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

Will, G.J.

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ACCEPTANCE, REJECTION, AND THE SOCIAL BRAIN IN ADOLESCENCE

TOWARD A NEUROSCIENCE OF PEER RELATIONS

Geert-Jan Will

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ACCEPTANCE, REJECTION, AND THE SOCIAL BRAIN IN ADOLESCENCE

TOWARD A NEUROSCIENCE OF PEER RELATIONS

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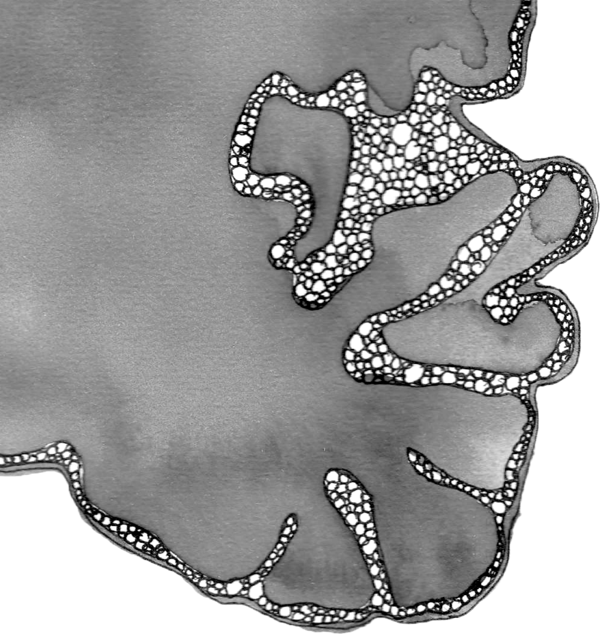

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Human beings have a fundamental need to form and maintain lasting positive relationships with others (Baumeister & Leary, 1995). These relationships are a source of companionship, intimacy, and support from infancy to old age. During childhood and adolescence, relationships with peers provide an important socialization context in which many important skills and psychological capacities develop. In interactions with peers, children and adolescents acquire key social skills (e.g. cooperation, conflict resolution) and cognitive abilities (e.g. emotion regulation, perspective taking) that are needed for successful functioning in a complex social environment (Bukowski, Buhrmester, & Underwood, 2011; Ladd, 1999; Rubin, Bukowski, & Parker, 2006).

The need for social connection is so vital that many problems arise when this need remains unsatisfied. Events that threaten our need for social connection, such as social exclusion and rejection, are highly distressing and can have detrimental consequences for well-being. Children and adolescents who are chronically rejected by their peers suffer from widespread impairments in daily life that can persist across development and into adulthood, ranging from poor academic achievement (DeRosier, Kupersmidt, & Patterson, 1994) and dropping out of school (Hymel, Comfort, Schonert-Reichl, & McDougall, 1996), to delinquency (Kupersmidt, Burchinal, & Patterson, 1995) and the development of psychopathology (Boivin, Hymel, & Bukowski, 1995; Coie, Terry, Lenox, Lochman, & Hyman, 1995; Parker & Asher, 1987). Therefore, it is of great importance to understand the developmental processes that play a role in the emergence and maintenance of peer group rejection.

The goal of this thesis was to examine the neurocognitive underpinnings of processes that play a role in sustaining peer rejection as well as those that are instrumental in gaining peer acceptance. The first part of the thesis focuses on the neurocognitive processes underlying subjective and behavioral responses to social exclusion, which have been hypothesized to play a crucial role in the emergence or maintenance of peer group rejection (Coie, 1990; Sandstrom, 2004). For example, children and adolescents who react to social exclusion with retaliatory vengeance might be more likely to elicit further rejection from their peer group than those who show behavior aimed at reconnecting after exclusion (Coie, 1990; Sandstrom, 2004). The second part of this thesis concentrates on the neural and psychological processes involved prosocial behavior, based on the widely established finding that frequent displays of prosocial behaviors, such as cooperating, helping, and sharing, are associated with both gaining and maintaining peer acceptance (Coie & Kupersmidt, 1983; Deković & Gerris, 1994; Layous, Nelson, Oberle, Schonert-Reichl, & Lyubomirsky, 2012). Understanding the neural and psychological mechanisms underlying reactions to social exclusion and prosocial behavior is therefore vital for a better understanding of the emergence and maintenance of peer rejection.

The remainder of this chapter sketches a conceptual framework for the empirical studies in this thesis. First, a working model is presented that was used for studying the developmental processes governing emergence and maintenance of peer rejection (1.2). Next, we highlight key findings from the literature on the neural and psychological processes involved in reactions to social exclusion (1.3) and those involved in prosocial behavior in the form of sharing of valuable resources (1.4). Together, the working model of peer group rejection and the findings from prior work on social exclusion and sharing behavior laid the foundations for the empirical studies described in this dissertation, of which the aims are summarized at the end of this chapter (1.5).

1.2 MECHANISMS OF EMERGENCE AND MAINTENANCE OF PEER REJECTION

Peer group acceptance and rejection reflect the collective valence of group members' sentiments toward individuals in the group. Acceptance and rejection can be reliably assessed through asking members of a peer group who they like most and who they like least (Bukowski, Sippola, Hoza, & Newcomb, 2000; Coie, Dodge, & Coppotelli, 1982; Newcomb & Bukowski, 1983). Children who receive many negative nominations (liked least) and who receive few positive nominations (liked most) are classified as having a rejected status[1].

Longitudinal studies have demonstrated that low levels of acceptance and high levels of rejection during childhood are associated with an array of negative adjustment outcomes, including poor academic achievement (DeRosier et al., 1994) and higher levels of both internalizing (Ladd & Troop-Gordon, 2003) and externalizing behavior problems (van Lier & Koot, 2010). Although the evidence for such longitudinal links is overwhelming, establishing longitudinal links between peer group rejection and adjustment difficulties does not provide insights into the developmental mechanisms through which peer sentiments impact later psychosocial adjustment. To better understand how peer group acceptance and rejection have their impact on adjustment, researchers have begun investigating the transactional relationship between the individual child and the way they are treated by their peer group (Coie, 1990; Sandstrom & Coie, 1999). Transactional models of peer relations posit that characteristics of

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[1] *Acceptance and rejection are interconnected, but not polar opposite, constructs. Children low in peer acceptance (those who receive few liked most nominations from their peers) do not necessarily have to be rejected by peers (through receiving many liked least nominations from their peers). Indeed, correlations between acceptance and rejection are negative and modest in size (Bukowski et al., 2000). Thus, although acceptance is often regarded as the opposite of rejection, it is more precise to see the opposite of accepted as 'not accepted' and the opposite of rejected as 'not rejected'.*

an individual child help to construct and shape their behavior in social interactions with peers, and interactions with peers in turn shape children's perceptions and dispositions (Ladd, 2003).

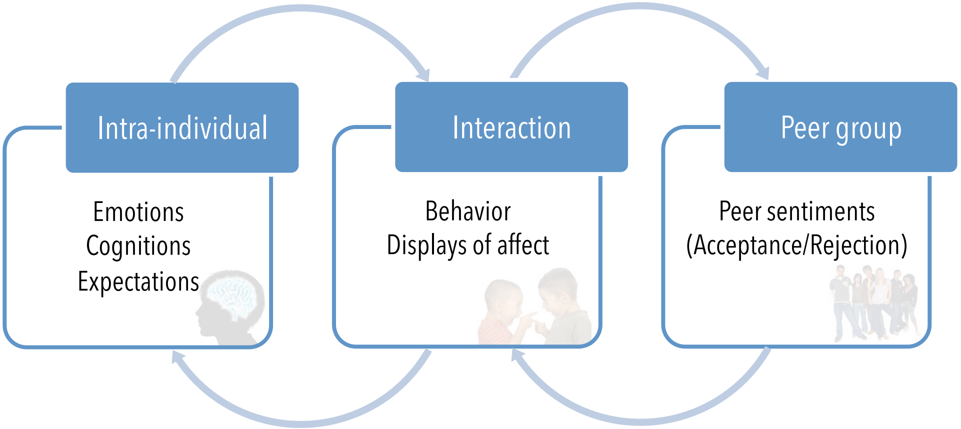


Figure 1.1. *A working model of processes playing a role in the emergence or maintenance of peer rejection at three levels of social complexity.*

Based on such transactional models, we propose a simplified model of the reciprocal interactions between individual children and their peer group that guided the hypotheses for the empirical studies in this thesis (see ***Figure 1.1***). The model is subdivided into three levels of social complexity comparable to a model proposed by Hinde (1979). To be specific, the model distinguishes between processes at the level of the individual child (i.e. intra-individual), those at the level of social interactions (i.e. interpersonal) and those at the level of the peer group.

Intra-individual processes such as emotions, cognitions, and expectations are the processes that individual children bring with them into social interactions. Social interactions are exchanges of sets of behaviors or overt displays of affect between two individuals. Social interactions with peers influence the individual's reputation and standing in the peer group (e.g. peer group acceptance and rejection). Importantly, processes at each level of social complexity both constrain and influence processes at the other levels.

In his transactional model of peer rejection, Coie (1990) distinguished between the so-called 'emergent phase' and the 'maintenance phase' of peer rejection. The emergent phase is characterized by specific interactions between a child and their peer group, which give rise to peer group rejection. For example, a child who has difficulties in perspective taking (intra-individual level) is less likely to consider the needs of other people and as a consequence refuses to share a toy with a classmate (interaction level). The refusal to share with his classmate can then trigger dislike in this member of the peer group. When this pattern of selfish behavior is shown consistently in interactions with other members of the peer group, individual member's disliking of the child may extend to a consensual disliking in the peer group (i.e. peer group rejection; group level).

A wealth of research supports these proposed links by showing that consensual disliking in the peer group arises from specific behaviors displayed in social interactions with peers. For example, rejected children show higher levels of aggressive and disruptive behaviors, more social withdrawal and lower levels of prosocial behavior in interactions with their peers than accepted children (Coie, Dodge, & Kupersmidt, 1990; Haselager, Cillessen, Van Lieshout, Riksen-Walraven, & Hartup, 2002; Newcomb, Bukowski, & Pattee, 1993). These behavioral propensities have been shown to precede peer group rejection and to elicit dislike in the emergent phase of peer rejection. For example, children with a rejected status in their school class rapidly become rejected when they enter a new group with unfamiliar peers (Hardy, Bukowski, & Sippola, 2002), and this is driven by rejected children's greater propensity for aggressive behaviors and lower levels of prosocial behavior (Coie & Kupersmidt, 1983; Dodge, 1983). After initial rejection in the emergent phase, some children may maintain their rejected status because they continue to show behaviors that are poorly tolerated by their peer group.

In the maintenance phase peer group rejection becomes stable, and cognitions, emotions and behaviors of both the individual child and its peers are changed in ways that sustain a rejected status. For example, chronic exposure to peer rejection has been shown to foster anxious or angry expectations about rejection (London, Downey, Bonica, & Paltin, 2007). Children with angry expectations about rejection show higher levels of distress in response to acute rejection experiences (e.g. a classmate refuses to work together on an assignment), and show increasingly higher levels of aggression and interpersonal difficulties in their peer group over time (Downey, Lebolt, Rincon, & Freitas, 1998). Thus, social-cognitive processes (intra-individual) shaped by prior interactions in the peer group play a role in sustaining behaviors that further consolidate peer group rejection. These examples show that the three levels in the model are heavily intertwined and influence each other both in the emergent phase and the maintenance of peer rejection.

The emergent phase and the maintenance phase in Coie's (1990) theory represent longer periods of time accruing multiple social interactions over the course of weeks, months or years. However, as can be seen from the examples described above, the developmental processes that contribute to the emergence or maintenance of rejection can be described at finer levels of analysis. That is, peer group rejection can be triggered or be maintained by recursive sequences between rejection-eliciting behaviors, the way the peer group reacts to those behaviors, and the impact of the reactions from the peer group on the rejected child's feelings, cognitions, and behavior.

The main goal of this thesis was to examine four such processes that play a role in the emergence and maintenance of a rejected status. Specifically, we examined the following processes at the intra-individual level and at the level of the interaction: i) subjective and neural responses to social exclusion, ii) behavioral reactions to social exclusion, iii) behavioral reactions to the exclusion of a peer, and iv) prosocial behavior in the form of sharing valuable resources. To investigate these processes, we used experimental social interaction paradigms in combination with functional Magnetic Resonance Imaging (fMRI), which is a neuroimaging technique that enables the study of brain function while participants are asked to perform a specific task. Furthermore, to gain a better understanding of how these processes at the intra-individual level and the level of the interaction are influenced by processes at the level of the peer group, we examined how these processes varied as function of chronic exposure to peer group rejection. The next sections describe the theories and empirical findings that provided the background for the empirical investigations of these four processes. To highlight each process' involvement in the emergence or maintenance of peer rejection, prior work will be discussed in the light of our working model.

1.3 REACTIONS TO SOCIAL EXCLUSION

Excluding a peer from a group or activity is one of the most common methods children and adolescents use to express dislike toward rejected peers (Coie et al., 1990). In child and adolescent peer groups, social exclusion can take the form of both *direct* refusals of entry to a group or activity (e.g. telling a child he cannot join a game) and *indirect* actions (e.g. ignoring a peer's requests to join a game, or not choosing a peer as a partner for a group activity) (Gazelle & Ladd, 2003). Although social exclusion is a distressing experience across the lifespan (Williams, 2007), adolescence has been hypothesized to be a developmental period during which reactions to exclusion are intensified. During adolescence, concerns about fitting in with the peer group peak (O'Brien & Bierman, 1988), and the failure to integrate oneself in a network of peers both reflects and precedes serious adjustment difficulties (e.g. social withdrawal, loneliness, or depressive symptoms) (Boivin et al., 1995; Prinstein & Aikins, 2004). It has been proposed that adolescence might be particularly stressful for those who were chronically rejected during childhood (Coie et al., 1990). Rejected children have fewer positive affiliations with peers in which many social skills are acquired (e.g. conflict resolution, negotiation) (Boivin & Hymel, 1997; Parker & Asher, 1993). Consequently, as they enter adolescence, chronically rejected children might lack the social skills needed for coping with the increased stresses of the adolescent peer world.

Although not every child with a rejected status is targeted for social exclusion, rejected children are more likely to be excluded from peer activities than their accepted counterparts. Moreover, adjustment difficulties associated with peer group rejection (e.g. school disengagement) are exacerbated among children who are both rejected and frequently excluded from peer activities (relative to non-excluded rejected children) (Buhs & Ladd, 2001; Buhs, Ladd, & Herald, 2006). Yet, the processes through which social exclusion may influence the maintenance of a rejected status are far from clear. Therefore, we examined three processes that could each play a unique role in the emergence or maintenance of peer rejection: i) subjective and neural responses to social exclusion, ii) retaliatory and prosocial reactions to social exclusion and iii) behavioral reactions to the exclusion of a peer.

Subjective and neural responses to social exclusion

The way a child responds to social exclusion has been argued to play an important role in determining whether exclusion forms an isolated incident as opposed to a recurring phenomenon (Ladd & Troop-Gordon, 2003; Sandstrom, Cillessen, & Eisenhower, 2003; Zakriski, Jacobs, & Coie, 1997). For example, children who immediately start crying in response to social exclusion are likely to be targeted for exclusion again. As such, heightened exclusion-related distress and associated neural activity might represent potential mechanisms at the intra-individual level of social complexity through which a rejected status might emerge or be maintained across development.

Neuroimaging studies have shown that the distress adolescents and adults report after they are excluded can be reliably linked to activity in neural systems processing negative emotions and emotion regulation (Eisenberger, 2012; Eisenberger, Lieberman, & Williams, 2003). After being ostensibly excluded by two strangers in a virtual ball-tossing game called Cyberball (Williams, Cheung, & Choi, 2000), children, adolescents, and adults report heightened levels of exclusion-related distress in the form of negative emotions (e.g. anger, sadness) and decreases in the satisfaction of vital human needs (e.g. belonging, self-esteem, control, and a meaningful existence) (Abrams, Weick, Thomas, Colbe, & Franklin, 2011; Sebastian, Viding, Williams, & Blakemore, 2010). Self-reports of such exclusion-related distress have been shown to correlate positively with neural activity in the anterior cingulate cortex (ACC) and anterior insula (AI) - brain regions involved in processing conflict and (negative) emotions - during the exclusion experience (Gunther Moor et al., 2012; Masten et al., 2009). Negative correlations have been found between self-reported distress and activity in the ventrolateral prefrontal cortex (vlPFC) – a region implicated in top-down regulatory control- suggesting that the vlPFC is involved in regulating the distress caused by exclusion (Eisenberger et al., 2003; Masten et al., 2009).

Neural activity in brain regions linked to the distressing aspect of exclusion has been shown to vary with individual and social factors characteristic of children with a rejected status. That is, ACC activity is exacerbated in individuals who anxiously expect rejection (DeWall et al., 2012; Masten et al., 2009) and who perceive lower levels of social support in their relationships (Eisenberger, Taylor, Gable, Hilmert, & Lieberman, 2007). To critically test whether neural processing of social exclusion shows associations with chronic peer group rejection, we examined subjective (i.e. mood and need satisfaction) and neural responses to social exclusion in adolescents with a history of chronic peer rejection and tested how their responses differed from those in adolescents with a history of stable peer acceptance (**Chapter 2**). Heightened neural reactivity to social exclusion might be an intra-individual process involved in attaining or maintaining a rejected status, given that a heightened emotional or neural reactivity to exclusion might reinforce or provoke excluders and consequently could promote progressively greater dislike in the peer group.

Behavioral reactions to social exclusion

A potential mechanism at the level of the interaction through which a rejected status among peers might emerge or is maintained, is the way children respond behaviorally to social exclusion (Sandstrom, 2004). For example, retaliatory reactions to exclusion are likely to elicit repeated instances of exclusion from the peer group. In contrast, controlling the urge to lash out against the bullies might stop exclusion, which is likely to have positive effects on peer status. Concurrent associations between peer status and coping with exclusion and other peer-related conflicts suggest that behavioral responses to exclusion might play a role in the maintenance of a rejected status. That is, children and adolescents with a rejected status report a more frequent use of aggressive coping styles when faced with social exclusion in a hypothetical scenario (Sandstrom, 2004) or a recalled conflict with a peer (Bowker, Bukowski, Hymel, & Sippola, 2000). On the contrary, accepted children more often deal with interpersonal anger in non-aggressive ways that minimize further conflict (Fabes & Eisenberg, 1992). Furthermore, prosocial reactions to negative peer treatment have been associated with greater psychological well-being in victims of bullying compared to victims of bullying who predominantly seek revenge (Flanagan, Hoek, Ranter, & Reich, 2012; Park, Enright, Essex, Zahn-Waxler, & Klatt, 2013)

To gain insight into the psychological and neural mechanisms underlying retaliatory and prosocial reactions to social exclusion, we turned to game theoretical paradigms derived from behavioral economics (Camerer, 2003; Rilling & Sanfey, 2011). These paradigms offer a context of social interactions where the decisions people make have actual consequences for their own and their interaction partner's well-being. In two-player exchange games such as the Dictator Game one player receives a valuable set of rewards (e.g. money or candy) from the experimenter and is then given the opportunity to propose a split of the rewards between themselves and a second player (Forsythe, Horowitz, Savin, & Sefton, 1994). In the Dictator Game, the second player cannot influence the distribution of resources and thus passively receives the amount of rewards that the first player is willing to share. Prior work using such economic exchange games has demonstrated that social decision-making depends on distinct, but interacting, networks of brain regions. Importantly, these networks have been shown to support different psychological processes involved in social decision-making, including cognitive/emotional processes involved in the detection of norm-violations (Güroğlu, van den Bos, van Dijk, Rombouts, & Crone, 2011; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011), cognitive-regulatory processes (e.g. impulse control; Steinbeis, Bernhardt, & Singer, 2012), and socio-cognitive processes (e.g. perspective taking; Güroğlu et al., 2011; van den Bos et al., 2011) .

To examine retaliatory and prosocial reactions to exclusion, we gave participants the opportunity to play a Dictator Game in which they could punish (i.e. retaliate) or forgive (i.e. act prosocial toward) the individuals who previously excluded them in Cyberball (i.e. the excluders). Participants could punish the excluders through decreasing their monetary outcomes or they could forgive them through refraining from punishment and sharing a sum of money equally with them. A better understanding of the neurocognitive mechanisms underlying these reactions can increase our understanding of the processes underlying children's decisions to seek revenge or reconnection after exclusion. Prior work has demonstrated that a tendency to retaliate against excluders (interaction level) has been shown to rely on cognitive control capacities (intra-individual level) in adults (Chester et al., 2013). In addition, prosocial motivations toward offenders have been linked to higher levels of socio-cognitive capacities such as perspective taking (i.e. the tendency to adopt another person's perspective; Brown, 2003) and higher levels of activity in neural circuitry implicated in thinking about other people's mental states (e.g. beliefs, intentions, and desires; Young & Saxe, 2009). Consequently, we anticipated that refraining from punishment and acting prosocial toward the excluders would be associated with activity in brain networks supporting cognitive control and perspective taking.

To test whether perspective taking and cognitive control are involved in prosocial reactions to exclusion, we first examined the neural processes involved in punishment and forgiveness of excluders in a sample of young adults (**Chapter 3**). The findings from this study laid the foundations for our next study in which we examined how the neural processes involved in punishment and forgiveness vary as a function of a history of chronic peer rejection and individual differences in cognitive control and perspective taking (**Chapter 4**). Given that aggressive reactions to exclusion are likely to aggravate the situation, we expected that finding links between chronic peer rejection and neural processes underlying behavioral reactions to exclusion would lead to a better understanding of how chronically rejected children might become trapped in a pattern of sustained rejection.

Behavioral reactions to the exclusion of a peer

The peer group plays a crucial role in determining whether a rejected child is targeted for exclusion or not. For example, the likelihood that children with a rejected status are victimized is higher in classrooms with fewer peers who stand up for victims of bullying compared to classrooms with more of such prosocial defenders (Kärnä, Voeten, Poskiparta, & Salmivalli, 2010). Indeed, observations in school playgrounds have shown that peers who stand up for victims of bullying are successful in stopping bullying in more than half of the time (Hawkins, Pepler, & Craig, 2001). Furthermore, victims who are defended by classmates are more accepted in their peer group and report higher levels of self-esteem, and lower levels of internalizing symptoms than non-defended victims (Sainio, Veenstra, Huitsing, & Salmivalli, 2010). Therefore, in addition to examining reactions to social exclusion at the level of the excluded child, we also investigated processes at the level of the peer group that play a role in stopping or enabling exclusion.

Specifically, we investigated intra-individual processes (i.e. mood and perspective taking) in uninvolved bystanders who witnessed the exclusion of a peer and who were subsequently given the opportunity to help the victim of exclusion and to punish the excluders. Advanced forms of perspective taking, such as inferring another person's feelings in the absence of explicit emotional cues (i.e. affective perspective-taking), have been shown to continue to develop across adolescence (Hoffman, 2000). Given the importance of such perspective-taking skills for prosocial behavior (Vaish, Carpenter, & Tomasello, 2009), we examined helping and punishment in various phases of adolescent development (from late childhood to young adulthood) and tested how individual and developmental differences in perspective taking contributed to performing those behaviors (**Chapter 5**). Identifying the socio-cognitive processes that motivate bystanders to help a victim of exclusion is important, given the positive effects of prosocial action toward victims of bullying in terms of well-being and peer status (Sainio et al., 2010).

1.4 SHARING

Prosocial behaviors such as helping, cooperating and sharing have been shown to been among the strongest predictors of peer acceptance across childhood and adolescence (Caprara, Barbaranelli, Pastorelli, Bandura, & Zimbardo, 2000; Caputi, Lecce, Pagnin, & Banerjee, 2012; Crick, 1996; Deković & Gerris, 1994; Parker & Asher, 1987; Zimmer-Gembeck, Geiger, & Crick, 2005). Prosocial behaviors have even been shown to have a *causal* effect on gaining acceptance among peers; both when they are displayed spontaneously (Coie & Kupersmidt, 1983) and when children are instructed to display them more often (Layous et al., 2012). Consequently, understanding the neural and psychological processes involved in prosocial behavior is critical for a better understanding of the emergence and maintenance of an accepted or rejected status.

A form of prosocial behavior that allows for the examination of several underlying neural and psychological processes and which has been studied extensively is: sharing of valuable resources. First of all, sharing decisions have consequences for both the well being of the person making the distribution and for the person receiving a portion of the resources. Therefore, it has been argued that socio-cognitive capacities such as perspective taking are needed to recognize the need in the other person in order to share with them (Güroğlu, van den Bos, & Crone, 2014). Furthermore, when humans distribute resources, considerations of fairness, that is a concern for an equal distribution based on a comparison of the needs of two or more parties, come into play. Already in infancy, humans prefer equal distributions to unequal distributions and show behaviors that are indicative of aversion to inequality (Schmidt & Sommerville, 2011; Sloane, Baillargeon, & Premack, 2012). Failing to share with a peer might thus rely on separate processes (e.g., failing to recognize the need of the other person, but also diminished aversion to inequality), which have been shown to be supported by separate neural networks. Perspective taking in social exchange is associated with activity in brain regions in the medial frontal and temporo-parietal cortex (Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2013; Güroğlu et al., 2011; van den Bos et al., 2011), whereas the detection of violations of fairness norms have been shown to activate brain regions involved in processing conflict and negative emotions (pre-Supplementary Motor Area/ACC and AI) (Chang & Sanfey, 2011; Güroğlu et al., 2011).

What mechanisms could underlie the typically found lower levels of prosocial behavior shown by rejected children relative to their accepted counterparts? First of all, rejected children's lower levels of prosocial behavior have previously been linked to a lesser understanding of other people's minds (e.g. less advanced 'theory of mind' skills) (Fink, Begeer, Hunt, & de Rosnay, 2014; Slaughter, Dennis, & Pritchard, 2002). Second, a diminished tendency to behave prosocially could also be associated with lower degrees of internal conflict or negative affect experienced when violating a fairness norm (e.g. when keeping all resources to oneself). To gain insights into these two underlying processes, we first examined the neural correlates of violations of fairness norms in sharing decisions in a sample of young adults (**Chapter 7**). Subsequently, to investigate whether the previously described mechanisms involved in sharing decisions show associations with peer group acceptance or rejection, we examined the neural correlates of sharing decisions in adolescents with a history of stable peer acceptance and adolescents with a history of chronic peer rejection (**Chapter 8**). A better understanding of the mechanisms underlying prosocial behavior at the intra-individual level and at the level of the interaction can provide valuable insights into the role of prosocial behavior in gaining or maintaining peer acceptance.

1.5 OUTLINE OF THIS THESIS

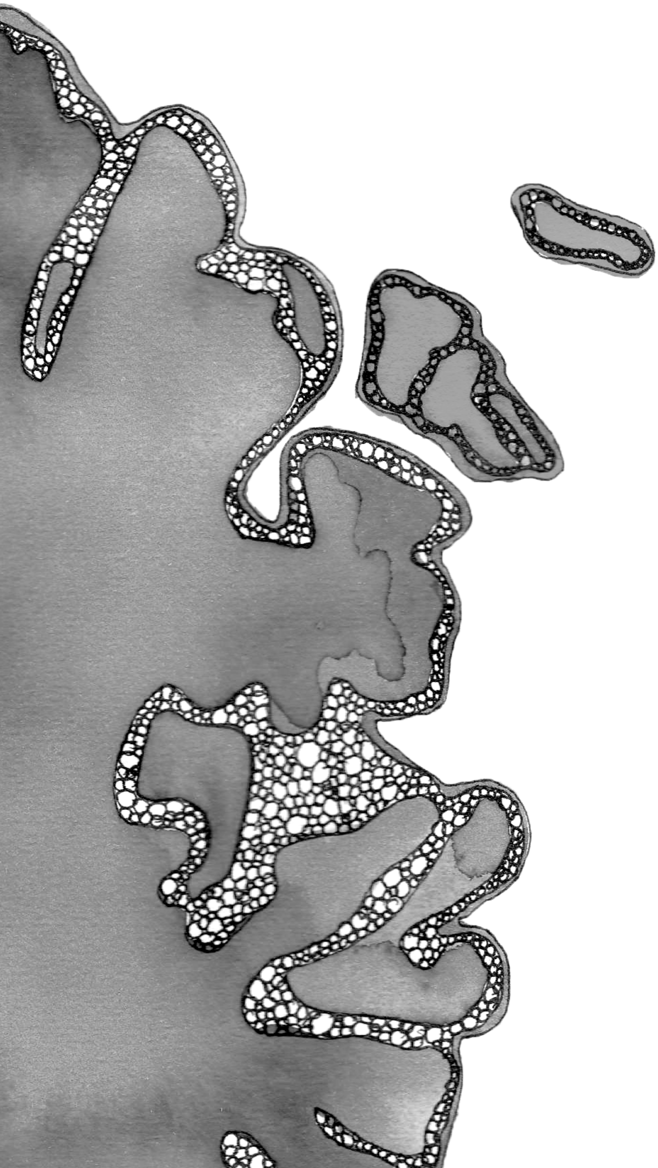
The overarching goal of this thesis was to examine the neural, psychological, and behavioral processes, which play a role in the emergence or maintenance of a rejected status. To explore these processes, we combined experimental paradigms borrowed from social psychology (Cyberball) and behavioral economics (economic games such as the Dictator Game) with neuroimaging methods from cognitive neuroscience (fMRI), and multi-informant survey measures on psychological and social functioning from developmental psychology (self-, peer, and parent-reports). The empirical studies were guided by our transactional model of peer interactions, which distinguished between processes at the level of the individual child (i.e. intra-individual), those at the level of social interactions and those at the level of the peer group. Together these studies not only aimed to advance our understanding of the processes that give rise to peer group rejection and its maintenance, but they also provide valuable insights into the affective, cognitive-regulatory, and socio-cognitive processes underlying social interactions in general.

The first part of this thesis (**Chapters 2-5**) focuses on the affective, cognitive and neural (intra-individual) processes underlying subjective and behavioral reactions to social exclusion (at the level of the social interaction) and how these processes varied as function of chronic peer group rejection (group level). **Chapter 2** describes a neuroimaging study that shows how sustained exposure to peer group rejection across six years of elementary school is associated with heightened neural responses to social exclusion in early adolescence. **Chapter 3** reports on a study that examined the neural correlates of retaliatory (i.e. punishment) and prosocial (i.e. forgiveness) reactions toward peers who previously excluded them in a sample of young adults. **Chapter 4** investigated how the neural processes involved in punishment and forgiveness of excluders in adolescence vary as a function of individual differences in chronic exposure to peer rejection, cognitive control capabilities and perspective-taking skills. **Chapter 5** describes a behavioral study that examined how affective perspective-taking skills contribute to individual and developmental differences (age 9-22) in third-party decisions to help victims of social exclusion and to punish excluders.

The second part of this thesis (**Chapter 6-8**) focuses on the neurocognitive (intra-individual) processes underlying sharing decisions (in social interactions) involving real costs and benefits for self and others and how these processes are associated with individual histories of sustained exposure to either high or low levels of peer acceptance (group level). **Chapter 6** presents a review of the evidence for the hypothesis that developmental changes in cognitive control and perspective-taking skills and their underlying neural circuitry are critical to understanding developmental changes in strategic thinking and an increased incorporation of other's perspectives into social decisions. **Chapter 7** describes a study on the neural correlates of violations of a fairness norm in sharing decisions in young adults. We examined neural activity when participants violated a norm of equality to benefit themselves, but also when they violated a norm of equality to benefit another person. **Chapter 8** investigated how activation of neural systems involved in the detection of norm-violations and those supporting perspective taking during sharing choices differs between adolescents who were stably accepted and adolescents who were chronically rejected during childhood. Finally, **Chapter 9** summarizes the results of the studies in this thesis and discusses the implications of the findings for understanding the mechanisms of emergence and maintenance of peer rejection.

PART I

REACTIONS TO SOCIAL EXCLUSION



CHAPTER 2

CHRONIC CHILDHOOD PEER REJECTION IS ASSOCIATED WITH HEIGHTENED NEURAL RESPONSES TO SOCIAL EXCLUSION DURING ADOLESCENCE

This chapter is published as:

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ABSTRACT

This functional Magnetic Resonance Imaging (fMRI) study examined subjective and neural responses to social exclusion in adolescents (age 12–15) who either had a stable accepted (n = 27; 14 males) or a chronic rejected (n = 19; 12 males) status among peers from age 6 to 12. Both groups of adolescents reported similar increases in distress after being excluded in a virtual ball-tossing game (Cyberball), but adolescents with a history of chronic peer rejection showed higher activity in brain regions previously linked to the detection of, and the distress caused by, social exclusion. Specifically, compared with stably accepted adolescents, chronically rejected adolescents displayed: 1) higher activity in the dorsal anterior cingulate cortex (dACC) during social exclusion and 2) higher activity in the dACC and anterior prefrontal cortex when they were incidentally excluded in a social interaction in which they were overall included. These findings demonstrate that chronic childhood peer rejection is associated with heightened neural responses to social exclusion during adolescence, which has implications for understanding the processes through which peer rejection may lead to adverse effects on mental health over time.

2.1 INTRODUCTION

Children and adolescents who are rejected by peers suffer from widespread impairments in mental health that can persist across development (Ladd, 2006; Ladd & Troop-Gordon, 2003; Prinstein & Aikins, 2004). A potential mechanism through which a rejected status among peers leads to mental health problems is a heightened emotional and neural reactivity to negative treatment that accompanies a rejected status (e.g., being ignored, harassed, excluded). For example, boys with a rejected status who are more distressed by a rejection experience have more externalizing behavioral problems than boys with a rejected status who show lower levels of reactive distress (Sandstrom et al., 2003). Similarly, adolescents who display enhanced neural responses to social exclusion are more likely to exhibit depressive symptoms 1 year later (Masten et al., 2011a). Given that children's social experiences in peer groups play a crucial role in shaping their perceptions and expectations about future social interactions (Crick & Dodge, 1994; Ladd, Ettekal, Kochenderfer-Ladd, Rudolph, & Andrews, 2014; London et al., 2007), sustained exposure to either high or low levels of peer group rejection is likely to have an impact on how adolescents respond to negative peer treatment, such as social exclusion. Therefore, we examined subjective and neural responses to social exclusion in adolescents who either had a stable accepted or a chronic rejected status among their classmates across six elementary school grades.

Chronic peer group rejection and psychosocial development

Adverse adjustment outcomes resulting from peer group rejection have been well documented. Peer group rejection has proven to be reliably assessed by asking children to nominate the classmates they like and dislike (Asher & Coie, 1990; Bukowski et al., 2000; Jiang & Cillessen, 2005; Parker & Asher, 1987). Children who receive many negative (dislike) nominations and who receive few positive (like) nominations are classified as having a rejected status (Asher & Dodge, 1986; Bukowski et al., 2000). A rejected status has been found to be highly stable across time and across different social contexts (Coie & Kupersmidt, 1983; Hardy et al., 2002; Jiang & Cillessen, 2005).

Moreover, a chronic rejected status has been prospectively linked to an array of impairments in daily life, ranging from poor academic achievement (DeRosier et al., 1994) to an increased incidence of both internalizing (Ladd & Troop-Gordon, 2003) and externalizing behavior problems (Sturaro, van Lier, Cuijpers, & Koot, 2011).

Transactional models of peer rejection posit that such impairments in daily life arise from a sustained pattern of reciprocal interactions between peers expressing their dislike and the way a rejected child responds to being disliked (Coie, 1990). For example, repeated exposure to rejection experiences (e.g., social exclusion) may elicit negative emotions (e.g., anger at exclusion) resulting in aggressive reactions, which in turn could trigger repeated instances of exclusion by the peer group ultimately giving rise to externalizing problems (Coie, 2004; Dodge et al., 2003). Internalizing problems have been hypothesized to arise from a similar developmental cascade in which repeated exposure to rejection experiences may amplify negative emotions (e.g., sadness, distress), which in turn heighten anxiety, lead to withdrawal or bolster psychological processes that underlie the development of internalizing disorders (e.g., low self-esteem, lower levels of trust in others) (Ladd et al., 2014; Troop-Gordon & Ladd, 2005). As such, a rejected status could be maintained across development through a heightened emotional or neural reactivity to negative treatment such as social exclusion. Understanding the mechanisms underlying the maintenance of a rejected status can aid in understanding why some children are able to deal with episodes of peer rejection without much difficulty whereas others become trapped in a pattern of sustained rejection and associated impairments in daily life (Sandstrom, 2004; Sandstrom & Coie, 1999).

Social exclusion: distress and neural correlates

Social exclusion is highly distressing and immediately threatens fundamental human needs, such as our need to belong, our need for control over our (social) environment and our needs for self-esteem and a meaningful existence (Baumeister & Leary, 1995; Williams, 2007). Relationships with peers are vital to satisfying these needs across the lifespan (Ladd, 1999; Rubin et al., 2006) and therefore we hypothesized that childhood peer acceptance and rejection have an impact on the extent to which these needs are threatened by social exclusion in adolescence. An experimental design, which has proven to be a reliable paradigm to elicit exclusion-related distress, is a virtual ball-tossing game called Cyberball (Williams et al., 2000). After being ostensibly excluded by two peers in Cyberball, children, adolescents and adults consistently report heightened levels of distress in the form of higher levels of negative mood (e.g., sadness and anger) and a decreased satisfaction of the need to belong, the need for control, self-esteem, and the need for a meaningful existence (Abrams et al., 2011; Gunther Moor et al., 2012; van Beest & Williams, 2006).

Functional Magnetic Resonance Imaging (fMRI) studies using the Cyberball game have identified a network of brain regions involved in processing exclusion-related distress of which three regions are most consistently found: the anterior cingulate cortex (ACC), the anterior insula (AI) and the ventrolateral prefrontal cortex (vlPFC) (Cacioppo et al., 2013; Eisenberger, 2012; Rotge et al., 2014). Higher levels of need threat have been associated with higher levels of activation in the AI and dorsal, ventral and subgenual regions of the ACC (Bolling et al., 2011a; Eisenberger et al., 2003; Gunther Moor et al., 2012; Masten et al., 2009). Consistent with the ACC and AI's involvement in processing conflict and (negative) emotions, these findings suggest that the ACC and AI are involved in processing the distress caused by exclusion. Negative associations have been found between self-reported need threat and activation in the vlPFC, suggesting that the vlPFC is involved in regulating the distress caused by exclusion (Bolling et al., 2011a; Eisenberger et al., 2003; Masten et al., 2009).

Notably, fMRI studies have also highlighted that activity in these brain regions during exclusion may be enhanced or attenuated depending on individual or social factors. Chronic peer group rejection may be one such social factor, and individual factors identified in previous research (e.g., sensitivity to rejection, an anxious attachment style, perceived social support) are likely characteristic of adolescents who have experienced chronic rejection. That is, higher levels of ACC activity during social exclusion have been observed in adolescents who reported to be more sensitive to rejection (Masten et al., 2009) and in adults with an anxious attachment style characterized by a vigilance to cues of rejection (DeWall et al., 2012). Furthermore, adults who perceived their daily social interactions to be more comforting and supportive showed dampened ACC activation during exclusion (Eisenberger et al., 2007) and young adults who spent more time with friends during late adolescence showed a similar pattern of reduced ACC and AI activity during exclusion (Masten, Telzer, Fuligni, Lieberman, & Eisenberger, 2012). Taken together, these findings suggest that people who are more sensitive to rejection or who have lower levels of (perceived) social support display higher levels of activity in brain regions involved in processing the distress caused by social exclusion. Consequently, it is likely that adolescents with a history of peer rejection, who are often more sensitive to rejection (London et al., 2007) and perceive lower levels of peer social support (Ladd et al., 2014) than adolescents with a history of peer acceptance, display enhanced neural responses in the ACC or AI when they are excluded.

The current study

To test the hypothesis that adolescents with a history of chronic peer rejection display enhanced neural responses to social exclusion compared to stably accepted adolescents, we recruited participants from a sample of adolescents who were followed yearly in their classrooms since they were 6 years old. We invited participants who were, across six elementary school grades, consistently nominated by their peers to be liked and almost never disliked (i.e., those with a stable high social preference among their peers, or, stably accepted adolescents) and participants who were consistently disliked and almost never liked (i.e., those with a chronic low social preference, or, chronically rejected adolescents), and examined differences in their subjective and neural responses to exclusion in Cyberball using whole-brain fMRI analyses. Based on previously found negative associations between concurrent social preference and self-reported distress after a mild social rejection experience (Sandstrom et al., 2003), we hypothesized that adolescents with a history of chronic rejection would report higher levels of distress (i.e., lower mood and need satisfaction) after exclusion compared to adolescents with a history of stable acceptance. We further hypothesized that adolescents with a history of peer rejection would show heightened activity in brain regions previously linked to the distressing aspect of social exclusion (e.g., ACC and AI) compared to adolescents with a history of stable acceptance. To test whether chronically rejected adolescents would also show neural reactivity indicative of a hypervigilance to cues of potential rejection, we investigated neural responses to events during which participants did not receive the ball in a social interaction in which they were overall included (i.e., incidental exclusion).

2.2 METHOD

Participants

The current study formed the eighth wave of a longitudinal study on the impact of elementary school social experiences on child behavioral, emotional and academic outcomes where participants were followed between the ages of 6 and 12. A total of 1,189 participants were followed annually from first to sixth grade of elementary school. Each year participants filled out a peer-nomination procedure (unlimited nominations), in which participants were asked to name the peers in their class who they liked most and liked least. An average social preference score (liked most minus liked least nominations) across the six waves was computed. Subsequently, participants were identified as chronically rejected if they were in the lower 10th percentile or as stably accepted if they were in the upper 10th percentile of that 6-year average social preference. By using a 10% threshold it was ensured that none of the chronically rejected adolescents were ever classified as sociometrically popular and none of the stably accepted adolescents were ever classified as having a rejected status across the six waves. Correlation coefficients between social preference scores of adjacent years ranged from .67 to .70 (all *p*s < .001), which is comparable to those reported in other studies (Salmivalli & Isaacs, 2005; Vitaro, Pedersen, & Brendgen, 2007). Participation rates of in the classrooms across cohorts and six annual assessments ranged from 88 - 99%, indicating that participation rates in the classroom nomination assessments were above recommended thresholds (Marks, Babcock, Cillessen, & Crick, 2013).

Based on these criteria, 219 adolescents were eligible for participation in the fMRI study. Of these youths, recent full contact information was available for 131 adolescents, who were subsequently approached for participation 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 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, gender, and average levels of anxiety and conduct problems across 6 years of elementary school (all *p*s > .19). A radiologist reviewed all anatomical scans, and one participant was excluded from the analyses due to an anomaly. Two participants were

Table 2.1 *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)	-1.62 (0.52)	1.16 (0.18)	< .001
Gender (% Male)	70.6	51.9	.22
Age	13.98 (0.77)	14.04 (0.58)	.78
Pubertal status (PDS)			
o Males	2.44 (0.77)	2.19 (0.59)	.36
o Females	3.17 (0.26)	2.72 (0.63)	.15
Race/Ethnicity (% Caucasian)	100	96.3	.44
IQ (WISC Similarities and Block Design)	95 (12.68)	100 (10.24)	.16
Current social competence (parent reported)	4.59 (0.62)	5.40 (0.57)	< .001
Anxiety during elementary school (teacher reported)[b]	0.41 (0.80)	-0.31 (1.01)	< .05
Conduct problems during elementary school (teacher reported)[b]	0.81 (1.39)	-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*

excluded from the analyses because their head movement parameters exceeded 1 voxel (3 mm) in at least one direction.

The remaining 44 participants had a mean age of 14.0 years (*SD* = 0.70; 26 males). Twenty-seven adolescents met our criteria for a history of stable peer acceptance (*M* age = 14.0; *SD* = 0.77; 14 male) and 17 for a history of chronic peer rejection (*M* age = 14.0; *SD* = 0.56; 12 male). 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 chronic peer rejection who were diagnosed with Attention-Deficit Hyperactivity Disorder (ADHD). Three of these participants with ADHD were on a stable dose of methylphenidates, but were medication-free on the day of scanning and the preceding day. One participant was on medication during scanning. The two groups of adolescents did not differ in gender, age, pubertal status, ethnicity, or IQ (all *p*s > .15; see ***Table 2.1***).

