t = 2.55$, $p < .05$, also after controlling for gender and ADHD diagnosis. Self-reported perspective-taking skills did not differ between groups ($p = .11$). Punishment behavior (inequality offers for excluders – inequality for includers in the BI and NCI conditions) was not correlated with behavioral regulation difficulties ($p = .39$) or perspective taking ($p = .19$).

Neuroimaging results

Punishment and forgiveness across the sample

Before we examined differences in brain responses between chronically rejected and stably accepted adolescents, we first investigated the neural correlates of punishment and forgiveness across the whole sample. The punishment contrast (Excluders inequality > Includers inequality) resulted in activation in bilateral ventral striatum bilateral ventral striatum (peaks at -12, 20, 7 and 9, 20, 4), right dlPFC (36, 29, 37) and bilateral parietal cortex (peaks at 30, -58, 61 and -45, -45, 52) (***Figure 4.3A***). The forgiveness contrast (Excluders equality > Includers equality) contrast resulted in activation only in the dmPFC (peak at 6, 47, 22; ***Figure 4.3B***).

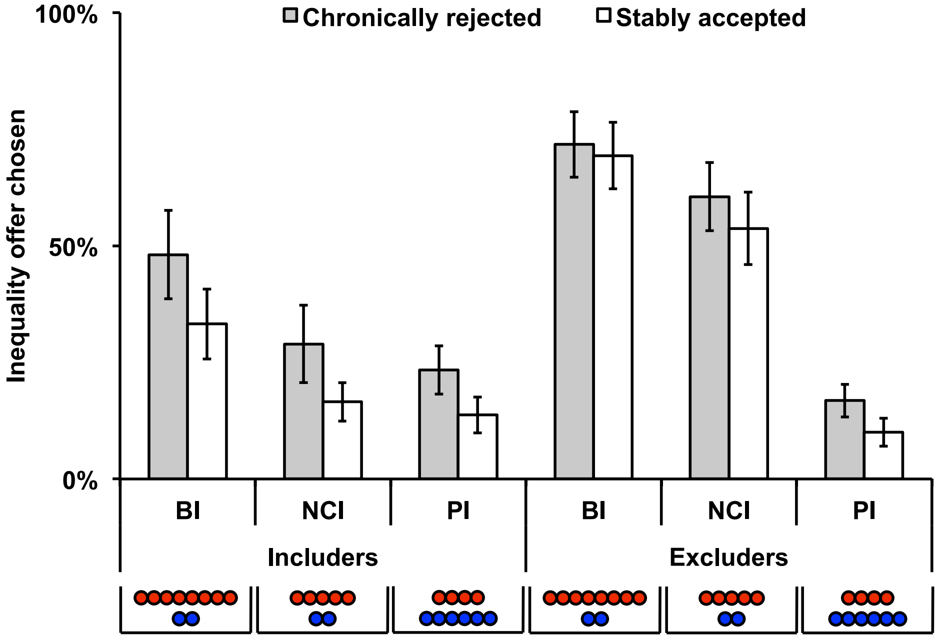

Figure 4.2 *Percentage of inequality offers chosen for includers and excluders in the three inequality conditions of the Dictator Game as a function of prior childhood peer status history. Unequal distributions were pitted against an equal distribution of money (five coins for the participant/five coins for the recipient). BI, beneficial inequality (8/2); NCI, non-costly inequality (5/2); PI, prosocial inequality (4/6).*