Chronically rejected adolescents had higher average levels of anxiety and conduct problems across 6 years of elementary school and they had lower levels of social competence at the moment of scanning than stably accepted adolescents (all *p*s < .05). Researchers and research assistants were familiar with the recruitment procedure based on childhood histories of acceptance and rejection, but were not informed about individual participants' peer status history to ensure blind assessments during data collection. All participants and their parents gave informed consent for the study. The medical ethical committee of the VU University Medical Center approved the longitudinal study and the MRI study was approved by the Leiden university medical ethical committee. After scanning, participants filled out a battery of questionnaires and were debriefed. Participants received a monetary compensation for participation and small gifts.

fMRI task: Cyberball

Participants were given a cover story, in which they were told that they were about to perform a mental visualization task and that this would be investigated by means of an online ball-tossing game (Williams et al., 2000). Accordingly, they were asked to imagine what the other players looked like, what kind of personalities they would have and in what kind of weather conditions the game would be played (Williams, 2007). It was explained that the players were unfamiliar peers and that they would be connected through the Internet. Unbeknownst to the participants, the behavior of the other players in Cyberball was preprogrammed. The other players in the game were depicted as cartoon characters with their names depicted below them (1 male; 1 female). The participants were represented by a hand in the middle of the screen and they could throw the ball to the left or right player with a button press of the index finger of the corresponding hand.

Participants first played an inclusion condition in which each player received the ball an equal amount of times (10 out of 30 throws). After filling out short questionnaires assessing mood and need satisfaction in the scanner (see below), participants played the exclusion condition where, after receiving the ball once at the start of the game and throwing it to one of the other players, they did not receive a single ball for the remainder of the game (28 out of 30 throws). Scans were acquired during two separate runs each lasting about 3 minutes. Participants' throws were self-paced, ball throws of the other players were preceded by a random jitter interval (100- 4000 ms) and it took 2 seconds before each throw reached the designated player. During debriefing, we administered a funneling suspicion probe about the authenticity of the players in Cyberball consisting of three open-ended questions (see supplementary material; 2.5). The number of participants who raised suspicions did not differ between the two groups (7 stably accepted vs. 6 chronically rejected adolescents), $\chi^2(1) = .4, p = .51$.

Questionnaires: Mood and need satisfaction

To assess exclusion-related distress we used self-report measures of mood and need satisfaction (Gunther Moor et al., 2012; Lelieveld, Gunther Moor, Crone, Karremans, & van Beest, 2013; Sebastian et al., 2010; Will, Crone, & Güroğlu, 2014). Mood and need satisfaction were assessed at three time points: (i) immediately after inclusion, (ii) immediately after exclusion, and (iii) approximately 30 minutes after exclusion (when participants came out of the scanner).

The Need Satisfaction questionnaire consisted of eight items taken from the Need Threat Scale (van Beest & Williams, 2006), with two questions assessing each of the following four needs: belonging, self-esteem, control and meaningful existence (see Supplementary ***Table S2.1***; 2.5). All need satisfaction items were rated on a scale from 1 (*not at all*) to 5 (*very much*) and negative items were recoded. Higher scores on this measure thus reflect satisfaction of these needs and lower scores reflect the threat of these needs. The mood questionnaire consisted of eight mood items (feeling good, bad, happy, sad, relaxed, tense, friendly and unfriendly (see Supplementary ***Table S2.1***; 2.5). All mood items were rated on a scale from 1 (*not at all*) to 5 (*very much*) and negative mood items (bad, sad, tense, unfriendly) were recoded.

Internal consistency of the need satisfaction scale proved to be good (Cronbach's $\alpha = .78$) and therefore, consistent with previous studies using Cyberball (van Beest & Williams, 2006; Williams et al., 2000), the four need scales were averaged to create an overall index of need satisfaction at each time-point, i.e., after inclusion, after exclusion and post-scanning. Internal consistency of the mood scale was acceptable (Cronbach's $\alpha = .67$) and the four mood constructs were averaged to create an overall index of mood at each time-point.

fMRI data acquisition

Participants were first familiarized with the scanner environment through the use of a mock scanner. Scans were acquired using a 3T Philips Achieva MRI system at the Leiden University Medical Center. Stimuli were projected onto a screen located at the head of the scanner bore using Authorware. Participants viewed the screen via a mirror mounted on the head coil. Foam inserts that surrounded the head were used to minimize head movement. First, we obtained a localizer scan for each participant. Second, T2*-weighted Echo-Planar Images (EPI) were obtained (repetition time (TR)= 2.2 sec, echo time (TE)= 30ms, sequential acquisition, 38 slices of 2.75 mm, field of view (FOV) = 220 × 220 × 114.68 mm) during two functional runs: Cyberball inclusion and exclusion. The first two volumes of each functional run were discarded to allow for equilibration of T1 saturation effects. Finally, we obtained a high-resolution 3D

T1-FFE scan for anatomical reference (TR = 9.76 ms, TE = 4.59 ms, flip angle = 8°, 140 slices, voxel size = 0.875 × 0.875 × 1.2 mm voxels, FOV = 224 × 177 × 168 mm) after the functional runs.

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). Functional images were slice-time corrected, realigned, co-registered to individual structural T1 scans, normalized to a T1 template, and spatially smoothed using an 8 mm, full-width at half-maximum isotropic Gaussian kernel. The normalization algorithm, resampled the volumes to 3 mm cubic voxels using a 12-parameter affine transformation and a nonlinear transformation involving cosine basic functions. All results are reported in MNI305 stereotactic space.

We analyzed the fMRI data using an event-related design based on previous studies (Gunther Moor et al., 2012; Will et al., 2014). Data were modeled as zero-duration events at the onset of a ball-toss and convolved with a canonical hemodynamic response function (HRF). Statistical analysis was carried out using a general linear model. Regressors were defined for three Cyberball events (throwing, receiving or a ball-toss between the two other players) and were analyzed separately for the inclusion game and the exclusion game. The model contained a basic set of cosine functions that high-pass-filtered the data and a covariate to control for run effects. 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 whole-brain one-tailed t-tests to examine the neural correlates of social exclusion and incidental exclusion across the sample. 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 whole-brain independent samples t-tests. Results were considered significant at an uncorrected threshold of $p < .001$ with a minimum cluster size of 10 contiguous voxels to balance between Type 1 and Type 2 errors (Lieberman & Cunningham, 2009). We also report which results remain significant using a whole-brain voxel-wise false discovery rate (FDR) correction ($p < .05$, > 10 voxels). We used the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002; http://marsbar.sourceforce.net/) to extract activity in functional regions of interest.

2.3 RESULTS

Self-reported distress

A repeated measures ANOVA with time point (3 levels: inclusion, exclusion, and 30 minutes after exclusion) as within-subjects factor for the composite score of need satisfaction and peer status history (2 levels: chronically rejected vs. stably accepted) as a between-subjects factor yielded a main effect of time point, $F(2, 84) = 221.73$, $p < .001$, $\eta_p^2 = .84$. Follow-up pairwise comparisons showed that need satisfaction assessed immediately following exclusion was lower than need satisfaction after inclusion ($p < .001$) and 30 minutes after exclusion ($p < .001$) (see ***Figure 2.1A***). The interaction effect between time point and peer status history was not significant ($p = .49$), indicating that effects of social exclusion on need satisfaction were

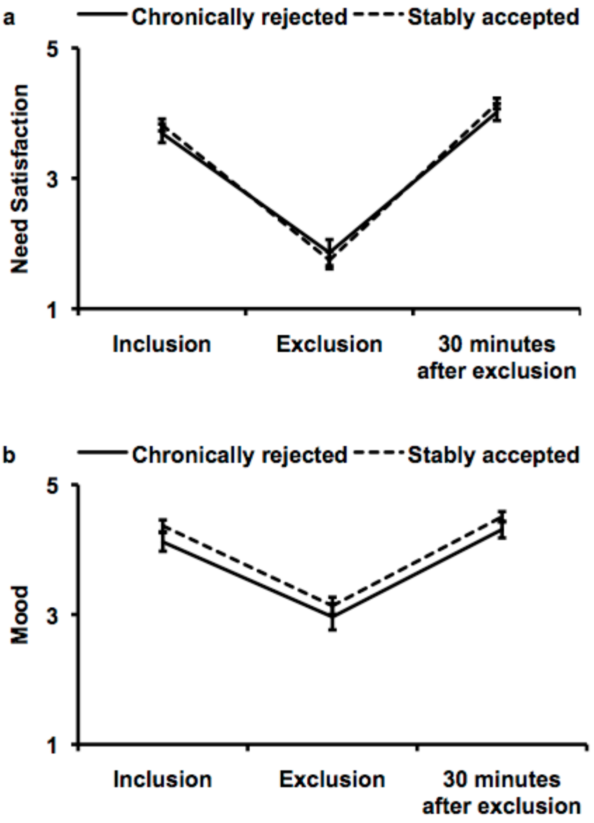


Figure 2.1 *A) Mean levels of a composite score of self-reported satisfaction of fundamental human needs (belonging, self-esteem, control and meaningful existence) assessed immediately after inclusion, exclusion and 30 minutes after exclusion. B) Mean levels of a composite score of mood assessed immediately after inclusion, exclusion and 30 minutes after exclusion (error bars represent standard errors of the mean).*

similar for stably accepted and chronically rejected adolescents.

Similarly, a repeated measures ANOVA with time point (3 levels: after inclusion, after exclusion and 30 minutes after exclusion) as within-subjects factor for overall mood with peer status history (2 levels: chronically rejected vs. stably accepted) as a between-subjects factor yielded a main effect of time point, $F(2, 84) = 98.24, p < .001, \eta_p^2 = .71$. Follow-up pairwise comparisons showed that mood assessed immediately following exclusion was lower than after inclusion ($p < .001$) and 30 minutes after exclusion ($p < .001$) (see ***Figure 2.1B***). The interaction effect between time point and peer status history was not significant ($p = .87$), indicating that effects of social exclusion on mood were similar for stably accepted and chronically rejected adolescents.

Neuroimaging results

Neural responses to social exclusion across the sample

Before we tested for differences in brain responses between chronically rejected and stably accepted adolescents, we first investigated the neural correlates of social exclusion across the whole sample. Three contrasts were used: two examining the neural correlates of social exclusion and a third contrast examining the neural correlates of incidental exclusion.

The first contrast, which compared activation on trials where participants did not receive the ball in the exclusion game with trials where participants received the ball in the inclusion game (Exclusion: not receiving the ball > Inclusion: receiving the ball), resulted in activation in a set of brain regions (***Figure 2.2A***), including ventral ACC/medial PFC (vACC/mPFC; peak voxel of cluster at -12, 47, 1), striatum (peak at -6, 17, -2), bilateral vlPFC (peaks at 27, 32, -11 and -45, 32, -8) and the dorsomedial PFC (peak at -6, 47, 46). The second contrast, which compared activation on trials where participants did not receive the ball in the exclusion game with trials where they did not receive the ball in the inclusion game (Exclusion: not receiving the ball > Inclusion: not receiving the ball), resulted in activation in the striatum (peak at -6, 17, -2) and the vACC (peak at -6, 44, 1) (***Figure 2.2B***).

To identify the neural regions associated with incidental exclusion, we compared activation on trials where participants did not receive the ball during the inclusion game with trials where participants received the ball during the same game (Inclusion: not receiving the ball > Inclusion: receiving the ball). This whole brain contrast resulted in increased activation in several brain regions, including bilateral inferior frontal gyrus (IFG; peaks at 36, 32, -11 and -39, 32, -11), medial PFC (peak at -9, 50, -5) and left vlPFC (peak at -54, 29, 7) (see ***Figure 2.2C***). All significant clusters (uncorrected and FDR corrected) are reported in Supplementary ***Table S2.2*** (2.5).

Neural responses to social exclusion associated with peer status history

To examine differences in brain responses between adolescents with a history of stable acceptance or chronic rejection, we ran whole-brain independent samples *t*-tests on all three contrasts outlined above. Chronically rejected adolescents showed increased activation in dACC (peak at -3, 41, 16) when they were excluded. That is, compared to stably accepted adolescents, chronically rejected adolescents showed higher dACC activity on events where they did not receive the ball during the exclusion game compared with events where they received the ball

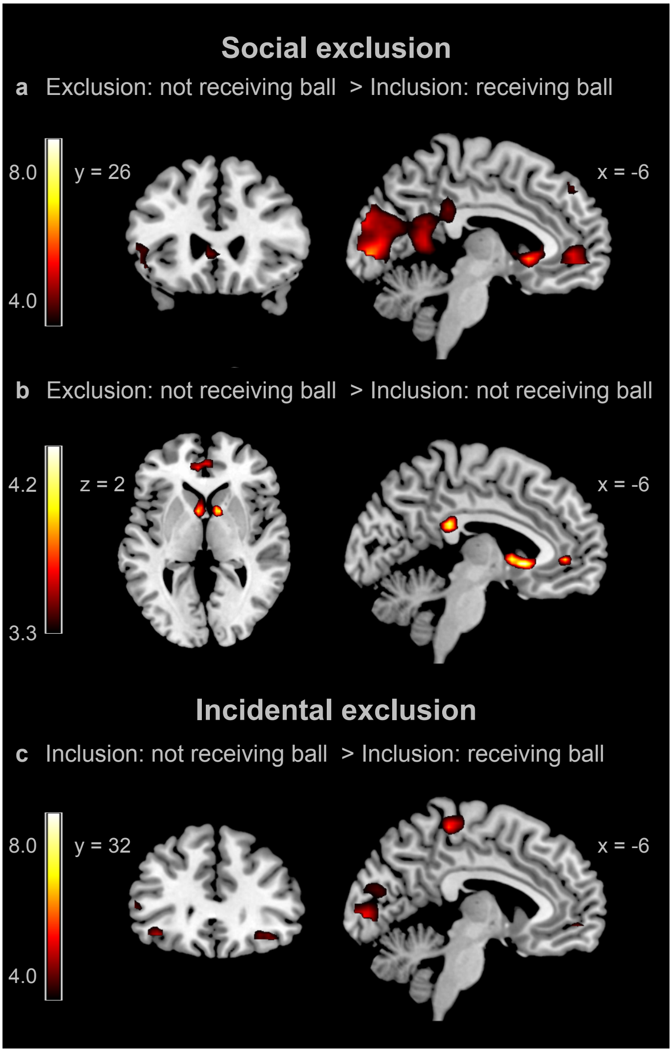
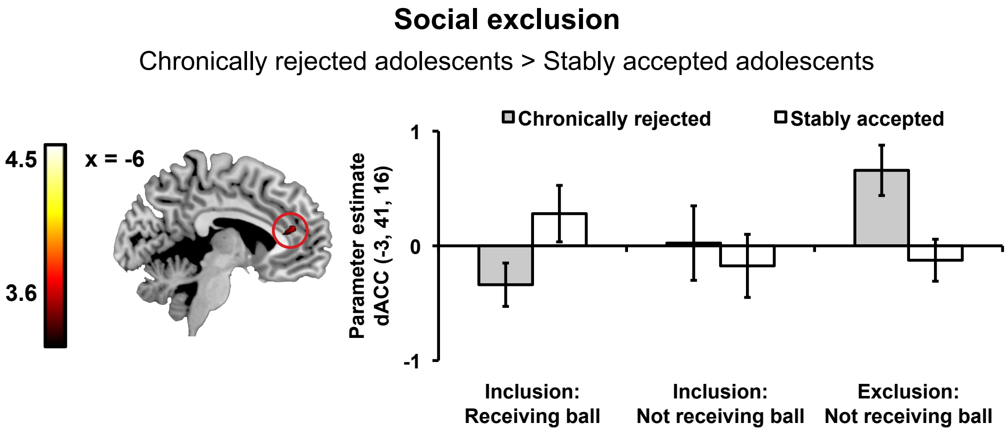


Figure 2.2 *Whole-brain results for the Cyberball interaction collapsed across peer status groups. (A) Social exclusion 1: Not receiving the ball during the exclusion game > receiving the ball during inclusion game. (B) Social exclusion 2: Not receiving the ball during the exclusion game > Not receiving the ball during inclusion game. (C) Incidental exclusion: Not receiving the ball during the inclusion game > receiving the ball during inclusion game.*


Social exclusion

Chronically rejected adolescents > Stably accepted adolescents

Figure 2.3 *Chronically rejected adolescents showed increased activation in the dorsal anterior cingulate cortex (dACC; -3, 41, 16) during social exclusion compared to stably accepted adolescents. Subject-level contrast values in this region of the dACC were extracted for events on which participants received the ball during the inclusion game, when they did not receive the ball during the inclusion game and when they did not receive the ball during the exclusion game and plotted to facilitate interpretation (error bars represent standard errors of the mean).*

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in the inclusion game (Chronically rejected adolescents [Exclusion: not receiving the ball - Inclusion: receiving the ball] > Stably accepted adolescents [Exclusion: not receiving the ball - Inclusion: receiving the ball]) (see ***Figure 2.3***).

Additionally, differences in neural responses to incidental exclusion were found. Specifically, a whole brain contrast showed that compared to stably accepted adolescents, chronically rejected adolescents showed increased activation in the pre- supplementary motor area (peak at -9, 23, 46), dACC (peak at -15, 29, 31) extending into left anterior prefrontal cortex [aPFC; peak at -36, 50, 13]), and right aPFC (peak at 24, 50, 13) on incidental exclusion trials (Chronically rejected adolescents [Inclusion: not receiving the ball - Inclusion: receiving the ball] > Stably accepted adolescents [Inclusion: not receiving the ball - Inclusion: receiving the ball]) (see ***Figure 2.4***).

A direct comparison between stably accepted and chronically rejected adolescents on the second social exclusion contrast (Exclusion: not receiving the ball > Inclusion: not receiving the ball) did not result in activation in regions associated with cognitive or affective processes. No regions showed higher activity in stably accepted adolescents than chronically rejected adolescents in any of the three contrasts. All significant clusters are reported in ***Table 2.2***.

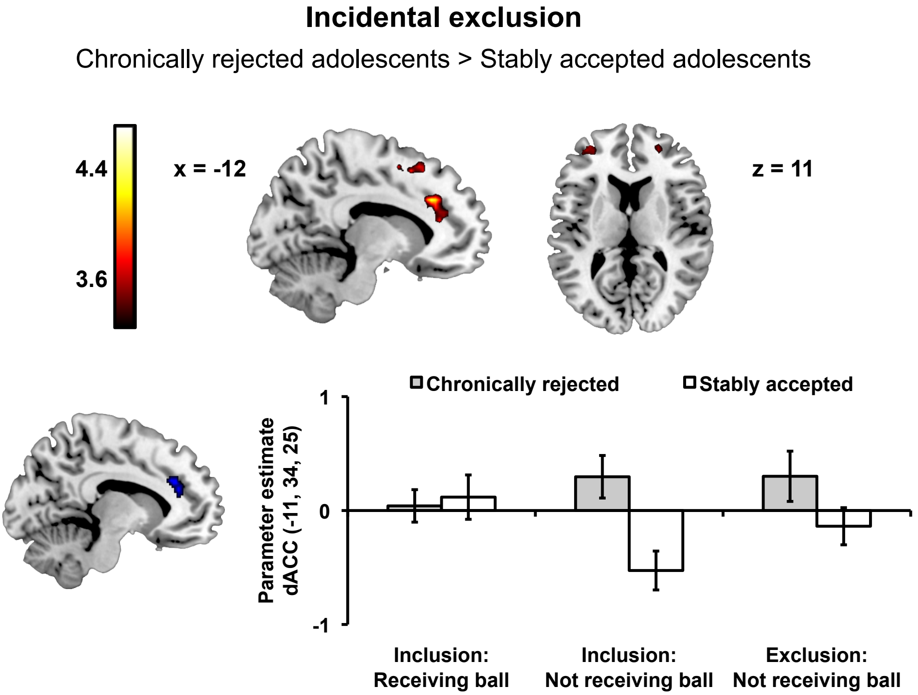


Figure 2.4 *Chronically rejected adolescents, compared to stably accepted adolescents, showed increased activation in the pre-supplementary motor area (-9, 23, 46), dorsal anterior cingulate cortex (dACC; -15, 29, 31) extending into left anterior prefrontal cortex (aPFC; -36, 50, 13), and right aPFC (24, 50, 13) during incidental exclusion. Subject-level contrast values in this region of the dACC (cluster of activation masked with an anatomical ROI of the ACC from the Automated anatomical labeling ROI library (Tzourio-Mazoyer et al., 2002) were extracted for events on which participants received the ball during the inclusion game, when they did not receive the ball during the inclusion game and when they did not receive the ball during the exclusion game and plotted to facilitate interpretation (error bars represent standard errors of the mean).*

2.4 DISCUSSION

The present study investigated differences in subjective and neural responses to social exclusion in adolescents who either had a stable accepted or a chronically rejected status across six elementary school grades. We first replicated previous findings, showing that a brief episode of social exclusion is distressing for adolescents (Gunther Moor et al., 2012; Sebastian et al., 2010) and that social exclusion is associated with activation in brain regions implicated in emotion processing and emotion regulation, such as the dorsal and ventral ACC, medial prefrontal cortex (mPFC), the striatum and vlPFC (Bolling et al., 2011a; Gunther Moor et al., 2012; Masten et al., 2009; Sebastian et al., 2011). Our findings extend the literature by showing that

Table 2.2 *Brain regions revealed by whole-brain analyses testing for peer status history differences in the Cyberball game (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Social exclusion: Chronically rejected adolescents > Stably accepted adolescents [Exclusion: not receiving the ball - Inclusion: receiving the ball]						
Postcentral gyrus	L	19	3.60	-45	-19	31
Anterior Cingulate cortex	L	17	3.48	-3	41	16
Superior Temporal gyrus	L	10	3.38	-60	-34	19
Social exclusion: Chronically rejected adolescents > Stably accepted adolescents [Exclusion: not receiving the ball - Inclusion: not receiving the ball]						
Heschl's gyrus	R	15	3.52	48	-22	10
Incidental exclusion: Chronically rejected adolescents > Stably accepted adolescents [Inclusion: not receiving the ball - Inclusion: receiving the ball]						
Anterior Cingulate cortex	L	148	4.21	-15	29	31
extending into:			3.70	-15	35	19
Middle Frontal gyrus (anterior prefrontal cortex)			3.45	-36	50	13
Superior Frontal gyrus/	L	26	3.56	-15	20	52
Supplementary Motor Area			3.49	-9	11	55
Superior Frontal gyrus (anterior prefrontal cortex)	R	11	3.40	24	50	13
Supplementary Motor Area	R	16	3.37	9	23	46

differences in sustained patterns of peer group acceptance and peer group rejection during the elementary school period are associated with differential neural processing of social exclusion in adolescence. That is, chronically rejected adolescents showed, in comparison to stably accepted adolescents: 1) increased activation in the dACC when they were excluded, and 2) increased activation in the dACC and aPFC during incidental exclusion events in a social interaction in which they were included.

Childhood peer status and self-reported distress after exclusion

Our results show that a brief episode of exclusion in Cyberball results in immediate distress in the form of decreased mood and need satisfaction and that chronically rejected adolescents and stably accepted adolescents report similar levels of distress. Our results partially overlap with the results from a previous study that examined individual differences in subjective distress after receiving a video message from another child telling the participants that he/she did not want to play with them (Sandstrom et al., 2003). Consistent with our findings, Sandstrom and colleagues (2003) found no differences in acute distress reported by accepted and rejected boys. However, their findings indicated that rejected girls reported higher levels of distress compared to accepted girls. Our sample was not large enough to test for such interactions between sex and peer status history in order to examine whether distress differed between rejected and accepted girls. Future studies with larger samples could test whether individual differences in self-reported distress associated with a stable high or low peer status might be different for boys and girls.

Additionally, methodological differences between paradigms used to elicit rejection-related distress may account for differences in results. That is, the relatively mild rejection experience in Sandstrom and colleagues' (2003) study could have allowed more room for individual differences in responses compared to the Cyberball paradigm. That is, meta-analyses have shown that exclusion in the Cyberball paradigm very reliably induces distress (large effect sizes of exclusion in Cyberball on mood and need satisfaction; D's between 1 and 2; Gerber & Wheeler, 2009), but also that the self-reports of such distress seem to be less amenable to moderation by individual differences, such as the participant's sex (Williams & Sommer, 1997), their levels of loneliness (Wesselmann, Wirth, Mroczek, & Williams, 2012) or social anxiety (Zadro, Boland, & Richardson, 2006). Thus, the strength of the Cyberball paradigm (i.e., its ability to reliably induce distress) might also be a limitation when investigating individual differences. A milder or more ambiguous rejection experience might allow for more variability in responses, which could be related to individual differences such as peer status.

Childhood peer status and neural responses to exclusion

The neuroimaging results show that neural responses to both social exclusion and incidental exclusion differ between adolescents who were chronically rejected and those who had a stable accepted status during childhood. Compared to stably accepted adolescents, chronically rejected adolescents showed heightened dACC activity during social exclusion. Our findings are in line with previous work showing enhanced dACC activation during exclusion in adolescents who are more sensitive to rejection (Masten et al., 2009), adults with low self-esteem (Onoda et al., 2010), adults who perceived their daily social interactions to be less comforting and supportive (Eisenberger et al., 2007) and young adults who spent less time with friends during late adolescence (Masten et al., 2012). Combining these previous findings with our results suggest that chronically rejected adolescents show an enhanced neural response to exclusion that they share with people who are more sensitive to rejection, who have lower levels of self-esteem and who have less satisfying social relations.

What could the higher levels dACC activity during exclusion reflect? The ACC is implicated in a wide variety of cognitive and emotional processes including conflict monitoring (Botvinick, Cohen, & Carter, 2004), expectancy violation (Somerville, Heatherton, & Kelley, 2006), physical pain and other negative emotions (Shackman et al., 2011), reactions to being treated unfairly (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003) and social exclusion (Eisenberger et al., 2003). It has been proposed that the ACC is central to a system involved in monitoring the extent to which autonomic/affective signals elicited by salient events interfere with goals or ongoing behavior and therefore require increased attention (Shenhav, Botvinick, & Cohen, 2013). Furthermore, it has been put forward that there is a functional dissociation between dorsal and ventral parts of the ACC (Somerville et al., 2006). That is, the dorsal ACC is connected with prefrontal, parietal and motor cortices, and is important for signaling conflict and integrating top-down and bottom-up processes (Shenhav et al., 2013). The ventral ACC is connected to regions involved in generating and processing affect, such as the amygdala, striatum, and AI, and has been implicated in integrating emotional and motivational valence of stimuli (Somerville et al., 2006).

Chronically rejected and stably accepted adolescents did not show differences in ventral ACC activity, suggesting that exclusion is emotionally salient irrespective of childhood peer status. This notion was mirrored by the similarities in self-reported distress after exclusion. Thus, although it could be hypothesized that chronic exposure to negative peer experiences might desensitize children's reactions to social exclusion, our findings suggest otherwise. Specifically, the finding that chronically rejected adolescents showed increased activation of the dACC compared to stably accepted adolescents suggests that a persistent low status among peers is associated with a neural signal possibly indicating increased conflict or salience associated with being excluded.

Notably, chronically rejected, compared to stably accepted, adolescents, showed enhanced activity in dACC and aPFC in response to incidental exclusion, that is, events during which they did not receive the ball in an interaction in which they were overall included. Higher levels of activity in the dACC and aPFC during exclusion in Cyberball have been shown to be associated with higher levels of rejection sensitivity (Masten et al., 2009), which has been defined as "the disposition to defensively (i.e., anxiously or angrily) expect, readily perceive, and overreact to social rejection" (Downey et al., 1998, p. 1074). Enhanced neural responses to not receiving the ball in the inclusion game in brain regions previously linked to a greater sensitivity to rejection suggest that chronically rejected adolescents might be more sensitive to cues of potential exclusion than stably accepted adolescents. Taken together, these findings show that adolescents with a history of chronic rejection exhibit heightened neural responses to actual and incidental exclusion, which could be indicative of a hypersensitivity or hypervigilance to exclusion.

One possible mechanism accounting for this hypersensitivity could be that chronically rejected adolescents have been exposed to higher levels of negative peer treatment similar to the treatment in Cyberball (being ignored or excluded) than the stably accepted adolescents. Although peer group rejection has been found to be predictive for experiencing peer victimization, including relational victimization (e.g., being left out or excluded from peer activities) (Salmivalli & Isaacs, 2005; van Lier & Koot, 2010), there are large individual differences in the extent to which children with a rejected status are victimized; both in terms of frequency and severity (Boivin et al., 1995; Boulton, 1999). Future studies should examine individual differences related to chronic exclusion/victimization using peer nominations of being excluded/victimized in a larger sample of chronically rejected adolescents. Such endeavors can shed light on the question of whether neural responses to social exclusion are particularly pronounced in adolescents who have been chronically excluded or victimized.

Limitations

Several limitations to the current study warrant consideration. First, although our study is the first demonstration of differences in neural responses to exclusion between adolescents with a history of stable peer acceptance and those with a history of chronic peer rejection, we cannot conclude that these differences are the result of their respective peer status histories. Although the more pronounced brain responses among chronically rejected adolescents could plausibly be attributed to their manifest social experiences, we cannot rule out that such differences were already present before elementary school and their emerging peer status. Future longitudinal studies investigating whether changes in peer status are linked to changes in brain response may shed more light into the question of direction of effects.

Second, our results are based on a comparison of two extreme groups on the outer ends of the social preference spectrum. Although a hypersensitivity to exclusion in adolescents with a history of rejection is highly consistent with both theoretical accounts of peer relations (Coie, 1990; Ladd & Troop-Gordon, 2003; Zakriski et al., 1997) and the development of rejection sensitivity (Downey et al., 1998; London et al., 2007), we cannot rule out the possibility that differences between the two groups are partly explained by a hyposensitivity to exclusion in the stably accepted adolescents. That is, a greater exposure to positive peer relations in the stably accepted group could have also had a dampening effect on neural responses to exclusion (Masten et al., 2012). Future research can inform this question by contrasting adolescents with a history of chronic rejection and acceptance with a sample of adolescents with a stable average peer status.

Third, our sample of chronically rejected adolescents contained adolescents with and without a clinical diagnosis of ADHD. Although removing the participants with ADHD from our analyses did not influence our findings, it is important to investigate whether neural responses to exclusion differ between chronically rejected children with ADHD and those without such a diagnosis.

Conclusions, implications and future directions

To conclude, the present study forms an important first step toward understanding how social exclusion might be experienced differently as a function of an adolescent's prior peer status history. Using neuroimaging methods we showed that, despite chronically rejected and stably accepted adolescents reporting similar negative feelings following exclusion, chronically rejected adolescents showed enhanced neural responses to social exclusion and incidental exclusion. Our findings shed light on the processes, occurring at the level of an individual child, through which peer rejection may lead to adverse effects on mental health over time. Crucially, adolescents who have been exposed to chronic peer rejection process the same exclusion experience differently on a neural level compared to adolescents who were not exposed to chronic rejection, which might not be easily captured by self-reports. Longitudinal studies have shown that peer rejection is a very persistent phenomenon, which can generalize across different social contexts. For example, when children with a rejected status in their classroom enter new social situations where they are unknown, they rapidly reestablish a rejected status (Coie & Kupersmidt, 1983; Hardy et al., 2002). Consistent with transactional models of peer rejection, children with a heightened neural reactivity to social exclusion might show more pronounced emotional or behavioral reactions to acute rejection experiences (e.g., social exclusion), which could in turn elicit repeated instances of rejection in a new social situation. Thus, sensitivity at the neural level might lead to more negative peer experiences that put adolescents with a history of peer group rejection at greater risk for developing mental health problems. However, more work is needed to definitively pinpoint the psychological processes that heightened neural responses in ACC and aPFC represent and how they affect subsequent psychosocial adjustment.

The current study lays the foundations for future work that can examine how neural responses to social exclusion among rejected adolescents might predict behavioral reactions to exclusion. For example, a heightened responsiveness to exclusion might be related to more aggressive reactions, which could sustain the cycle of repeated instances of rejection and increasingly more behavioral problems in which chronically rejected children might have become trapped. Similarly, a heightened neural reactivity to exclusion might be related to anxious expectations of rejection leading to withdrawal from social interactions. Finally, the current findings can inform interventions aimed at reducing rejected children's social difficulties by targeting their hypersensitivity to exclusion. Neuroimaging studies of emotional reappraisal have shown that emotion regulation strategies can alter emotion-related neural activity (Ochsner, Silvers, & Buhle, 2012). An interesting future direction would be to test whether emotion regulation strategies could be used to attenuate the heightened neural response to exclusion and how attenuation of the response might influence subsequent acceptance in the peer group. Ultimately, a neurocognitive perspective on the complex interplay between peer relations and psychosocial development may contribute to our understanding of which rejected children are at risk for developing problems and how subjective and neural responses to exclusion might predict adjustment trajectories.

2.5 SUPPLEMENTARY MATERIAL

Table S2.1

Assessment of Need Satisfaction and Mood following Inclusion, Exclusion and 30 minutes after exclusion (when participants came out of the scanner). All items were rated on a scale from 1 ('not at all') to 5 ('very much'). (R) = reversed scored.

Construct	Item
Need satisfaction	
Belonging	1. I had the feeling that I belonged to the group during the game. 2. During the game I felt connected with one or more players.
Control	3. I had the feeling that the other players decided everything. (R) 4. I felt in control over the game.
Self esteem	5. I felt good about myself. 6. My self-esteem was high.
Meaningful existence	7. During the game it felt as if my presence was not meaningful. (R) 8. I had the feeling that my presence during the game was important.
Mood	During the game I felt: 1. Good 2. Bad (R) 3. Happy 4. Sad (R) 5. Relaxed 6. Tense (R) 7. Friendly 8. Unfriendly (R)

Table S2.2

Brain regions revealed by whole-brain contrasts during the Cyberball game across the sample (all thresholded p < *.001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Social exclusion (Exclusion: not receiving the ball > Inclusion: receiving the ball)						
Calcarine gyrus/Cuneus	L	1376	6.70	-12	-97	4*
			6.63	-12	-88	1*
			5.70	12	-88	1*
Caudate	L	82	5.26	-6	17	-2*
			3.17	9	8	1*
Ventral Anterior Cingulate cortex/	L	174	4.62	-12	47	1*
Medial Prefrontal cortex			4.10	0	50	-5*
			3.99	12	47	-2*
Precentral gyrus	L	64	4.57	-39	-16	40*
Inferior Frontal gyrus	R	47	4.37	27	32	-11*
			3.76	36	35	-11*
Inferior Frontal gyrus (vlFPC)	L	89	4.28	-45	32	-8*
			4.12	-24	32	-11*
			3.84	-36	32	-11*
Superior Temporal gyrus/	R	46	3.76	66	-10	4*
Posterior Insula			3.49	42	-19	4*
			3.37	54	-10	7*
Superior Frontal gyrus (dmPFC)	L	22	3.63	-6	47	46*
Superior Temporal gyrus	L	13	3.54	-66	-28	4*
Social exclusion (Exclusion: not receiving the ball > Inclusion: not receiving the ball)						
Caudate	L/R	79	4.00	-6	17	-2
			3.86	12	8	1
			3.84	6	17	-2
Posterior Cingulate	L/R	56	3.88	-6	-34	25
			3.88	0	-34	19
Ventral Anterior Cingulate cortex/	L/R	38	3.72	-6	44	1
Medial Prefrontal cortex			3.19	12	47	-2

Incidental exclusion (Inclusion: not receiving the ball > Inclusion: receiving the ball)						
Cuneus/Calcarine gyrus	L	648	6.66	-12	91	1*
			6.12	12	-85	4*
			3.91	27	-79	5*
Paracentral Lobule/Precentral gyrus	L	350	4.90	-6	-34	61*
			4.63	15	-31	64*
Poscentral gyrus			4.49	-18	-34	76*
Posterior Insula/		88	4.69	36	-13	19*
Precentral gyrus			4.00	39	-16	37*
Precentral gyrus	L	24	4.58	-39	-16	40*
Fusiform gyrus	R	106	4.47	27	-40	-14*
			4.09	33	-40	-14*
Inferior Frontal gyrus	L	19	4.18	-39	32	-11*
Middle Temporal gyrus	L	20	3.88	-60	-7	-17*
Postcentral gyrus	R	10	3.87	63	-7	22*
Hippocampus	L	16	3.87	-30	-10	-23*
Inferior Frontal gyrus	R	18	3.75	36	32	-11*
Medial Prefrontal cortex	L	12	3.75	-9	50	-5*
Inferior Frontal gyrus (vlPFC)	L	13	3.66	-54	29	7*
Parahippocampal gyrus/	L	26	3.55	-24	-37	-14*
Fusiform gyrus			3.28	-33	-31	-17*

Suspicion probe about authenticity of peers in Cyberball game

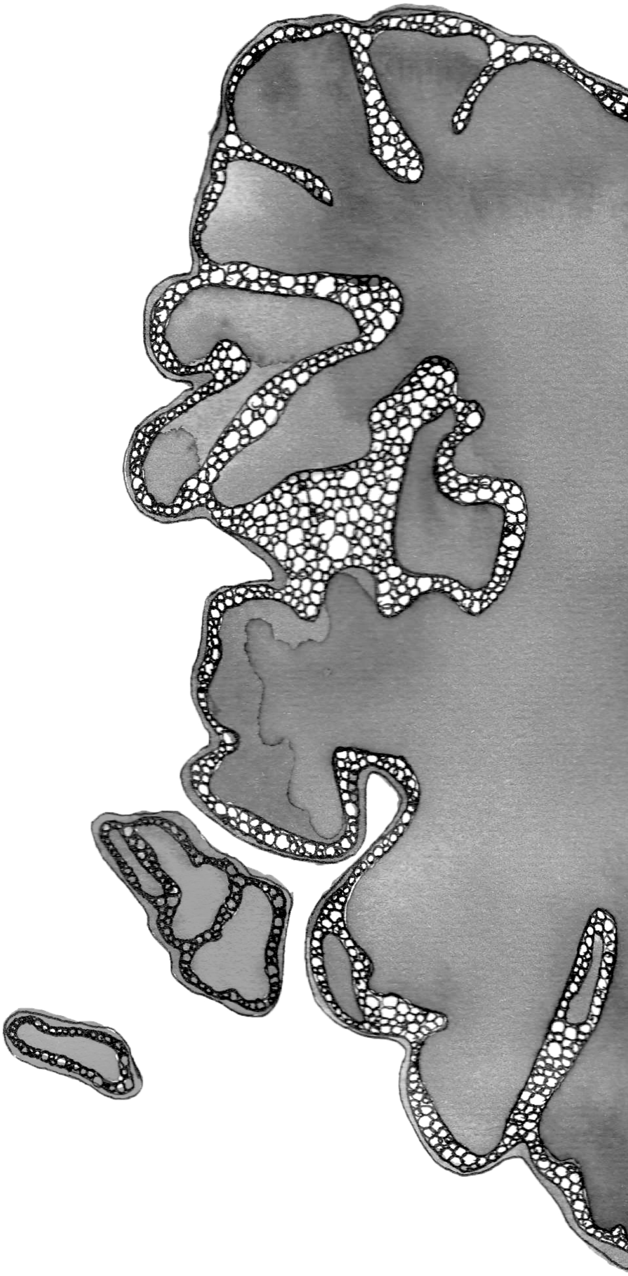
Decreases in need satisfaction and mood across the sample provide evidence that participants felt excluded and less accepted after exclusion in Cyberball, showing that the manipulation had an effect.

Using an explicit check, such as “Did you believe that the other players were real people?” often proves not to be very reliable as people very easily deduct from the question that they were deceived and in turn confess to having had suspicions all along. Therefore, we administered a funneling suspicion probe during a debriefing interview, which included three open ended questions:

1. “What did you think of the ball game?”
2. “How did you like being connected through the Internet with the other players?”
3. “What do you think this study was about?”

In response to the first question 3 participants raised suspicion about either the players in the Cyberball game not being real people (*n* = 2) or that the players were told not to throw to ball to the participant (*n* = 1). In response to the second question an additional 8 were doubtful about the connection being real and in response to the final question 1 participant raised doubts about the interaction being real.

The number of participants who raised suspicions about the authenticity of the players in Cyberball did not differ between the two peer status history groups (7 stably accepted vs. 6 chronically rejected adolescents), $\chi^2(1) = .4$, $p = .51$.



CHAPTER 3

ACTING ON SOCIAL EXCLUSION: NEURAL CORRELATES OF PUNISHMENT AND FORGIVENESS OF EXCLUDERS

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ABSTRACT

This functional magnetic resonance imaging study examined the neural correlates of punishment and forgiveness of initiators of social exclusion (i.e. 'excluders'). Participants divided money in a modified Dictator Game between themselves and people who previously either included or excluded them during a virtual ball-tossing game (Cyberball). Participants selectively punished the excluders by decreasing their outcomes; even when this required participants to give up monetary rewards. Punishment of excluders was associated with increased activation in the pre-supplementary motor area (pre-SMA) and bilateral anterior insula. Costly punishment was accompanied by higher activity in the pre-SMA compared with punishment that resulted in gains or was non-costly. Refraining from punishment (i.e. forgiveness) was associated with self-reported perspective-taking and increased activation in the bilateral temporoparietal junction, dorsomedial prefrontal cortex, dorsal anterior cingulate cortex, and ventrolateral and dorsolateral prefrontal cortex. These findings show that social exclusion can result in punishment as well as forgiveness of excluders and that separable neural networks implicated in social cognition and cognitive control are recruited when people choose either to punish or to forgive those who excluded them.

3.1 INTRODUCTION

Social exclusion is a highly distressing experience and poses a severe threat to fundamental human needs, such as our need to belong and a need for control (Baumeister & Leary, 1995; Williams, 2007). In response to social exclusion, people often attempt to restore their thwarted needs in subsequent social interactions. For example, after people are excluded they show increased levels of prosocial behavior toward potential new sources of affiliation, which possibly reflects a motivation to seek renewed acceptance and restore a sense of belonging (Maner, DeWall, Baumeister, & Schaller, 2007). Furthermore, victims of exclusion selectively decrease prosocial behavior toward the specific individuals who excluded them (Hillebrandt, Sebastian, & Blakemore, 2011) and are even willing to aggress against them (Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007), which has been suggested to be an attempt to regain a sense of control (Williams, 2007). However, not everyone chooses to aggress against those who excluded them (Chester et al., 2013) and some might even decide to forgive the initiators of exclusion (i.e. the excluders). This study set out to investigate punishment as well as forgiveness of excluders and the neural correlates of these behavioral reactions to social exclusion.

A series of neuroimaging studies have identified a network of brain regions involved in emotional reactions to social exclusion using a virtual ball-tossing game called Cyberball (Bolling et al., 2011b; Eisenberger et al., 2003; Sebastian et al., 2011). After being excluded in Cyberball, people report heightened levels of sadness and anger and lowered levels of a sense of belonging, self-esteem, control and meaningful existence (van Beest & Williams, 2006; Zadro, Williams, & Richardson, 2004). Such exclusion-related distress has been positively associated with activation in brain regions involved in processing negative affect, such as the anterior insula (AI) and dorsal, ventral and subgenual regions of the anterior cingulate cortex (ACC) (Bolling et al., 2011b; Eisenberger et al., 2003; Masten et al., 2009). Activity in the ventrolateral prefrontal cortex (vlPFC), a region implicated in emotion regulation, has been found to be negatively related to distress after exclusion (Bolling et al., 2011b; Eisenberger et al., 2003).

Although these studies have informed us on the neural correlates of processing and regulating exclusion-related distress, the neural correlates of social behavior *after* an episode of exclusion have received less attention. A recent study showed that although participants showed low levels of trust toward peers who previously excluded them, reinforcement signals in the striatum still guided learning from the trustworthiness of excluders and enabled sustaining trust (Fareri, Chang, & Delgado, 2012). In a Dictator Game - where profits are not dependent on the second player's decisions - people kept more money to themselves and shared less with excluders, which was associated with increased activation in dorsal ACC (dACC), AI, the temporoparietal junction (TPJ) and lateral regions of the PFC (Gunther Moor et al., 2012). How activation in these regions relates to punishment of excluders or refraining thereof (i.e.

forgiveness) is not yet clear, because these prior studies' experimental designs did not provide a dissociation between a self-oriented motive aimed at maximizing one's own profits and other-oriented motives aimed at increasing (Fareri et al., 2012) or decreasing (Gunther Moor et al., 2012) another person's profits.

The goals of this study were threefold: (i) to examine whether people punish excluders when it does not result in monetary gains or when they have to pay to punish, (ii) to investigate how activation in brain regions involved in punishment of norm-violators is differentially sensitive to gains and losses for the punisher, and (iii) to examine the neural correlates of forgiving excluders (i.e. refraining from punishment by equally sharing with excluders when sharing was not confounded by strategic motivations aimed at maximizing personal profits) (Brüne, Juckel, & Enzi, 2013; McCullough, Worthington, & Rachal, 1997). We modified the Dictator Game in such a way that participants could choose to either forgive excluders by sharing a sum of money equally with them, or to punish them and punishment could coincide with: (i) gains (beneficial inequality), (ii) no monetary consequences (non-costly inequality), or (iii) losses (costly inequality).[1] We regarded unequal distributions as punishment and equal distributions as forgiveness only in interactions with peers who violated a social norm during Cyberball, i.e. the excluders. Therefore, to get a clean measure of punishment, we examined unequal distributions allocated to excluders relative to unequal distributions allocated to includers.

We hypothesized that participants would punish excluders by reducing the excluders' monetary rewards (i.e. choosing more unequal distributions for excluders than for includers). We predicted punishment to be inflicted most often when it led to monetary gains (i.e. beneficial inequality) and least often when it was costly, with non-costly inequality at an intermediate position. Based on previous neuroimaging studies we expected brain regions implicated in reward processing (striatum), negative affect (AI) and the detection of norm-violations (pre-supplementary motor area [pre-SMA]/ACC) to be involved in delivering punishment (Baumgartner, Gotte, Gugler, & Fehr, 2012; De Quervain, 2004; Sanfey et al., 2003; Strobel et al., 2011).

Participants could forgive the excluders, defined as refraining from retaliation and acting prosocial toward the offenders despite the offenders' hurtful actions (McCullough et al., 1997), by sharing a sum of money equally with them (Brüne et al., 2013). Prior studies have demonstrated that adopting a transgressor's perspective facilitates forgiveness (Brown, 2003;

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[1] *We included a prosocial inequality condition (where inequality offers would result in sharing more than half of the stake) in order to avoid automaticity in responding, such that inequality for excluders always indicated punishment. Thus, it served as a filler condition to prevent predictability of the task, and keep participants engaged. We excluded the prosocial inequality condition from the analyses investigating punishment and forgiveness because the prosocial inequality condition did not offer participants the opportunity to punish (because excluders' outcomes could not be reduced) nor to forgive (since there is no possibility to refrain from punishment).*

Exline, Baumeister, Zell, Kraft, & Witvliet, 2008). Consequently, we tested whether higher levels of self-reported perspective-taking would be related to lower levels of punishment behavior toward excluders. We hypothesized that forgiveness would coincide with increased activation in brain regions implicated in 'theory of mind' and perspective taking, such as the dorsomedial prefrontal cortex (dmPFC) and the TPJ (Lamm, Batson, & Decety, 2007; Young & Saxe, 2009). Furthermore, cognitive control has been shown to play an important role in refraining from aggression against excluders (Chester et al., 2013) and control-related brain regions, such as regions of the lateral PFC are activated when people share equally with peers who previously treated them unfairly (Brüne et al., 2013). Accordingly, we predicted that forgiving excluders would also be associated with activity in regions of the lateral PFC, consistent with their involvement in cognitive control in social decision-making (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Steinbeis et al., 2012).

3.2 METHODS

Participants

Twenty-eight right-handed healthy volunteers were recruited through local advertisements and gave informed consent for the study. Two participants were excluded from the analyses because they expressed doubts about the cover story. The remaining 26 participants had a mean age of 20.7 years (SD = 1.97, 16 females). All participants indicated to be healthy and reported no contraindications for fMRI (e.g. no head injuries, no history of neurological or psychiatric disorders). All anatomical scans were reviewed and cleared by a radiologist; no anomalies were reported. After scanning, participants filled out several questionnaires and were debriefed. Participants received €25 for participation and an additional amount of money, which was told to be determined by their decisions in the Dictator Game. In reality, each participant received an extra €5. The study was approved by the university's medical ethical committee.

fMRI tasks

Cyberball

Participants were instructed that they were about to perform a mental visualization task by means of an online ball-tossing game with two other participants in the experiment (Williams et al., 2000). Participants were told that they were about to interact with other participants who were present at the experiment site and with whom they would not meet face-to-face after the experiment. In reality, all ball tosses by the other players were preprogrammed. The participants were represented by a cartoon hand along with their own name and the other players were displayed as two cartoon characters accompanied by one male and one female name (***Figure 3.1A***). Participants could throw the ball to a player on their right or their left side by a button press with the index finger of the corresponding hand. Participants first played the inclusion condition where each of the three players received the ball an equal number of times (10 out of 30 trials). Next, participants played the exclusion condition with two novel players, during which they received the ball once at the start of the game. After throwing it to one of the players they did not receive the ball on any of thefollowing 28 trials. Scans were acquired during two separate runs that lasted approximately 3 min each. Throwing was self-paced. Ball throws lasted 2 s and were preceded by a random jitter interval (100–4000 ms).

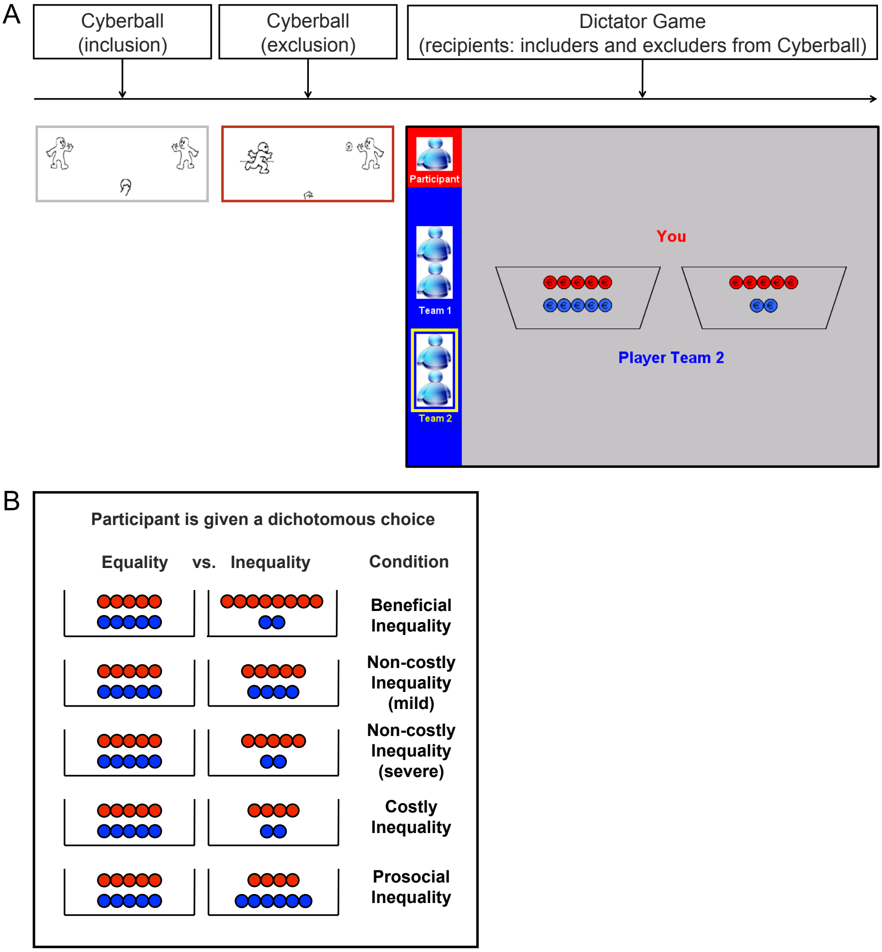

Figure 3.1 *(A) Experimental procedure. Participants carried out the following tasks in the scanner: (i) Cyberball inclusion with two anonymous peers, (ii) Cyberball exclusion by two novel anonymous peers, (iii) Dictator Game in which participants divided money between themselves (depicted with red coins) and the players from the Cyberball games (i.e. includers and excluders; depicted with blue coins). (B) Five different forms of inequality; each trial consisted of a dichotomous choice between an equal distribution and one of these five forms of inequality.*

Dictator Game

After Cyberball, participants were given the opportunity to divide coins between themselves and one player from either the first or the second ball game, that is, Team 1 and Team 2, respectively. It was emphasized that coins were valuable and that a randomly selected allocation would be converted into real money, which both allocators (the participants) and recipients would receive at the end of the experiment. Furthermore, the Dictator Game was introduced as the final game of the experiment. Therefore, it was unlikely that the participants anticipated further interactions with the includers and excluder.

Participants were given a dichotomous choice between an equal distribution of five coins for themselves and five for the recipient (5/5) and one of five different unequal distributions (***Figure 3.1B***). These five unequal distributions were as follows and should all be interpreted relative to the alternative equal (5/5) distribution: beneficial inequality (eight coins for the participant and two coins for the recipient: 8/2), mild non-costly inequality (5/4), severe non-costly inequality (5/2), costly inequality (4/2) and (costly) prosocial inequality (4/6). Although in the non-costly inequality conditions choosing the inequality option instead of the equal distribution had no consequences for the participant's own earnings, beneficial inequality was *advantageous* and costly inequality was *disadvantageous* to the participant.

We did not include a condition with neutral recipients with whom the participants had not interacted before, because this would increase the length of the task with 150% and this could lead to greater trial-to-trial variability, e.g. bigger differences in emotional valence between the first and final trials of the task possibly due to negative emotions toward excluders diminishing over time. Moreover, previous work has repeatedly shown that: (i) although exclusion elicits negative affect, inclusion does not elicit positive affect (Maner et al., 2007; Wesselmann et al., 2012; Will, van den Bos, Crone, & Güroğlu, 2013) and (ii) treatment of includers does not differ from treatment of neutral interaction partners or people with whom participants had not interacted before (Fareri et al., 2012; Gunther Moor et al., 2012; Güroğlu, Will, & Klapwijk, 2013; Hillebrandt et al., 2011). The Dictator Game consisted of 180 trials (18 trials per condition; 5 inequality conditions × 2 recipients) and was administered in three runs of 210 volumes each, lasting about 23 min in total. After a fixation screen with a jittered duration (M = 1540 ms; SD = 1221 ms; min = 550 ms; max = 7700 ms optimized with Opt-Seq2, Dale, 1999; surfer.nmr.mgh.harvard.edu/optseq/) participants were presented with a decision screen that showed (i) which distributions they could choose from and (ii) who the recipient would be (***Figure 3.1A***). Responses could be made by a button press with the index finger (left bucket) or middle finger (right bucket) of the right hand. As soon as participants made a decision 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 1 s. Trials without a response consisted of <1% of all trials and were excluded from further analyses.

Questionnaires

Mood reports and need satisfaction

To measure exclusion-related distress, we assessed mood and need satisfaction at three time points: (i) after inclusion, (ii) after exclusion and (iii) after the Dictator Game (outside the scanner). The mood questionnaire consisted of eight mood items (feeling good, bad, happy, sad, relaxed, tense, friendly and unfriendly). The need satisfaction questionnaire consisted of eight items (two items assessing each need) taken from the need threat scale including ratings of belonging, self-esteem, control and meaningful existence (van Beest and Williams, 2006). All items were rated on a scale from 1 (*not at all*) to 5 (*very much*) and negative items were recoded. Lower scores on these measures reflect distress, i.e. need threat and lower mood.

Trait perspective-taking

Participants completed the perspective-taking subscale of the Interpersonal Reactivity Index (IRI; Davis, 1983) to assess dispositional perspective-taking, i.e. the tendency to adopt another person's point of view (e.g. "When I get mad at someone, I try to imagine what they might be thinking"). 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 University Medical Center. Stimuli were projected onto a screen located at the head of the scanner bore using Authorware (Cyberball) and E-prime (Dictator Game). Participants viewed the screen via a mirror mounted on the head coil. Foam inserts that surrounded the head were used to minimize head movement. The following scans were acquired: (i) a localizer scan, (ii) T2*-weighted Echo-Planar Images (EPI; repetition time = 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 five functional runs, (iii) high-resolution T1-weighted and T2-weighted anatomical scans (with the same slice prescription as the EPIs). The first two volumes of each functional run were discarded to allow for equilibration of T1 saturation effects.

fMRI data analysis

MRI data were preprocessed and analyzed using SPM5 statistical parametric mapping image analysis software (Wellcome Trust Centre for Neuroimaging, University College London). Images were slice-time corrected, realigned, corrected for motion, spatially smoothed using an 8-mm FWHM Gaussian filter, and spatially normalized to EPI templates. Translational movement parameters never exceeded 1 voxel (< 3 mm) in any direction for any subject or 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.

Data were modeled as zero-duration events at the onset of a ball-toss (Cyberball) or the decision screen (Dictator Game) (Gunther Moor et al., 2012; Lelieveld et al., 2013) and convolved with a canonical hemodynamic response function (HRF). Statistical analysis was carried out using a general linear model (GLM). Regressors were defined for three Cyberball events (a ball-toss between virtual peers, throwing, or receiving the ball) and were analyzed separately for the inclusion game and the exclusion game. Regressors were defined separately for equality and inequality choices made in each of the five inequality conditions in the Dictator Game and analyzed separately for the includers and the excluders. This model consisted of 20 decision-related regressors (i.e. inequality condition [5] × recipient [2] × choice [2]), a regressor indicating missed trials, and a covariate for each run to control for run effects (3), which resulted in a GLM with a total of 24 predictors. To investigate the main effect of interacting with the excluders compared with includers in the Dictator Game (Excluders > Includers), we contrasted all decisions for excluders with all decisions for includers in conditions where participants could punish or forgive (i.e. all conditions except prosocial inequality). To test how activation in regions derived from the 'Excluders > Includers' contrast was differentially sensitive to personal gains when punishing excluders, we employed a region of interest (ROI) approach (see below). To investigate the neural correlates of punishment, we contrasted inequality decisions for excluders with equality decisions for excluders (Excluders inequality > Excluders equality). Finally, to examine forgiveness we contrasted equality decisions for excluders with equality decisions for includers (Excluders equality > Includers equality). For the latter two contrasts, we only considered the four Dictator Game conditions involving punishment and forgiveness (i.e. all conditions except prosocial inequality). Both GLMs 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. One-tailed t-tests were considered significant at an uncorrected threshold of $p < .001$ with a minimum cluster size of 10 contiguous voxels to balance between Type 1 and Type 2 errors (Lieberman & Cunningham, 2009). We also report which results remain significant using a whole-brain voxel-wise false discovery rate (FDR) correction ($p < .05$, >10 voxels).

For ROI analyses, we used the MarsBaR toolbox (Brett et al., 2002; http://marsbar.sourceforce.net/) to extract activity in functionally defined ROIs in the 'Excluders > Includers' contrast (in the Dictator Game) about which we had a priori hypotheses, i.e. pre-SMA/ACC, left and right AI. For each ROI, the blood oxygenation level dependent (BOLD) signal across functional clusters of voxels was averaged and the center of mass is reported. For all ROI analyses, effects were considered significant at $p < .017$, based on a Bonferonni correction for multiple comparisons ($p = .05/3$ ROIs).

3.3 RESULTS

Behavioral data

Need satisfaction and mood. Consistent with previous studies (van Beest & Williams, 2006; Williams et al., 2000) the four need scales were averaged to create an overall index of need satisfaction at each time-point, i.e. after inclusion, after exclusion and after the Dictator Game. Similarly, the four mood constructs were averaged to create an overall index of mood at each time-point[2]. A repeated measures ANOVA with time point (3 levels: inclusion vs. exclusion vs. after the Dictator Game) as within-subjects factor for the composite score of need satisfaction yielded a main effect of time point, $F(2, 48) = 219.37, p < .001, \eta_p^2 = .90$. Overall need satisfaction measured after inclusion ($M = 3.7$) declined during exclusion ($M = 1.7$) and returned to pre-exclusion levels after the Dictator Game ($M = 4.1$). A repeated measures ANOVA with time point (3 levels: inclusion vs. exclusion vs. after the Dictator Game) as within-subjects factor for overall mood yielded a main effect of time point, $F(2, 48) = 50.73, p < .001, \eta_p^2 = .68$. Overall mood measured after inclusion ($M = 4.4$) dropped during exclusion ($M = 3.5$) and returned to pre-exclusion levels after the Dictator Game ($M = 4.5$).

Punishment of the excluders in the Dictator Game

To investigate whether excluders were punished, a repeated measures ANOVA was performed with inequality condition (5 levels: beneficial inequality, non-costly mild inequality, non-costly severe inequality, costly inequality and prosocial inequality) and recipient (2 levels: includers vs. excluders) as within-subjects factors and the percentage of unequal offers as the dependent variable. These analyses resulted in main effects of recipient, $F(1, 25) = 27.149, p < .001, \eta_p^2 = .52$ and inequality condition, $F(4, 100) = 31.93, p < .001, \eta_p^2 = .56$, and a significant recipient × inequality condition interaction, $F(4,100) = 13.80, p < .001, \eta_p^2 = .36$. Unequal distributions were chosen more often for excluders than for includers in each condition, (all *p*s < .01), except for the prosocial inequality condition ($p = .09$) (see ***Figure 3.2A***). Post hoc pairwise comparisons showed that, in exchange with the excluders, beneficial inequality was chosen more than the two non-costly inequality options ($p < .05$), which were chosen at similar rates (p =.09) and more than costly inequality, (all *p*s <.01). A similar analysis for the includers showed that the beneficial inequality was chosen more often than the other forms of inequality, $p < .01$.

Perspective taking and forgiveness

A negative correlation between self-reported perspective-taking and punishment frequency

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[2] *Univariate analyses on the separate needs and mood constructs demonstrated that each need and each mood construct yielded the same results as the overall indexes.*

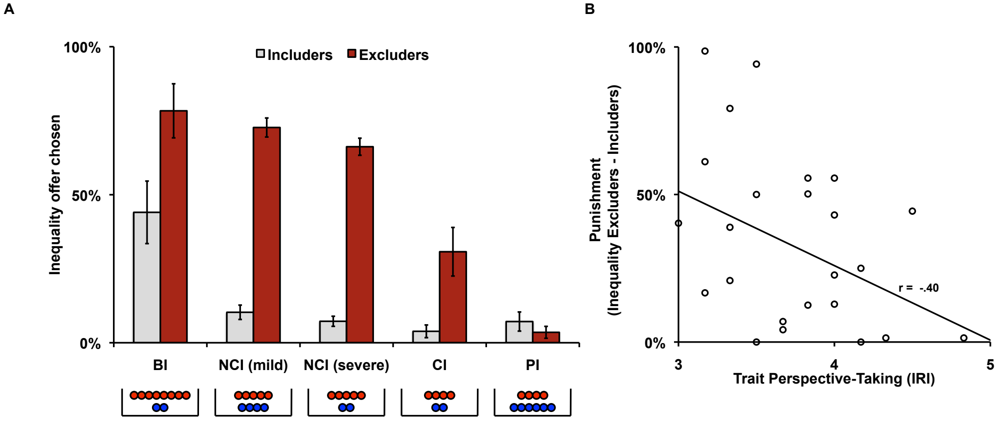

Figure 3.2 *(A) Mean percentages of trials on which participants chose an unequal distribution in the Dictator Game for players who previously included and excluded them during Cyberball (error bars represent standard errors of the mean). Each form of inequality is displayed on the x-axis (red coins for participants; blue coins for the recipients). Unequal distributions were pitted against an equal distribution of money (5 coins for the participant / 5 coins for the recipient). BI = beneficial inequality; NCI = non-costly inequality; CI = costly inequality; PI = prosocial inequality; (B) Self-reported trait perspective-taking was negatively associated with punishment of the excluders (difference between unequal distributions chosen for excluders and includers).*

(percentage of inequality offers to the excluders – percentage inequality offers to the includers in all conditions except prosocial inequality), $r = -.40$, $p < .05$, confirmed that perspective taking is important for forgiving excluders (see ***Figure 3.2B***). Perspective-taking skills were unrelated to exclusion-related distress (mood after exclusion, $r = .30$, $p = .14$, and need satisfaction after exclusion, $r = .21$, $p = .29$).

Neuroimaging results

fMRI results Cyberball

To examine the neural correlates of social exclusion, we compared activation on trials where participants did not receive the ball in the exclusion game with trials where participants received the ball in the inclusion game (Exclusion: not receiving the ball > Inclusion: receiving the ball). This whole-brain contrast resulted in activation in several regions, including the medial PFC (mPFC; peak at 3, 45, -15) and subgenual ACC (sgACC; peak at -9, 24, -6) (see ***Figure 3.3A***). A regression analysis with need satisfaction as a predictor revealed a positive correlation in the ventral ACC (peak at 6, 42, 3) and the right vlPFC/insula (peak at 45, 21, -3) (see ***Figure 3.3B***). All significant clusters are reported in Supplementary ***Table S3.1***.

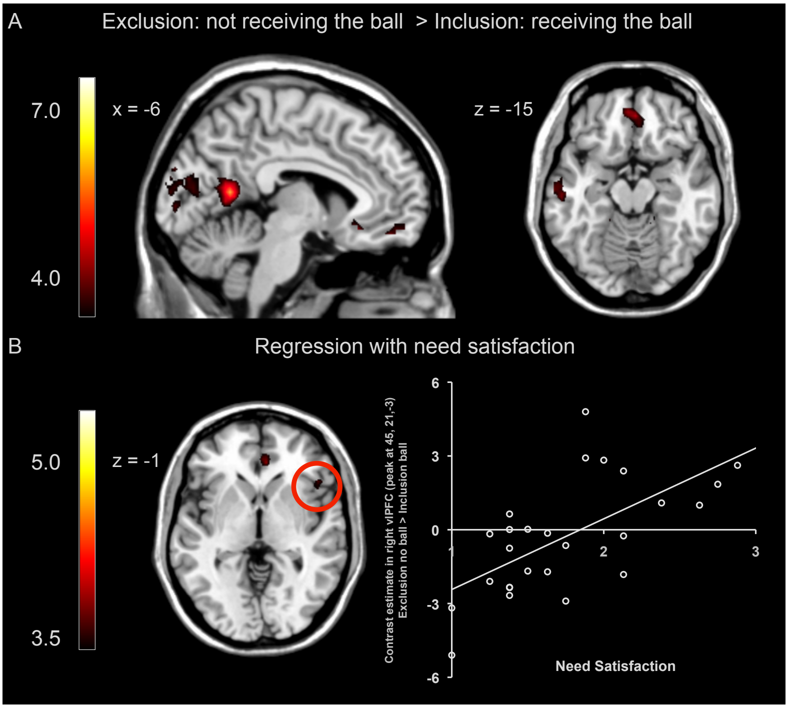

Figure 3.3 *Whole-brain results from the Cyberball interaction. (A) Not receiving the ball during the exclusion game > receiving the ball during inclusion gam resulted in activation in the mPFC (peak at 3, 45, -15) and sgACC (peak at -9, 24, -6) (B) A whole-brain regression analysis showed that activity in the 'Exclusion: not receiving the ball > Inclusion: receiving the ball' contrast was positively associated with need satisfaction after exclusion in the right ventrolateral prefrontal cortex (vlPFC; peak at 45, 21, -3).*

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fMRI results Dictator Game

Decision-making with excluders.

To investigate brain regions that were more active when making a decision in the Dictator Game for excluders compared to includers, we conducted a whole-brain analysis collapsed across the four Dictator Game conditions involving punishment (i.e., all conditions except prosocial inequality) and collapsed across choices. The 'Excluders > Includers' contrast resulted in increased activation in the pre-SMA (peak at 3, 21, 60) and bilateral AI (peaks at 30, 21, -9 and -30, 21, -15) (see ***Figure 3.4***). All areas of activation are listed in ***Table 3.1***.

Punishing excluders.

To examine the neural correlates of punishment, we conducted a whole-brain analysis and ROI analyses. A whole-brain contrast between inequality choices for excluders and equality

Table 3.1 *Brain regions revealed by whole-brain contrasts when participants made an allocation in the Dictator Game with excluders vs. includers as recipients (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Excluders > Includers						
Middle Cingulate cortex	R	31	4.13	3	-6	30
Precentral gyrus	L	13	3.84	-42	0	21
Pre-Supplementary Motor Area	R	20	3.83	3	21	60
Inferior Parietal lobe	L	59	3.81	-48	-45	57
			3.80	-54	-45	42
			3.70	-57	-36	48
Anterior Insula (extending into	R	14	3.64	36	24	-18
Inferior Frontal gyrus)			3.41	30	21	-9
Inferior Frontal gyrus (Lateral PFC)	R	17	3.61	42	42	-18
Anterior Insula (extending into	L	15	3.55	-30	21	-15
Inferior Frontal gyrus)			3.25	-36	21	-9
Includers > Excluders						
Superior Occipital gyrus	L	62	4.04	-12	-99	12
			3.40	-15	-96	0

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. PFC = Prefrontal cortex.

choices for includers (Excluders inequality > Excluders equality) collapsed across the four Dictator Game conditions involving punishment (i.e. all conditions except prosocial inequality) did not result in significant clusters of activation. To investigate how activation in the pre-SMA/ ACC, left and right AI were differentially sensitive to self-gain while punishing the excluders, we performed functional ROI analyses based on these regions obtained from the 'Excluders > Includers' contrast reported earlier.

First, using activation levels in each ROI during inequality choices for the excluders as the dependent variable, we conducted three separate repeated measures ANCOVAs for each brain region with inequality condition (4 levels: beneficial inequality, non-costly mild inequality, non-costly severe inequality, and costly inequality) as a within-subjects factor and punishment frequency as a covariate. We controlled for punishment frequency because of the involvement

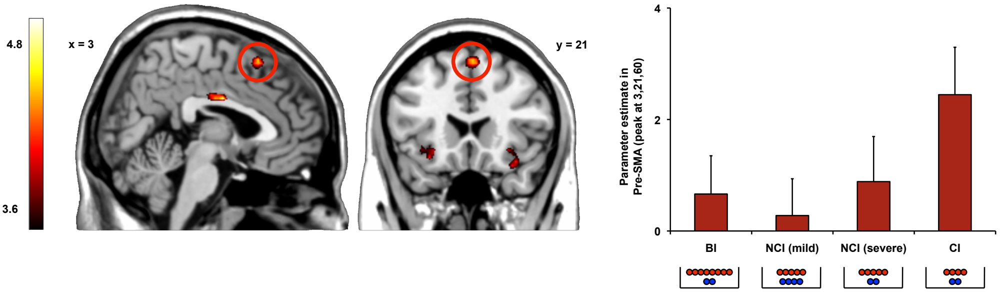


Figure 3.4 *Activation of pre-SMA (peak at 3, 21, 60) when choosing unequal offers for excluders in the four different punishment conditions (error bars represent standard error of the mean). BI = beneficial inequality; NCI = non-costly inequality; CI = costly inequality*

of the pre-SMA/ACC and AI in deviations from default response patterns (Güroğlu, van den Bos, Rombouts, & Crone, 2010; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009) and to control for the amount of trials contrast values were based on. These analyses yielded a main effect of Inequality condition in the pre-SMA, *F*(3, 33) = 5.17, *p* < .01, η_p^2 = .32, qualified by more activity for costly inequality choices compared to the three other inequality choices for excluders (***Figure 3.4***). Activity in left (*p* = .27) and right AI (*p* = .12) did not differ between inequality choices after controlling for punishment frequency.

Second, we correlated activation in the ROIs with the frequency of inequality choices made in each condition. These analyses yielded a negative correlation between BOLD response and costly punishment frequency in the pre-SMA (*r* = -.64, *p* < .017) and right AI (*r* = -.63, *p* < .017). Thus, the participants who less often opted for costly punishment exhibited higher BOLD responses in these regions when they chose costly punishment.

Forgiving excluders.

To investigate which brain regions were involved in forgiveness of excluders we contrasted equality choices for excluders with equality choices for includers in the four Dictator Game conditions involving punishment and forgiveness (i.e., all conditions except prosocial inequality). This comparison (Excluders equality > Includers equality) revealed activity in the right TPJ (peak at 57, -57, 45), dmPFC (peak at 3, 42, 36), right vlPFC (peak at 42, 42, -15) and the right AI (peak at 30, 21, -9). A subsequent whole-brain regression analysis with punishment frequency as a predictor revealed a positive correlation in the left and right TPJ (peaks at -51, -48, 36 and 45, -54, 36), dmPFC (peak at -15, 60, 24), as well as in the Pre-SMA/ACC (peaks at -6, 18, 51 and 9, 36, 36), bilateral AI (peaks at -30, 21, -6 and 33, 18, -12) and dorsolateral and ventrolateral PFC (peaks at -30, 51, 0 and 33, 54, 9) (***Figure 3.5***). Thus, participants who punished more often recruited the left and right TPJ, dmPFC, lateral PFC and Pre-SMA/ACC and bilateral AI to a greater extent when they forgave the excluders. All significant clusters are reported in ***Table 3.2***.

Table 3.2 *Brain regions revealed by whole-brain contrasts when participants shared the stake equally in the Dictator Game with excluders vs. includers (all thresholded* p < *.001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Excluders equality > Includers equality						
Superior Frontal Gyrus (dmPFC)	R	272	4.16	12	30	57
extending into:			3.93	12	21	66
Pre-Supplementary Motor Area/						
Dorsal Anterior Cingulate Cortex			3.90	21	36	54
Inferior Frontal gyrus (Lateral PFC)	R	21	3.81	42	42	-15
Temporoparietal junction	R	87	3.79	57	-57	45
			3.61	48	-63	48
			3.60	57	-51	51
Middle Frontal gyrus	R	60	3.76	42	24	51
			3.29	48	24	30
			3.27	45	12	48
Anterior Insula extending into:	R	20	3.64	30	21	-9
Inferior Frontal gyrus			3.45	36	21	-15
			3.42	30	18	-24
Superior Frontal Gyrus (dmPFC)	R	15	3.57	15	66	21
Angular Gyrus	L	28	3.44	-57	-60	39
			3.42	-45	-69	48
			3.32	-42	-63	42
Middle Frontal gyrus	L	15	3.40	-36	18	54
			3.26	-30	18	54
Positive correlation with punishment frequency (percentage inequality for excluders – percentage inequality for includers)						
Temporoparietal junction	L	550	5.23	-51	-48	36*
			4.69	-51	-39	42*
			4.40	-54	-27	39*
	R	320	5.15	45	-54	36*
			4.27	24	-60	42*
			4.05	57	-54	42
Superior Frontal Gyrus (extending into:	L	557	5.20	-33	18	54*
Pre-Supplementary Motor Area /			4.68	-6	18	51
Dorsal Anterior Cingulate cortex)			4.57	9	36	36*

Anterior Insula	L	17	4.56	-30	21	-6*
Lateral PFC (dlPFC/vlPFC)	L	90	4.47	-30	51	0*
			3.71	-33	54	-9*
			3.59	-42	48	3*
Middle Frontal gyrus	L	110	4.39	-42	30	24*
			4.04	-36	9	36*
			3.90	-39	18	27*
Thalamus/Pallidum	L	41	4.01	-9	-9	3*
			3.97	-12	0	-3
			3.77	-3	-18	-6*
Middle Frontal gyrus	R	100	3.98	42	24	30*
			3.92	45	30	24*
			3.89	51	24	30*
Inferior Frontal gyrus	R	15	3.94	45	24	9*
			3.23	51	21	3*
Precentral gyrus	L	17	3.76	-30	-6	48*
			3.47	-21	-9	48*
Superior Frontal gyrus (dmPFC)	R	15	3.73	15	60	24
Anterior Insula	R	15	3.72	33	18	-12*
Middle Occipital gyrus	R	11	3.62	39	-72	24*
Lateral PFC (dlFPC)	R	12	3.50	33	54	9*
Posterior Cingulate cortex	R	13	3.42	9	-27	30*
			3.30	9	-30	24*
			3.30	3	-33	27*
Includers equality > Excluders equality						
No significant activations						

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. * = also significant using FDR correction, $p < .05$, > 10 voxels). dmPFC = Dorsomedial prefrontal cortex; dlPFC = Dorsolateral prefrontal cortex; vlPFC = Ventrolateral prefrontal cortex

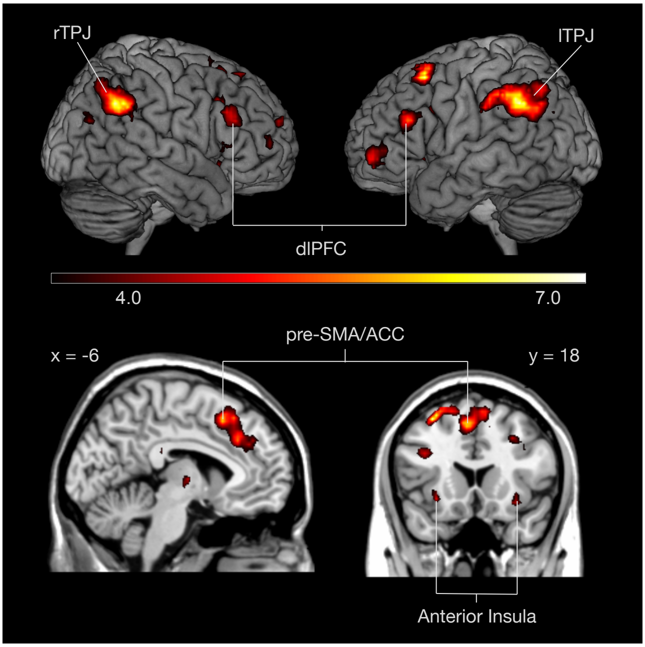


Figure 3.5 *A regression analysis for the 'Excluders equality > Includers equality' contrast with punishment frequency as a regressor resulted in activation in: left and right TPJ (peaks at -51, -48, 36 and 45, -54, 36), dorso- and ventrolateral regions of the PFC (peaks at -30, 51, 0 and 33, 54, 9), pre-SMA/ACC (peaks at -6, 18, 51 and 9, 36, 36) and bilateral AI (peaks at -30, 21, -6 and 33, 18, -12).*

3.4 DISCUSSION

The current fMRI study set out to investigate how experiencing social exclusion relates to subsequent punishment and forgiveness of excluders and the neural correlates of such decisions. We replicated previous findings showing that social exclusion in Cyberball is distressing (van Beest & Williams, 2006; Zadro et al., 2004) and associated with activation in brain regions involved in processing negative affect (sgACC and vACC), emotion regulation (vlPFC) and social evaluation (mPFC) (Eisenberger et al., 2003; Gunther Moor et al., 2012; Sebastian et al., 2011). We extend previous work by showing that participants punished excluders, not only when punishment coincided with monetary gains (Gunther Moor et al., 2012) but also when punishment had no monetary consequences and even when it was costly to punish. This corroborates research showing that people selectively decrease prosocial behavior toward excluders (Maner et al., 2007), possibly to reestablish a sense of control over their social world (Williams, 2007). Through our modification of the Dictator Game, we could distinguish a motivation to reduce the excluders' outcomes from a selfish motivation to maximize one's own outcomes. Although excluders were punished in each condition, punishment was inflicted the most when it resulted in monetary gains and participants punished less when they had to give up money to do so. Taken together, our behavioral findings provide strong evidence for the notion that social exclusion leads to punishment of excluders and that personal outcome maximization plays an important role in these decisions.

Consistent with prior work demonstrating that punishment of unfairness coincides with activity in the pre-SMA/ACC and bilateral AI (Güroğlu et al., 2010; Sanfey et al., 2003), we show that this network is also important for punishing a non-economic norm-violation. In the pre-SMA, we found a dissociation between costly punishment and punishment that resulted in gains or was non-costly. Higher activation in the pre-SMA during costly punishment might suggest increased motor conflict when deciding to punish the excluders compared with forms of punishment that incur no costs or yield gains (Garavan, Ross, Kaufman, & Stein, 2003). Inequality choices were more infrequent than equality choices in the costly inequality condition, which might be related to a possible motor conflict due to a prepotent response of choosing equality (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Nonetheless, after controlling for differences in punishment frequency, the pre-SMA was still more active for costly inequality than the other inequality choices. Future, studies could scrutinize whether choosing costly punishment is indeed associated with increased conflict and what the nature of this possible conflict might be. AI activity did not differ across inequality conditions. Based on the notion that the four forms of inequality reduced the recipients' outcomes, but differed in consequences for self-gain, our results suggest that the AI might not be sensitive to consequences for self-gain when punishing norm-violators (Sanfey et al., 2003) or dividing resources unequally (Corradi-Dell'Acqua, Civai, Rumiati, & Fink, 2013). The pre-SMA/ACC and the AI are part of a network that is important for encoding representations of the physiological state of the body and the integration of cognitive and emotional processes (Chang, Yarkoni, Khaw, & Sanfey, 2013; Singer, Critchley, & Preuschoff, 2009). Activation in this cingulo-insular network has been associated with negative affective states, such as anger (Denson, Pedersen, Ronquillo, & Nandy, 2009) and disgust (Jabbi, Bastiaansen, & Keysers, 2008). The 'Excluders inequality > Excluders equality' contrast did not result in clusters of activation, perhaps because the brain regions associated with punishing the excluders (pre-SMA and AI) were similarly activated during forgiveness. Possibly, increased activation in the pre-SMA/ACC and insula reflects higher levels of negative affect associated with a renewed interaction with the excluders in general, or more specifically with violating a norm of equality in order to punish (Zaki & Mitchell, 2011), which may also be experienced when sharing equally with them. The pre-SMA/ACC–insula network's involvement in deviations from a default response pattern (Güroğlu et al., 2010; van den Bos et al., 2009) was also supported by two findings in this study: (i) participants who punished more often recruited the pre-SMA/ACC and insula when they forgave the excluders and (ii) people who less often opted for costly punishment exhibited greater activation in the pre-SMA and right insula when they chose costly punishment. No activation in reward-related brain regions (e.g. striatum or orbitofrontal cortex) was found when participants punished the excluders, which may be due to methodological differences between our Dictator Game and other punishment paradigms used in previous studies, e.g. classic costly punishment paradigms (Baumgartner et al., 2012; Strobel et al., 2011) or administration of electric shocks to norm-violators (Hein, Silani, Preuschoff, Batson, & Singer, 2010; Singer et al., 2006). People high and low in trait perspective-taking were similarly hurt by exclusion, but people who reported higher levels of perspective-taking skills more often decided to forgive the excluders despite their hurt feelings. Forgiveness, which has been defined as an attempt to preserve the relationship with a norm-violator despite prior inflictions of harm (McCullough, Kurzban, & Tabak, 2013), has been associated with motivational changes, including (i) becoming less motivated to retaliate against a wrongdoer and (ii) becoming more concerned with the wrongdoer's well-being (McCullough, Fincham, & Tsang, 2003; McCullough et al., 1998; McCullough et al., 1997). It is plausible that both of these motivations apply to our behavioral index of forgiveness. Moreover, sharing equally with excluders is likely to result from a non-strategic prosocial motivation, because decisions in the Dictator Game were not confounded by strategic considerations to ultimately maximize personal gains and the amount of money participants gave to the excluders could not be influenced by the excluders (e.g. through rejection or punishment). This, in combination with the positive relationship with perspective-taking, suggests that sharing equally with the excluders is a prosocial tendency, which is likely to reflect an attempt to affiliate with the excluders (McCullough et al., 1997; Molden & Maner, 2013).

It has been argued that the 'perceived likelihood of affiliation' is a critical precondition for initiating efforts at social reconnection based on findings showing that people gave less money to a new interaction partner after being rejected when they expected not to actually meet their new partner face-to-face (Maner et al., 2007; Molden & Maner, 2013). In this study, participants were told that the recipients in the Dictator Game were unfamiliar, anonymous others and that there would be no face-to-face interaction after the experiment. An important consideration for future research is how expectations about future interactions with the excluders might influence forgiveness behavior and its neural correlates.

When participants forgave the excluders, they recruited regions of the 'mentalizing' network, such as the left and right TPJ and the dmPFC and regions involved in cognitive conflict and control, such as the dACC and the lateral PFC. Although activation in the mentalizing network has previously been linked to forgiveness of moral transgressions in hypothetical scenarios (Young & Saxe, 2009), here we show for the first time that bilateral TPJ and dmPFC are activated during actual forgiveness behavior involving real costs and benefits for self and offenders. A positive relationship between punishment frequency and activation in these regions suggests that people who punished more often might engage in increased mental state reasoning Koster-Hale & Saxe, 2013) or perspective taking (Lamm et al., 2007) when forgiving. Forgiving was furthermore associated with activation in brain regions implicated in cognitive conflict and control (dACC and lateral PFC). These regions are activated when people counter their own response tendencies, for instance when they overcome a selfish impulse

(Knoch et al., 2006) or when they share equally with unfair people (Brüne et al., 2013). A role for cognitive control in forgiveness of excluders is in line with recent findings showing that people who performed relatively worse on an external measure of cognitive control were more likely to aggress against excluders than high performers (Chester et al., 2013). Taken together, activation in the mentalizing network and control-related brain regions during equal sharing with excluders suggests that higher demands on mental state reasoning have to be met and that possibly a prepotent response to retaliate has to be controlled in order to forgive excluders.

Several limitations to this study should be noted. First, the amount of trials varied across conditions due to the participants' relatively stable decision-making patterns. Second, although a recent study used a similar operationalization of forgiveness (Brüne et al., 2013), we did not collect self-report measures of trait forgiveness to validate our index of forgiveness. Further research is thus required to validate our measure of forgiveness by linking it to cognitive and motivational aspects associated with forgiveness and to determine in what way our measure reflects an attempt at reaffiliation after being excluded.

Despite these limitations, the current results advance our understanding of the neural correlates of social interactions with excluders. Such insights are of crucial importance to understand how social exclusion exerts its detrimental effect on people's lives. That is, chronic peer rejection has been associated with detrimental consequences for mental health and is further related to lower levels of prosocial behavior (Cillessen & Rose, 2005) and higher levels of aggression (Dodge et al., 2003). Such behavioral problems contribute to a mutually reinforcing pathway between repeated instances of rejection and increasingly more behavioral problems, which might exacerbate the psychosocial problems associated with rejection (Sturaro et al., 2011). Importantly, interventions that train aggressive victims to take their bullies perspective and to forgive them improve behavioral adjustment and psychological well-being (Park, Enright, Essex, Zahn-Waxler, & Klatt, 2013). Ultimately, a mechanistic understanding of the reciprocal relationship between aggressive (e.g. punishing) and prosocial (e.g. forgiving) responses to exclusion and neural and cognitive development has the potential to give us more insights on what might be the best way to act on social exclusion.