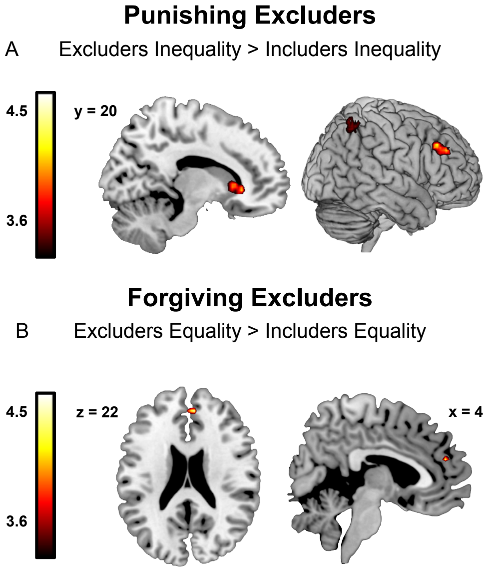

Figure 4.3 *(A) Both groups of adolescents showed increased activity in bilateral ventral striatum (peaks at -12, 20, 7 and 9, 20, 4), right dlPFC (36, 29, 37) and bilateral parietal cortex (peaks at 30, -58, 61 and -45, -45, 52) when punishing the excluders (Excluders inequality > Includers inequality) and (B) Both groups of adolescents showed increased activity in dmPFC (peak at 6, 47, 22) when forgiving the excluders (Excluders equality > Includers equality)*

Individual differences associated with chronic peer group rejection, perspective-taking skills and behavioral regulation problems

To examine how neural processes involved in punishment and forgiveness of exclusion varied as a function of childhood peer rejection, we compared the two groups using two-sample *t*-tests on both contrasts outlined above. A two-sample *t*-test on the punishment contrast (Excluders inequality > Includers inequality) showed that chronically rejected and stably accepted adolescents showed no differential brain activity during punishment of excluders. However, during forgiveness of excluders (Excluders equality > Includers equality), chronically rejected adolescents showed enhanced activity in lPFC (peak at 36, 44, 4) and dorsal striatum (peak at 9, 11, 10) (***Figure 4.4***). No regions showed higher levels of activity in stably accepted adolescents compared to chronically rejected adolescents during either punishment or forgiveness.

To explore how individual differences in perspective taking and executive control were associated with punishment and forgiveness behavior and neural activity during forgiveness, we ran two whole-brain regression analyses on the forgiveness contrast (Excluders equality > Includers equality) with self-reported trait perspective-taking skills or parent-reported behavioral regulation problems as predictors. Participants with higher levels of perspective taking showed higher levels of activity in a region of the dmPFC (peak at -3, 50, 37) during forgiveness, which overlapped with the cluster of activation obtained in the main forgiveness contrast (***Figure 4.5A***). Participants with more behavioral regulation problems showed more activity in the right dorsal AI (peak at 37, 17, 10) and the pre-SMA/ACC (peak at 3, 11, 55) when they forgave the excluders (***Figure 4.5B***)

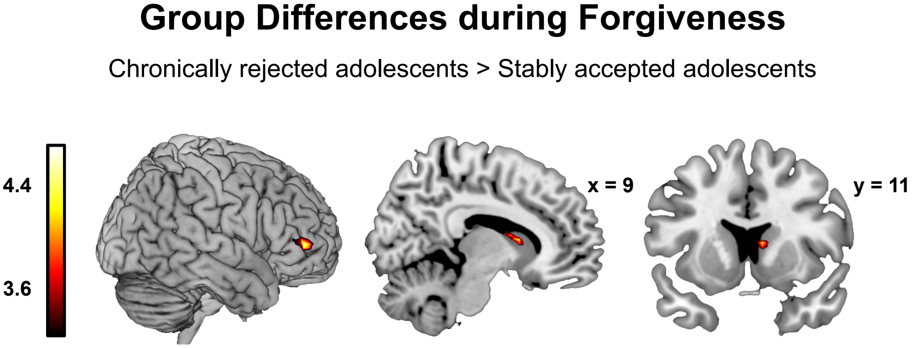

Figure 4.4 *Chronically rejected adolescents showed enhanced activity in lPFC (peak at 36, 44, 4) and dorsal striatum (peak at 9, 11, 10) compared to stably accepted adolescents during forgiveness of excluders. Subject-level contrast values in lPFC were extracted and plotted to facilitate interpretation.*