3.5 SUPPLEMENTARY MATERIAL

Table S3.1 *Brain regions revealed by whole-brain contrasts during the Cyberball game (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Exclusion no ball > Inclusion ball						
Calcarine gyrus/Cuneus	L	783	5.45	-15	-93	-6*
			4.85	15	-99	6*
			4.69	18	-93	15*
Precuneus/Lingual gyrus	L	85	4.76	-6	-57	12*
			3.45	-15	-63	-6*
Middle Temporal gyrus	L	134	4.42	-51	9	-30*
			4.31	-54	0	-24*
			3.66	-60	-9	-18*
Medial Prefrontal cortex	R	45	3.85	3	45	-15*
			3.47	-12	57	-6*
Subgenual Anterior Cingulate cortex	L	15	3.79	-9	24	-6*
			3.47	0	27	-9*
Lingual gyrus	L	16	3.61	-18	-39	-12*
Positive correlation with need satisfaction after the exclusion game						
Superior Frontal gyrus	L	22	4.37	-18	24	54
Ventral Anterior Cingulate cortex	R	35	4.30	6	42	3
Inferior Frontal gyrus/Anterior Insula	R	19	3.71	45	21	-3
Positive correlation with self-reported perspective-taking skills						
No significant clusters of activation						
Positive correlation with need satisfaction after the exclusion game						
No significant clusters of activation						
Inclusion ball > Exclusion no ball						
Inferior Parietal lobule extending into:	L	5059	6.42	-36	-39	45*
Postcentral gyrus	R		6.33	33	-33	48*

Postcentral gyrus	L		6.32	-33	-33	54*
Middle Temporal gyrus extending into:	L	280	5.06	-45	-66	0*
Middle Occipital gyrus			4.43	-51	-75	0*
			3.70	-33	-99	-6*
Middle Temporal gyrus	R	364	4.87	48	-66	-3*
			4.79	48	-57	3*
			4.42	60	-63	-3*
Insula (mid) extending into:	L	200	4.80	-39	-3	9*
Inferior Frontal gyrus			4.70	-51	9	0*
			4.27	-54	9	21*
Middle Cingulate cortex	L	58	4.76	-12	-24	42*
Cerebellum Crus 1	R	95	4.66	39	-57	-30*
			3.48	51	-57	-33*
			3.26	30	-69	-30*
Inferior Frontal gyrus	R	286	4.60	57	9	9*
			4.38	57	12	21*
			4.37	54	12	-6*
Thalamus	L	27	4.46	-9	-24	6*
			4.02	-12	-12	3*
Middle Occipital gyrus	R	41	4.29	33	-78	30*
Middle Frontal gyrus	L	151	4.14	-36	39	15*
			3.96	-27	36	24*
			3.84	-42	39	27*
Thalamus	R	17	4.08	12	-18	6*
Insula	L	18	4.07	-33	21	6*
Middle Frontal gyrus	R	98	3.98	33	42	36*
			3.70	36	45	24*
Middle Cingulate cortex	R	10	3.69	9	-18	45*
Cerebellum 6	L	27	3.69	-33	-57	-30*
Exclusion no ball > Inclusion no ball						
Caudate	L	11	3.90	-3	12	0
Cuneus	L	25	3.74	-6	-93	15
Middle Cingulate cortex	R	30	3.74	3	-30	21
			3.37	3	-21	33
Lingual gyrus	R	20	3.65	18	-45	-3
Cuneus	R	11	3.41	3	-78	27

Inclusion no ball > Exclusion no ball						
Precuneus	R	174	4.76	12	-66	60*
			4.06	-12	-63	60*
Inferior Parietal Lobule	L	155	4.41	-42	-45	48*
			3.58	-54	-33	48*
			3.46	-27	-45	51*
Superior Temporal gyrus	R	45	4.33	66	-42	12*
			3.83	63	-36	21*
Middle Frontal gyrus	R	79	4.28	30	0	51*
			4.01	30	3	63*
			3.67	33	9	57*
Inferior Frontal gyrus	L	11	4.08	-33	33	9
Middle Temporal gyrus	R	140	4.06	57	-69	0*
			3.88	54	-60	6*
			3.70	45	-63	0*
Inferior Frontal gyrus	R	41	3.87	54	9	21*
Inferior Parietal lobule/	R	69	3.77	42	-42	51*
Superior Parietal lobule			3.58	42	-45	60*
Middle Temporal gyrus	L	58	3.75	-51	-72	9*
			3.63	-42	-66	6*
Superior Frontal gyrus/	L	28	3.65	-24	-9	63
Middle Frontal gyrus			3.59	-30	0	54
Inclusion no ball > Inclusion ball						
Cuneus/Calcarine gyrus	R	333	5.89	18	-102	9*
			3.94	9	-93	30*
			3.64	15	-81	9*
Middle Occipital gyrus	L	208	4.86	-24	-99	15*
			4.60	-15	-96	-9*
			4.43	-18	-105	12*
Middle Temporal gyrus	L	55	4.31	-51	6	-33*
			3.60	-51	-3	-30*
			3.58	-57	-12	-24
Inferior Frontal gyrus	R	21	4.10	42	33	-15*
Inferior Frontal gyrus	L	13	3.87	-39	33	-15
Inclusion ball > Inclusion no ball						
Inferior Parietal lobule extending into:	L	5283	6.59	-42	-30	42*

Supramarginal gyrus/			6.36	-60	-24	42*
Supplementary Motor Area			6.27	-12	-9	66*
Inferior Frontal gyrus extending into:	R	1898	6.02	51	9	0*
Insula	L		5.88	-45	3	-3*
Thalamus	L		5.39	-12	-18	9*
Cerebellum 6	R	219	5.03	33	-60	-27*
			3.59	30	-72	-27*
Inferior Temporal gyrus	R	266	4.91	42	63	-6*
			4.39	39	-54	-3*
Middle Temporal gyrus	R		3.97	51	-54	0*
Cerebellum 6	L	154	4.69	-33	-51	-30*
			4.61	-21	-54	-24*
Middle Occipital gyrus	L	142	4.47	-45	-69	0*
Middle Frontal gyrus	L	75	4.08	-33	39	30*
			3.77	-27	33	30*
			3.37	-39	45	15*
Middle Frontal gyrus	R	76	3.94	33	45	33*
			3.67	39	45	27*
			3.62	33	39	27*
Vermis 4 5	R	20	393	3	-60	-9*
Precuneus	L	46	3.73	-9	-75	42*
Superior Occipital gyrus			3.47	-21	-72	30*
Superior Parietal gyrus			3.14	-18	-66	39*

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.

Table S3.2 *Brain regions revealed by whole-brain analyses testing for sex differences* for the 'Excluders > Includers' contrast in the Dictator Game (all thresholded* p *< .001 uncorrected, > 10 voxels).*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Males ([Excluders – Includers] > Females [Excluders – Includers])						
Middle Temporal gyrus	L	125	4.35	-51	0	-21

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.

*We explored sex differences in all reported whole-brain contrasts. Direct comparisons between males and females on the Cyberball, punishment (Inequality excluders > Equality excluders) and Forgiveness (Equality excluders > Equality includers) contrasts did not result in significant clusters of activation. Also the ROI analysis investigating differences between inequality conditions did not yield sex differences.

Supplementary analysis

Punishment of the excluders in the Dictator Game: time effects

To investigate whether punishment frequency progressively declined during the Dictator Game, we tested whether punishment frequency was lower in the second and third run of the experiment (each run lasted 7.7 minutes). First, a repeated measures ANOVA was performed with inequality condition (5 levels: beneficial inequality, non-costly mild inequality, non-costly severe inequality, costly inequality and prosocial inequality), recipient (2 levels: includers vs. excluders) and run (3 levels: run 1, 2 and 3) as within-subjects factors and the percentage of unequal offers as the dependent variable. This analysis resulted in a main effect of run, $F(2, 50) = 6.56$, $p < .01$, $\eta_p^2 = .21$ and significant interaction effects of run × inequality condition, $F(8,200) = 2.52$, $p < .05$, $\eta_p^2 = .09$ and run × inequality condition × recipient, $F(8,200) = 3.53$, $p < .01$, $\eta_p^2 = .12$.

To further investigate these interaction effects, we ran two follow-up repeated measures ANOVAs for each recipient separately with inequality condition (5 levels) and run (3 levels) as within-subjects factors and the percentage of unequal offers as the dependent variable. For the includers, there was no main effect run ($p = .276$) and no significant run × inequality condition ($p = .173$). For the excluders this analysis yielded both a main effect of run, $F(2, 50) = 6.60$, $p < .01$, $\eta_p^2 = .21$ and a significant interaction effect of run × inequality condition, $F(8,200) = 3.82$, $p < .005$, $\eta_p^2 = .13$. This effect was driven by the costly inequality condition, $F(2,50) = 8.72$, $p < .005$, $\eta_p^2 = .26$, showing that costly Inequality for the excluders was chosen more in the first run (37%) compared to the second (18%; $p < .05$) and third run (17%, $p < .05$), in which costly inequality was chosen at similar rates (*p* = 1). There was no significant main effect of run in the beneficial inequality (*p* = .766), mild non-costly inequality (*p* = .054), severe non-costly inequality (*p* = .057) and prosocial inequality (*p* =.506) conditions (see Supplementary ***Figure S3.1***). Together, these results show that punishment is executed less during the later stages of the experiments when participants have to give up money to punish the excluders.

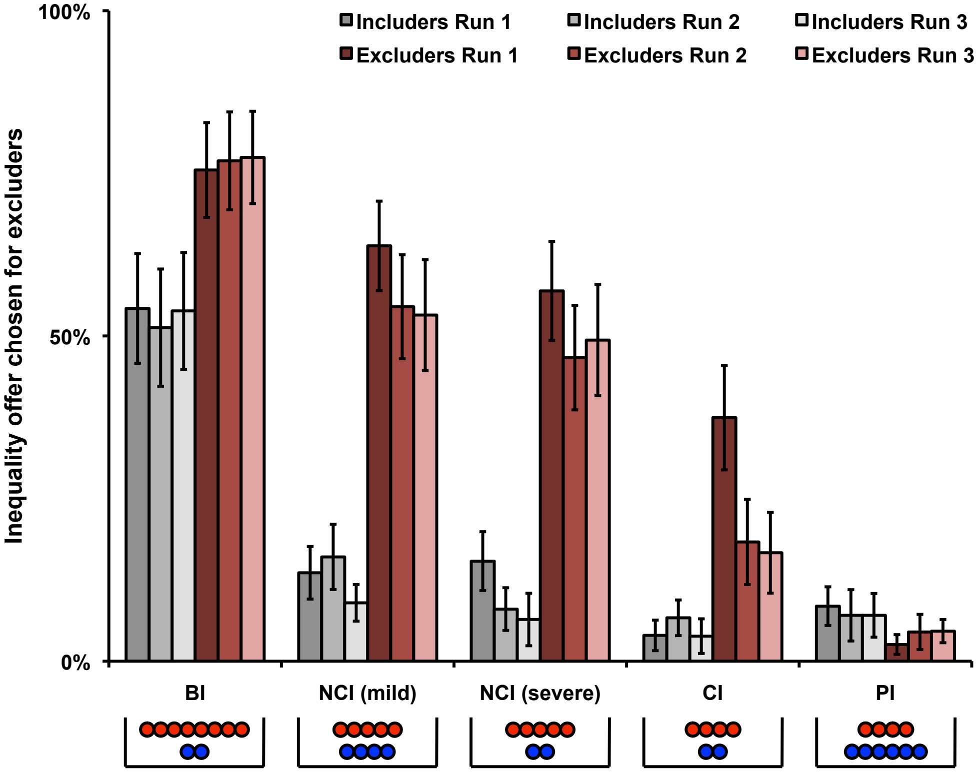


Figure S3.1 *Mean percentages of trials on which participants chose an unequal distribution in each run of the Dictator Game (each run consisted of 60 trials and lasted 7.7 minutes) for players who previously included and excluded them during Cyberball (error bars represent standard errors of the mean). Each form of inequality is displayed on the x-axis (red coins for participants; blue coins for the recipients). Unequal distributions were pitted against an equal distribution of money (5 coins for the participant / 5 coins for the recipient). BI = beneficial inequality; NCI = non-costly inequality; CI = costly inequality; PI = prosocial inequality*

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

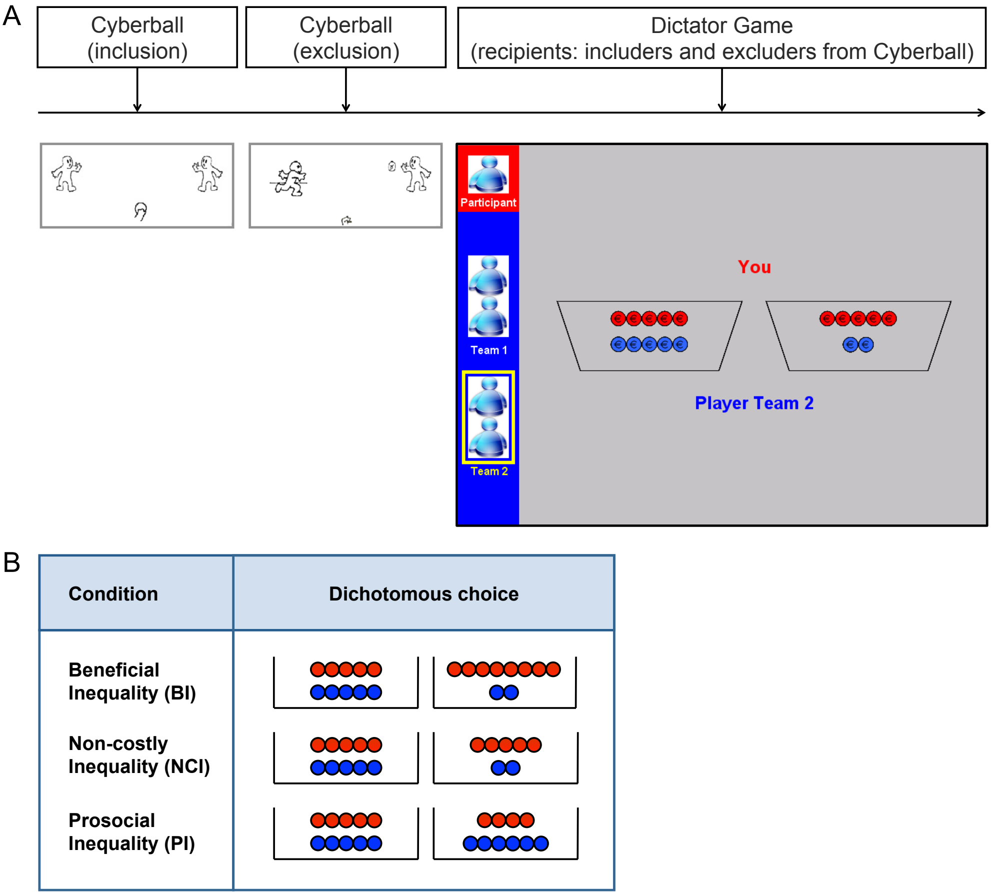


Figure 4.1 *(A) Experimental procedure: Participants carried out the following tasks in the scanner: (i) Cyberball inclusion with two anonymous peers (includers), (ii) Cyberball exclusion by two novel anonymous peers (excluders), and (iii) Dictator game in which participants distributed money between 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***).

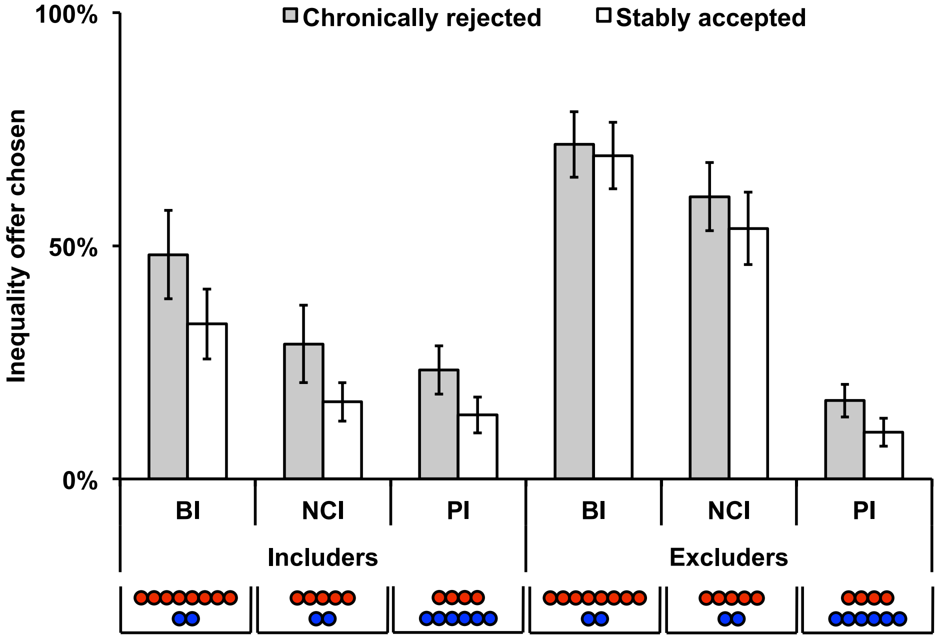


Figure 4.2 *Percentage of inequality offers chosen for includers and excluders in the three inequality conditions of the Dictator Game as a function of prior childhood peer status history. Unequal distributions were pitted against an equal distribution of money (five coins for the participant/five coins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

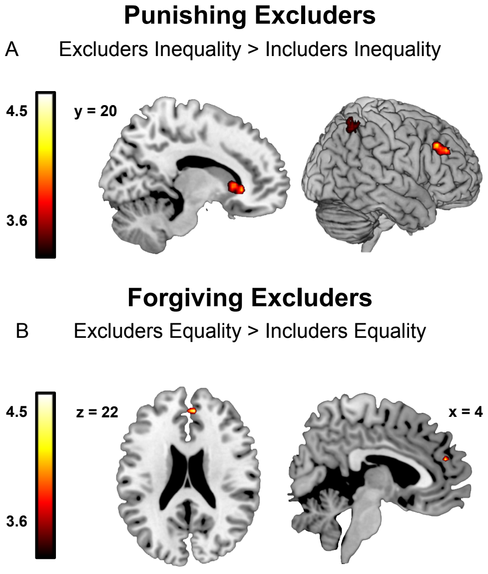


Figure 4.3 *(A) Both groups of adolescents showed increased activity in bilateral ventral striatum (peaks at -12, 20, 7 and 9, 20, 4), right dlPFC (36, 29, 37) and bilateral parietal cortex (peaks at 30, -58, 61 and -45, -45, 52) when punishing the excluders (Excluders inequality > Includers inequality)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

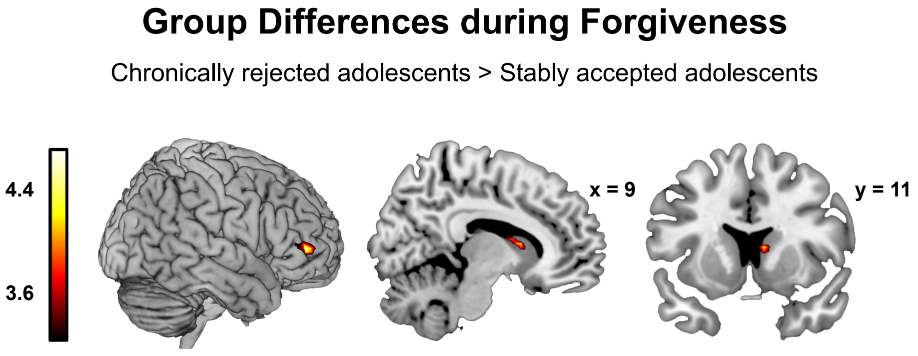


Figure 4.4 *Chronically rejected adolescents showed enhanced activity in lPFC (peak at 36, 44, 4) and dorsal striatum (peak at 9, 11, 10) compared to stably accepted adolescents during forgiveness of excluders. Subject-level contrast values in lPFC were extracted and plotted to facilitate interpretation.*

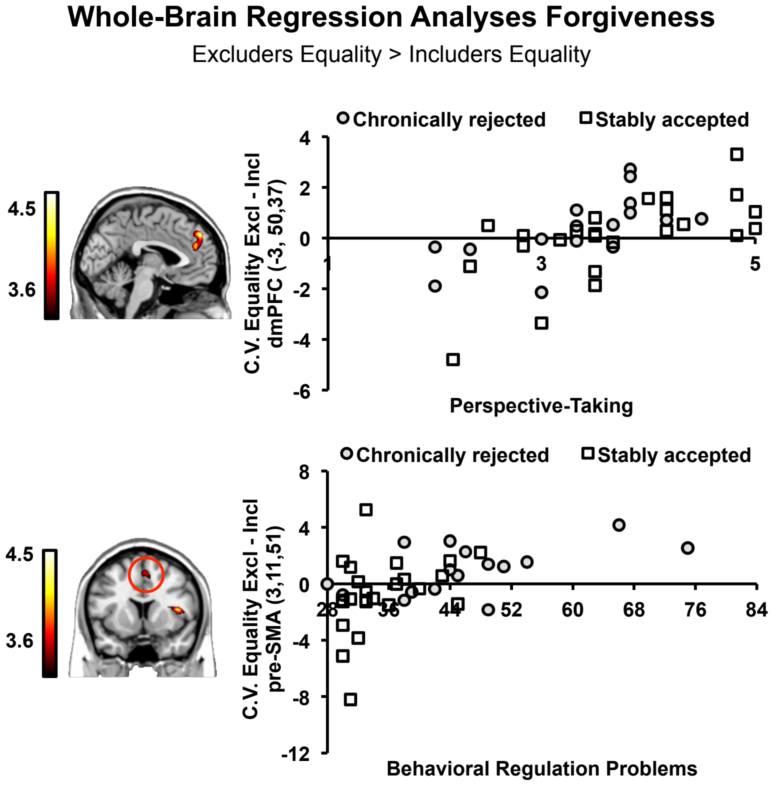


Figure 4.5 *(A) A whole brain regression analysis on the 'Excluders equality > Includers equality' contrast with self-reported perspective-taking skills as a predictor resulted in activation in an overlapping region of dmPFC (peak at -3, 50, 37); (B) A whole brain regression analysis on the 'Excluders 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.

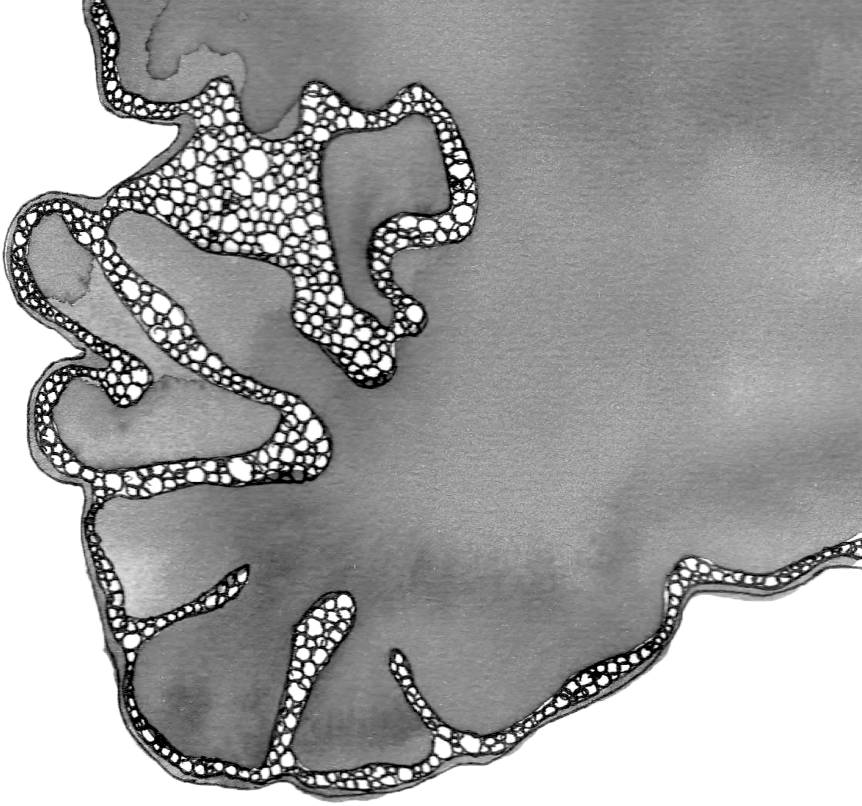
4.5 SUPPLEMENTARY MATERIAL

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*



CHAPTER 5

ACTING ON OBSERVED SOCIAL EXCLUSION: DEVELOPMENTAL PERSPECTIVES ON PUNISHMENT OF EXCLUDERS AND COMPENSATION OF VICTIMS

This chapter is published as:

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ABSTRACT

This study examined punishment of excluders and compensation of victims after observing an instance of social exclusion at various phases of adolescent development. Participants (*n* = 183; age 9 to 22 years) were first included in a virtual ball-tossing game, Cyberball, and then *observed* the exclusion of a peer. Subsequently, they played economic games in which they divided money between themselves and the including players, the excluders, and the victim. The results demonstrate a gradual age-related increase in money given to the victim from age 9 to 22 and a gradual decrease in money allocated to the excluders from age 9 to 16 with an increase in 22-year-olds. Affective perspective-taking predicted both compensation of the victim and punishment of the excluders. Taken together these results show that across adolescence individuals sacrifice an increasingly bigger share of their own resources to punish excluders and to compensate victims and that taking the perspective of the victim enhances these decisions.

5.1 INTRODUCTION

Adolescence is a developmental period characterized by a social reorientation away from primary caregivers and toward the peer group (Brown, 2004). In the transition from childhood to adolescence, youths spend more time with peers and become increasingly concerned about integration within the peer group (O'Brien & Bierman, 1988; Steinberg & Morris, 2001). As concerns about peer acceptance rise, social exclusion becomes a dominant form of peer victimization during early adolescence (Brown, 1990). Social exclusion has been linked to a variety of negative outcomes, such as loneliness, depression, and poor academic achievement (Juvonen, Nishina, & Graham, 2000; Rigby, 2000). Even witnessing peer harassment, including social exclusion, has been associated with negative consequences for psychosocial well-being (Nishina & Juvonen, 2005).

Observing the exclusion of another person elicits negative affect similar to the distress caused by self-experienced exclusion (Masten, Morelli, & Eisenberger, 2011; Wesselmann, Bagg, & Williams, 2009). When people are asked to take the targeted person's perspective and "imagine themselves in their shoes" their own distress is even exacerbated (Wesselmann et al., 2009). People are likely to engage in prosocial acts toward the victim of exclusion, such as such as helping, sharing, and comforting. These behaviors are possibly motivated by an affective response congruent with the perceived distress of the victim (Batson, Early, & Salvarani, 1997). Indeed, increased activation in brain regions sensitive to 'social pain' during the observation of social exclusion has been associated with increased prosocial concern toward the victim, both in adults (Masten et al., 2011b) and in adolescents (Masten, Eisenberger, Pfeifer, & Dapretto, 2010).

Prior research has demonstrated that during adolescence social interactions become progressively more prosocial and that these changes are related to an increased capacity for perspective taking (Eisenberg, Carlo, & Murphy, 1995; Eisenberg, Miller, Shell, McNalley, & Shea, 1991). Core components of perspective taking, such as a 'theory of mind,' mature before adolescence as children acquire the ability to understand that other people's mental states might differ from their own (Wellman, Cross, & Watson, 2001). However, more advanced forms of perspective taking, such as affective perspective-taking, undergo crucial developmental changes during adolescence (Hoffman, 2000; Selman, 1980). Affective perspective-taking can be defined as the ability to put oneself in the shoes of another person in order to infer what the other is feeling without explicit emotional cues. Given the importance of affective perspective-taking for prosocial behavior (Eisenberg, Cumberland, Guthrie, Murphy, & Shepard, 2005), developmental change in understanding the distress in a target of social exclusion would be expected to enhance prosocial responding toward such a victim.

The current study set out to investigate the development of social interactions with victims and initiators of social exclusion (i.e., the excluders) and how these changes are related to developing perspective-taking skills. We hypothesized that developmental changes in perspective-taking skills are related to both increased prosocial behavior toward the victim and decreased prosocial behavior toward the excluders. These questions were addressed using experimental games with real monetary consequences in combination with self-reported *trait* perspective-taking skills and an index of *state* affective perspective-taking.

Economic games and social development

Studies employing economic paradigms, such as the Ultimatum Game (UG), have proven to be effective in examining developmental differences in perspective-taking skills (Güroğlu, van den Bos, & Crone, 2009; Takagishi, Kameshima, Schug, Koizumi, & Yamagishi, 2010). The UG is a simple two-person economic game in which the first player (i.e., the proposer) proposes a division of a certain amount of money (i.e., the stake). The second player (i.e., the responder) can then either accept the proposed split and both players are paid accordingly, or decide to reject the offer which results in neither player receiving anything (Güth, Schmittberger, & Schwarze, 1982). An alternative version of this game is the Dictator Game (DG), in which the second player (i.e., the recipient) does not have the possibility to reject (Forsythe et al., 1994). Offering an equal split in the DG therefore represents costly prosocial behavior, since the allocator sacrifices personal gain in order to share half of the money with the recipient. In the UG, however, offering half of the stake might also reflect strategic fairness, as self-gain is maximized by proposing a fair offer in order to decrease the probability of rejection (Pillutla & Murnighan, 1995).

Basic fairness considerations concerning anonymous others do not undergo considerable developmental changes during adolescence (Güroğlu, et al., 2009). This is reflected by the notion that 9-year-old children's DG offers do not differ from DG offers made by adolescents and adults. However, with increasing age, adolescents typically show more strategic behavior by offering more money in the UG than in the DG (Leman, Keller, Takezawa, & Gummerum, 2009). Based on this notion, a growing body of research has suggested an age-related increase in incorporating the perspective of others in social decision making across adolescence (Güroğlu, et al., 2009; Sutter, 2007; van den Bos, Westenberg, Van Dijk, & Crone, 2010).

Importantly, decisions in these economic games are strongly influenced by prior experiences with, and social knowledge about, the people these games are played with (Delgado, Frank, & Phelps, 2005; Fehr & Fischbacher, 2003). For instance, people differ in their DG allocations toward players who previously included or excluded them (Gunther Moor, et al., 2012). That is, both adolescents and young adults offer an equal split of the stake to players who previously included them in a virtual ball-tossing game, but selectively punish excluders by offering them less than half of the stake. Notably, early- and mid-adolescents have been shown to opt for a more severe punishment than young adults by offering the excluders even less money (Gunther

Moor, et al., 2012). The question then arises whether this propensity to punish excluders develops in a similar manner when participants witness the exclusion of a peer and thus are not a victim themselves (Gunther Moor, et al., 2012).

Previous research has shown that when uninvolved bystanders witness social exclusion from a third-party perspective they direct prosocial behavior toward the victim (Masten et al., 2011b). Furthermore, adults display a tendency for altruistic punishment (i.e., voluntarily incurring costs to punish others who violated social norms), even when they are not part of the interaction themselves (Fehr & Fischbacher, 2004; Fehr & Gächter, 2002). Could there be a similar motivation to punish excluders? And is the willingness to sacrifice rewards in order to compensate victims or to punish excluders the same across development? Acting based on third-party observations of peers' behavior is crucial for the development of adolescents' peer relationships, as they often infer through these observations whether they want to interact with a specific peer. Thus, considering the continued development of perspective-taking skills involved in making such inferences about peers' behavior (Hoffman, 2000; Selman, 1980), we hypothesized that both prosocial behavior displayed toward the victim and third-party punishment of the excluders would differ at various phases of adolescent development.

The present study

The aim of the present study was to investigate developmental differences in interactions with victims and excluders after observing an instance of social exclusion and its relation with perspective taking. Accordingly, participants in distinct phases of adolescent development in the age range of 9–22 years (pre-adolescence to young adulthood) were first included in a virtual ball-tossing game (i.e., Cyberball) and then observed the exclusion of a peer in the same game. Subsequently, they played one-shot versions of two different economic games in which they could divide money between themselves and the including players, the excluders, and the victim from the Cyberball interactions.

The first goal of the study was to examine developmental differences in how another person's prior behavior during an observed episode of social exclusion (i.e., whether he or she was a victim or a perpetrator) impacts prosocial behavior toward these excluders and victims in a DG. DG offers reflect generosity and a preference for fairness, because the recipient has no influence on how the stake is split. Thus, each amount of money transferred to the recipient is a form of costly prosocial behavior.

The second goal was to examine whether individuals are also willing to pay to punish excluders in an Altruistic Punishment/ Compensation Game (APCG; Leliveld, van Dijk, & van Beest, 2012). In this game, participants can either do nothing or invest some money, which is then multiplied by 3 and either added to (compensation) or subtracted from (punishment) the other player's total. In the DG compensation is costly, but punishment (i.e., withholding money) also leads to maximization of one's own outcomes. Furthermore, in the DG, an equal split (5/5) can be offered as a form of compensation but can also be offered to avoid an unequal distribution of money (inequity aversion). In the APCG the least costly option (not investing any points at all) results in an equal allocation. Thus, by employing two different games we aimed to disentangle motivations to punish excluders from selfmaximization (maximizing one's own outcomes) and motivations to compensate the victim from inequity aversion. We predicted that with increasing age, participants would differentiate more between recipients based on prior experiences with these peers. Accordingly, we expected an age-related increase in money allocated to the victim and an age-related decrease in money allocated to the excluders.

The third goal of the current study was to explore the relationship between perspective taking and the age-related changes in these punishment and compensation behaviors. Accordingly, we obtained a self-report measure of the ability to take someone else's perspective (trait) and a state measure of affective perspective-taking, in which participants were probed for inferences about the distress of the victim of exclusion. 'Trait' measures reflect people's stable dispositions that may generalize to different types of situations, but 'state' measures are more directly linked to a specific situation. We predicted age-related increases in both trait perspective-taking and state affective perspective-taking. We expected the latter to result in an increased understanding of the affective state of the victim (e.g., mood) with age, such that older participants were expected to perceive the mood of the victim to be lower than their own mood. Given the positive relationship between prosocial behavior and both dispositional and situationally induced perspective-taking (Eisenberg et al., 2005), we examined how both forms of perspective-taking were related to developmental and individual differences in compensation of the victim and punishment of the excluders.

5.2 METHOD

Participants

One hundred and ninety-two participants were recruited from local schools in urban and suburban areas in the west of the Netherlands. Nine participants (five 9-year-olds and four 11-year-olds) who failed to write down the IDs of the other Cyberball players (which were necessary to identify each player in the economic games) during at least one of the two Cyberball games were excluded from the analyses. The total of 183 participants included in the analyses were subdivided into five age groups: 9-year-olds (*n* = 27, *M* age = 9.0, *SD* = 0.49, 17 girls), 11-year-olds (*n* = 44, *M* age = 10.7, *SD* = 0.70, 21 girls), 14-year-olds (*n* = 46, *M* age = 13.7 years, *SD* = 0.66, 22 girls), 16-year olds (*n* = 42, *M* age = 16.4, *SD* = 0.58, 18 girls) and 22-year-olds (*n* = 24, *M* age = 22.1, *SD* = 2.45, 15 women). Nine and 11-year-olds attended primary schools; 14- and 16-year-old participants attended college-preparatory high schools and the 22-year-olds were college students. Gender distributions did not differ across the five age groups, $\chi^2(4) = 4.2$, $p = .38$. Sixty participants only played the DG and thus 132 participants played the DG and the APCG. The distribution for the participants who also played the APCG into five age groups was as follows: 9-year-olds ($n = 27$, M age = 9.0, SD = 0.49, 17 girls), 11-year-olds ($n = 28$, M age = 11.1, SD = 0.61, 11 girls), 14-year-olds ($n = 23$, M age = 14.1 years, SD = 0.41, 11 girls), 16-year olds ($n = 21$, M age = 16.4, SD = 0.51, 10 girls) and 22-year-olds ($n = 24$, M age = 22.1, SD = 2.45, 15 females). Gender distributions did not differ across the five age groups, $\chi^2(4) = 4.50$, $p = .34$.

No data were collected about the children and adolescents' ethnicity. School records indicated that the ethnic composition was as follows: 60.6% of the children and 42.7% of the adolescents had two parents with a Dutch background, and 39.4% of the children and 56.2% of the adolescents had either one or two parents who belonged to ethnic minorities (e.g., Surinamese, Antillean, Moroccan, Turkish) or were born in another country. The majority of the 22-year-olds (79.2 %) had two Dutch parents; 12.5 % had at least one non-Dutch parent; 8.3% had missing data on ethnicity. No information was collected about the language(s) spoken in the home and family socioeconomic status.

Materials

Cyberball

Participants played a modified version of the virtual ball-tossing game called 'Cyberball' (Williams et al., 2000). At the start of the experiment participants were told that they were about to play an online ball-tossing game with unfamiliar, anonymous peers at another school with whom they were connected through the Internet. In reality, all throws by the other players were preprogrammed. Furthermore, it was explained that all players would receive a point for every time that he or she would catch the ball. Additionally, it was emphasized that points were valuable and would be converted into money, which participants would receive upon completion of the experiment. In order to avoid possible influence of familiarity with the names on decisions in the economic games, players in the Cyberball game were given player IDs (e.g., player 421). Participants carried out the two Cyberball games in a fixed order (i.e., first the 'inclusion condition' followed by the 'observed exclusion condition') based on prior research that employed a within-subject design (Gunther Moor, et al., 2012; Masten et al., 2011b). By doing so, participants had a feeling for how the game worked and were familiarized with the social nature of the game and the possible consequences of exclusion. In the inclusion condition participants played with two players (includers) where each of the three players received the ball an equal number of times (10 out of 30 trials). Participants could throw the ball to either one of the players by a mouse click on the player's ID. Next, participants played the observed exclusion condition during which they witnessed the exclusion of an unfamiliar peer by two novel players (excluders). Both excluders and the excluded player (victim) were novel players with unique player IDs. In this game, the victim received the ball once at the start of the game and did not receive the ball on any of the following 28 trials. Following the standard cover story used in the Cyberball experiments, participants were instructed to imagine what the other players looked like, what kind of personalities they would have and how the game would be played in real life (Williams, 2007). In the current study, to keep the participants further engaged in the task, they were asked to keep track of the number of times each player received the ball during both Cyberball games. They could write down the IDs of each player on a form with a depiction of the characters in the game and score each player's ball possession. The player IDs were of use during the economic games and other questions about the Cyberball players later in the experiment. Participants were omitted from further analyses when they failed to write down these IDs.

Economic games

Following the two games of Cyberball, participants played one-shot version of economic games with each player (i.e., the two includers, two excluders and the victim). Participants were informed that they would be allocators and that the other players would be recipients. It was emphasized that their decisions determined both their own payoffs and those of the recipients. Furthermore, the economic games were introduced as the final games of the experiment. Consequently, it was clear to the participants that their allocations would have no consequences for possible future interactions, and the allocations were therefore not confounded by strategic motivations.

Dictator Game.

In the Dictator Game the participants were asked to divide a set of 10 points between themselves and each recipient. Participants could choose from seven fixed divisions, namely: 10 points for themselves, 0 for the other player (10/0); 8 for themselves, and 2 for the other player (8/2); 6 for themselves, 4 for the other player (6/4); 5 for themselves, 5 for the other player (5/5); 4 for themselves, 6 for the other player (6/4); 2 for themselves, 8 for the other player (2/8); or 0 for themselves, 10 for the other player (0/10). These divisions were depicted by numbers on the computer screen from left to right with the 5/5 option in the middle of the screen.

Altruistic Punishment/Compensation Game.

The Altruistic Punishment/Compensation Game (APCG) is based on classic altruistic punishment studies, where a third-party individual (C) can invest money in order to punish a violator (A) of economic fairness norms in an exchange with B (Fehr & Gächter, 2002). For each point used to punish, A's outcomes are reduced by 3 points. In the modified version introduced by Leliveld et al. (2012), there is also an altruistic compensation condition where participants can choose to compensate the victim of inequality (B) by increasing B's outcomes by 3 points for each point paid. In the current experiment, participants were given 10 points, of which they could invest 0, 1, 2, or 3 points to either compensate or punish each player (the two includers, two excluders and the victim). For each point invested, three points would be either added to (compensation) or subtracted from (punishment) the outcome of the recipient. To make the task clear to participants of all ages and to keep the number of decision-moments to a minimum, participants could choose from seven fixed divisions: three compensation options (7 points for themselves and 19 for the other player [7/19], 8 for themselves and 16 for the other player [8/16], 9 for themselves and 13 for the other player [9/13]), one equitable option (10 for themselves, 10 for the other player [10/10]), and 3 punishment options (9 for themselves and 7 for the other player [9/7], 8 for themselves and 4 for the other player [8/4], or 7 for themselves and 1 for the other player [7/1]). These divisions were depicted by numbers on the computer screen from left to right with the 10/10 option in the middle of the screen.

Mood reports and state affective perspective-taking

Mood ratings were taken at three time points: (i) at baseline prior to playing the first Cyberball game, (ii) after inclusion, and (iii) after the observed exclusion condition. Besides reporting their own mood, participants were asked to give an estimate of the victim's mood. This perceived mood of the victim was used to calculate an index of state affective perspective-taking, defined as the discrimination between mood of the self and perceived mood of the victim (mood self–mood victim). The mood questionnaire consisted of eight mood items (feeling good, bad, happy, sad, relaxed, tense, friendly and unfriendly; see also Gunther Moor, et al., 2012). All of the mood items were rated on a scale from 1 (*not at all*) to 7 (*very much*) and negative mood items (bad, sad, tense, unfriendly) were recoded. Internal consistency of the scale proved to be adequate (Cronbach's α >.69 at each time point). Therefore, all eight items were averaged to calculate a composite score for mood.

Trait perspective-taking

Participants completed the perspective taking subscale (six items) of the Interpersonal Reactivity Index (IRI; Davis, 1983) to assess dispositional perspective taking, i.e., the tendency to adopt another person's point of view (e.g., "I sometimes try to understand my friends better by imagining how things look from their perspective"; "When I get mad at someone, I try to imagine what they might be thinking"). All items were rated on a scale from 1 (*not at all*) to 5 (*very much*). Internal consistency of the subscale was adequate (Cronbach's α = .67) resulting in all six items to be averaged to a composite score of self-reported trait perspective-taking.

Procedure

First, permission was obtained from teachers and school authorities. Next, informed consent was acquired from the parents of all participating children and adolescents. Children and adolescents filled out the perspective taking subscale of the IRI in their classroom, while their teacher and two researchers were present. Subsequently, participants were taken to separate quiet testing rooms in their school where they completed the Cyberball games, mood ratings and economic games on a laptop in approximately 30–45 min. At the end of the experiment, the participants were fully debriefed in their classroom. They were told that total profits in their class ranged from €1.70 - 2.30 and that each participant would be paid €2. Adults were recruited through flyers and the university's course credits system. After signing consent forms, they were tested in separate testing booths in a lab at the university. They were debriefed immediately after the experiment. Finally, adult subjects could opt either for course credit or an endowment of money (€6.50), in addition to the amount they earned during the game. The procedure was approved by the local ethics committee.

Data-analysis

Points that were allocated to the two includers and the two excluders were averaged separately and submitted to a within-subject analysis of point transfer to the includers, excluders and the victim. Since DG and APCG allocations were not distributed normally, the data were analyzed using comparable nonparametric tests as well. These analyses yielded the same results as the parametric tests. In case Mauchly's test indicated that the assumption of sphericity had been violated, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

5.3 RESULTS

Age differences in fairness considerations following observed social exclusion

The first question that was tested was whether fairness considerations toward includers, excluders and the victim differ at various phases of adolescent development. To this end, a repeated measures ANOVA was performed with recipient (3 levels: includers vs. excluders vs. victim) as the within-subjects factor and age group (5 levels: 9-, 11-, 14-, 16- and 22-years) as the between-subjects factor for number of points transferred in the DG. There was a significant main effect of recipient, $F(2, 356) = 48.86, p < .001, \eta_p^2 = .22$, and a significant interaction effect between recipient and age group, $F(8, 356) = 5.04, p < .001, \eta_p^2 = .10$. There was no main effect of age group, $F(4,178) = 1.63, p = .17, \eta_p^2 = .04$.

Post hoc repeated measures ANOVAs were performed for each age group separately to further examine the interaction effect. These analyses demonstrated that there was a significant effect of recipient for 11-, 14-, 16-, and 22-year-olds (all ps $< .01$, all $\eta_p^2 > .14$), but not for 9-year-olds, $F(2, 52) = 1.44, p = .247$, $\eta_p^2 = .05$. These analyses further revealed that: (i) 11-year-olds transferred more points to the victim as opposed to the other recipients (both ps $< .01$), there was no difference between points allocated to the includers and the excluders (p = .17), and (ii) participants in the three older age groups allocated most points to the victim, fewer to the includers and fewest to the excluders (all ps < .05; see ***Figure 5.1***).

Regression analyses with age as a predictor for each recipient separately confirmed that there was an age-related linear increase in points allocated to the victim, $F(1,181) = 6.34$, $p < .05$, $r = .18$, and no age difference in points allocated to the includers, $F(1,181) = 1.63$, $p = .20$, $r = .09$. With respect to the excluders there was no significant linear decrease with age, $F(1,181) = 0.38$, $p = .54$, $r = .05$, but a significant quadratic trend, $F(2,180) = 3.75$, $p < .05$, $r = .20$. Examination of this quadratic trend indicated a gradual decrease in points allocated to the excluders with age across adolescence with a negative peak around age 16, followed by an increase in young adults. Taken together, these findings indicate that with increasing age participants differentiated more between excluders and victims, with includers being in an intermediate position.

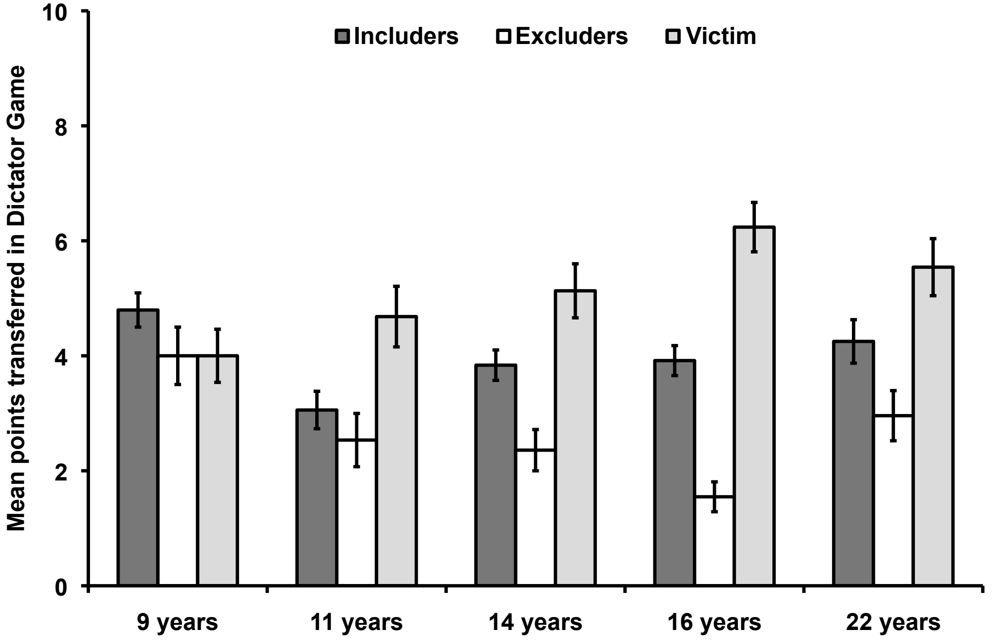

Figure 5.1 *Mean points transferred in the Dictator Game to the three different recipients previously encountered in the Cyberball games displayed for each age group (error bars represent standard errors of the mean).*

Age differences in altruistic punishment of excluders and compensation of the victim

To investigate developmental differences in altruistic punishment of excluders and compensation of victims, a repeated measures ANOVA was performed with recipient (3 levels: includers vs. excluders vs. victim) as the within-subjects factor and age group (5 levels: 9-, 11-, 14-, 16- and 22-years) as the between-subjects factor and the number of points allocated in the APCG as the dependent variable. There was a significant main effect of recipient, $F(2, 236) = 63.04, p < .001, \eta_p^2 = .35$ and a significant interaction effect between recipient and age group, $F(8, 236) = 4.78, p < .001, \eta_p^2 = .14$. There was no main effect of age group, $F(4,118) = 0.46, p = .77, \eta_p^2 = .02$.

Post hoc repeated-measures ANOVAs were performed for each age group separately to further investigate the interaction effect. These analyses demonstrated that there was a significant effect of recipient for all age-groups (all ps $< .05$, all $\eta_p^2 > .12$), except for 11-year-olds, $F(2, 54) = 2.81, p = .087, \eta_p^2 = .09$. These analyses further revealed that: (i) 9-year-old children transferred more points to the victim as opposed to the other recipients (both ps $< .05$), but there was no difference between points awarded to the includers and the excluders ($p = .74$), and (ii) 14-year-olds significantly awarded less points to the excluders ($p < .01$ compared to the includers and victim), but did not significantly differentiate between the victim and the includers ($p = .50$); and iii) participants in the two older age groups granted most points to the victim, fewer to the includers and fewest to the excluders (all ps $< .01$; see ***Figure 5.2***).

Regression analyses with age as a predictor for each recipient separately demonstrated that there were no age-related changes in points granted to the victim and to the includers (all $F(1,121) < 1.98, p > .16$). With respect to the excluders, however, we found a quadratic trend, $F(2,120) = 5.27, p < .01$, which indicated a gradual decrease in the number of points granted to the excluders with age across adolescence with a peak at 16 years, followed by an increase in the young adults.

Mood and state affective perspective-taking

To investigate the influence of observing social exclusion on mood, a repeated measures ANOVA was performed with time point (4 levels: baseline, inclusion, exclusion, and victim) as the within-subjects factor and age group (5 levels: 9-, 11-, 14-, 16- and 22-years) as the between-subjects factor for overall mood scores. There was a significant main effect of time point, $F(3, 531) = 235.81, p < .001, \eta_p^2 = .57$ and a significant interaction effect between time point and age group, $F(12, 531) = 2.43, p < .05, \eta_p^2 = .05$. There was no main effect of age group, $F(4,177) = 1.52, p = .20, \eta_p^2 = .03$.

Post hoc repeated measures ANOVAs showed that there was no significant difference in mood between baseline and inclusion ($p = .14$). However, mood scores significantly dropped following observed exclusion ($p < .001$) and this did not differ between age groups ($p = .87$).

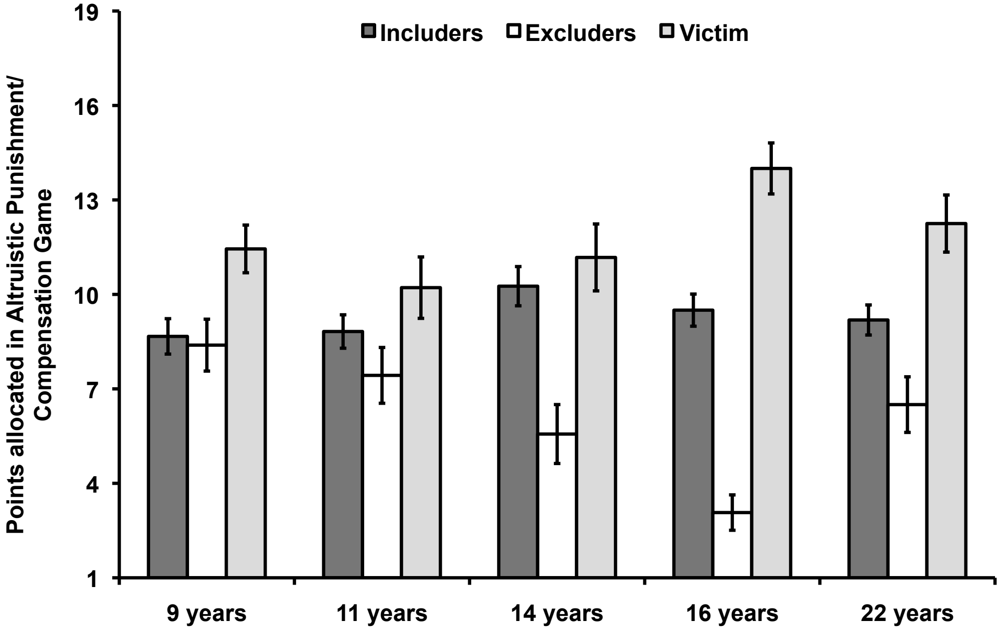

Figure 5.2 *Mean points allocated in the Altruistic Punishment/ Compensation Game to the three different recipients previously encountered in the Cyberball games displayed for each age group (error bars represent standard errors of the mean).*

Thus, participants in each age group reported lower mood after observing the exclusion of a peer. Furthermore, these analyses revealed developmental differences in state affective perspective-taking, such that 9-year-olds did not report a difference between their own mood and the mood of the victim ($p = .32$), while participants of the other age groups perceived the mood of the victim to be lower than their own mood (all ps < .001; see ***Figure 5.3***).

Perspective taking and exchange behavior

The two measures of perspective taking were not significantly correlated, $r = -.07, p = .38$, indicating that these measures reflect independent aspects of perspective-taking skills. The analyses examining the relation between perspective-taking and allocations in the DG toward the victim and the excluder were thus performed separately for our self-report measure of trait perspective-taking and state affective perspective-taking. Affective perspective-taking correlated positively with age ($r = .16, p < .05$). A multiple regression analysis with affective perspective-taking and age as predictors significantly predicted compensation of the victim (DG allocation victim – DG allocation includers), $R^2 = .04, F(2, 179) = 3.95, p < .05$. However, only affective perspective-taking was a significant predictor of compensation of the victim, β =

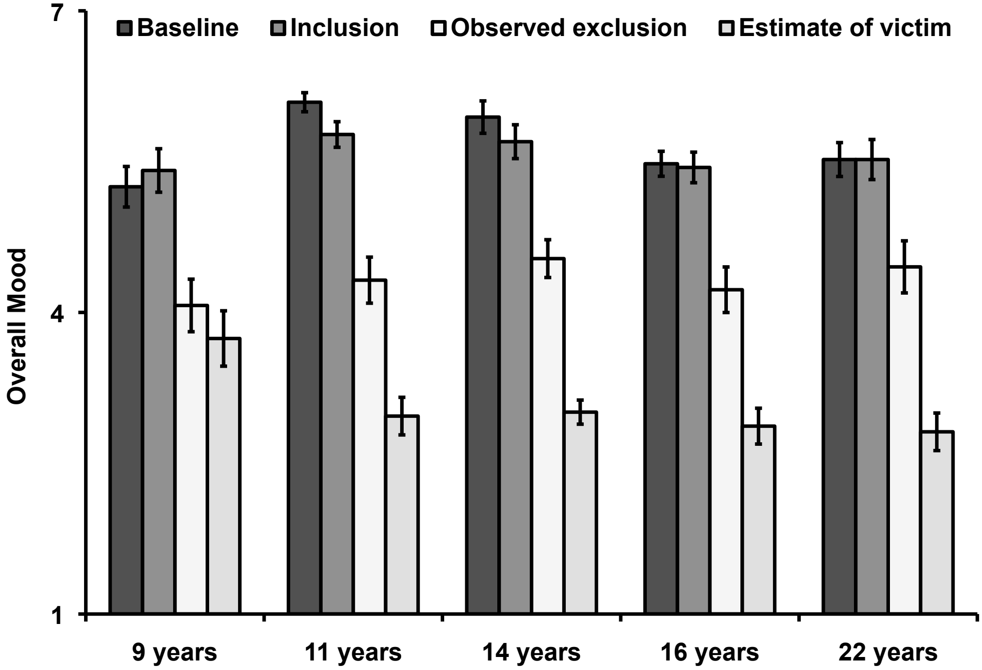

Figure 5.3 *Overall mood ratings for each of the five age groups at different time points: at baseline, after being included, after observing the exclusion of a peer, and a mood estimate for the victim of exclusion (error bars represent standard errors of the mean).*

.166, $t(179) = 2.24, p < .05$, whereas age was not, $\beta = .098$, $t(179) = 1.32, p = .19$. With respect to punishment of the excluders (DG allocation excluders – DG allocation includers) we found a similar effect, $R^2 = .04$, $F(2, 179) = 3.43, p < .05$. Again, age was not a significant predictor, $\beta = - 0.097$, $t(179) = -1.31, p = .19$, but affective perspective-taking was, $\beta = -0.15$, $t(179) = -2.03$, $p < .05$. Thus, individual differences in estimating the mood of the victim to be lower than one's own mood were related to an increase in point transfer in the DG toward the victim and a decrease toward excluders, when controlling for age.

Self-reported trait perspective-taking scores as measured by the IRI subscale also correlated with age ($r = .20, p < .01$). A multiple regression analysis with trait perspective-taking and age as predictors did not predict compensation of the victim (DG allocation victim – DG allocation includers), $R^2 = 0.03$, $F(2, 175) = 2.46, p = .09$. Neither trait perspective-taking, $\beta = -.112$, $t(175) = -1.48$, $p = .14$, nor age, $\beta = .146$, $t(175) = 1.91$, $p = .06$, were significant predictors in this model. Also punishment of the excluders (DG allocation excluders – DG allocation includers) could not be predicted by trait perspective-taking, $R^2 = .02$, $F(2, 175) = 1.48, p = .23$. Again, IRI perspective-taking was not a significant predictor, $\beta = -0.53$, $t(175) = -0.69, p = .49$, and neither was age in this model, $\beta = -0.108$, $t(175) = -1.41$, $p = .16$.

5.4 DISCUSSION

The current study set out to investigate punishment of excluders and compensation of victims after observing an instance of social exclusion at various phases of adolescent development. The results make four significant contributions to the literature on the development of social decision making with peers and perspective taking. First, observers of social exclusion show age-related differential treatment of victims and excluders when making decisions about fairness. Second, altruistic punishment of the excluders displayed a protracted developmental pattern compared to altruistic compensation of the victim. Third, we obtained evidence of developmental differences between late childhood and early adolescence in a state measure of affective perspective-taking, defined as the discrimination between mood of the self and perceived mood of the victim. Fourth, individual differences in affective perspective-taking predicted both more pronounced compensation of the victim and stronger punishment of the excluders.

Fairness considerations following observed social exclusion

The first main finding is that fairness considerations toward victims and excluders differ at various points of adolescent development. With increasing age, participants shared more of their money with the victim and less with the excluders, compared to the includers. This result adds to the growing body of evidence that during adolescence fairness considerations become less strictly egalitarian and progressively more complex. That is, adolescents incorporate gradually more social information when deciding what is fair or not, e.g., their interaction partner's intentionality (Güroğlu, et al., 2009) or individual contributions to a group effort (Almås, Cappelen, Sørensen, & Tungodden, 2010). Furthermore, our results show that 9-year-olds on average shared 40 to 50% of the stake with unfamiliar peers (regardless of the recipient's prior behavior). This supports the notion that a preference for equal outcomes develops as a strong motivator in fairness considerations prior to entering adolescence (Blake & McAuliffe, 2011; Fehr, Bernhard, & Rockenbach, 2008). Further, while treatment of the victim and the excluders differed between age groups, we found no developmental differences in mood levels following observed exclusion. This result suggests a crude automatic affective response to the social exclusion of another person (Wesselmann et al., 2009), which develops before adolescence.

Punishment of excluders and compensation of the victim

While altruistic punishment and compensation have been shown to be crucial for the enforcement of social norms and maintenance of large-scale cooperation (Fehr & Gächter, 2002; Yamagishi, 1986), its developmental trajectory has remained largely overlooked (but see Kenward & Dahl, 2011; Kenward & Östh, 2012). Here, we show that third-party decision making (e.g., altruistic punishment and compensation) in a setting of observed social exclusion differs at various points across adolescent development. Moreover, altruistic punishment and compensation were shown to have differential developmental patterns. With respect to compensation of the victims, the results of the two games show slightly different patterns. In the DG, participants allocated progressively more points to the victim compared to the other players, with increasing age. This suggests an increased concern for the excluded peer and more compensation behavior at the expense of the participants' own gain. However, when comparing the two games, the 9-year-olds displayed more compensation behavior in the APCG than in the DG. It could be that 9-year-olds give more precedence to norms of distributive equality, which is reflected in their sharing of 40% to 50% of the stake with all recipients. Consequently, when offering each recipient an equal split (regardless of prior behavior), compensation of the victim would require offering more than 50% of the stake, which could have been regarded as too generous. In the APCG on the other hand, compensating the victim was less costly (ranging from 10 to 30% of the stake) and yielded a relatively easier way for compensation (as three times the offer was given to the recipient). Thus, the context of the game (i.e., the possible options) may have guided participants to more compensation in the APCG.

The second important issue was whether children and adolescents exhibit third-party punishment of excluders and how this develops across adolescence. Here, we differentiated between beneficial punishment (in the DG) and costly or altruistic punishment (in the APCG). Results from both games in the present study demonstrate the same slower developmental trajectory compared to compensation. Furthermore, analyses also revealed an age-related quadratic trend, showing that adults punished less severely than 16-year-olds. This was not likely due to an age-related increase in self-maximization after age 16, because the quadratic trend was also observed in the DG, where adults allocated more money to the excluders than the adolescents. This corroborates previous findings on a developmental decrease between late adolescence and early adulthood in punishment severity using a DG (Gunther Moor, et al., 2012) and a Costly Punishment Game (van den Bos, van Dijk, & Crone, 2012) when participants are victims of a social norm-violation themselves.

What could account for these developmental declines in punishment severity between late adolescence and young adulthood? First, while the negative affect associated with witnessing social exclusion might be similar for adolescents and adults, adults might punish less severely due to increased levels of emotion regulation. Emotions, such as anger, have been associated with an increased likelihood of altruistic punishment (Seip, Van Dijk, & Rotteveel, 2009) and age-related decreases in costly punishment are mediated by decreases in anger (van den Bos, et al., 2012). Other possibilities include developmental differences in social desirability, involvement in the situation and social norms. It could be that adolescents view social exclusion as a more critical transgression compared to young adults, which in turn demands more rigorous punishment. Indeed, the extent to which adolescents worry about peer acceptance has been found to increase during adolescence and to decline around age 17–18 (Kloep, 1999). Furthermore, adolescents perceive peer evaluations as crucial determinants of self-worth (O'Brien & Bierman, 1988). Nonetheless, this hypersensitivity to rejection in adolescence cannot explain why the 16-year-olds demonstrated more punishment behavior than the 14-year-olds. In future research it will be of considerable interest to examine these different explanations for the developmental trend in punishment following observed exclusion.

Punishment, compensation, and perspective taking

The developmental difference between late childhood and early adolescence in affective perspective-taking is supported by research demonstrating continued development of affective theory of mind during adolescence (Sebastian et al., 2012). Importantly, the index of state affective perspective-taking not only predicted increased prosocial behavior toward the victim but also decreased prosocial behavior toward the excluders. What could account for the result that the state measure of affective perspective-taking is a better predictor of behavior toward excluders and the victim than individual differences in dispositional perspective-taking? Perhaps it is the specific nature of the situation (e.g., social exclusion) that does not elicit prosocial responses in individuals generally high in trait perspective-taking, or conversely, witnessing social exclusion might evoke punishment and compensation behavior also in individuals low in trait perspective taking. Our findings suggest that people not only have to possess the tendency to adopt someone else's point of view, but actually have to infer the affective state of the victim to be lower than their own in order to act more prosocially toward them as a result.

Consequently, we believe that our index of the discrimination between mood of the self and perceived mood of the victim could be a valuable measure for assessing state affective perspectivetaking. By employing a difference score as opposed to merely using perceived mood of the victim we control for personal distress, which might result from the observation of exclusion. Personal distress is a self-oriented aversive emotional response to the apprehension of another person's affective state and has been associated with decreases in prosocial behavior (Decety & Meyer, 2008). Nonetheless, the findings of the current study do not allow us to determine precisely whether the developmental differences in affective perspective-taking are due to an inability to inhibit one's own perspective when asked about another person's perspective or a failure to deduct the victim's distress (Birch & Bloom, 2004; Decety & Meyer, 2008). Future research could address this issue and further investigate the links between this state measure of affective perspective-taking and measures of dispositional perspective-taking.

Limitations

Several limitations to the current study should be considered. First, it could be argued that our study was susceptible to demand characteristics, e.g., an artifact that could make participants aware of the study's goals, which possibly could have influenced their behavior. We aimed to reduce possible consequences of demand characteristics by using economic games to measure social behavior. That is, economic games are anonymous, so concerns about participants presenting themselves as more generous, empathic or moral were likely reduced. Moreover, the participant's decisions had actual consequences for their payoffs.

Second, to make our data comparable to the adult literature on altruistic punishment and compensation, we used a version of Cyberball in which ball possession resulted in receiving points (van Beest & Williams, 2006). Behavior in the economic games thus reflects other-regarding preferences aimed at increasing or decreasing another person's welfare, either motivated by a concern for economic fairness or a pure motivation to compensate or punish. Future research should test whether a study design where exclusion does not have monetary consequences results in different patterns of punishment and compensation behavior.

Third, future studies should examine the developmental trends in punishment and compensation behavior longitudinally using comparable paradigms in order to rule out the role of possible cohort differences and to further study the role of participant characteristics that might be associated with the developmental effects.

Conclusions and future directions

The current findings revealed developmental differences across adolescence in treatment of victims and initiators of social exclusion. With increasing age, adolescents sacrificed an increasingly bigger share of their own resources to compensate victims of social exclusion and to punish excluders. Our results confirm the hypothesis that affective perspective taking is important for acting prosocially in situations where the victim's feelings need to be inferred without explicit emotional cues. Independent of age, people who perceived the mood of the victim to be lower than their own, showed increased prosocial behavior toward the victim and punished the excluders.

To conclude, a better understanding of the development of the cognitive and affective mechanisms underlying social decision-making processes is indispensible for the study of social and moral development across adolescence. While elucidating developmental differences is a crucial first step, future research should investigate individual differences in children and adolescents' reactions to social exclusion and other forms of victimization. Individual differences related to peer status, pubertal development, or rejection sensitivity are highly relevant and might be particularly crucial in identifying those children and adolescents who are at risk for developing psychosocial problems.

PART II

SHARING

CHAPTER 6

A NEUROCOGNITIVE PERSPECTIVE ON THE DEVELOPMENT OF SOCIAL DECISION-MAKING

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ABSTRACT

In this chapter we review evidence for the hypothesis that developmental changes in the abilities to control impulses and to take other people's perspective are crucial in understanding age-related changes in social behavior. Studies that have examined the developmental roots of prosocial behavior and (strategic) fairness using experimental economic games show that other-oriented concern and a preference for fairness emerge early in development. Continued development of intentionality understanding and strategic behavior in bargaining situations suggest that perspective taking and cognitive control undergo extended development and continue to contribute to changes in social behavior well into adolescence. Furthermore, functional developmental neuroimaging studies have shown that these behavioral changes are accompanied by an increased recruitment of brain regions implicated in impulse control (e.g. dorsolateral prefrontal cortex) and perspective taking (e.g. temporo-parietal junction). Together these studies show that developmental changes in impulse control and perspective taking and their underlying neural circuitry are associated with progressively more strategic thinking and an increased incorporation of other's perspectives into social decision-making across development.

6.1 INTRODUCTION

Beginning early in ontogeny humans show levels of sociality that surpass those of other species (Tomasello & Vaish, 2013). For example, 1-year-old toddlers help others to achieve a goal by pointing toward, or picking up, objects that are needed to successfully complete an action without any explicit request or reward (Warneken & Tomasello, 2006). Despite the early emergence of key social tendencies, social behavior continues to develop and grow in complexity across childhood and adolescence. Children expand their behavioral repertoire with social tactics, such as teasing and deception, and they increasingly learn to take other people's feelings into account in their social responses (Burnett & Blakemore, 2009a). For instance, whereas preschoolers mainly use deception to their own benefit, school-aged children increasingly start to use deception to protect other's feelings (e.g. telling 'white lies') (Talwar, Murphy, & Lee, 2007).

Developmental changes in social behavior are thought to be supported by developmental changes in general cognitive functions like impulse control and specific social cognitive functions such as the ability to adopt another person's perspective (e.g. perspective taking). Controlling impulses is of crucial importance for the regulation of social behavior and continues to develop across childhood and adolescence (Davidson, Amso, Anderson, & Diamond, 2006; Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005). Children acquire a core component of perspective taking when they develop an understanding that other people's mental states might differ from their own (Wellman et al., 2001). Even though this 'theory of mind' emerges before adolescence, more advanced forms of perspective taking needed to act on the understanding of other people's mental states continue to develop during adolescence (Dumontheil, Apperly, & Blakemore, 2010; Selman, 1980). This rather protracted development of both impulse control and perspective taking is likely to contribute to developmental changes in social behavior across adolescence and into adulthood. This implication is central in the neurobiological models of social development which posit that continued structural development of the brain is associated with functional changes in brain networks implicated in cognitive control and social cognition, which in turn contribute to developmental changes in social behavior (Blakemore, 2008; Crone & Dahl, 2012; Nelson, Leibenluft, McClure, & Pine, 2005).

In this chapter we review evidence for the hypothesis that the gradual development of impulse control and perspective-taking skills are associated with progressively more strategic thinking and an increased incorporation of other's intentions in social decision-making. In the following sections, we first describe why paradigms from behavioral economics provide valuable tools to study developmental changes in social behavior and its underlying mechanisms (6.2). Subsequently, we describe the age-related behavioral changes in these games (6.3), followed by evidence linking these behavioral changes to children's developing abilities to control selfish impulses and to take other people's perspective (6.4). Next, we focus on functional neuroimaging studies showing that social decision-making in adults relies on separable, but interacting, networks in the brain (6.5). Finally, we review recent neuroimaging studies demonstrating differential development of the brain networks involved in social decision-making (6.6), supporting the proposition that increased intentionality understanding and strategic motivations in social decision-making are associated with developmental changes in these networks.

6.2 WHY USE ECONOMIC GAMES TO STUDY SOCIAL DEVELOPMENT?

To investigate the psychological and neural mechanisms underlying social decision-making, psychologists and neuroscientists have turned to game theoretical paradigms derived from behavioral economics (Rilling & Sanfey, 2011). These paradigms offer a context of social interactions where the decisions people make have actual consequences for their own and their interaction partner's outcomes. Two of these games, namely the Ultimatum Game and the Dictator Game, have proven to be valuable tools to study concerns about fairness. In these two-player exchange games one player (i.e., the proposer) is given a set of valuable rewards, such as money, candy or stickers and is given the opportunity to propose a split of the rewards between themselves and a second player. In the Ultimatum Game the second player (i.e., the responder) can either accept or reject the proposal. If the proposal is accepted, both players receive their part of the stake as proposed. In case of rejection, neither of the players receives anything (Güth et al., 1982). The Dictator Game is different in the sense that the responder (i.e., the recipient in this case) does not have the power to reject the proposal and thus passively receives the amount of rewards that the first player transfers (Forsythe et al., 1994).

Game theoretical models assume that humans are rational decision-makers who act to maximize personal outcomes (Camerer, 2003). Accordingly, game theory predicts that Ultimatum Game proposers would make the smallest offer possible and that responders would accept any offer greater than zero. However, findings show that (adult) proposers and responders do not follow the game theoretical predictions: proposers offer most often an equal split and responders usually reject offers smaller than 20% of the stake (Camerer, 2003). In the Dictator Game, there is no possibility for reciprocation or retribution for the recipient, so game theory would predict that proposers would keep the entire set of rewards to themselves. Interestingly, proposers in the Dictator Game rarely act in accordance with these predictions. Adult humans transfer on average 20 to 30% of the stake to anonymous others with 50% of the stake typically being one of the most frequently occurring offers (Forsythe et al., 1994; Hoffman, Mccabe, Shachat, & Smith, 1994). These deviations from the game theoretical predictions suggest that people not only have an interest in maximizing their own payoffs but also have a concern for the other person's outcomes. Importantly, whereas the positive offers in the Dictator Game reflect other-regarding concern, the comparatively larger offers in the Ultimatum Game suggest that strategic considerations aimed at reducing the possibility of rejection also play a role in decisions about fairness. In addition, the consistently found rejections of unfair Ultimatum Game offers suggest an aversive response to receiving less than the proposer (known as 'disadvantageous inequity aversion') and rejection of the offer possibly provides the responder with a way of correcting such inequity (Fehr & Schmidt, 1999).

Using these games for developmental research offers several advantages (Gummerum, Hanoch, & Keller, 2008). First, an important advantage is that the same paradigm can be used across a wide age range (from children as young as 3 years old to adults), enabling meaningful comparisons between different age groups. Second, the structured nature of the games makes it possible to quantify complex social behavior, which makes them useful for neuroimaging research. Third, these games allow for experimental manipulations where subcomponents of social decision-making, such as understanding another person's intentions and controlling selfish impulses, can be disentangled. Such subcomponents of decision-making might be differentially sensitive to developmental change. For example, emotional reactions to unfairness might mature earlier than an understanding of an interaction partner's intentions, which might depend on slowly developing cognitive functions. Psychological and neural mechanisms underlying such sub processes can further be investigated by relating age-related and age-independent individual differences in behavior and neural activation to external measures of cognitive control (e.g. inhibition tasks) or perspective taking (e.g. theory of mind tasks). By doing so, one can examine how different cognitive functions and their underlying neural substrates are involved in developmental changes in social behavior.

6.3 DEVELOPMENT OF A PREFERENCE FOR FAIRNESS

Concern for another person's wellbeing has strong developmental roots and emerges at very young ages. Twelve- to 18-month old infants willingly engage in instrumental helping of an adult who has dropped (Warneken & Tomasello, 2006) or misplaced (Liszkowski, Carpenter, & Tomasello, 2008) an object that is needed to complete an action and during the second year of life toddlers start to comfort others in distress (Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). Nonetheless, infants and toddlers are much more reluctant to show prosocial behavior when it is costly, i.e. when they have to give up some of their own possessions to benefit another person (Svetlova, Nichols, & Brownell, 2010). Developmental studies employing the Dictator Game have shown that although children tend to keep most of the resources to themselves, the size of their donations increase with age between the ages of 3 and 8 (Benenson, Pascoe, & Radmore, 2007; Blake & Rand, 2010; Smith, Blake, & Harris, 2013) and no longer differs from donations made by adults after age 9 (Gummerum, Keller, Takezawa, & Mata, 2008; Güroğlu et al., 2009; Steinbeis et al., 2012).

Interestingly, this developmental increase in costly sharing is not due to developmental differences in explicit knowledge about what constitutes a fair (i.e., in most cases equal) distribution of resources. Infants as young as 15 months already expect resources to be distributed equally as indicated by prolonged eye gazes in situations when resources are distributed unequally between two recipients compared to situations where both recipients receive an equal amount of resources (Schmidt & Sommerville, 2011; Sloane, Baillargeon, & Premack, 2012). A recent study showed that, although 3 year-olds do not differ from 8-year-olds in their judgments about what constitutes an equal division of rewards, they still tend to keep more than half of the rewards to themselves in a Dictator Game and the willingness to give away half of the rewards increases between the ages of 3 to 8 (Smith et al., 2013). Furthermore, converging evidence from developmental investigations of rejections of unequal distributions confirms that the willingness to incur costs to avoid unequal outcomes ("I'd rather receive nothing than less than the other") increases between age 3 and 8 (Blake & McAuliffe, 2011). Also when distributing resources, 8-year-olds appear not to choose a distribution that favors a peer; even when this has no consequences for their own outcomes (Fehr et al., 2008; Shaw et al., 2013; Shaw & Olson, 2012). Taken together, these findings suggest that a developing sense of fairness makes children increasingly enforce equality when this is costly, but that it does not make them necessarily more generous or tolerant of higher outcomes for a peer.

Investigations of proposer behavior in the Ultimatum Game show that not only a prosocial concern about the other person's profits or equal outcomes plays a role in fairness considerations, but also that strategic considerations aimed at reducing the possibility of rejection come into play. That is, adults tend to offer higher shares of the stake (closer to an equal split of the rewards) when the second player can punish unfair offers (e.g. by rejecting them in an Ultimatum Game) (Fehr & Fischbacher, 2004b; Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007). As such, the difference in Ultimatum Game and Dictator Game offers provides a measure of strategic social behavior. During late childhood (age 7-10), children start making higher Ultimatum Game proposals compared to Dictator Game allocations, but their Ultimatum Game proposals are still smaller than those proposed by adults (Harbaugh, 2003). During adolescence, the difference between Ultimatum Game and Dictator Game offers becomes progressively greater, suggesting a developmental increase in strategic behavior across adolescence (Güroğlu et al., 2009; Leman et al., 2009). The results from these studies also demonstrate that the increasing discrepancy between Ultimatum Game and Dictator Game offers is driven by increasingly higher Ultimatum Game offers and that Dictator Game offers made by children in late childhood do not differ from adult Dictator Game offers (Güroğlu et al., 2009; Steinbeis et al., 2012). Taken together these studies show that a prosocial tendency to share resources with another person emerges early in development, but social behavior seems to become increasingly strategic across childhood and adolescence.

6.4 IMPULSE CONTROL AND PERSPECTIVE TAKING

Strategic bargaining depends on the notion that unfair Ultimatum Game proposals can be punished, while Dictator Game proposals cannot. Recently, it was demonstrated that strategic bargaining assessed as the difference between Ultimatum Game and Dictator Game offers is associated with the developing capacity to control impulses (Steinbeis et al., 2012). The difference between the number of rewards transferred in the Ultimatum Game and in the Dictator Game increased between the ages of 6 and 14 (see ***Figure 6.1A***). Furthermore,

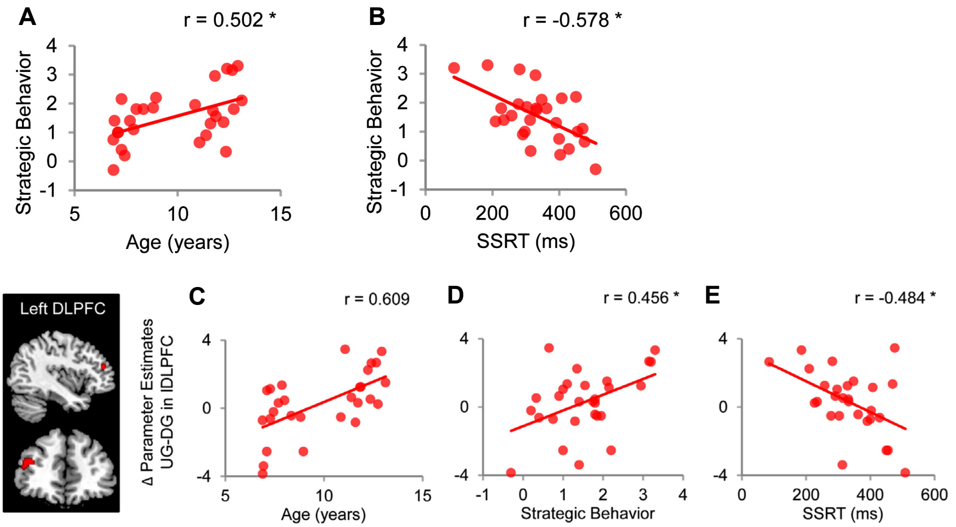

Figure 6.1 *Age-related changes in strategic behavior and recruitment of the left dorsolateral prefrontal cortex (dlPFC): (A) Strategic behavior (Ultimatum Game (UG) proposals – Dictator Game (DG) proposals) increased with age; (B) More strategic behavior was associated with better performance on a measure of impulse control (lower stop-signal reaction times [SSRTs] represent enhanced impulse control); (C) Older children recruited the left dlPFC to a larger extent when making offers in the UG compared to the DG; (D) More strategic behavior was associated with higher activation in left dlPFC when making offers in the UG compared to the DG; (E) Higher levels of impulse control were associated with higher activation levels in left dlPFC when making offers in the UG compared to the DG. Adapted from Steinbeis et al. (2012) reprinted with permission.*

irrespective of age, children and adults who were better at controlling a prepotent motor response in a stop-signal reaction time (SSRT) task, also showed more strategic behavior (see ***Figure 6.1B***). These findings suggest that strategic social behavior relies on the capacity to implement behavioral control over a selfish impulse of keeping all resources to oneself in situations where selfish behavior can be punished.

In addition, it has been argued that proposers have to take the responder's perspective in order to infer what kind of offers is likely to be rejected (Singer, 2006; Singer & Fehr, 2005). Indeed, 4-5 year old children who passed a false-belief task (a task to probe the acquisition of a theory of mind), more often proposed a fair offer in the Ultimatum Game than same-aged peers who failed to pass this task (Takagishi et al., 2010). Furthermore, children with deficits in perspective taking such as children with autism spectrum disorders tend to propose self-serving unfair offers in the Ultimatum Game (Sally & Hill, 2006). Interestingly, a prosocial tendency to share at least some part of one's resources with a peer in a Dictator Game is no different in children with autism spectrum disorders, suggesting that perspective-taking abilities are especially important when social interactions have a strategic component.

Further evidence for a role of perspective taking in decisions about fairness comes from studies that have shown that identical unfair Ultimatum Game offers (in terms of monetary outcomes) are rejected at different rates, depending on the alternative offer that was available to the proposer (Falk, Fehr, & Fischbacher, 2003). Specifically, an unfair offer is less often rejected when the proposer had no better alternative (e.g., a less unfair distribution of the stake) compared to cases where the proposer indeed had a fair alternative to share the stake equally. This suggests that responders not only judge the fairness of an offer by its absolute value or the relative profits in comparison with the proposer's profits, but also in terms of the proposer's intentions behind an unfair offer. Several studies examining developmental differences in responses to unfair Ultimatum Game offers with varying alternative options indeed showed interesting age differences in such intentionality understanding in fairness considerations (Güroğlu et al., 2009; Sutter, 2007). A comparison of four age groups in distinct phases of development (9 year-old pre-adolescents, 12 year-old early adolescents, 15 year-olds mid-adolescents and 18-year-old late adolescents/young adults) showed that rejection rates of an unfair offer where the proposer had no other alternative decreased between the ages of 9 and 18. Furthermore, 9-year-olds rejected monetarily identical unfair offers regardless of whether the proposer had a fair alternative, no alternative or an even more unfair alternative. With increasing age, adolescent proposers and responders flexibly adapted their bargaining behavior in accordance with the alternative that is available to an unfair distribution, suggesting an age-related increase in the incorporation of the proposer's intentionality behind an unfair offer ("it is unfair, but there was no better alternative") into the decision-making process (Güroğlu et al., 2009).

The role of perspective taking in social decision-making has also been investigated using another economic game called the Trust Game (Berg, Dickhaut, & McCabe, 1995). In the Trust Game the first player (the trustor) is given the choice of either splitting the stake with a second player (the trustee) or transferring the entire endowment to the trustee and let the trustee split the stake. When the trustor decides to trust the trustee by transferring everything, the stake is multiplied (usually by 3 or 4). The trustee can reciprocate trust by sharing this higher stake equally, or defect trust and keep all the money. Developmental studies have shown that the frequency of trusting the second player continues to increase during adolescence (Sutter & Kocher, 2007; van den Bos et al., 2010). Furthermore, young adults and older adolescents show higher levels of reciprocity than early adolescents and children (van den Bos et al., 2010). Moreover, these age differences are most pronounced in situations where the trustor takes a larger risk of losing money by trusting the second player (van den Bos et al., 2010). Trust-decisions become riskier when the amount of money that can be lost in case of defection increases. In adults, riskier trust-decisions are met by higher levels of reciprocity, which possibly reflects a recognition of the trustor's positive intentions and an appreciation of the risk the trustor took by investing in the trustee (Malhotra, 2004; Pillutla, Malhotra, & Murnighan, 2003). Van den Bos and colleagues (2010) showed that 9-year-olds did not reciprocate more when the trustor took a larger risk than when he/she took a relatively lower risk. This 'risk-dependent' reciprocity gradually increased across adolescence, again suggesting a continuing increase in the sensitivity to other people's intentions well into adulthood.

Taken together, behavioral studies employing different economic exchange paradigms consistently show that cognitive development related to both impulse control and perspective taking play a crucial role in understanding age-related changes in social behavior. In the following sections, we will review results from neuroimaging studies that provide converging evidence for the role of impulse control and perspective taking in social decision-making.

6.5 NEURAL NETWORKS INVOLVED IN SOCIAL DECISION-MAKING

Neuroimaging studies have elucidated a role for three distinct, but interacting, brain networks in social decision-making: a basic affective network, a cognitive regulatory network, and a mentalizing network (see ***Figure 6.2***) (Rilling & Sanfey, 2011). We will first briefly summarize findings that provide support for the notion that these three networks contribute to social decision-making. Subsequently, we will review the evidence from developmental functional magnetic resonance imaging (fMRI) studies that show that these networks are differentially sensitive to developmental change. Findings from these studies support the hypothesis that asynchronous development of these systems is associated with age-related increases in strategic social behavior and intentionality understanding in social interactions.

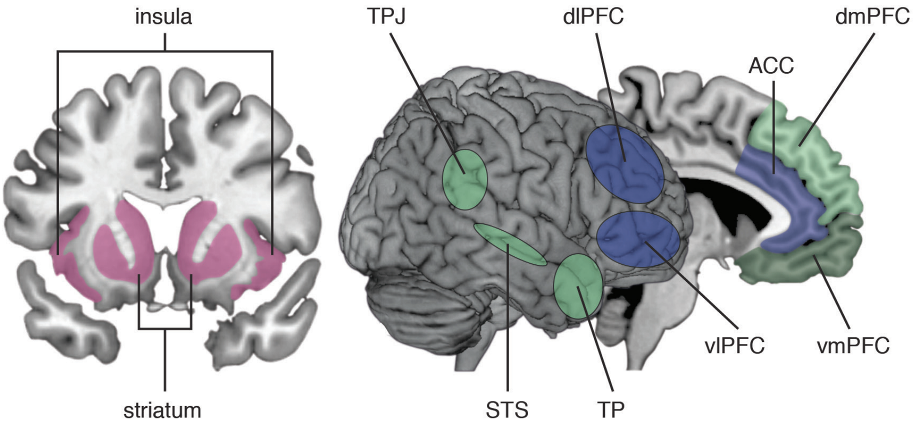

Figure 6.2. *Schematic representation of brain networks involved in social decision-making: basic affective network (pink), cognitive-regulatory network (blue), and mentalizing network (green). TPJ = temporo-parietal junction; STS = Superior Temporal Sulcus; TP = temporal pole; dlPFC = dorsolateral Prefrontal Cortex; vlPFC = ventrolateral Prefrontal Cortex; ACC = Anterior Cingulate Cortex; dmPFC = dorsomedial Prefrontal Cortex; vmPFC = ventromedial Prefrontal Cortex.*

First, neural structures implicated in the processing of basic positive and negative affect, such as the anterior insula (AI) (Sanfey et al., 2003), ventral striatum (Tabibnia, Satpute, & Lieberman, 2008) and the amygdala (Haruno & Frith, 2010) are involved in biasing social decisions, i.e. whether certain social stimuli should be approached (associated with a positive emotional signal) or avoided (associated with a negative emotional signal). For example, increased activation of the AI, a brain region that is involved in encoding representations of the physiological state of the body and negative affect such as disgust, anger and sadness, has been associated with unreciprocated trust (Rilling et al., 2008) and receiving unfair offers in an Ultimatum Game (Sanfey et al., 2003). Interestingly, the AI is activated not only when people receive unfair offers, but also when people observe someone else receiving an unfair offer (Corradi-Dell'Acqua et al., 2013) and when people have to divide resources unequally themselves (Hsu, Anen, & Quartz, 2008). In contrast, activation of the ventral striatum, a region important for processing rewards, has been associated with mutual cooperation in a prisoner's dilemma (Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b) and receiving an equal split of the stake in the Ultimatum Game (Tabibnia et al., 2008). Based on such findings, it has been argued that brain structures involved in basic emotion processing might play a role in signaling pleasantness (ventral striatum) and unpleasantness (AI) of social interactions and consequently might give rise to the maintenance or elimination of such interactions.