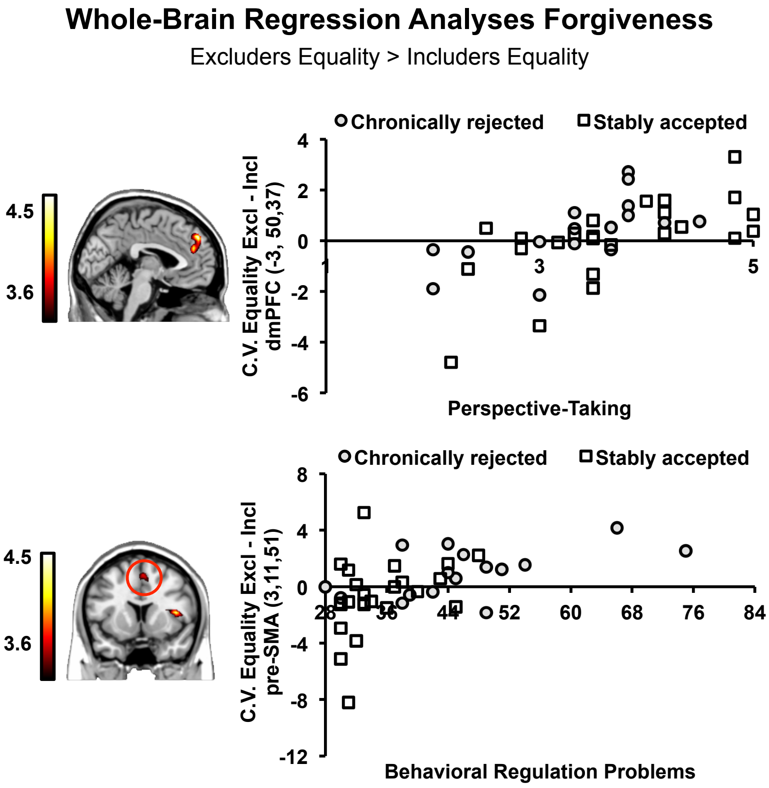

Figure 4.5 *(A) A whole brain regression analysis on the 'Excluders equality > Includers equality' contrast with self-reported perspective-taking skills as a predictor resulted in activation in an overlapping region of dmPFC (peak at -3, 50, 37); (B) A whole brain regression analysis on the 'Excluders equality > Includers equality' contrast with parent-reported behavioral regulation problems as a predictor resulted in activation in the pre-SMA/ACC (peak at 3, 11, 55) and in the right dorsal AI (peak at 37, 17, 10). C.V. = contrast value.*

4.4 DISCUSSION

This study examined the neural processes involved in punishment and forgiveness of excluders and how these processes vary as a function of chronic peer rejection. The first main finding was that both chronically rejected and stably accepted adolescents punished the excluders by selectively decreasing their monetary outcomes; both when punishment resulted in gains and when punishment had no monetary benefits. Social exclusion thus elicits a tendency to retaliate against the sources of exclusion even when this does not result in material gain, which is not modulated by exposure to high levels of peer rejection.

The second main finding was that punishment was associated with heightened activity in the ventral striatum, the dlPFC and parietal cortex in both groups of adolescents. The ventral striatum has previously been shown to be involved in processing both primary (e.g. food) and social rewards, including punishment of unfair interaction partners (Singer et al., 2006). Furthermore, ventral striatum activation during punishment has been shown to correlate with the self-reported desire for revenge and has therefore been suggested to code for the rewarding aspect of retaliation. Activation in the dlPFC has been linked to punishing criminal intent (Buckholtz et al., 2008) and economic unfairness (Güroğlu et al., 2011). The dlPFC - in concert with the parietal cortex - has been proposed to integrate different value signals and execute a punishment response among competing response options (Buckholtz & Marois, 2012).

Contrary to our hypotheses, chronically rejected adolescents did not show lower levels of forgiveness than stably accepted adolescents. Nonetheless, despite both groups displaying similar levels of forgiveness behavior, meaningful differences emerged on a neural level. To be specific, the third main finding was that chronically rejected adolescents, compared to stably accepted adolescents, displayed higher levels of activity in the dorsal striatum and the lPFC when they forgave the excluders. The dorsal striatum is strongly connected with a dorsal fronto-parietal network that plays a vital role executive control (Haber & Knutson, 2010; van den Bos, Rodriguez, Schweitzer, & McClure, 2014). Together with the chronically rejected adolescents' higher levels of behavioral regulation difficulties (indexing problems in inhibition, shifting and emotional control), heightened activity in this dorsal fronto-striatal network suggests that chronically rejected adolescents have to exert greater levels of control in order to act prosocial toward those who previously excluded them. This dovetails with findings showing that executive control skills are positively related to displays of prosocial behavior, social competence, and peer acceptance (Eisenberg, Vaughan, & Hofer, 2009; Spinrad et al., 2006).