Second, brain regions that are involved in the processing of basic positive and negative affect interact with a cognitive regulatory network including the dorsal anterior cingulate cortex (dACC) and regions in the prefrontal cortex (PFC), such as the ventrolateral prefrontal cortex (vlPFC) and the dorsolateral prefrontal cortex (dlPFC) (Rilling & Sanfey, 2011). Activation in this cognitive regulatory network has been associated with cognitive control over selfish impulses and allows individuals to act in a goal-directed manner when there is a conflict between self-interest and social norms (Knoch et al., 2006; Sanfey et al., 2003). For example, activation in lateral regions of the PFC has been associated with strategic bargaining (Spitzer et al., 2007) and temporarily disrupting activity in the dlPFC using repetitive transcranial magnetic stimulation decreases rejection rates of unfair offers in an Ultimatum Game, while leaving explicit fairness judgments unaffected (Knoch et al., 2006). These findings suggest that control-related brain regions are of crucial importance for the regulation of (strategic) social behavior.

Third, when making social decisions, affective and cognitive regulatory regions interact with a third system, namely the mentalizing network. The mentalizing network includes the left and right temporo-parietal junction (TPJ), superior temporal sulci, ventral and dorsal regions of the medial PFC and the temporal poles (Frith & Frith, 2010; Saxe, Carey, & Kanwisher, 2004). Regions in this network are consistently identified in tasks that probe reasoning about other people's mental states (i.e., mental state reasoning or mentalizing), for instance when people have to infer other people's thoughts, beliefs or desires (Blakemore, den Ouden, Choudhury, & Frith, 2007; Saxe & Kanwisher, 2003). Moreover, taking other people's perspective in economic exchange has repeatedly been associated with activation in regions of the mentalizing network, such as the TPJ (Güroğlu et al., 2010) and the dorsomedial PFC (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a; van den Bos et al., 2009).

6.6 UNDERSTANDING CHANGING SOCIAL BEHAVIOR FROM A DEVELOPMENTAL NEUROSCIENCE PERSPECTIVE

Longitudinal research examining changes in brain structure over time has shown that different brain regions reach maturity at different ages (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2003). That is, sensorimotor regions in the occipital and parietal lobes reach maturity first, followed by other parts of the cortex in a posterior to anterior direction. In particular, the dlPFC and the TPJ are among the brain regions latest to fully mature, developing well into early adulthood, which in turn might (partially) explain a similar protracted developmental pattern in their associated functions, such as impulse control (dlFPC) and perspective taking (TPJ). Indeed, models of functional brain development have posited

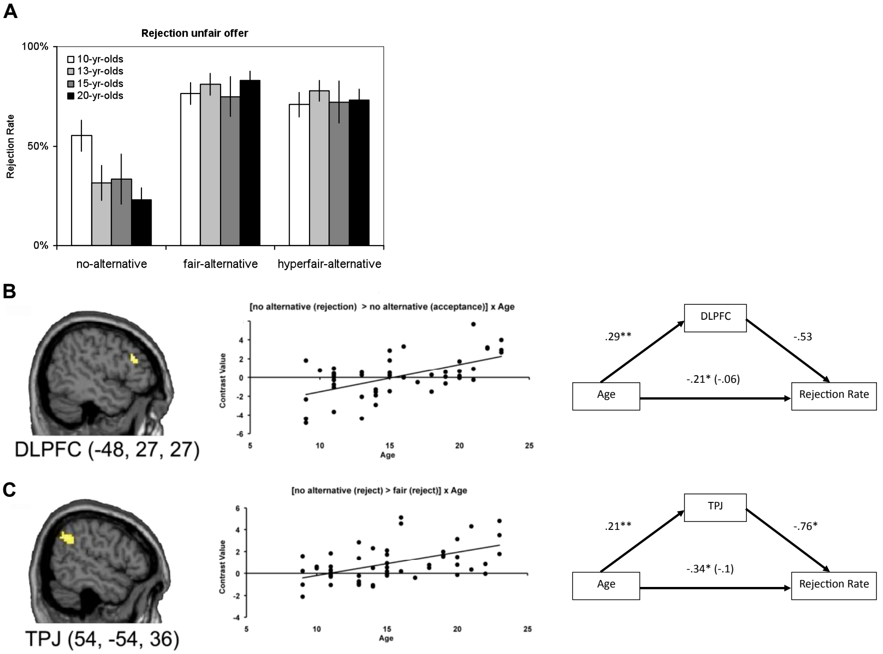

__Figure 6.3__ Age-related changes in intentionality understanding in fairness are mediated by age-related increases in recruitment of the dorsolateral prefrontal cortex (dlPFC) and the temporo-parietal junction (TPJ): (A) Rejection rates of unfair offers when the proposer could not make a fair offer decrease with age; (B) Rejection of unfair offers when the proposer could not make a fair offer is associated with increased recruitment of the dlPFC (B) and TPJ (C); the age-related changes in behavior are mediated by neural activation in these regions. Adapted from Güroğlu et al. (2011) reprinted with permission.

that structural brain development might underlie emerging contributions of late maturing brain networks to social behavior (Blakemore, 2008; Crone & Dahl, 2012). Importantly, whereas affective networks including subcortical brain structures might reach maturity during childhood or puberty, regions of the cognitive regulatory network and the mentalizing network show continued structural changes well into the second and third decades of life (Goddings et al., 2013; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2012). This interplay between structural and functional brain development could underlie a developmental asynchrony between earlier maturing affective reactions to unfairness (associated with activity in basic affective network) and continued development of strategic considerations and intentionality understanding in social decision-making (associated with later maturing cognitive regulatory and mentalizing networks).

To investigate developmental changes in the neural networks involved in fairness-related decision-making Güroğlu and colleagues (2011) examined the neural correlates of intentionality understanding in reactions to unfairness in four phases of development: 10 year-olds, 13 year-olds, 16 year-olds and a young adults aged 20. Their results showed that age was positively associated with TPJ and dlPFC activity when participants were confronted with an unfair offer where the proposer had no alternative to making an unfair offer (see ***Figure 6.3A***). Rejection rates of such unfair offers decreased across adolescence, which again suggests that with age, adolescents become increasingly sensitive to the proposer's intentions behind an unfair proposal. Furthermore, mediation analyses showed that age-related decreases in rejection rates in this 'no alternative' condition were fully mediated by activation in the dlPFC (***Figure 6.3B***) and the TPJ (***Figure 6.3C***). Moreover, no developmental differences were observed in dACC and bilateral AI activation during reactions to unfair proposals. Together these findings suggest that the detection of violations of fairness norms and underlying neural responses in the AI and dACC mature prior to entering adolescence and that the continued development of intentionality understanding in decisions about fairness across adolescence is accompanied an age-related increase in neural activity in brain regions important for perspective taking (i.e., TPJ) and impulse control (i.e., dlPFC).

The importance of the emerging contribution of dlPFC to the development of strategic social behavior was elegantly demonstrated by Steinbeis and colleagues (2012) in a study where they asked children (ages 6-13) to be a proposer in both the Ultimatum Game (where unfair offers can be punished) and a Dictator Game (where there is no sanction to unfair offers). They showed that activity in both left and right dlPFC when making Ultimatum Game proposals compared to Dictator Game proposals correlates positively with two measures of strategic behavior: 1) the difference between Ultimatum Game and Dictator Game offers (***Figure 6.1D***) and 2) the difference between Ultimatum Game offers and the proposers' beliefs about the smallest acceptable offer to the responder. Moreover, they also showed that activity in the left dlPFC when making Ultimatum Game proposals compared to Dictator Game proposals increases between the ages of 6 and 13 (***Figure 6.1C***).

The involvement of brain regions in both the cognitive regulatory network (e.g. dlPFC) and the mentalizing network (e.g. the dorsomedial prefrontal cortex and the TPJ) in perspective taking in social interactions has also been studied using the Trust Game. Neuroimaging studies with adult participants have demonstrated the involvement of the dorsomedial prefrontal cortex (dmPFC) in decisions to trust (Rilling et al., 2004a), as well as in decisions to defect (McCabe, Houser, Ryan, Smith, & Trouard, 2001; van den Bos et al., 2009). Given the importance of the dmPFC in for self-referential thinking (Amodio & Frith, 2006), it has been suggested that these findings reflect an increased attention to one's own outcomes because both decisions involve maximization of payoffs (i.e., trust decisions lead to a multiplication of the stake and defect decisions lead to sure gains). Decisions to trust another person have also been shown to coincide with TPJ activation, which increases with age into adulthood (Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2013). In addition, TPJ activity has also been associated with receiving trust, in particular in situations in which people received trust from a trustor who took a larger risk by trusting them (van den Bos et al., 2009), suggesting that the TPJ is involved in shifting attention to the trustor's perspective when evaluating the risk he/she took.

To investigate the development of the neural correlates of reciprocity and the role of perspective taking herein, van den Bos and colleagues (2011) examined trustee behavior in three different age groups (early adolescents aged 12–14 years; mid adolescents aged 15–17 years; and young adults aged 18–22 years). They showed that receiving trust (compared to receiving no trust) was associated with increased activation in the left TPJ and right dlPFC and that activation in these regions increased linearly with age. Importantly, higher levels of risk taken by the trustor were associated with higher levels of activation of the TPJ and the dlFPC during reciprocity choices. Moreover, they showed that participants of all ages activated the dmPFC during defection, but that early adolescents also activated the dmPFC when they reciprocated trust. This latter result corroborates findings from developmental functional neuroimaging studies that show an age-related decrease in dmPFC activity during mentalizing in theory of mind tasks across adolescence (Blakemore et al., 2007; Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007) and an age-related increase in functional specificity of the TPJ to processing information about people's mental states compared to other forms of social information (Gweon, Dodell-Feder, Bedny, & Saxe, 2012; Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009). It has been suggested that the age-related shift in the relative contributions of the dmPFC and the TPJ to social reasoning might tip early adolescents toward more self-oriented choices (associated with higher mPFC activation) and late adolescents toward more other-oriented choices (associated with higher TPJ activation) (Crone, 2013).

6.7 CONCLUSIONS AND FUTURE DIRECTIONS

In this chapter we reviewed evidence for the notion that the abilities to control impulses and to take others' perspectives when making social decisions undergo extended development, and that these behavioral changes can be traced to brain networks involved in social decision-making developing at different rates. Much of this evidence comes from studies employing experimental paradigms with economic games, which have proven to be valuable tools for studying the development of social behavior and in particular for successfully dissecting sub processes involved in social decision-making. Behavioral studies show that other-oriented concern and a preference for fairness have strong developmental roots. Greater sensitivity to others' intentions and more strategic behavior in bargaining situations provide evidence that continued development in perspective taking and impulse control contribute to changes in social behavior that occur across adolescence. Finally, these behavioral changes are accompanied by an increased recruitment of regions involved in impulse control (e.g. dlPFC) and perspective taking (e.g. TPJ) in decisions where perspectives of interaction partners have to be effectively weighed against self-interest and social norms.

While elucidating developmental differences in recruitment of the dlPFC and TPJ and their involvement in social decision-making is a crucial first step, many fundamental questions remain unanswered. First, it is important not only to understand how the different brain regions (such as the TPJ or the dlPFC) are differentially recruited across development, but also how these regions interact and communicate with one another. For example, increased functional connectivity between regions of the mentalizing network (e.g. pSTS/TPJ) and brain structures implicated in the computation of reward (e.g. ventral MPFC) has been associated with higher levels of prosocial behavior in adults (Hare, Camerer, Knoepfle, & Rangel, 2010). Functional connectivity in the cognitive regulatory network (Fair et al., 2008) and the mentalizing network (Burnett & Blakemore, 2009b; Klapwijk et al., 2013) changes across adolescence, suggesting that developmental changes in functional connectivity may further contribute to changes in social behavior.

Second, the majority of developmental functional neuroimaging studies are based on cross-sectional data sets with participants of different ages. Although cross-sectional studies are an excellent first step to demonstrate developmental *differences*, there is a great need for longitudinal studies of social brain development. Longitudinal designs rule out the role of possible cohort differences and can give us insight on actual developmental *changes* within participants. One of the major questions in the field of developmental neuroimaging centers around the specific contributions of maturational processes relative to environmental or societal influences on the development of (social) behavior. For example, children who are accepted by their peers during childhood express higher levels of prosocial behavior and show advanced development of empathy and theory of mind compared to children who are rejected by their peers (Slaughter et al., 2002). Longitudinal studies can provide insights on how developmental trajectories of individual characteristics (such as long-term peer acceptance or rejection by peers) are related to social cognitive development and how they relate to developmental trajectories of both brain structure and function. An increased understanding of this intricate interplay between a dynamic social context and a maturing brain will be crucial for developing interventions that can help children and adolescents in navigating their increasingly complex social worlds.

CHAPTER 7

NEURAL CORRELATES OF ADVANTAGEOUS AND DISADVANTAGEOUS INEQUITY IN SHARING DECISIONS

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ABSTRACT

Humans have a strong preference for fair distributions of resources. Neuroimaging studies have shown that being treated unfairly coincides with activation in brain regions involved in signaling conflict and negative affect. Less is known about neural responses involved in violating a fairness norm ourselves. Here, we investigated the neural patterns associated with inequity, where participants were asked to choose between an equal split of money and an unequal split that could either maximize their own (advantageous inequity) or another person's (disadvantageous inequity) earnings. Choosing to divide money unequally, irrespective who benefited from the unequal distribution, was associated with activity in the dorsal anterior cingulate cortex, anterior insula and the dorsolateral prefrontal cortex. Inequity choices that maximized another person's profits were further associated with activity in the ventral striatum and ventromedial prefrontal cortex. Taken together, our findings show evidence of a common neural pattern associated with both advantageous and disadvantageous inequity in sharing decisions and additional recruitment of neural circuitry previously linked to the computation of subjective value and reward when violating a fairness norm at the benefit of someone else.

7.1 INTRODUCTION

Although economic models assume that the maximization of personal gains is the main motivation when distributing resources, investigations of actual decision-making have shown that fairness concerns play an important role in social interactions (Fehr & Schmidt, 1999). Indeed, the evidence is overwhelming: people have a preference for fair outcomes and, all else being equal, acting fairly is generally the expected social norm (Fehr & Fischbacher, 2004a; ; Henrich et al., 2005; Kahneman, Knetsch, & Thaler, 1986; Tabibnia & Lieberman, 2007) and equality is often used as a cognitive heuristic in decision-making (Civai, Rumiati, & Rustichini, 2013). In search of proximate mechanisms it has been shown that equal distributions are perceived as rewarding, both indicated by self-reported ratings of fair divisions of resources as well as reward-related neural activation patterns associated with these choices (Tabibnia, Satpute, & Lieberman, 2008; Tricomi, Rangel, Camerer, & O'Doherty, 2010; Turillo, Folger, Lavelle, Umphress, & Gee, 2002). Further, being treated unfairly leads to anger (Srivastava, Espinoza, & Fedorikhin, 2009) and has been associated with activation of neural networks involved in conflict and negative affect (Güroğlu, van den Bos, Rombouts, & Crone, 2010; Güroğlu, van den Bos, van Dijk, Rombouts & Crone, 2011, Sanfey et al., 2003). Finally, when confronted with unfair treatment and given the power to retaliate, people generally reject inequitable distributions of resources, even when this is costly for them (Fehr & Schmidt, 1999; Güth et al., 1982; Straub & Murnighan, 1995).

Despite this strong preference for equity and the aversion toward inequity, people often make inequity choices, such as when inequity is more advantageous for the self. For example, people aim to increase relative advantage over others (Fehr & Schmidt, 1999) and when a high social position is experimentally induced they become more selfish and display higher levels of immoral behavior, such as cheating and lying (Piff, Stancato, Côté, Mendoza-Denton, & Keltner, 2012). It is thus crucial to gain a better understanding of the neural mechanisms underlying inequity decisions in order to better understand when and why we decide to divide resources in an unequal fashion. The current study aimed to investigate the neural responses associated with inequity in sharing decisions when maximization of outcomes for the self or another person is in conflict with the equity norm.

Using allocation tasks such as the 'Dictator Game' where participants divide a certain amount of rewards (i.e., the stake) between themselves and another player without sanctions or reputation-related consequences, many studies have shown that people often give away a nontrivial amount of the stake to anonymous others, with an equitable 50-50 split being the most frequent allocation (Camerer & Thaler, 1995; Fehr et al., 2008; Fehr & Gächter, 2002; Forsythe et al., 1994; Raihani & McAuliffe, 2012). Nonetheless, such a preference for fairness is highly sensitive to different aspects of the (social) context in which they occur (Bardsley, 2008; Fehr et al., 2008; Güroğlu, van den Bos, & Crone, 2009; Koch & Normann, 2008; Steinbeis

& Singer, 2013). For example, a preference for equity decreases when the costs of establishing equal outcomes increase, supporting the crucial role of self-outcome maximization in fairness considerations. Furthermore, people seem to be less tolerant to receiving less than other people (i.e., disadvantageous inequity) compared to receiving more than others (i.e., advantageous inequity) (Fehr et al., 2008; Fehr & Gächter, 2002; Güroğlu et al., 2010; Güroğlu et al., 2011; Blake & McAuliffe, 2011). In other words, fairness considerations are not solely shaped by other-regarding preferences and prosocial intentions, but also by self-outcome maximization and aversion to disadvantageous inequity (Güroğlu et al., 2009; Steinbeis & Singer, 2013).

Studies investigating the neural mechanisms associated with inequity have predominantly focused on the perception and receipt of unfair treatment (Corradi-Dell'Acqua et al., 2013; Güroğlu et al., 2010; Güroğlu et al., 2011; Sanfey et al., 2003; Tabibnia et al., 2008; Wright et al., 2011). These studies have consistently shown involvement of the dorsal anterior cingulate cortex (dACC) and the anterior insula (AI) in perceiving unfairness. Interestingly, studies have shown heightened AI activity when people themselves are the target of unfair treatment (Sanfey et al., 2003) and when they see someone else receiving an unfair offer (Corradi-Dell'Acqua et al., 2013). Based on the AI's domain general role in providing anticipatory emotional signals in decision-making (Dosenbach et al., 2006; Kuhnen & Knutson, 2005) and the dACC and AI's involvement in neural representations of bodily arousal states (Craig, 2003; Critchley, 2005), it has been argued that the dACC and AI play an important role in guiding our social behavior to follow social norms (Rilling & sanfey, 2011). Behaviors in response to unfairness have been consistently associated with activation in the dorsolateral prefrontal cortex (dlPFC), which has been suggested to reflect increased regulation of a default prepotent reaction to unfair offers (Güroğlu et al., 2010; Knoch, Gianotti, Baumgartner, & Fehr, 2010; Knoch et al., 2007; Knoch et al., 2006; Spitzer et al., 2007; Steinbeis et al., 2012; van't Wout, Kahn, Sanfey, & Aleman, 2005; Wright et al., 2011). Although these findings overall support the idea that equity is perceived as a social norm, fewer studies have investigated how neural responses to unfairness might be different when making inequity decisions. Two studies investigating allocation of resources to others who had previously excluded the participants from a social interaction have shown the involvement of the dACC – AI network when sharing unequally with those excluders (Gunther Moor et al., 2012; Will et al., 2014). In the current study, we aimed to investigate whether inequity choices are processed differently than equity choices and how this depends on the benefit for the self and the other. For this purpose, we investigated inequity choices in different experimental conditions that aimed to disentangle inequity that is advantageous for the self from inequity that is advantageous for another person (while leaving the decision-maker's own outcome unaffected).

First, based on previous findings, we expected higher AI and dACC activity when making inequity choices in general (Hsu, Anen, & Quartz, 2008; Zaki & Mitchell, 2011). A central question was whether the AI and dACC response subseries a general role through acting as a 'social alarm system' that is activated in response to both advantageous and disadvantageous inequity, i.e. regardless of whether the participants themselves or another person benefits from the inequity. If equity were perceived as the social norm, we would expect higher levels of AI and dACC activity in making inequity choices across different conditions that differ in relative outcomes for self and other. However, if other-regarding (prosocial) outcomes were perceived as the social norm, we would expect increased levels of activation in this network when making choices that ensure equity, but also lead to less optimal outcomes for others.

Second, we tested the hypothesis that inequity choices that lead to benefit of others is associated with activation in neural circuitry previously linked to reward-processing. This hypothesis is based on prior studies wherein participants were the allocators of resources and that showed that neural regions implicated in the computation of subjective value and reward play an important role in resource distribution (Hsu et al., 2008; Zaki & Mitchell, 2011). Although the paradigms used in these studies differed considerably, these prior studies showed that reward-related brains regions (e.g. the striatum and ventromedial PFC [vmPFC]) were associated with choosing outcomes that maximized the amount of joint resources. However, paradigms in these studies did not investigate two core processes of fairness considerations, namely, choices that incur costs to the self (Hsu et al., 2008) and a fair alternative to making inequity choices (Zaki & Mitchell, 2011). In the current study, we included similar experimental conditions that involved a fair alternative to inequity and that also differed in respective possible costs and benefits for the self and the other. We expected that choices indicating other-regarding preferences through a maximization of the other's outcomes would result in increased activation in reward-related brain regions, such as the striatum and the vmPFC.

7.2 METHODS

Participants and procedure

Twenty-eight young adults (*M* = 20.7 years, *SD* = 1.91; 11 male) were recruited through local advertisements. All participants were right-handed and did not report any contraindications for fMRI. Before scanning participants were familiarized with the scanner environment using a mock scanner. After scanning, they filled out a battery of questionnaires, and received €25 for their participation and an additional amount of money, which was told to be determined by their decisions in the allocation games. In reality everyone received an additional €2. The current study was conducted in accordance with the ethical standards of the American Psychological Association as expressed in the Declaration of Helsinki. All participants provided written informed consent for the study. The study was approved by the Leiden University Medical Center (LUMC) ethics committee. A radiologist reviewed all anatomical scans; no anomalies were reported.

fMRI task description

Participants played the role of the allocator in a set of three modified dictator games (Fehr et al., 2008). In each game the participants were asked to distribute coins between themselves and an anonymous other player based on preset dichotomous choices. One of the two options was always a fair (equal) distribution of coins, i.e. one coin for the self and one coin for the other (1/1). The alternative distribution in the three games were as follows: (i) one coin for the self and zero coins for the other (i.e., 1/0) in the advantageous competitive inequity game, where the inequity choice maximized the difference between self and other without gains relative to the equity choice, (ii) two coins for the self and zero coins for the other (i.e., 2/0) in the advantageous self-maximizing inequity game, where the inequity choice maximized outcomes for the self, and (iii) one coin for the self and two coins for the other (i.e., 1/2) in the disadvantageous prosocial inequity game, where the inequity choice signified other-regarding (i.e., prosocial) concerns.

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/). On the left hand side of this screen, participants were also presented with the name of the other player (see ***Figure 7.1A***). This was followed by the decision screen where participants were presented with two distributions (i.e., two buckets with coins in them) they could choose between. In each distribution coins for the self were indicated in red and coins for the other were indicated in blue. Participants had 4000ms to make a choice. Upon making a choice, the bucket of their choice was encircled in red and this was displayed until the end of 5000 ms in total. In case of no response within the 4000 ms period, participants were presented a screen with "Too late!" for the duration of 1000 ms. Trials without a response consisted of less than 1% of all trials and were excluded from further analyses. Prior to scanning participants were provided with instructions (see Supplementary material) and practiced the game (6 trials) on a computer. During the scanning session participants played a total of 60 trials, with 20 trials of each game, in randomized order. The location of the equal distribution was counterbalanced across trials. All trials were presented in one block lasting about 8 minutes.

On each trial, the first name and the first letter of the surname of both the participant and the recipient were displayed on screen to ensure anonymity, but also to emphasize the notion that participants would play each trial with a new player (see ***Figure 7.1A***). Participants were told that random trials would be selected and their choices on these trials would determine their final earnings in the task. Prior to the experiment, participants were explained that the recipients were participants in the study and it was also emphasized that their decisions would have consequences for the other players' earnings. None of the participants reported disbelief in the cover story that their offers influenced other players' outcomes.

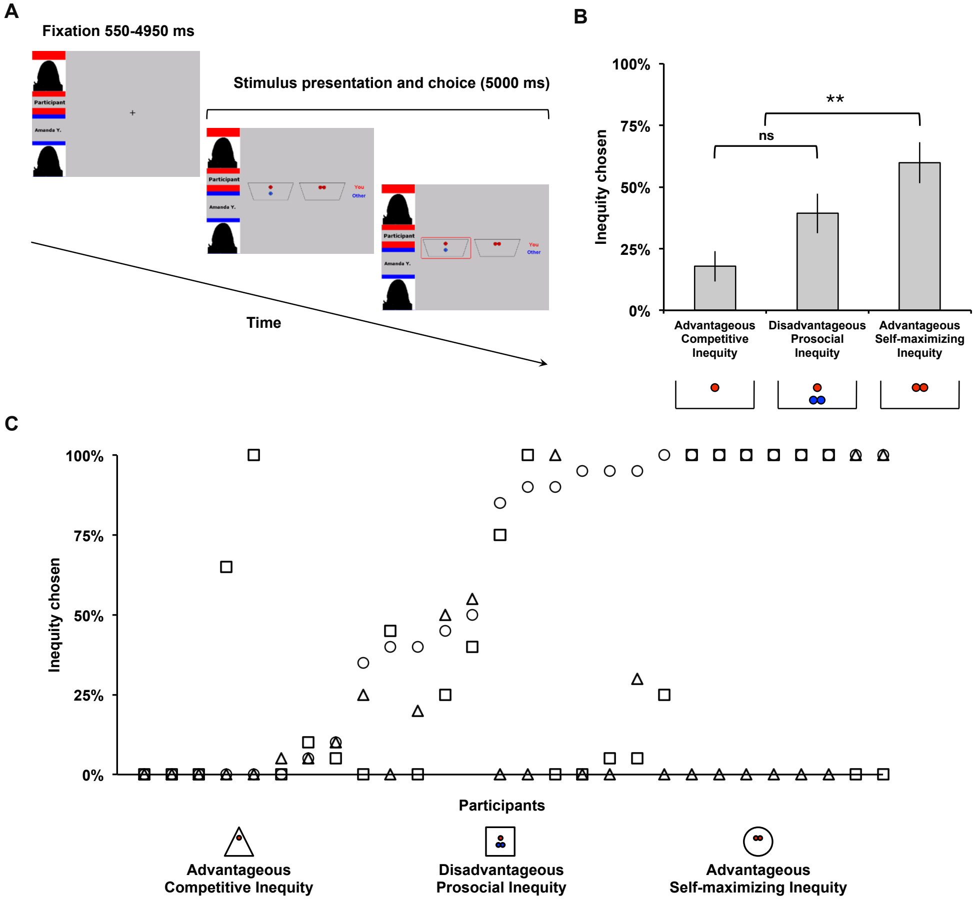

Figure 7.1 *Visual display of the fMRI task and frequency of inequity choices. (A) Visual display of events presented in the one trial of the fMRI task. Each trial started with a jittered fixation cross lasting 550-4950 ms. The following screen displayed the name of the participant in red (here 'Participant') and the name of the recipient (here 'Amanda Y.'). This screen also presented the available choice options for distributing the coins (here advantageous self-maximizing inequity game; 1/1 vs 2/0) with red and blue coins indicating the share for the participant and the recipient, respectively. The participant had a maximum response time of 4000ms to make a choice. Upon response, the chosen distribution was encircled in red (here 1/1) until the end of the 5000 ms. (B) Percentage of inequity choices made in each of the three games.* $^{**}p < .001$, $^{*}p < .05$. *(C) Percentage of inequity choices made by each participant in each of the three games.*

fMRI data acquisition

Scanning was carried out at the University Medical Centre using a 3.0 T Philips Achieva. The scanning procedure included: (i) a localizer scan, (ii) T2*-weighted whole-brain echo planar images (EPI) measuring the bold-oxygen-level-dependent (BOLD) signal (TR = 2.2 s, TE = 30 ms, slice matrix = 80 × 80, slice thickness = 2.75 ms, slice gap = 0.28 mm, field of view (FOV) = 220 mm), (iii) high-resolution T1- and T2- weighted matched bandwidth anatomical images with the same slice prescriptions as the EPIs. Functional data were acquired in a single functional run of 210 volumes; the first two volumes were discarded to allow for equilibration of T1 saturation effects. The task was programmed in E-prime and was projected onto a screen that was viewed through a mirror fastened upon the head coil assembly. Head movement was restricted by the use of foam inserts around the head.

fMRI data analysis

Image pre-processing and analysis was conducted using SPM8 software (Wellcome Trust Centre for Neuroimaging, University College London). Pre-processing included slice-time correction, realignment, spatial normalization to EPI templates, and smoothing with a Gaussian filter of 8 mm full-width at half maximum. Movement parameters in all directions were below 1.08 mm for all participants and all scans. The fMRI time series were modeled by a series of events convolved with a canonical hemodynamic response function (HRF). The data were modeled at stimulus onset of the decision screen with zero duration and based on the game (3 levels: advantageous competitive inequity, advantageous self-maximizing inequity and disadvantageous prosocial inequity) and participant's choice (2 levels: equity or inequity), resulting in a 3 × 2 full factorial model that included six regressors. 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 repeated measures ANOVA. The full-factorial ANOVA has an unbalanced design because not all participants made all choices and thus the number of observations included in each cell of the design differed. For this reason we also conducted follow-up analyses examining the t-contrasts of Inequity > Equity for each game separately. Mean percentage of inequity offers in each game was used in regression analyses to test for brain-behavior relations in a GLM model based on the game (collapsed across choices; 3 levels: advantageous competitive inequity, advantageous self-maximizing inequity and disadvantageous prosocial inequity). The fMRI analyses were conducted at the threshold of $p < .001$ uncorrected with a voxel threshold of 10 functional voxels to balance between Type 1 and Type 2 errors (Lieberman & Cunningham, 2009). Regions of interest (ROI) analyses were further conducted on the regions obtained from the whole-brain analyses using the MarsBaR toolbox in SPM8 (Brett et al., 2002; http://marsbar.sourceforce.net/). All results are reported in the MNI305 (Montreal Neurological Institute) stereotactic space.

7.3 RESULTS

Behavioral results

An examination of response patterns of the participants showed that they had strong preferences for equity or inequity choices, which depended on the costs for self and other (see ***Table 7.1***). A detailed overview of these choices per participant can be seen in ***Figure 7.1C***. Percentage of inequity choices across the three conditions was compared using a repeated measure ANOVA, which yielded a significant main effect of game, $F(2,54) = 8.4, p = .001, \eta_p^2 = .24$ (***Figure 7.1B***). Participants chose the inequity distribution more often in the advantageous self-maximizing inequity condition ($M = .60$, $SD = .43$) than in the disadvantageous prosocial inequity condition ($M = .39$, $SD = .44$; $F[1,27] = 4.90, p < .05, \eta_p^2 = .15$) and in the advantageous competitive inequity condition ($M = .18$, $SD = .33$; $F[1,27] = 21.98, p < .001, \eta_p^2 = .45$). Inequity choices in the latter two conditions did not differ significantly from each other ($p = .09$). There was also a significant correlation between inequity choices in the disadvantageous prosocial inequity and the advantageous competitive inequity conditions, $r = -.41, p < .05$.

Table 7.1 *Frequency (and percentage) of participants making 100% equity, 100% inequity or both choices across the trials per game.*

Game	100% Equity	100% Inequity	Both
Disadvantageous prosocial inequity (1/2)	10 (37.5%)	8 (28.6%)	10 (37.5%)
Advantageous competitive inequity (1/0)	17 (60.7%)	3 (10.7%)	8 (28.6%)
Advantageous self-maximizing inequity (2/0)	6 (21.4%)	9 (32.1%)	13 (46.4%)

Neuroimaging results

In order to examine the neural correlates of equity and inequity choices, we examined the 'Inequity > Equity' and reverse contrasts within the 3 (game) × 2 (choice) ANOVA. The 'Inequity > Equity' *t*-contrast revealed a network of regions comprising bilateral AI (peaks at -30, 21, -12; 19 and 27, 24, -9), right inferior frontal gyrus (peak at 54, 21, 18), dACC (peaks at 6, 39, 21 and 0, 24, 36), and dorsolateral (peak at 27, 45, 36) and ventrolateral PFC (peak at 30, 54, -3) Activation levels obtained from ROI analyses in right AI is plotted for demonstration purposes in a bar graph of activation per game and offer (***Figure 7.2***). The reverse contrast (Equity > Inequity) did not yield any clusters of activation and the game by choice interaction also did not result in significant activation. Thus, AI, dACC and dlPFC were activated in response to choosing an unequal distribution of resources, regardless of the consequences of this distribution for self or other in terms of maximizing outcomes or costs.

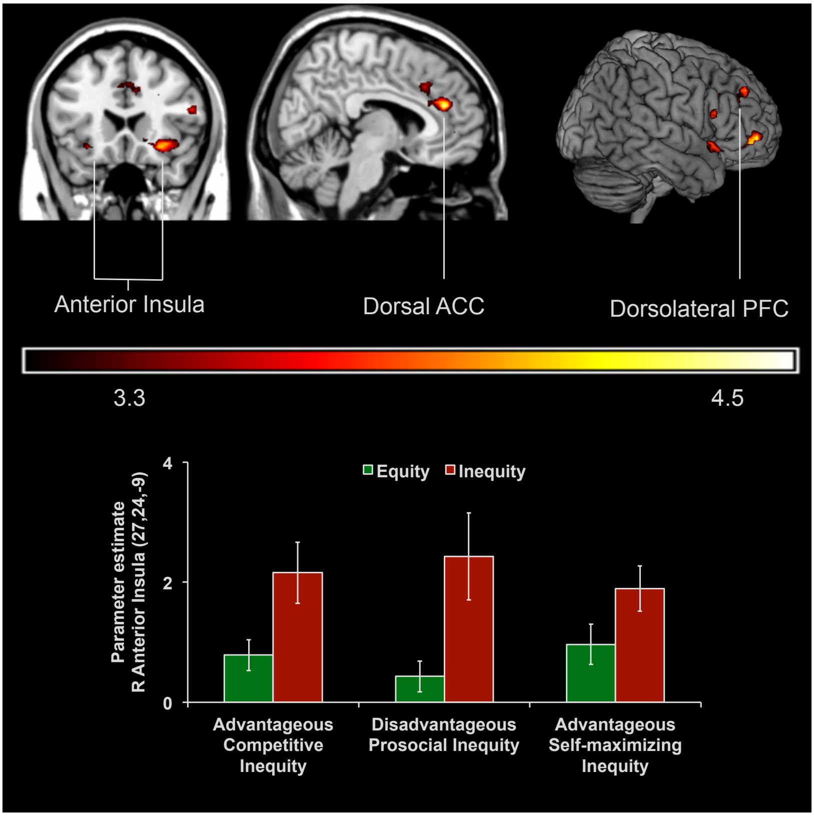

Figure 7.2 *Brain regions from the 'Inequity > Equity' contrast in the 3 (game) × 2 (choice) full factorial ANOVA. Bar graph displays contrast estimates obtained from ROI analysis in right AI (peak at 27, 24, 29) for inequity and equity choices in the three conditions. Error bars indicate* SEM.

Next, in order to examine inequity related neural responses in more depth, we focused on the 'Inequity > Equity' and reverse contrasts in the context of each of the three games separately using *t*-tests. The 'Equity > Inequity' contrast did not yield activation in any of the three games. We also did not detect any regions for the 'Inequity > Equity' contrasts in the advantageous competitive (n = 8) and the Advantageous Self-maximizing (n = 13) games at the chosen threshold, but note that the effects reported above are partially replicated at a more lenient threshold[1].

The 'Inequity > Equity' contrast in the disadvantageous prosocial inequity condition (n =10) yielded increased activation in the vmPFC (peak at 6, 48, 0), ventral striatum (peak at 12,

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[1] *See Supplementary **Table S7.1** for an overview of the regions of activation in the 'Inequity > Equity' contrasts per condition at the* p < *.005, minimum 10 voxel threshold.*

21, 0), and right AI (peak at 45, 15, -6) during inequity choices than equity choices (***Figure 7.3***; activation levels obtained from ROI analyses in ventral striatum and vmPFC are plotted for demonstration purposes in a bar graph of activation per game and offer). Importantly, here the inequity choices were not only disadvantageous for the self relative to the other player, but also beneficial for the other player. Post hoc ROI analyses showed that higher activation in these regions during inequity than equity was specific for the disadvantageous prosocial inequity game; inequity and equity related activity in the advantageous competitive and advantageous self-maximizing inequity games did not differ significantly in any of the regions (all *p*s > .25).

Finally, we examined brain-behavior relations by conducting whole-brain regressions where inequity choice frequency was included as a regressor in activations involved in the 'disadvantageous prosocial inequity game (collapsed across choices) – null contrast' ($n = 28$). This approach enabled us to examine the relation between frequency of inequity choices and brain activation across the complete sample of 28 participants, whereas the previously reported inequity vs. equity and reverse contrasts could be examined only among the 10 participants who had made both equity and inequity choices in the disadvantageous prosocial inequity condition. This analysis resulted in a set of regions in which activation correlated positively with inequity choices, including the precuneus (peak at -9, -57, -48), vmPFC (peak at 15, 45, 0), and dlPFC (peak at 24, 39, 42) (***Figure 7.4***; the relation between dlPFC activation and frequency of inequity offers is demonstrated in a scatterplot). There was no activation in brain regions of interest in the brain-behavior correlations for the other two games (see Supplementary ***Table S7.2***).

7.4 DISCUSSION

The current study set out to investigate the common and distinct neural responses associated with inequity decisions involved in maximizing outcomes for the self or another person. Our behavioral results demonstrate that participants more often chose unequal distributions in situations where their own profits could be maximized relative to alternatives where they could maximize the other person's profits. The neuroimaging findings showed that choosing inequity regardless of whether it entails benefits for the other is associated with increased activation in the AI, dACC and dlPFC. In addition, decisions to distribute resources unequally, but in a way that benefits another person's profits additionally coincided with increased activation in ventral striatum, vmPFC, precuneus and dlPFC. Taken together, our findings show that there is a common neural response to making advantageous and disadvantageous inequity choices, which resembles the pattern of neural activity previously associated with being treated unfairly (Corradi-Dell'Acqua et al., 2013; Güroğlu et al., 2010; Güroğlu et al., 2011; Sanfey et al., 2003). Furthermore, we show a distinct neural response associated with prosocial inequity,

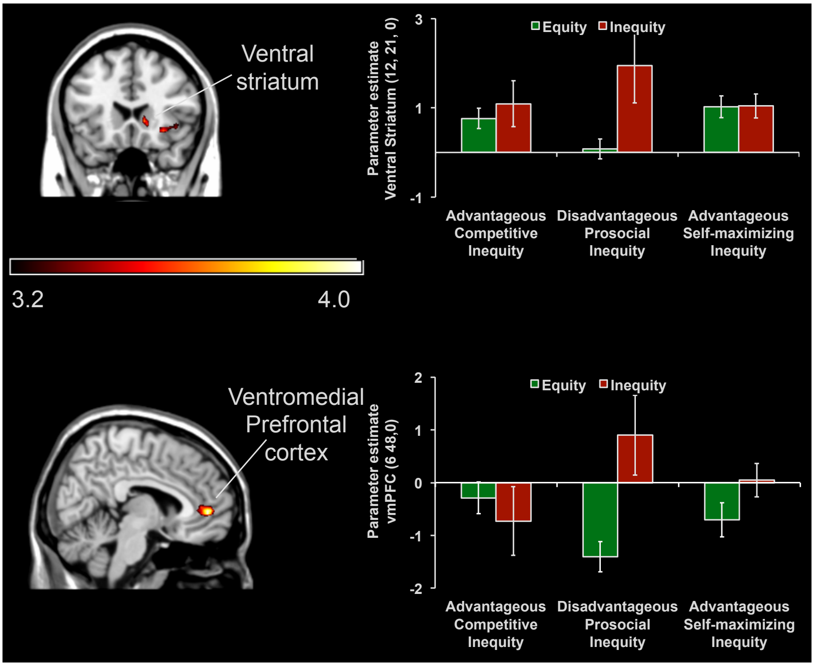

Figure 7.3 *Ventral striatum (peak at 12, 21, 0) and vmPFC (peak at 6, 48, 0) from the 'Inequity > Equity' contrast in the disadvantageous prosocial inequity condition. Bar graphs display contrast estimates obtained from ROI analyses for inequity and equity choices in the three conditions. Error bars indicate* SEM.

which suggests that violating a fairness norm in order to increase another person's outcomes is processed differently on a neural level compared to selfish violations of a fairness norm.

Our behavioral findings show that participants adjusted their behavior depending on the available alternatives to an equal split. In doing so, it seems that different principles interact to guide decision-making when distributing resources: a social norm of equity, (possible) costs for the self, and a concern for outcomes of others relative to the self. Whereas an equal distribution was the most preferred option when it did not involve possible costs to the allocator (i.e., the participant), equal distributions became less preferred when it was costly to establish them. This finding is in line with previous studies on fairness preferences, which show that, although an equal split is used as a cognitive heuristic, contextual factors related to the relevance of self-interest systematically shifts preferences away from an equal split (Civai et al., 2013). Preference for an equal distribution was not only influenced by absolute costs, as in the Advantageous Self-maximizing Inequity condition, but also in terms of relative costs compared to the other

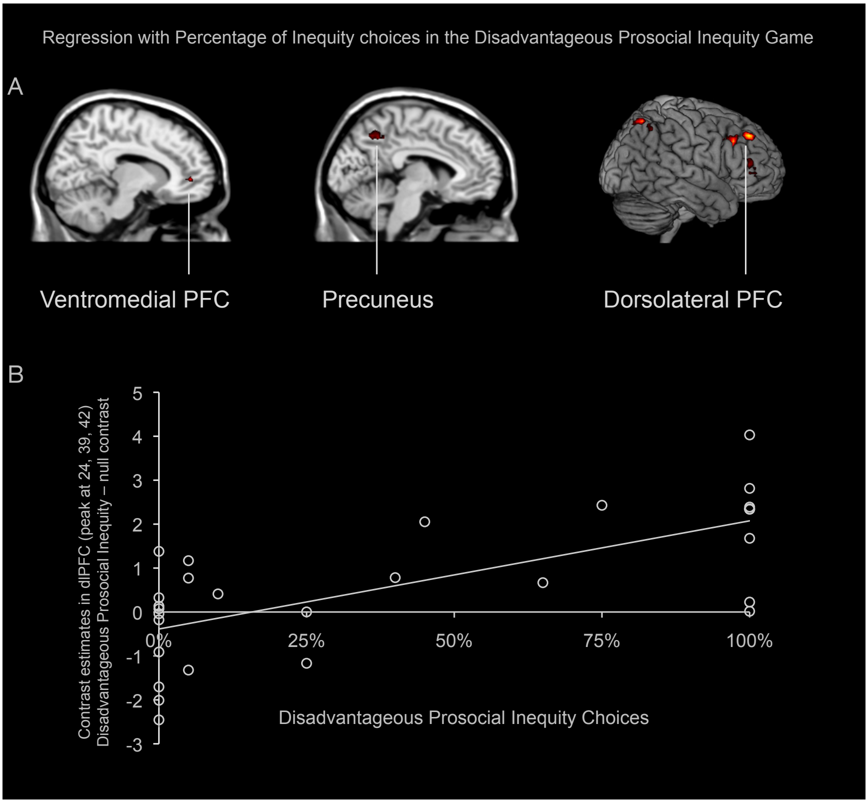

***Figure 7.4** (A) A whole-brain regression analysis showed that neural activity during the disadvantageous prosocial inequity game was positively associated with the frequency of inequity choices in the vmPFC (peak at 15, 45, 0), precuneus (peak at - 9, -57, -48), and dlPFC (peak at 24, 39, 42. (B) Scatter plot displays contrast estimates for the disadvantageous prosocial inequity condition on the y-axis and behavior (% inequity) on the x-axis (N = 28).*

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player, as in the Disadvantageous Prosocial Inequity condition. This latter finding demonstrates that a preference for equal outcomes does not necessarily have to be grounded in a prosocial motivation, but might also result from the desire to avoid receiving lower payoffs than another person (Fehr & Schmidt, 1999).

Neuroimaging results further show that there is a common neural response in dACC, bilateral AI and dlPFC to both advantageous and disadvantageous inequity. This suggests that a general neural mechanism is implicated in signaling deviations from a fairness norm in sharing decisions, regardless of who benefits from the unequal distribution of goods. Our findings corroborate previous findings showing that both advantageous and disadvantageous inequity were associated with AI activity (Yu, Calder, & Mobbs, 2014) and a heightened medial frontal negativity (Wu, Hu, van Dijk, Leliveld, & Zhou, 2012), which has been interpreted as suggesting the involvement of the dACC-AI network in norm and associated expectancy violations. The dACC and the AI are part of a 'salience network' that serves an important domain general role in integrating cognitive and emotional signals when processing motivationally salient information (Botvinick et al., 2004; Chang et al., 2013). Activation in this network has been associated with error processing (de Bruijn, de Lange, Von Cramon, & Ullsperger, 2009), uncertainty (Singer et al., 2009), conflict (Shenhav et al., 2013) and violations of a social norms (Chang et al., 2013; Civai, Crescentini, Rustichini, & Rumiati, 2012; Corradi-Dell'Acqua et al., 2013; Klucharev, Hytonen, Rijpkema, Smidts, & Fernandez, 2009; Montague & Lohrenz, 2007).We extend previous research by showing that the AI and dACC are also activated when creating inequity in choices that involve possible costs to the self and a fair alternative to inequity, both of which are core components of fairness considerations previously not investigated using fMRI.

Increased dlPFC activity during both advantageous and disadvantageous inequity choices relative to equity choices fits with findings from a recent study showing dlPFC involvement in both advantageous and disadvantageous inequity in a game in which participants received less or more money than another person after performing a perceptual task (Fliessbach et al., 2012). Based on its role in cognitive control and goal-directed behavior it has been argued that dlPFC activity in social decision-making tasks reflects increased control over prepotent responses that are aimed to maximize self-gain (Knoch et al., 2006; Spitzer et al., 2007; Steinbeis et al., 2012; Wright et al., 2011). Our results suggest that dlPFC activity might reflect higher levels of executive control required to violate a salient social norm regardless of whether this maximizes gains for the self or someone else. The notion that this is not restricted to maximizing outcomes for the self was supported by our individual differences analyses that showed that participants who more often chose outcomes that maximize the profits of the other over an equal distribution recruit the dlPFC to a greater extent when doing so.

In addition to a common neural pattern associated with inequity, we also found that violations of a fairness norm in the Disadvantageous Prosocial Inequity condition were associated with activation in the striatum and the vmPFC. Activation in these regions associated with such prosocial behavior that leads to better outcomes for another person is in line with prior findings showing that the striatum not only responds to primary rewards, but also to social rewards such as charitable donations (Harbaugh, Mayr, & Burghart, 2007), maximizing another person's outcomes (Zaki & Mitchell, 2011), and mutual cooperation in a prisoner's dilemma paradigm (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b). Moreover, individual differences analyses showed that the more frequent people showed this other-outcome maximizing behavior, the more they activated the vmPFC and the precuneus. The vmPFC is not only important for the encoding the subjective value of rewards (Levy & Glimcher, 2012; Rangel & Hare, 2010), but is also part of a network, including the precuneus, dorsomedial prefrontal cortex and the temporo-parietal junction (Saxe et al., 2004; Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009) important for mental state-reasoning (Blakemore et al., 2007; Moriguchi et al., 2007) and perspective taking (Lamm et al., 2007). Moreover activation in the mPFC has been shown to be associated with processing one's own and other people's actions and intentions in economic games (Halko, Hlushchuk, Hari, & Schürmann, 2009; Rilling et al., 2004a). Acting in a way that does not necessarily benefit outcomes for the self, but is beneficial to another person's gains might thus possibly require increased levels of perspective taking. It would be recommended for future studies to assess self-reported subjective value associated with individuals' choices of advantageous and disadvantageous inequity in order to be able to examine how experience of reward is related to the neural signal associated with these choices.

Several limitations of the current study should be noted. One of the main challenges of the current research design is related to individual differences in observed behavior. As indicated by the behavioral patterns (see ***Figure 7.1C***), the majority of participants were consistent in their choices within a certain condition, which might be considered desired given that this consistency reflects stable individual preferences and implies that participants did not choose randomly. However, this resulted in relatively small numbers of observations in several neuroimaging analyses where choice-related neural activation was examined based on contrasts of inequity versus equity choices per condition. For example, although there was a main effect of the 'Inequity > Equity' contrast across conditions, these effects could not be observed when this contrast was examined per condition separately at the chosen threshold, but was only evident at more lenient threshold levels. In addition, the results may represent the neural activity of individuals who are ambiguous about equity choices, and in future research it should be examined whether these also represent choices of individuals with strict equity norms. Previous behavioral studies using the three allocation games have also examined profiles of individual behavior patterns (Fehr et al., 2008; Steinbeis & Singer, 2013). In the current study, our sample size did not allow us to examine the neural correlates of individual behavioral profiles. Future studies employing larger sample sizes should aim to examine individual differences in neural activation related to profiles of behavior.

The individual differences in observed behavior also resulted in an unbalanced design in our fMRI analysis. In other words, due to the fact that not all participants made all choices in each game, it was not possible to conduct a balanced full-factorial analysis with the same number of observations in each cell of the design. Future studies can aim to manipulate the study design in order to obtain a more balanced response pattern or, as indicated above, aim for larger sample sizes that will enable to examine individual differences based on choice profiles. Furthermore, the current study did not employ self-report explicit measures about cognitive and affective processes related to making (inequity) choices. Future research should include measures about beliefs on fairness norms, affect related to inequity choices or autonomic measurements, such as heart rate, which can provide the researchers with additional measures in interpreting behavioral and neural findings.

The current results offer a number of avenues for future research. For example, our current design did not allow for a dissociation between joint-outcome maximization and maximization of another person's outcomes in the disadvantageous inequity (1/2) choices. Future studies could include a condition where the 1/1 option is pitted against a 2/1 distribution, in which the latter choice would both be self- and joint outcome maximization (Meuwese, Crone, de Rooij, & Güroğlu, 2014). A contrast between the 2/1 and 1/2 choices could disentangle joint outcome maximization from person-specific (self vs. other) outcome maximization. Furthermore, using the same set of three allocation tasks (Fehr et al., 2008; Steinbeis & Singer, 2013) and other paradigms (Blake & McAuliffe, 2011; Shaw & Olson, 2012) it has been shown that across development children and adolescents increasingly start enforcing equality between the ages of 3 and 13. Recent developmental work has shown that developmental changes in late maturing brain regions such as regions of the mentalizing network and the lateral PFC are associated with developmental increases in intentionality understanding and strategic considerations in fairness decisions (Güroğlu et al., 2011; Steinbeis et al., 2012). It would be of great interest to relate behavioral changes in both advantageous and disadvantageous inequity choices to brain development, because taking a developmental perspective has the potential to enhance not only our understanding of social development, but could also provide insights into adult social decision-making and its underlying mechanisms.

Taken together, the current results further inform our understanding of an important aspect of human social behavior, that is, when and why we decide to divide resources unequally. We show that violations of an equity norm, both with selfish (i.e., advantageous) and prosocial (i.e., disadvantageous) outcomes, are associated with a common neural response in the salience network. Furthermore, prosocial violations of a simple fairness norm were associated with activation in brain regions that code for primary and more complex social rewards (Hsu et al., 2008; Zaki & Mitchell, 2011) and switching attention to another person's perspective (Halko et al., 2009; Lamm et al., 2007; Rilling et al., 2004a). These findings show that neural networks implicated in social cognition, domain general cognitive functions and emotional processes are important for both following social norms and for violating such norms when these violations serve a more prosocial purpose than the norm itself.

7.5 SUPPLEMENTARY MATERIAL

Table S7.1 *Regions of neural activation from the 'Inequity > Equity' contrast per allocation game at the threshold of* p *< .005 uncorrected, > 10 voxels.*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Disadvantageous prosocial inequity condition: Inequity > Equity						
Dorsolateral Prefrontal cortex	L	24	3.49	-30	36	36
	R	28	3.47	27	42	36
Lateral Prefrontal cortex	R	10	2.94	45	39	18
Ventromedial Prefrontal cortex	-	238	3.99	6	48	0
Anterior Insula	R	209	3.69	45	15	-6
Striatum			3.63	12	21	0
	L	111	3.37	-18	-3	-6
Precuneus	L	33	3.53	6	-42	45
	-	52	3.10	-6	-72	33
Inferior Frontal gyrus	L	15	3.46	-54	15	18
	R	35	3.24	33	21	30
Temporoparietal junction	R	36	3.29	48	-36	45
	L	18	3.03	-51	-54	42
Posterior Temporal gyrus	L	20	3.44	-57	-51	0
Advantageous self-maximizing inequity condition: Inequity > Equity						
Pallidum	R	34	3.46	24	-6	3
Ventrolateral Prefrontal cortex	R	24	3.06	36	45	-3
Advantageous competitive inequity condition: Inequity > Equity						
Dorsal Anterior Cingulate cortex	-	49	3.39	9	39	21
Somatosensory cortex	R	17	3.12	36	-3	27

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.

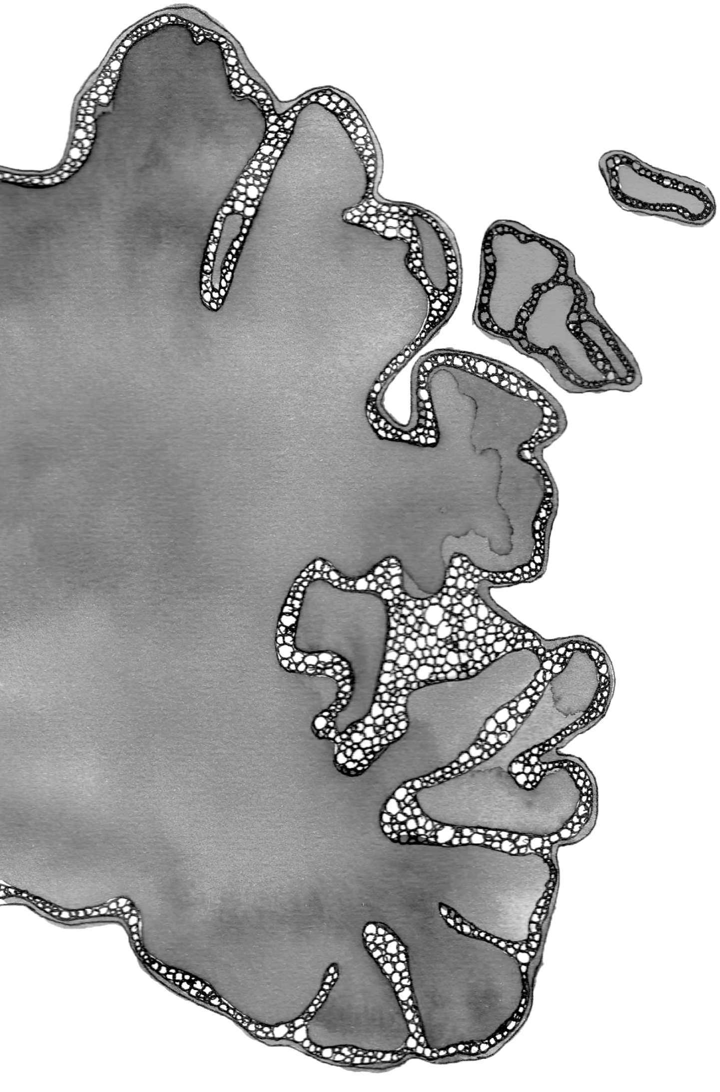
Table S7.2 *Regions of neural activation from whole-brain regression analyses with frequency of inequity choices per game as a regressor.*

Brain region	L/R	Voxels	*z*	MNI coordinates		
				x	y	z
Positive correlation with frequency inequity choices						
Advantageous self-maximizing inequity – null contrast						
Posterior Cingulate cortex	-	17	3.71	-3	27	36
Dorsolateral Prefrontal cortex	R	10	3.47	27	42	36
Advantageous competitive inequity – null contrast						
Cuneus	L	27	3.86	36	21	15
Negative correlation with frequency inequity choices						
Advantageous competitive inequity – null contrast						
Cuneus	R	18	3.91	18	-78	27
Putamen	R	12	3.26	30	9	0

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.

Task instructions for the allocation game

In this 'allocation game' you may decide how coins will be divided between you and another player. You can always choose between two options to divide the coins. This is what the game looks like (display is shown with an example of two buckets with red and blue coins in each). The red coins are for you and the blue coins are for the other player. In this example you see on the left side a bucket with one red coin. You receive one coin and the other player receives no coins. On the right side you see a bucket with one red and one blue coin. You receive one coin and the other player also receives one coin. Here is another example: on the left side you see a bucket with one red and one blue coin. You receive one coin and the other player receives one coin. On the right side you see a bucket with one red and two blue coins. You receive one coin and the other player receives two coins. You may choose how the coins will be distributed. Press the button number 1 using your right index finger to choose the left option and button number 2 using your right middle finger for the option on the right. Be careful: you have five seconds to make a decision. At the end of the game the computer will choose several random trials to determine how much each player has earned. These trials determine what you earn, but also how much the other players will earn. In other words, your choices have consequences on how much everyone will earn at the end of the game. Once you have made a choice, your choice will be encircled in red on the screen. In this example, the right option is chosen (slide showing right bucket with one red and two blue coins being encircled in red). So in that case you would earn one coin and the other player would earn two coins. You will play each round with another anonymous player. These players are not present today and have agreed to participate in the experiment on a future testing day. On each trial you see your name in red above on the left; the name of the other player will appear in blue below on the left side. If you have questions, you may ask them now. If you don't have any other questions, you will now play several practice trials with no human participant as the second player, but a computer.



CHAPTER 8

LONGITUDINAL LINKS BETWEEN CHILDHOOD PEER ACCEPTANCE AND THE NEURAL CORRELATES OF SHARING

This chapter is submitted as:

Will, G.-J., Crone, E. A., van Lier, P. A. C., & Güroğlu, B. (submitted). Longitudinal links between childhood peer acceptance and the neural correlates of sharing.

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.

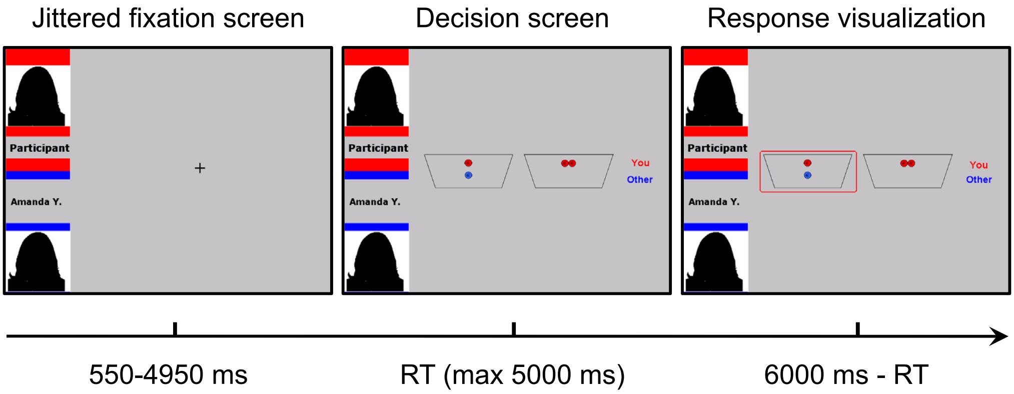


Figure 8.1 *Visual display of events presented in the one trial of the fMRI task. Each trial started with a fixation cross with a jittered duration (550–4950 ms). Subsequently, participants were presented a decision screen containing: the name of the participant in red, the name of the recipient in blue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

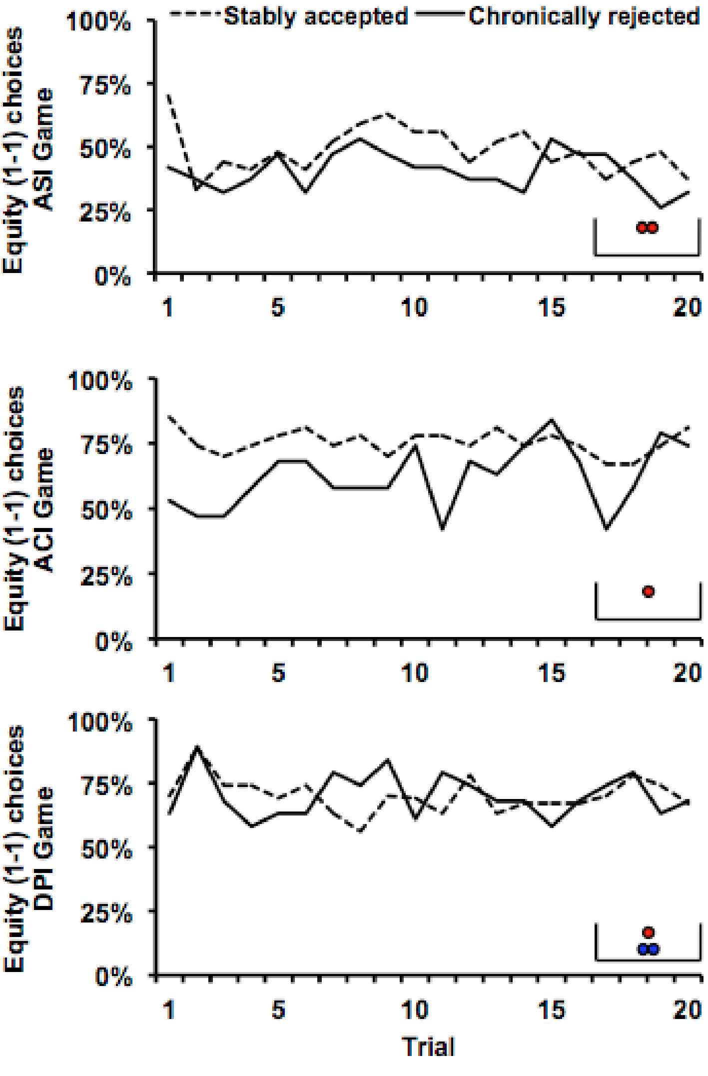


Figure 8.2 *Percentage of equity offers chosen by stably accepted and chronically rejected adolescents in each of the three equity games plotted as a function of trial number. The equity offer (which was always 1 coin for the participant and 1 coin for the recipient) was pitted against an alternative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

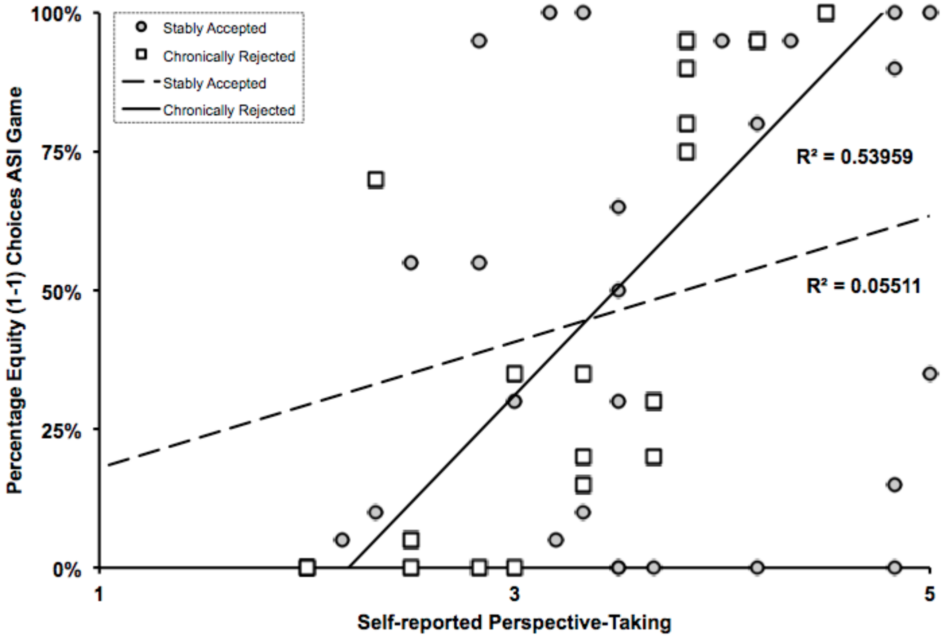


Figure 8.3 *Chronically rejected participants who reported higher levels of perspective taking were more likely to give up a reward to share equally (choosing 1-1 instead of 2-0 in the advantageous self-maximizing inequity Game). In the stably accepted group, no relation between perspective taking and 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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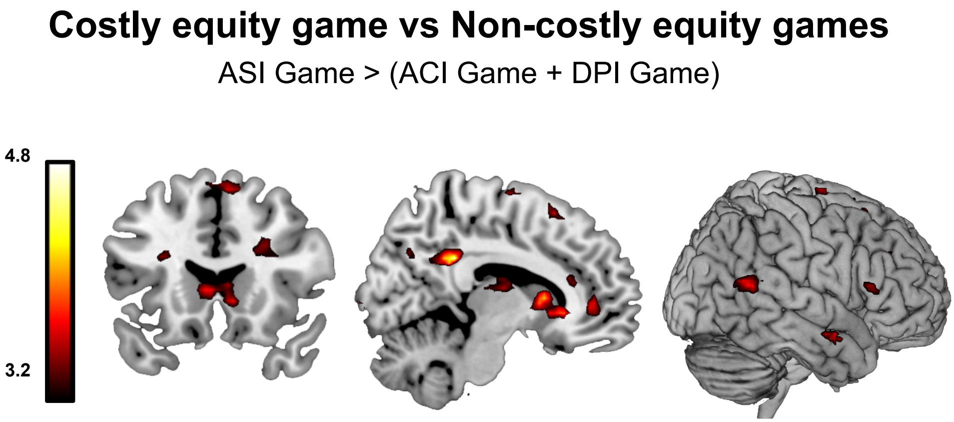
[1] *Although the current paper focused on the question how neural processes during sharing decisions vary as a function of peer status history, we also tested whether our prior findings on the neural correlates of inequity choices replicated (Güroğlu, Will, & Crone, 2014). The results of this analyses are reported in the Supplementary material and show that our prior findings partially replicate (see 8.5).*



Costly equity game vs Non-costly equity games

ASI Game > (ACI Game + DPI Game)

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]).*

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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

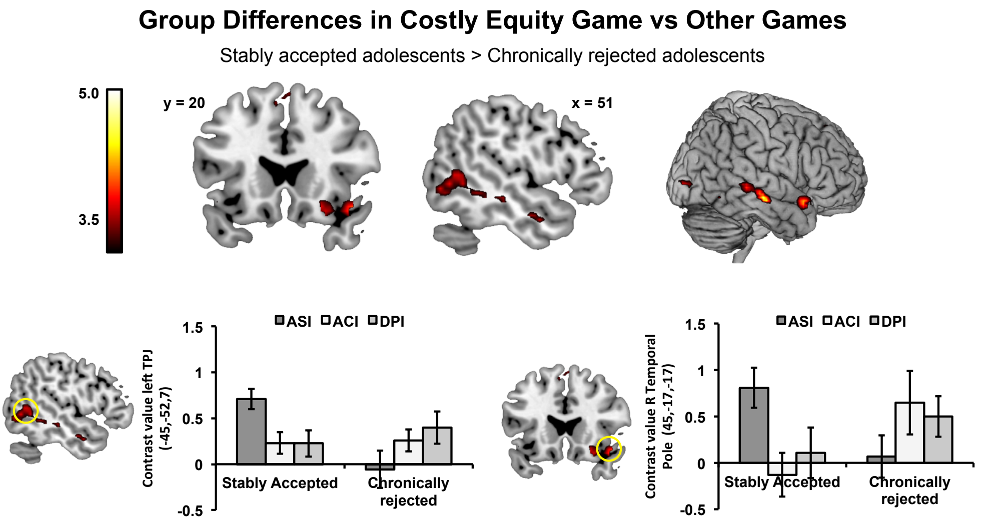


Figure 8.5 *Stably accepted adolescents exhibited heightened activity in left pSTS/TPJ (peak at -45, -52, 7), right IFG/AI (peak at 27, 23, -14), right Temporal pole (peak at 45, 17, -17) and pre-SMA (peak at -3, 23, 55) compared to chronically rejected adolescents in the advantageous self-maximizing 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)	Group, Mean (*SD*) 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.

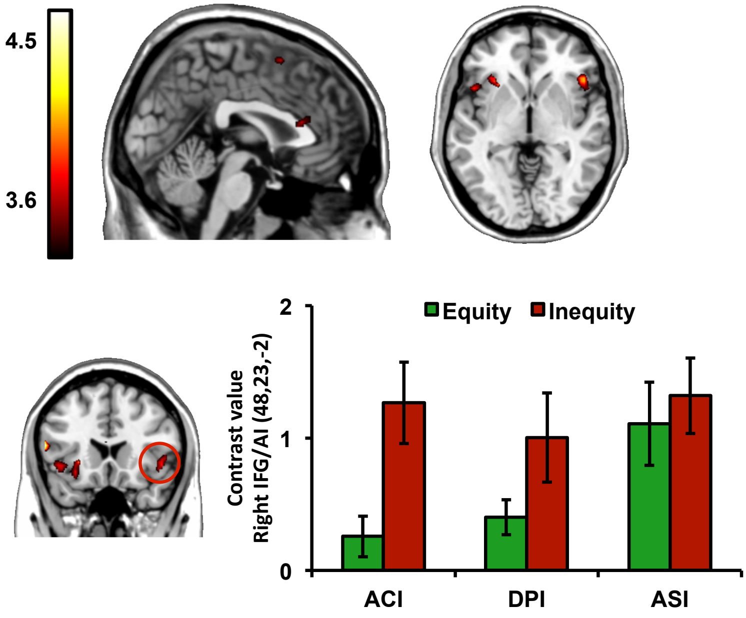
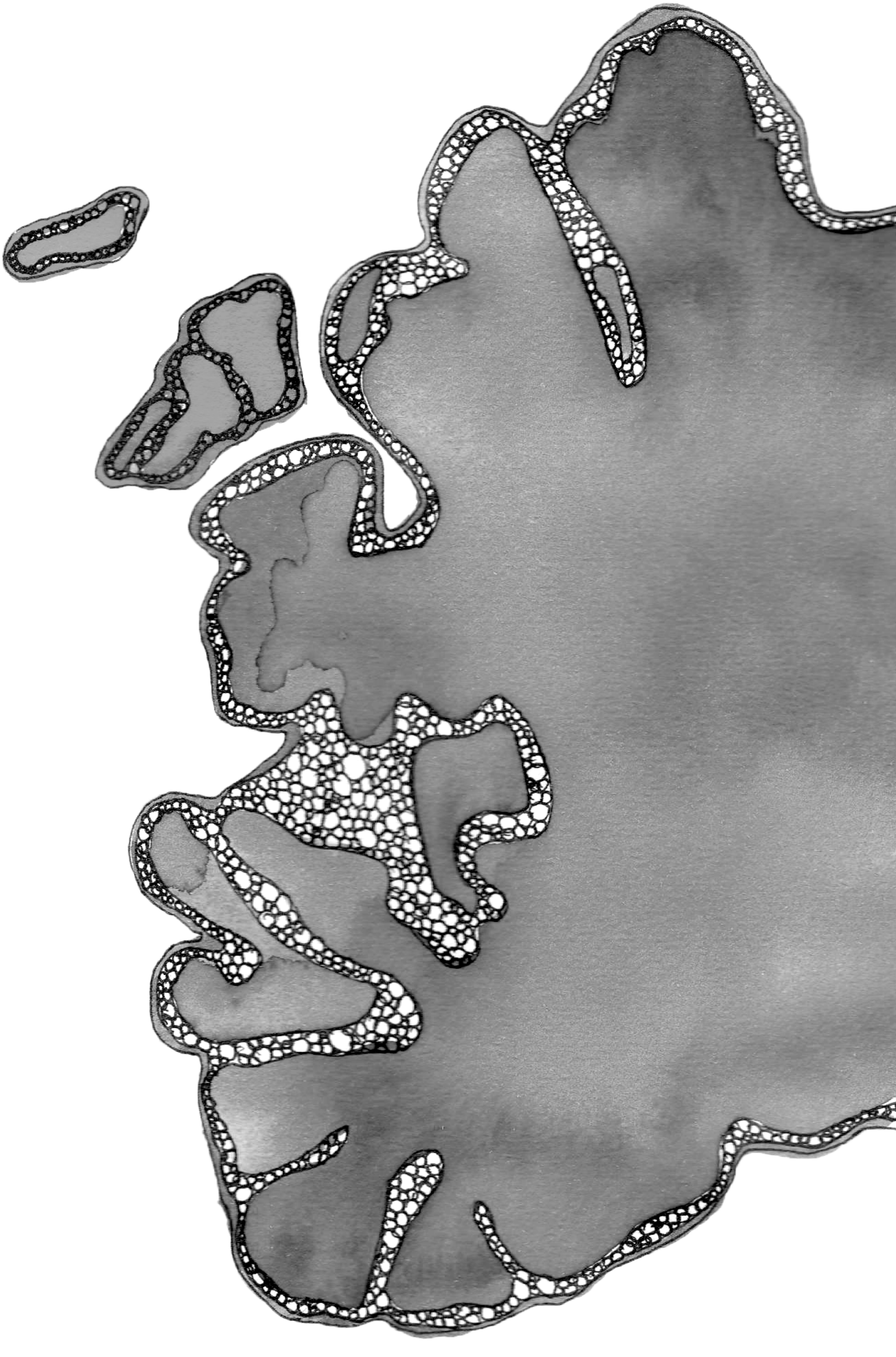


Figure S8.1 *Network of brain regions from the 'Inequity > Equity' contrast collapsed across equity games and across peer status history groups;* $p < .001$*, 10 voxel threshold. Bar graph displays contrast estimates obtained from ROI analysis in right AI (MNI 48, 23, -2) for inequity and equity choices 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.



CHAPTER 9

SUMMARY AND GENERAL DISCUSSION

9.1 INTRODUCTION

The goal of this thesis was to examine the neurocognitive underpinnings of processes that play a role in the emergence and maintenance of peer group rejection. Transactional models of peer rejection posit that peer group rejection *emerges* from a consistent display of behaviors that are poorly tolerated by the rejected child's peer group (Coie, 1990). These models further propose that once rejection has become stable in the peer group, cognitions and behaviors of both the rejected child and the members of the rejected child's peer group are changed in ways that *maintain* peer group rejection. Drawing on such transactional models, we created a simplified model of peer rejection, which guided the empirical studies in this thesis. This model distinguished between processes at the level of the individual child (i.e. intra-individual), those at the level of social interactions (i.e. interpersonal) and those at the level of the peer group.

At the interpersonal level, we examined retaliatory and prosocial reactions to social exclusion and prosocial behavior in the form of resource sharing with strangers. At the intra-individual level, we examined subjective (i.e. mood and need satisfaction) and neurocognitive processes that underlie behavioral reactions to exclusion and sharing. Furthermore, to gain a better understanding of how these intra- and interpersonal processes are influenced by processes at the group level, we investigated how these processes varied as function of chronic exposure to peer group rejection. Given the crucial role the peer group has in stopping social exclusion and alleviating the distress experienced by a victim of exclusion (Sainio et al., 2010; Salmivalli, 2010), we also examined socio-cognitive processes (intra-individual level) of uninvolved bystanders who witnessed the exclusion of a peer and were subsequently given the opportunity to help the victim of exclusion and to punish the perpetrators (interaction level).

In this chapter, the findings of the studies in this thesis are summarized and discussed within the framework of our working model. First, the main findings of each chapter are summarized (9.2). This summary is accompanied by a graphical summary of the neural correlates of the intra- and interpersonal processes involved in social decision-making (see ***Figure 9.1***). Second, because the findings of each separate study were mainly discussed in a (developmental) cognitive neuroscience framework, the general discussion will concentrate on how the findings fit into the broader 'peer relations' literature and how they relate to the mechanisms of emergence and maintenance of peer rejection (9.3-9.6). The final section of this thesis is dedicated to the advantages of an integration of developmental cognitive neuroscience with traditional peer relations research followed by several directions for future research (9.7) and concluding remarks (9.8).

9.2 SUMMARY

Chapter 2 examined how subjective and neural responses to social exclusion in adolescence vary as function of chronic exposure to peer rejection. We recruited a group of adolescents who were chronically rejected by their peers and a group of adolescents who had a stable accepted status across six elementary school grades. Participants were first included and subsequently excluded in the Cyberball paradigm (Williams et al., 2000) in an MRI scanner. Both groups of adolescents reported similar decreases in mood and need satisfaction after being excluded, demonstrating that a brief episode of social exclusion is distressing for adolescents irrespective of childhood peer status. On a neural level, differences between the two groups emerged. Specifically, chronically rejected adolescents, compared with stably accepted adolescents, exhibited heightened activity in the dorsal anterior cingulate cortex (dACC) during social exclusion. When incidentally excluded in a social interaction in which they were overall included, chronically rejected adolescents showed heightened activity in the dACC and anterior prefrontal cortex (aPFC). A heightened neural reactivity to continuous exclusion and incidental exclusion could be associated with more pronounced emotional or behavioral reactions to negative peer treatment (e.g. lashing out against peers who may or may not have intended to exclude them), which instigate further negative peer treatment. Consequently, a heightened neural reactivity to negative peer treatment might be a mechanism through which chronically rejected adolescents initially became rejected or through which they maintained their rejected status across elementary school.

The main goal of the study reported in **Chapter 3** was to examine the neural processes underlying retaliatory and prosocial reactions to exclusion in a sample of young adults. Participants played a modified Dictator Game in which they could choose to either punish (i.e. retaliate against) the excluders by decreasing their monetary outcomes or to refrain from punishment and forgive (i.e. act prosocial toward) them by sharing the stake equally with them. Additionally, punishment could result in monetary gains, losses, or could have no monetary consequences. Participants punished the excluders when this resulted in monetary gains, but also when this had no monetary consequences and even when punishment was costly. Punishment of excluders was associated with activation in pre-supplementary motor area (pre-SMA) and bilateral anterior insula (AI; see ***Figure 9.1***). Whereas AI activity was not sensitive to monetary consequences when punishing excluders, pre-SMA activity was higher for costly punishment relative to punishment that resulted in monetary gains or had no monetary consequences. Analyses of individual differences showed that people who were more inclined to take other people's perspectives were more likely to forgive the excluders. Forgiveness was associated with increased activation in brain regions supporting perspective taking (temporo-parietal junction [TPJ] and dorsomedial prefrontal cortex [dmPFC]) and cognitive control

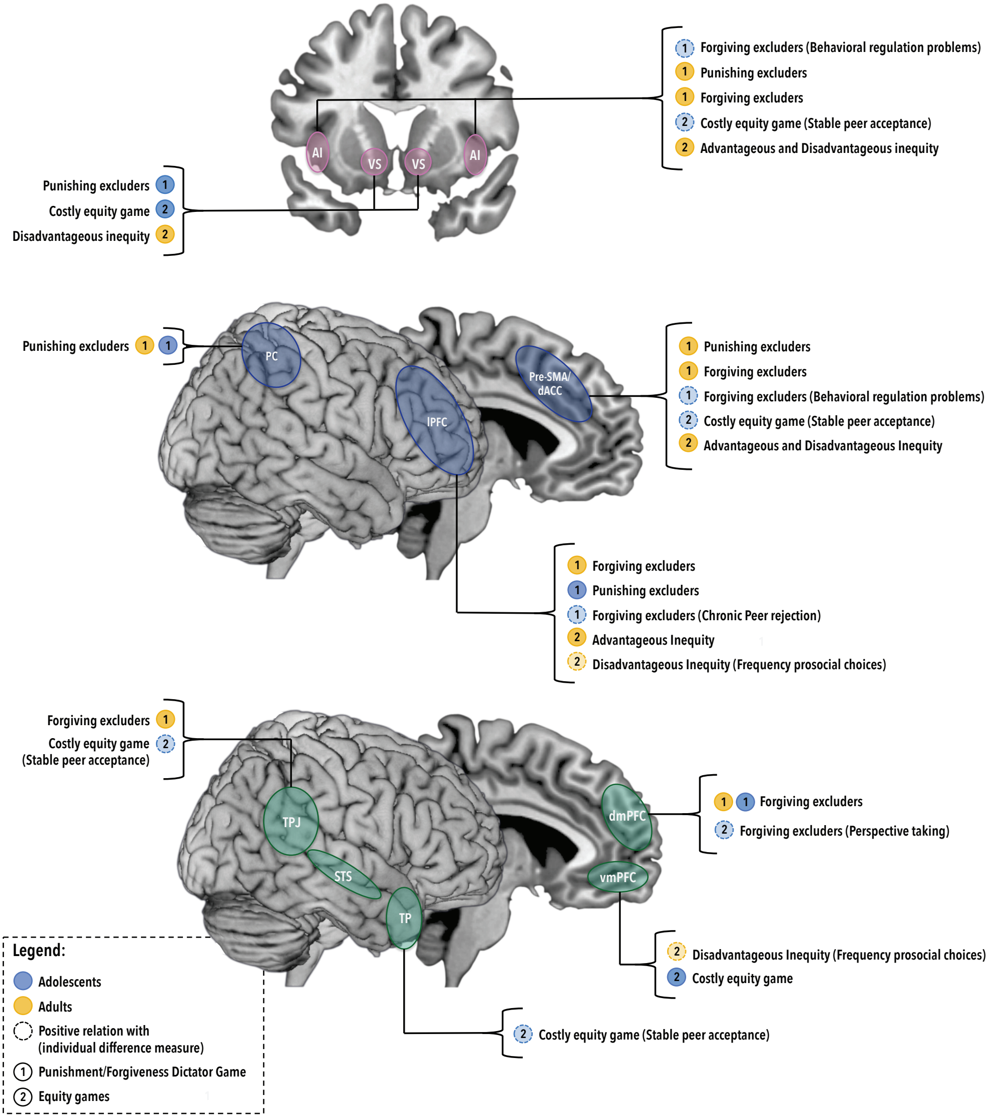


Figure 9.1 *Summary of the activations in three brain networks involved in social decision-making: basic affective network (pink), cognitive-regulatory network (blue) and mentalizing network (green). AI = anterior insula, VS = ventral striatum, PC = parietal cortex, lPFC = lateral Prefrontal Cortex, pre-SMA = pre-supplementary motor area, dACC = dorsal Anterior Cingulate Cortex, TPJ = temporo-parietal junction, STS = Superior Temporal Sulcus, TP = temporal pole, dmPFC = dorsomedial Prefrontal Cortex, vmPFC = ventromedial Prefrontal Cortex.*

(dACC and dorsolateral prefrontal cortex [dlPFC]). This suggests that perspective taking and cognitive control are two intra-individual processes underlying prosocial reactions to social exclusion. These findings laid the foundations for investigating how those neural processes vary as a function of childhood peer rejection.

Accordingly, in **Chapter 4**, a group of adolescents with a history of chronic peer rejection and a group of adolescents with a history of stable peer acceptance were given the opportunity to punish or to forgive individuals who excluded them in Cyberball. Similar to adults, adolescents punished the excluders by decreasing their monetary outcomes. Punishment of the excluders was associated with activity in ventral striatum, dlPFC and parietal cortex. Neither punishment behavior nor associated neural activity was modulated by individual differences in peer status history, perspective taking or behavioral regulation problems. Despite both groups showing similar levels of punishment and forgiveness, chronically rejected adolescents exhibited more activity in the dorsal striatum and the lateral PFC (lPFC) during forgiveness than stably accepted adolescents. Based the role of the dorsal striatum and lPFC in executive control, heightened activity in these regions during forgiveness might indicate that chronically rejected adolescents have to exert greater levels of control in order to act prosocial toward individuals who previously excluded them. During forgiveness, individual differences in perspective taking correlated positively with activity in the dmPFC and individual differences in behavioral regulation problems correlated positively with pre-SMA/ACC and AI. These findings demonstrate that individual differences in exposure to chronic peer rejection impact neural activity during prosocial, but not retaliatory reactions to social exclusion. Together they provide insights into several intra-individual processes underlying behavioral reactions that could provoke excluders and consequently could play a role in the maintenance of a rejected status.

Chapter 5 examined developmental differences in helping a victim of exclusion and punishing excluders after witnessing social exclusion. Participants between the ages of 9 and 22 were first included by two peers in Cyberball and subsequently witnessed the social exclusion of a peer by two excluders in Cyberball. Next, they played two types of economic games in which they distributed money between themselves and the peers who included them in the first game (i.e. the includers), the victim of exclusion, and the excluders. The results showed that, with increasing age participants were more likely to altruistically allocate a share of their rewards to the victim. Older adolescents were more likely to punish the excluders than younger adolescents and children. Adults were more merciful in their punishment than adolescents. This quadratic age-related pattern was found both when punishment was beneficial to the participants' own outcomes and when it was costly. Affective perspective-taking (i.e., discriminating between the victim's mood and one's own mood after exclusion) continued to develop in emerging adolescence. Individual differences in affective perspective-taking predicted higher levels of prosocial behavior toward the victim and more pronounced punishment of the excluders, which remained after controlling for age. Taken together, these findings demonstrate that the capacity to understand the distress in a victim of exclusion is important for social action in response to the negative treatment of a peer, in particular in situations where the victim's feelings need to be inferred without explicit emotional cues.

Chapter 6 reviewed the existing literature on the development of prosocial and strategic social behavior from infancy to young adulthood. This review showed that prosocial concern and a preference for fairness emerge very early in development. Nonetheless, across childhood and adolescence, prosocial behavior increases in complexity evidenced by a greater sensitivity to other people's perspectives and more strategic social behavior. Developmental cognitive neuroscience studies showed that developmental increases in the complexity of social behavior were associated with developmental changes in impulse control and perspective taking and the neural circuitry supporting those capacities. The final two chapters were dedicated to uncovering how prosocial behavior in the form of resource sharing and associated neural activity might vary as a function of chronic peer rejection or acceptance.

First, **Chapter 7** mapped the neural processes underlying aversion to unequal distributions of resources in sharing decisions. Young adults played economic games ('equity games') in which they could distribute money in an equal manner, or in unequal manner, which could be beneficial to their own outcomes or to another person's outcomes. Neuroimaging analyses revealed a common neural response associated with both advantageous and prosocial disadvantageous inequity in the dACC, AI and dlPFC, which is a network previously found to be implicated in the reception of unfair treatment. Prosocial disadvantageous inequity was associated with additional activation in the ventral striatum and ventromedial prefrontal cortex, which are regions implicated in the computation of subjective value and processing both social and non-social rewards. These findings laid the foundations for examining whether neural processes associated with violations of fairness norms and those associated with perspective taking in sharing decisions vary as a function of a history of chronic peer rejection or stable peer acceptance.

To test this hypothesis, a group of adolescents with a history of chronic peer rejection and a group with a history of stable peer acceptance played the equity games while undergoing fMRI (**Chapter 8**). Behavioral results showed that stably accepted adolescents were more likely to share equally than chronically rejected adolescents, but only when this was non-costly. When equity was costly, perspective-taking skills moderated the association between peer status history and prosocial behavior. Specifically, chronically rejected adolescents who reported higher levels of perspective taking shared more often than chronically rejected adolescents who reported lower levels of perspective taking. Neuroimaging analyses showed that stably accepted adolescents exhibit higher levels of activity in brain regions supporting perspective taking (e.g. TPJ/pSTS and temporal pole) and the detection of social norm-violations (pre-SMA and AI) than chronically rejected adolescents during choices where equity was costly. These findings provide insights into the mechanisms at the intra-individual level of social complexity, which might underlie the often-found heightened propensity for prosocial behavior in accepted children and adolescents.