The fourth main finding was that analyses of individual differences yielded insights into cognitive processes underlying refraining from punishment. Two mechanisms have been shown to be involved in succeeding or failing to refrain from retaliation after being excluded: i) the ability to take other people's perspectives (Will et al., 2014) and ii) the ability to cognitively control impulses (Chester et al., 2013). Our findings show that these two mechanisms are associated with activity in functionally separable neural networks. That is, during forgiveness, perspective-taking skills scaled with activity in the dmPFC, which is a hub in the theory of mind network (Koster-Hale & Saxe, 2013) and behavioral regulation problems correlated positively with activity in the pre-SMA/ACC and dorsal AI. A meta-analysis has shown that the dorsal AI (overlapping with the cluster in our study) is strongly connected to the pre-SMA/ACC and dlPFC and is implicated in executive control functions, including inhibition and switching (Chang et al., 2013). Taken together, these findings show that individual differences in cognitive functions can be reliably linked to activity in functionally separable neural networks supporting social cognition (e.g. dmPFC) or executive control (e.g. ACC and dorsal AI) and they underscore the importance of examining individual differences in neural processes underlying prosocial reactions to social exclusion.

Several limitations of this study deserve to be mentioned. First, the data do not speak to the causal question whether observed differences in forgiveness-related neural activity were caused by chronic peer rejection, or whether they reflect a propensity that was already present before the emergence of a rejected peer status. Future longitudinal studies should investigate whether adolescents that end up with a rejected status already show these differences earlier in development. Second, differences between the two groups could both be the result of greater exposure to negative peer interactions in the rejected group or greater exposure to positive peer interactions in the accepted group. Future studies should compare rejected adolescents to adolescents with a so-called 'average' social status to disentangle the influence of positive and negative experiences in the peer group on neural processing involved in social behavior. Third, our sample of chronically rejected adolescents was relatively small. Rejected adolescents form a heterogeneous group consisting of aggressive and non-aggressive subtypes (Ladd, 2006). Future research with larger samples could test whether the absence of behavioral differences between the two groups in our study could be due to heterogeneity in the rejected group.

In conclusion, our results show that punishment and forgiveness of excluders rely on distinct neural networks implicated in emotional and cognitive processes involved in social decision-making. Although chronically rejected adolescents were equally likely to forgive excluders as stably accepted adolescents, they displayed enhanced recruitment of the dorsal striatum and lPFC when forgiving excluders, suggesting that they might have to exert greater levels of executive control in order act prosocial toward peers who excluded them. Consequently, our results have implications for understanding the processes through which peer rejection's adverse effects are transmitted across development.

A greater demand on executive control functions might entail greater difficulties controlling retaliatory responses to negative treatment in the heat of the moment of their everyday interactions with peers. In turn, retaliatory responses are likely to provoke excluders, which could elicit renewed instances of exclusion and thereby further consolidate a rejected status in the peer group (Sandstrom, 2004). A priority for future research is therefore to further examine longitudinal associations between behavioral reactions to social exclusion, peer status, and different subcomponents of cognitive control (e.g. inhibition, shifting, emotion regulation tasks) to get a better understanding of which executive functions might underlie prosocial reactions to exclusion. Such endeavors can inform research that could test whether training of executive functions might facilitate adaptive social responses to exclusion, which ultimately could lead to greater acceptance among peers.

4.5 SUPPLEMENTARY MATERIAL

Table S4.1 *Participant characteristics.*

	Group, Mean (*SD*)		
Characteristics and Questionnaires	Chronically Rejected (n = 18)	Stably Accepted (n = 25)	p-value[a]
Mean Social Preference[b] (selection variable)	-1.59 (0.52)	1.17 (0.18)	< .001
Gender (% Male)	72	52	.18
Age	14.0 (0.78)	14.1 (0.57)	.64
Pubertal status (PDS)			
o Males	2.41 (0.75)	2.11 (0.54)	.26
o Females	3.17 (0.26)	2.68 (0.65)	.12
Race/Ethnicity (% Caucasian)	100%	96%	.39
IQ (WISC Similarities and Block Design)	95 (12.32)	101 (10.23)	.13

[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*