9.3 DO PEER EXPERIENCES SHAPE NEURAL RESPONSES TO SOCIAL EXCLUSION?

Chronically rejected adolescents, compared to stably accepted adolescents, showed elevated levels of activation in the ACC and aPFC, which they share with people who are more distressed by social exclusion (Eisenberger et al., 2003) and people who have anxious expectations about interpersonal rejection (DeWall et al., 2012; Masten et al., 2009). Heightened neural responses to exclusion might be a correlate of an intra-individual process (e.g. a hypersensitivity to exclusion), which could play an important role in attaining or maintaining a rejected status. A hypersensitivity to negative peer treatment could account for observations that children with a rejected status rapidly reestablish a rejected status when they enter new groups of peers (Coie & Kupersmidt, 1983; Hardy et al., 2002). Children with a heightened neural reactivity to social exclusion might overreact to negative peer treatment (e.g., social exclusion) in social interactions with peers, which could in turn lead to consensual disliking in the new peer group. As such a heightened neural reactivity might be a potential mechanism through which chronically rejected adolescents initially became rejected or through which they maintained their rejected status over time.

Theories on the development of rejection sensitivity, rooted in attachment theory (Bowlby, 1973), have proposed that repeated exposure to interpersonal rejection by close others, such as parents (Feldman & Downey, 1994), but also peers (London et al., 2007), makes individuals more sensitive to interpersonal rejection. Individuals high in rejection sensitivity are more likely to defensively expect, readily perceive, and overreact to social rejection (Downey & Feldman, 1996). Individuals high in rejection sensitivity experience greater levels of rejection by peers (London et al., 2007), are more distressed by rejection in the lab, and experience greater difficulties in interactions with peers over time (Downey et al., 1998). A greater tendency to anxiously or angrily expect rejection thus often leads to maladaptive responses, which could elicit further rejection and thereby paradoxically fulfill the anxious expectations about being rejected.

The development of anxious and angry expectations about rejection as a consequence of chronic exposure to peer rejection is consistent with social information processing models of peer interactions (Crick & Dodge, 1994). These models propose that expectations about social interactions are shaped by past experiences with peers. For example, in comparison with accepted children, rejected children perceive their peers to be less supportive and trustworthy (Ladd et al., 2014), and aggressive-rejected children adolescents are more likely to see provocation in ambiguous social situations (De Castro, Veerman, Koops, Bosch, & Monshouwer, 2002). Consistent with both attachment theory and social information processing models, it could be that a history of chronic peer rejection has sensitized adolescents to both actual exclusion and to cues signaling potential exclusion. Our findings showing that chronically rejected adolescents show heightened neural reactivity to incidental exclusion provide preliminary evidence for such a notion.

To conclude, elucidating associations between a history of chronic peer rejection and heightened neural responses to social exclusion is a crucial first step toward understanding how experiences in the peer group shape neural responses to social exclusion. However, given that brain responses were measured at a single time point the question remains: have the group differences in neural processing of social exclusion gradually increased over the years due to differential exposure to positive and negative interactions with peers? Or is the heightened neural reactivity to exclusion a reflection of underlying (dys)functions (e.g. problems in emotional regulation), which might have played a role in the emergence of peer group rejection, but remained stable across development? To be able to answer those questions, longitudinal designs are required to critically test whether the heightened neural responses to social exclusion are merely incidental to a rejected status or whether they become greater over time as a function of exposure to peer rejection (see 9.7 for a more elaborate discussion of this notion).

9.4 THE ROLE OF EXECUTIVE FUNCTIONS IN PROSOCIAL REACTIONS TO SOCIAL EXCLUSION

Our studies examining retaliatory and prosocial reactions to exclusion yielded important insights into both intra- and inter-personal processes involved in the emergence or maintenance of peer rejection. The first main result is that we found evidence of neural signatures of two cognitive processes underlying refraining from punishment and acting prosocial toward excluders: perspective taking and cognitive control (**Chapters 3 and 4**). Refraining from punishment and acting prosocial toward the excluders was associated with increased activity in brain regions supporting perspective taking (e.g. dmPFC and TPJ) and brain regions supporting cognitive control (ACC, dorsolateral and ventrolateral PFC). Those who punished more often showed greater activation in these regions when decided to forgive the excluders, suggesting that people engage in higher levels of perspective taking and effortful control in order overcome a (pre-potent) punishing response. Furthermore, individual differences in perspective taking were associated with activity in the mentalizing network (i.e. dmPFC) and individual differences in behavioral regulation problems (i.e. problems in inhibition, cognitive shifting and emotional regulation) scaled with pre-SMA/ACC and dorsal AI activity during forgiveness.

Crucially, both social cognition (e.g. 'theory of mind' abilities) and executive functioning are positively associated with displays of prosocial behavior and peer acceptance (Caputi et al., 2012; Spinrad et al., 2006). Consistent with prior work demonstrating links between executive functioning and peer acceptance, chronically rejected adolescents exhibited more behavioral regulation problems and they recruited control-related brain regions (e.g. dorsal striatum and lateral PFC) to a greater extent than stably accepted adolescents when they acted prosocial toward the excluders. A greater demand on neural circuitry implicated in cognitive control during prosocial reactions to exclusion could be a correlate these reactions being more effortful for adolescents who were chronically rejected. Consequently, in the heat of the moment of their daily experiences with peers, they might be more likely to exhibit behaviors that reinforce or provoke aggressors, which put them at a greater risk for further peer group rejection. Based on the lateral PFC's domain general role in cognitive control and self-regulation in social decisions (Knoch et al., 2006; Strang et al., 2014), it is tempting to interpret heightened lPFC activity during forgiveness as a neural correlate of the suppression of a punishing response. However, given that another subregion in the lPFC was also more active during punishment of excluders, more research is needed to pinpoint what heightened lPFC activity during forgiveness of excluders might reflect.

A promising approach to further investigate this question is using laboratory tasks to assess different executive functions (e.g. inhibition, shifting, emotion regulation) and subsequently relate performance on those tasks to individual differences in prosocial behavior and peer status. Using such an approach, it has been shown that aggressive-rejected children have more difficulties in shifting attention away from negative emotions than non-aggressive-accepted children (Wilson, 2003). Interestingly, difficulties in shifting attention predicted slower reactions in sharing a toy with two other children who had previously excluded the participants from a play activity (which parallels sharing of money with peers who previously excluded participants from ball-tossing in Cyberball in **Chapters 3 and 4**). Future work could expand this literature by examining longitudinal associations between relevant executive functions and behavioral reactions to exclusion and other forms of peer hassles. Such an endeavor can inform intervention research that could test whether training executive functions might have positive affects on peer acceptance.

9.5 THE IMPORTANCE OF AFFECTIVE PERSPECTIVE-TAKING FOR REACTIONS TO THE EXCLUSION OF A PEER

When observing the exclusion of a peer, affective perspective-taking (actively inferring the mood of the victim of exclusion) proved to be an important prerequisite for costly helping of a victim and for punishing excluders (**Chapter 5**). In contrast, cognitive perspective-taking (i.e. the ability to adopt another person's point of view) was not associated with helping and punishment behavior. These findings suggest that children and adolescents not only have to possess the ability to adopt someone else's point of view, but also actively have to infer the affective state of the victim in order to act prosocial toward them. Although peer rejection is not synonymous with peer exclusion, rejected children are excluded more often than accepted children and the negative treatment that rejected children receive from peers is likely to further cement their rejected status (Boivin & Hymel, 1997; Buhs & Ladd, 2001; Buhs et al., 2006). Consequently, elucidating individual and developmental differences in the willingness to help victims or to punish excluders may lead to a better understanding of processes at the level of the peer group that play a role in the emergence and rejection of peer rejection.

Bullying research has shown that peers play a vital role in stopping social exclusion and other forms of bullying (Salmivalli, 2010). Peers can sustain bullying by: i) actively assisting bullies during bullying episodes, ii) by reinforcing the bullies' behavior through giving them positive feedback (e.g. laughing or cheering), or iii) through remaining passive bystanders. Crucially, peers can also put a stop to bullying by actively defending the victim by taking their side, comforting them or by standing up against the bully (Hawkins et al., 2001). Consistent with our findings, those who defend victims in real-life bullying episodes report high levels of both cognitive components of empathy (e.g. understanding other people's emotions) as well as affective components (e.g. vicarious sharing of emotions) (for a review, see van Noorden, Haselager, Cillessen, & Bukowski, 2014). However, not all children who feel empathy for their bullied peers choose to intervene in a bullying situation in real-life. There is evidence to suggest that high levels of affective empathy only predict standing up for a victim when children and adolescents also have a high peer status (Caravita, Di Blasio, & Salmivalli, 2009; Pöyhönen, Juvonen, & Salmivalli, 2010). Future studies should incorporate measures of peer status as well as roles in bullying situations (e.g. defender, reinforcer, assistant) to gain a better understanding of the complex interplay between individual (e.g. empathic abilities) and contextual (e.g. peer status) factors involved in prosocial responses to the exclusion of a peer. Finally, bullying intervention programs often incorporate perspective-taking instructions, but they are not always as effective as they aim to be (van Noorden et al., 2014). One reason could be that some forms of perspective taking might not be as efficient as others for interventions in bullying situations. Our results underline the importance of distinguishing between different forms of perspective taking (i.e. affective vs. cognitive) and their consequences for social action in particular in bullying episodes where victims do not show overt signs of discomfort.

9.6 SHARING IS CARING

A result that consistently emerges from studies across this thesis is that perspective taking and underlying neural circuitry are important for prosocial behavior. That is, the capability to put oneself into the shoes of another person correlated with a variety of prosocial behaviors, including forgiveness of excluders (**Chapter 3)**, helping of a victim of exclusion (**Chapter 5**), and equally sharing resources with strangers (**Chapter 8**). Furthermore, heightened activity in brain regions supporting perspective taking was found during forgiveness (i.e. TPJ and dmPFC; **Chapter 4**), during choices to maximize another person's profits (precuneus and mPFC; **Chapter 7**) and during decision-making in the equity game where fairness was costly (TPJ and temporal pole; **Chapter 8**) (see ***Figure 9.1)***. Taken together, these findings suggest that brain regions of the mentalizing network are involved in switching attention to the perspective of another person in order to act prosocial toward them (Koster-Hale & Saxe, 2013; Mitchell, 2008). During costly sharing decisions, stably accepted adolescents exhibited higher activity in regions of the mentalizing network (TPJ and temporal pole) compared to chronically rejected adolescents, which possibly reflects higher levels of other-oriented thinking during social decisions. Lesser engagement of the mentalizing network during social choices might underlie a reduced tendency to engage in spontaneous other-oriented thinking which might lead to low levels of prosocial behavior. In other words, a child with a rejected status might be less likely to spontaneously engage in other-oriented thinking in social interactions, which could be an intra-personal process underlying their lower levels of prosocial behavior in interactions with peers, which could have played a role in the emergent phase of peer rejection.

On a final note, the maintenance of a rejected status across several years might prevent rejected children from developing the skills they need to gain peer acceptance. Recent studies have shown that children who have a better understanding of other people's mental states (i.e. theory of mind skills) are better liked now and in the future (Fink et al., 2014; Slaughter et al., 2002). Importantly, longitudinal links between theory of mind skills and future peer acceptance were mediated by prosocial behavior (Caputi et al., 2012). These findings suggest that theory of mind skills are shaped in positive interactions with peers and that prosocial behavior toward peers seems to give access to those interactions. Rejected children have fewer positive peer interactions (Boivin & Hymel, 1997) and relationships (e.g. fewer friendships; Parker & Asher, 1993). Therefore, they are likely to have fewer opportunities for developing the socio-cognitive skills and social behaviors that grant them access to positive interactions with peers, keeping them trapped in a web of rejection. Future prospective longitudinal designs incorporating laboratory assessments of theory of mind tasks, assessments of peer status and neuroimaging methods can give valuable insights into how the neural circuitry underlying perspective taking is shaped by interactions with peers and how functional changes in this neural circuitry are associated with changes in peer acceptance.

9.7 TOWARD A NEUROSCIENCE OF PEER RELATIONS

The results of the studies described in this thesis show that a neurocognitive approach to studying peer relations is successful in providing novel insights into the processes at the intra-individual and interactional level of social complexity and their associations with long-term experiences in the peer group. Hereby we show that an integration of developmental cognitive neuroscience of peer interactions with traditional peer relations research can advance the understanding of key questions in both fields. The following sections elaborate on the advantages of a joint enterprise, which could eventually give way to a neuroscience of peer relations. First, we will delineate how the neural systems involved in peer interactions can be better understood through the incorporation of key insights from peer relations research. Subsequently, we will describe in what way neuroscience can help peer relations researchers answer their questions. Finally, we will put forth an integrated research agenda of directions for future research.

How peer relations research may advance neuroscience

First, cognitive neuroscience studies investigating social relations can benefit from a rich body of knowledge on multiple aspects of children's relationships with peers. For example, in cognitive neuroscience studies operationalizations of complex relationships like friendships have often been rather crude (e.g. friendship as a dichotomous variable: friend or no friend). Through intense study of friendships, peer relations researchers have uncovered multiple meaningful dimensions of friendship, including positive dimensions such as protection and companionship, but also negative dimensions such as conflict (Bukowski, Motzoi, & Meyer, 2009). Whereas friendships characterized by high levels of protection or companionship have been linked to positive outcomes (e.g. protection from victimization and lower levels of internalizing problems; Hodges, Boivin, Vitaro, & Bukowski, 1999), friendships characterized by high levels of conflict are related to negative outcomes (e.g. greater risk of being victimized and higher levels of internalizing problems; La Greca & Harrison, 2005). Neuroimaging studies, which have incorporated such knowledge, have shown that neural responses to winning money for a friend are associated with positive aspects of friendship (e.g. closeness, safety, help), but not with negative aspects (e.g. conflict) (Braams, Peters, Peper, Güroğlu, & Crone, 2014). This study demonstrates that measuring multiple aspects of friendships yields a nuanced picture of neural processes involved in complex social relationships.

Second, peer relations research has a strong track record in defining different types of peer experiences. In cognitive neuroscience, terms such as rejection and exclusion are often used interchangeably, despite strong evidence indicating that these are distinct phenomena that show unique associations with adjustment outcomes (e.g. exacerbated school adjustment difficulties in children who are both rejected and excluded by peers; Buhs & Ladd, 2001; Buhs et al., 2006). Theories and hypotheses about neural systems involved in peer interactions can be improved through incorporation of theories and definitions from peer relations research.

Third, developmental cognitive neuroscientists have begun examining the development of neural processes using longitudinal designs. Peer relations researchers have experience in designing complex longitudinal models to establish causal effects. Consequently, cognitive neuroscientists could work together with peer relations researchers to better understand longitudinal patterns.

Fourth, neurobiological models of adolescent social interactions are likely to improve as a result of a greater understanding of the socialization experiences that help shape a developing brain. Neural processes can be better understood through identifying in what way they vary with socially relevant factors and in what when they are resistant to such factors (context-independent). Peer relations research has shown that children's social behavior is guided by their expectations and perceptions of their social world, which are shaped by peer experiences (Ladd et al., 2014; Salmivalli & Isaacs, 2005). Crucially, in order for experiences to change cognitions and behaviors, they must have an impact on brain structure and functioning. Peer researchers and neuroscientists should join forces to develop a theoretical framework of how brain and cognition develop as a consequence of bidirectional interactions between a maturing brain and (social) experiences.

How neuroscience may advance peer relations research

There are several ways in which a cognitive neuroscience approach can give insights into the affective, regulatory, and socio-cognitive processes underlying peer interactions. First, neuroscience methods can provide insight into processes that cannot always be observed in overt behavior or subjective reports, which are usually assessed after a social interaction has happened.

Second, phenotypically dissimilar behaviors (e.g., aggressive behavior vs. withdrawal from social interactions) may result from similar underlying processes (e.g. heightened emotional reactivity to negative peer treatment). Neuroscience can help elucidate such common underlying phenomena, which could then be targeted in interventions. Likewise, apparently similar looking behaviors might be the product of different underlying processes.

Third, neuroscience can give insights into the biological mechanisms that mediate the effects of social experiences (e.g. stressful events in the peer context) and (mental) health problems (e.g. psychosomatic complaints, internalizing, or externalizing problems). For example, it has been widely established that positive and lasting relationships with others are associated with better physical and mental health (Cacioppo, Hawkley, & Berntson, 2003; Slavich, O'Donovan, Epel, & Kemeny, 2010). To fully understand how the social environment affects physical and mental health, it is important to understand links between the social environment and brain functioning.

Fourth, there has been increasing interest in how the peer environment works together with genetic factors to shape social behavior (Brendgen, 2012). However, there are multiple levels of explanation between the level of the genes coding for specific proteins in the body and the level of behavior. Neural responses could therefore be used as endophenotypes, which serve as biological markers that are intermediate between genes and behavior.

Fifth, neurobiological findings can help extend and constrain current theories on peer relations in childhood and adolescence. For example, brain networks sub serving complex cognitive functions such as executive control and perspective taking have been shown to continue to develop structurally and functionally well into the second and third decades of life (Crone & Dahl, 2012; Mills et al., 2012; Shaw et al., 2008). As reviewed in **Chapter 6** these changes in the brain have been shown to importantly map onto developmental changes in social behavior, which has many implications for understanding associations between peer relations and cognitive development. Theories on peer relations in childhood and adolescence could be improved by taking into account the protracted developmental trajectory of complex (social) cognitive functions.

Future directions

The previously described advantages of joining forces between neuroscience and peer relations research open up several exciting avenues for future research. To inspire collaborations between developmental neuroscientists and peer researchers, the following sections describe several of them. They are structured in such a way that each recommendation has the potential to advance our understanding of the neuroscience of peer interactions, but at the same time can elucidate processes underlying peer interactions that are of interest to peer researchers.

Longitudinal designs

Throughout the discussion, several directions for future research were mentioned. The majority of those recommendations call on the need for longitudinal designs to study actual developmental changes within participants. Longitudinal studies with multiple neuroimaging assessments and long-term classroom assessments could give us insights in the transactional relationship between (functional) brain development and influences from the (social) environment. For example, rejected children who show greater neural reactivity to negative peer treatment might be more likely to overreact to negative peer treatment in their classrooms, which could increase the likelihood that they will be victimized. Rejected children who are victimized might show increasingly greater reactivity to emotional stimuli, giving rise to a developmental cascade, which could result in the emergence of externalizing and internalizing problems. Such prospective longitudinal designs could ultimately be instrumental in discovering 'biomarkers' (e.g. heightened neural reactivity to negative peer treatment) that can help identify children and adolescents who run a greater risk for developing psychopathology (e.g. internalizing behavioral problems).

Paradigm development

Using longitudinal designs to study the neural correlates of social interactions places limits on the use of certain experimental paradigms. For example, it seems reasonable to infer that a second or third exposure to social exclusion in Cyberball has a different emotional impact compared to the first time someone is excluded in this game. This could hinder the interpretation of longitudinal effects in brain regions processing emotions. Furthermore, the paradigms used in the context of this thesis used deception to give participants the impression that they engaged in actual social interactions. Given that deception warrants debriefing about the nature of the deceit, it is a challenge for the future to develop inventive social interaction paradigms that can be used for longitudinal neuroimaging research.

In addition to methodological considerations, there are also theoretical considerations encouraging paradigm development. For example, the immediate distress in response to exclusion was not modulated by peer status history. However, research has shown that chronic exposure to stress has been linked to a prolonged stress response, which is possibly associated with an inability to recover from stress (Juster, McEwen, & Lupien, 2010). A task for future research could be to develop paradigms that can reliably assess recovery from a peer stressor (e.g. harassment or exclusion). A working hypothesis would be that children who have been chronically rejected or victimized show dysregulated recovery from peer stressors, which could play a role in the maintenance of a rejected status.

Connectivity

The neuroimaging studies in this thesis successfully showed that activity in brain regions known to be part of specialized neural networks varied as a function peer status history. However, cognitions, emotions, and behaviors are the product of complex interactions within and between specialized networks. Using a method called psychophysiological interaction (PPI), it has been shown that functional coupling between the vlPFC – a brain region involved in regulating the distress caused by social exclusion - and the vACC – a region linked to the distressing aspect of exclusion - increases with age, possibly reflecting age-related increases in emotion regulation capacities (Bolling et al., 2011a). Crucially, poor emotion regulation might be one of the intra-personal factors underlying displays of negative affect or rejection-eliciting behaviors that play a role in the emergence or maintenance of a rejected status (Graziano, Keane, & Calkins, 2007). Relating measures of functional connectivity during emotion-processing tasks to measures of peer status can advance our understanding of both neural systems involved in emotion regulation and the role of emotion regulation difficulties in the maintenance of peer rejection.

Another promising approach to study how brain networks interact is examining *structural* connectivity. Diffusion tensor imaging (DTI) can be used to examine fractional anisotropy (FA), which is an index of the integrity of white matter tracts connecting different brain regions in a neural network. The relevance of studying structural connectivity between brain regions for psychosocial developmental processes has recently been demonstrated by a study showing that higher levels of structural integrity of white matter tracts between the striatum and prefrontal cortex is associated with a greater capacity for controlling the impulse to choose an immediate smaller reward instead of a larger delayed reward (Peper et al., 2013). Studying functional or structural connectivity between regulatory brain regions (e.g. PFC) and regions involved in processing basic emotions (e.g. striatum) can give us more insights into the mechanisms underlying problematic peer relations in rejected children.

Computational approaches to decision-making

Studies described in this thesis have shown that social decisions are the product of activity in distinct neural networks and that activity in these networks varies as a function of chronic peer rejection. For example, **Chapter 8** showed that stably accepted adolescents exhibited higher levels of activity in pre-SMA and TPJ during sharing decisions than chronically rejected adolescents. However, the precise nature of the computations performed by these brain regions remains to be discovered. A tool to learn more about the computations sub served by neural networks is computational modeling, which provides a quantitative framework to examine the relation between specific computational processes and brain activity.

Neuroimaging studies employing computational approaches have successfully linked different computational processes to activity in pre-SMA and TPJ in social decisions. Pre-SMA activity has been linked to a discrepancy detection parameter in fairness decisions (e.g., the discrepancy between expectations about what is fair and actual received treatment; Chang & Sanfey, 2011). TPJ activity has been linked to expectation matching (e.g., giving the amount of money to another person that would be perceived as fair by the other person; Chang, Smith, Dufwenberg, & Sanfey, 2011). Using computational models to decompose social decision-making in children with different peer status histories and link them to neural activity can give more insights into the processes (e.g. reduced sensitivity to violations of social norms) underlying individual differences in social behavior and their relation to peer acceptance.

9.8 CONCLUSIONS

Peer group rejection is a very pervasive phenomenon. Rejection can emerge as soon as children enter formal schooling and for some children rejection remains a reality throughout childhood and adolescence with detrimental consequences for mental health and school adjustment. Therefore, it remains critical to continue to study the developmental mechanisms involved in the emergence and maintenance of peer rejection. The studies described in this thesis show that a developmental cognitive neuroscience approach provides valuable insights into the affective, regulatory, and socio-cognitive processes that underlie behaviors thought to play a role in the emergence and maintenance of a rejected status. Prospective longitudinal designs, measures of brain connectivity, and computational models of decision-making offer promising approaches to further advance our understanding of the neural systems underlying (problematic) peer relations and the computations they sub serve.

To conclude, although peer rejection is a pervasive phenomenon, not all children who are rejected at one point in time are rejected later in life (Hardy et al., 2002; Jiang & Cillessen, 2005; Sandstrom & Coie, 1999). This thesis aimed to gain a better understanding of the mechanisms involved in the maintenance of peer rejection by comparing adolescents who maintained a rejected status throughout elementary school with adolescents with a history stable peer acceptance. Future studies could advance our understanding of the mechanisms involved in the maintenance peer rejection by studying the development of children who were initially rejected by peers, but who become more accepted over time. Studying the development of those children will further increase our understanding of why some children get caught in a vicious cycle of peer rejection that perpetuates itself over time, whereas others are able to escape this cycle and become better accepted by their peers.

NEDERLANDSE SAMENVATTING

Inleiding

De mens heeft een fundamentele behoefte om relaties aan te gaan met anderen (Baumeister & Leary, 1995). Deze behoefte om toe te behoren (de zogenaamde 'need to belong') is zo fundamenteel dat allerlei problemen ontstaan op het moment dat deze behoefte niet bevredigd wordt. Gebeurtenissen die deze behoefte bedreigen zoals buitengesloten of afgewezen worden, leiden op de korte termijn tot hevig psychologisch ongemak. Op de lange termijn heeft chronische blootstelling aan sociale uitsluiting of afwijzing zeer ernstige gevolgen: van slechtere prestaties op school (DeRosier et al., 1994; Hymel et al., 1996) tot het ontwikkelen van psychische problemen zoals angst en depressie (Boivin et al., 1995; Coie et al., 1995) en zelfs crimineel gedrag (Kupersmidt et al., 1995). Daarom is het van groot belang om de mechanismen te begrijpen die een rol spelen bij het ontstaan en de instandhouding van langdurige afwijzing.

Het doel van de in dit proefschrift beschreven onderzoeken was om de neurocognitieve mechanismen in kaart te brengen die een rol spelen bij de instandhouding van sociale uitsluiting als ook de mechanismen die belangrijk zijn voor het vertonen van gedrag dat leidt tot acceptatie. In het eerste deel van dit proefschrift staan de neurocognitieve processen centraal die ten grondslag liggen aan reacties op sociale uitsluiting. De manier waarop iemand reageert op uitsluiting bepaalt in sterke mate of het slechts bij een eenmalige uitsluiting blijft, of dat het een terugkerend fenomeen wordt. Kinderen en adolescenten die fel reageren op uitsluiting zouden hun pestkoppen kunnen provoceren en op die manier vaker tot slachtoffer van uitsluiting gemaakt worden dan kinderen die zich sociaal opstellen en proberen weer aansluiting te vinden bij hun klasgenoten (Coie, 1990; Sandstrom, 2004). Om beter te begrijpen waarom jongeren op een bepaalde manier reageren op uitsluiting hebben we niet alleen hun subjectieve reacties op uitsluiting onderzocht, maar ook hun gedragsmatige reacties bestudeerd en gekeken naar wat er in hun hersenen gebeurt tijdens en na uitsluiting.

In het tweede deel van dit proefschrift staan de neurocognitieve processen centraal die een rol spelen bij het tonen van prosociaal gedrag: gedrag met als doel het welbevinden van een ander te vergroten. Prosociale gedragingen zoals iemand helpen, samenwerken of iets met iemand delen, spelen een belangrijke rol bij het verwerven van acceptatie in een groep en het in stand houden van deze acceptatie (Coie & Kupersmidt, 1983; Deković & Gerris, 1994; Layous et al., 2012). Vanwege de cruciale rol die prosociaal gedrag vervult in het verwerven van acceptatie in een groep hebben we de psychologische en neurale mechanismen onderzocht die belangrijk zijn voor prosociaal gedrag in de vorm van het gunnen van geld aan een ander.

Om de neurocognitieve mechanismen die ten grondslag liggen aan reacties op uitsluiting en prosociaal gedrag in beeld te brengen, hebben we gebruik gemaakt van experimentele sociale interactie paradigma's in combinatie met een beeldvormende techniek genaamd functionele kernspintomografie (functional magnetic resonance imaging of fMRI). fMRI is een methode die het mogelijk maakt om psychologische processen te relateren aan activiteit in de hersenen (neurale processen) terwijl mensen een taak uitvoeren in een MRI scanner. Ook hebben we bij de deelnemers aan onze onderzoeken en bij hun ouders en klasgenoten vragenlijsten afgenomen om meer te weten te komen over verschillende psychologische vermogens zoals: het vermogen om je in een ander te verplaatsen en een situatie vanuit hun perspectief te bekijken (perspectief-nemen) en het vermogen tot het reguleren van je gedrag. Eerst hebben we de neurale en psychologische processen die betrokken zijn bij reacties op uitsluiting en prosociaal gedrag onderzocht in een groep jongvolwassenen. Om beter te begrijpen hoe deze neurocognitieve processen samenhangen met langdurige acceptatie en afwijzing in een groep van leeftijdsgenoten (c.q. de *peer groep*), hebben we deze processen ook onderzocht in adolescenten met een geschiedenis van langdurige afwijzing en in adolescenten met een geschiedenis van langdurige acceptatie.

Acceptatie en afwijzing in peer groepen (bijvoorbeeld klassen van kinderen) kunnen op een betrouwbare manier gemeten worden door alle leden van de groep twee vragen te stellen: "Wie vind je het aardigst/met wie ga je het liefst om?" en "Wie vind je het minst aardig/met wie ga je het minst graag om?" (Bukowski et al., 2000; Coie et al., 1982; Newcomb & Bukowski, 1983). Door de antwoorden van alle leden van de groep te combineren, kan de mate waarin ieder individu geaccepteerd en afgewezen is door alle andere leden van de groep in kaart worden gebracht. Kinderen die door zeer weinig klasgenoten als 'aardig' en door zeer veel klasgenoten als 'niet aardig' worden gezien worden volgens deze methode geclassificeerd als kinderen met een 'afgewezen' status. Longitudinale onderzoeken - waarbij acceptatie en afwijzing van kinderen gedurende langere tijd meerdere keren is gemeten - hebben aangetoond dat afwijzing door leeftijdsgenoten voorspellend is voor een reeks aan negatieve levensuitkomsten, o.a. slechte schoolprestaties (DeRosier et al., 1994), internaliserende problematiek (bijv. angst en depressieve klachten; Ladd & Troop-Gordon, 2003) en externaliserende problematiek (bijv. agressief en normoverschrijdend gedrag; van Lier & Koot, 2010). Hoewel de relatie tussen groepsgewijze afwijzing en het ontstaan van dit soort problematiek tientallen keren is aangetoond, weten we nog vrij weinig over de mechanismen die er voor zorgen dat groepsgewijze afwijzing ontstaat en hoe deze in stand blijft gedurende de kindertijd en de adolescentie. Daarom hebben wij ingezoomd op verschillende processen die daarbij een rol zouden kunnen spelen. Als eerste hebben we processen onderzocht die een rol spelen in het stoppen of in stand houden van sociale uitsluiting.

Deel I: Reacties op sociale uitsluiting

Een klasgenoot buitensluiten is één van de manieren waarop kinderen en adolescenten het vaakst uiting geven aan een negatieve (groeps-)attitude jegens deze persoon (Coie et al., 1990).

Sociale uitsluiting is een manier van pesten die zowel direct als indirect kan plaatsvinden. Directe uitsluiting is het expliciet laten weten dat een ander niet mee mag doen met een activiteit. Indirecte uitsluiting is impliciet en kan zich uiten in het negeren van een klasgenoot of hem/haar niet te vragen om mee te doen aan een activiteit (Gazelle & Ladd, 2003). Alhoewel sociale uitsluiting een vervelende ervaring is in alle fasen van het leven (Williams, 2007), is er evidentie voor de hypothese dat sociale uitsluiting extra pijnlijk is gedurende de adolescentie. Adolescenten maken zich meer zorgen over acceptatie door leeftijdsgenoten dan volwassenen (O'Brien & Bierman, 1988). Daarnaast is het niet kunnen vinden van een plek in een groep van leeftijdsgenoten tijdens de adolescentie vaak een symptoom of voorloper van psychosociale problemen (Boivin et al., 1995; Prinstein & Aikins, 2004).

De adolescentie zou met name erg stressvol zijn voor tieners die langdurig zijn afgewezen door hun klasgenoten (Coie et al., 1990). Langdurig afgewezen adolescenten hebben minder positieve interacties met leeftijdsgenoten gehad (Boivin & Hymel, 1997; Parker & Asher, 1993), waardoor zij minder de kans hebben gehad om sociale vaardigheden te ontwikkelen die nuttig zijn voor het omgaan met alle veranderingen tijdens de overgang van de kindertijd naar de volwassenheid. Op het moment dat zij voor het eerst naar de middelbare school gaan, missen zij sociale vaardigheden die nodig zijn om op een adequate manier met alle nieuwe sociale ervaringen van de adolescentie om te gaan. Indien ze worden buitengesloten zouden zij mogelijke heftiger hierop kunnen reageren. Heftigere reacties kunnen op hun beurt juist weer leiden tot meer afwijzing en uitsluiting met alle negatieve gevolgen van dien voor hun schoolprestaties en psychische gezondheid.

Niet ieder kind dat een afgewezen status heeft in zijn/haar klas wordt ook regelmatig buitengesloten. Desalniettemin, worden afgewezen kinderen wel veel vaker buitengesloten dan kinderen die in hoge mate geaccepteerd zijn in hun klas. Bovendien lopen kinderen die zowel buitengesloten als afgewezen worden een grotere kans op het ontwikkelen van psychosociale problemen (Buhs & Ladd, 2001; Buhs et al., 2006). Om meer te leren over de processen die een rol spelen bij reacties op uitsluiting en hoe deze samenhangen met groepsgewijze afwijzing hebben wij drie processen onderzocht: i) subjectieve (negatieve gedachten en gevoelens) en neurale reacties op uitsluiting; ii) gedragsmatige reacties op uitsluiting en de neurale processen die daarbij betrokken zijn en iii) gedragsmatige reacties op uitsluiting van een leeftijdsgenoot.

In **Hoofdstuk 2** hebben we met behulp van vragenlijsten en fMRI de relatie onderzocht tussen een geschiedenis van jarenlange afwijzing en subjectieve en neurale reacties op uitsluiting. Om dit te onderzoeken hebben we jongeren (12-15 jaar) uitgenodigd wiens acceptatie en afwijzing door klasgenoten gedurende zes jaar (groep 3 tot en met groep 8 van de basisschool) was gemeten. Sommige jongeren werden gedurende die zes jaar langdurig afgewezen en anderen werden juist langdurig geaccepteerd door hun klasgenoten. Om de reacties van beide groepen (langdurig afgewezen en geaccepteerde jongeren) op sociale uitsluiting te testen speelden zij twee keer een online balspel genaamd 'Cyberball' (Williams et al., 2000) terwijl ze in de MRI scanner lagen.

In beide spellen werden de deelnemers gekoppeld aan twee onbekende leeftijdsgenoten met wie ze via een knoppenkast en een computerscherm een bal konden overgooien. In het eerste spel kregen de deelnemers even vaak de bal als de twee onbekende leeftijdsgenoten. Ze werden dus betrokken in het spel. In het tweede spel werden de deelnemers gekoppeld aan twee nieuwe leeftijdsgenoten. Aan het begin van het tweede spel kregen de deelnemers de bal nog wel één keer toegespeeld, maar daarna sloten de andere twee spelers de deelnemers buiten door de bal niet meer naar hen te gooien. Na uitsluiting rapporteerden beide groepen een verlaagde stemming (ze voelden zich bijvoorbeeld verdrietiger) en lagere niveaus van gevoelens van toebehoren, zelfvertrouwen, controle over de sociale omgeving en een betekenisvol bestaan. Langdurig afgewezen jongeren rapporteerden negatieve gevoelens die niet te onderscheiden waren van de negatieve gevoelens die de geaccepteerde jongeren rapporteerden. De fMRI resultaten lieten zien dat de chronisch afgewezen jongeren meer activiteit vertoonden in de dorsale anterieure cingulate schors (of cortex) (dACC) - een soort neuraal alarmsysteem - op het moment dat zij werden buitengesloten in het balspel (spel 2). Deze verhoogde activiteit in de dACC was ook te zien op de momenten dat zij de bal incidenteel niet kregen in het spel waarin ze wel betrokken werden (spel 1). Deze incidentele uitsluiting ging ook gepaard ging met verhoogde activiteit in de anterieure prefrontale schors. Deze verhoogde neurale reactiviteit in dACC en prefrontale schors is eerder gevonden bij mensen die hypergevoelig zijn voor afwijzing en bij mensen die angstige of agressieve verwachtingen over afwijzing te hebben (Masten et al., 2009; DeWall et al., 2012). De verhoogde neurale reactiviteit op uitsluiting bij langdurig afgewezen adolescenten kan dus één van de mechanismen zijn die hebben bijgedragen aan gedachten, gevoelens en/of gedrag dat heeft geleid tot het ontstaan van groepsgewijze afwijzing.

Het tweede onderzochte proces dat een rol speelt in het ontstaan en/of in stand houden van uitsluiting is: de gedragsmatige reactie op uitsluiting. Om de neurocognitieve processen in kaart te brengen die een rol spelen bij gedragsmatige reacties op uitsluiting hebben we in **Hoofdstuk 3** de neurale processen onderzocht die gepaard gaan met wraakzuchtige en prosociale reacties op uitsluiting. We hebben een groep jongvolwassenen (in de leeftijd van 18-25) gevraagd om geld te verdelen tussen henzelf en leeftijdsgenoten die hen eerder hadden betrokken of eerder hadden buitengesloten in Cyberball. De deelnemers konden ervoor kiezen om wraak te nemen op de uitsluiters door hen minder geld te gunnen ('straffen') of om af te zien straf en het geldbedrag eerlijk te delen met de uitsluiters ('vergeving'). Straffen kon samengaan met financiële winsten, verliezen of kon geen invloed hebben op de financiële uitkomst van de deelnemers. De resultaten lieten zien dat de deelnemers de uitsluiters straften wanneer dit leidde tot financieel gewin, maar ook wanneer er geen gevolgen waren voor de eigen uitkomsten en zelfs als straffen gepaard ging met financiële verliezen. Het straffen van de uitsluiters ging gepaard met activiteit in de pre-supplementaire motorische schors (pre-SMA) en de anterieure insula (AI) van de deelnemers. De pre-SMA werd bovendien meer geactiveerd op het moment dat straffen financieel kostbaar was in vergelijking met straf met financiële winst of geen financiële gevolgen. Deelnemers die rapporteerden zich in het dagelijks leven vaker te verplaatsen in een ander (c.q. vaker andermans 'perspectief nemen') kozen er vaker voor om eerlijk te delen met de uitsluiters. Het eerlijk delen van het geldbedrag, 'vergeving', ging gepaard met activiteit in hersengebieden in netwerken die belangrijk zijn om je te kunnen verplaatsen in een ander (temporo-parietale junctie [TPJ] en dorsomediale prefrontale schors [dmPFC]) en gebieden die belangrijk zijn voor het reguleren van gedrag (dACC en dorsolaterale prefrontale schors [dlPFC]).

Deze resultaten ondersteunen de hypothese dat perspectief-nemen en het reguleren van je gedrag (door cognitieve controle) belangrijke psychologische vermogens zijn om je prosociaal op te stellen tegenover leeftijdsgenoten die je net hebben buitengesloten. In vergelijking met jongeren die geaccepteerd zijn in hun klas, zijn afgewezen jongeren veel vaker geneigd om agressief te reageren op conflicten met klasgenoten waardoor deze conflicten vaker escaleren (Fabes & Eisenberg, 1992; Rabiner et al., 1990). Daarnaast hebben zij minder goed ontwikkelde sociaal-cognitieve vaardigheden en hebben zij moeite met het reguleren van hun gedrag en het beheersen van impulsen en negatieve gevoelens (Dodge et al., 2003; Eisenberg et al., 1997; Fink et al., 2014). Op basis van deze bevindingen, verwachtten wij dat activatie van de neurale systemen die belangrijk zijn voor sociale cognitie en gedragsregulatie tijdens vergeving varieert op basis van langdurige blootstelling aan afwijzing.

Om deze hypothese te testen, hebben we langdurig afgewezen jongeren en langdurig geaccepteerde jongeren (net als de volwassenen in **Hoofdstuk 3**) de mogelijkheid gegeven om de leeftijdsgenoten die hen hadden buitengesloten in het balspel te straffen of te vergeven (**Hoofdstuk 4**). De resultaten lieten zien dat, net zoals volwassenen, beide groepen adolescenten de uitsluiters straften door hen vaker minder geld te gunnen. In beide groepen, ging straffen gepaard met activiteit in het ventrale striatum, dlPFC en de pariëtale schors. Tijdens vergeving werden er individuele verschillen gevonden in de mate waarin de neurale netwerken die belangrijk zijn voor sociale cognitie en gedragsregulatie werden geactiveerd. Ten eerste vertoonden langdurig afgewezen jongeren tijdens vergeving een verhoogde activiteit in een controle netwerk in het brein (dorsale striatum en laterale PFC) ten opzichte van de langdurig geaccepteerde jongeren. Daarnaast werd er tijdens vergeving hogere activiteit gevonden in de dmPFC (een deel van het sociale cognitie netwerk) in deelnemers die hogere niveaus van perspectief-neem-vaardigheden rapporteerden. Jongeren waarvan hun ouders rapporteerden dat zij problemen hadden in het reguleren van hun gedrag vertoonden verhoogde activiteit in de pre-SMA en de dorsale AI (netwerken betrokken bij gedragsregulatie). Deze bevindingen laten zien dat hersenactiviteit tijdens prosociale reacties, maar niet tijdens wraakzuchtige reacties, op uitsluiting varieert op basis van een blootstelling aan langdurige afwijzing, sociaal-cognitieve vaardigheden en problemen in gedragsregulatie. Samen bieden ze inzicht in verschillende intra-individuele processen die betrokken zijn bij reacties op uitsluiting die een rol spelen bij de instandhouding van langdurige uitsluiting.

Het derde onderzochte proces dat een rol speelt bij de instandhouding of de beëindiging van uitsluiting in een groep is de gedragsmatige reactie op uitsluiting van een ander. Eerder onderzoek heeft laten zien dat kinderen die getuige zijn van een pest-situatie er in meer dan 50% van de gevallen voor kunnen zorgen dat het pesten stopt (Hawkins et al., 2001). Bovendien rapporteren pestslachtoffers die getroost of beschermd worden door een klasgenoot hogere niveaus van psychisch welbevinden dan slachtoffers die niet geholpen worden (Sainio et al., 2010). Daarom hebben we in **Hoofdstuk 5** de ontwikkeling van perspectief-nemen en reacties op de uitsluiting van een leeftijdsgenoot onderzocht. Deelnemers in vijf leeftijdsgroepen (van 9 tot en met 22 jaar) werden eerst zelf betrokken in Cyberball alvorens zij toekeken hoe een onbekende leeftijdsgenoot werd buitengesloten door twee uitsluiters. Vervolgens speelden zij twee verschillende economische spellen waarin zij geld verdeelden tussen henzelf en een leeftijdsgenoot. Deze ontvanger van het geld kon iemand zijn die de deelnemers had betrokken in het eerste balspel, een van de uitsluiters uit het tweede balspel of het slachtoffer van de uitsluiting. Resultaten lieten zien dat naarmate de deelnemers ouder waren, zij een groter deel van hun geld weggaven aan het slachtoffer van uitsluiting. Oudere adolescenten (14- en 16-jarigen) straften bovendien de uitsluiters ook strenger dan de jongere deelnemers (9-11-jarigen) door hen minder geld te gunnen dan de spelers uit het eerste balspel en het slachtoffer. Volwassenen (22-jarigen) straften de uitsluiters ook, maar zij gunden de uitsluiters meer geld dan de adolescenten. Deze kwadratische relatie tussen leeftijd en strafgedrag werd zowel in het eerste spel gevonden waarin straffen de deelnemers geld opleverde als in het tweede spel waarin straffen de deelnemers juist geld kostte. Deelnemers in alle leeftijdsgroepen die zich inleefden in het slachtoffer en rapporteerden dat het slachtoffer zich slechter moest voelen dan zijzelf waren prosocialer naar het slachtoffer toe en straften de uitsluiters strenger. Deze bevindingen laten zien dat het vermogen om je in te leven in een ander en om te begrijpen dat uitsluiting leidt tot negatieve gevoelens bij een slachtoffer belangrijk is om actie te ondernemen na het zien van uitsluiting van een leeftijdsgenoot. Met name in situaties waarin adolescenten de gevoelens van een ander moeten inschatten zonder dat zij daarbij gebruik kunnen maken van expliciete aanwijzingen van negatieve gevoelens (bijvoorbeeld gezichtsuitdrukkingen of verbale indicatoren van verdriet).

Deel II: Eerlijk delen

Het vaak vertonen van prosociaal gedrag is een van de sterkste voorspellers van de mate waarin een kind geaccepteerd is alsmede zijn/haar toekomstige acceptatie (Caprara et al., 2000; Caputi et al., 2012; Crick, 1996; Deković & Gerris, 1994; Zimmer-Gembeck, et al., 2005). Het vertonen van prosociaal gedrag heeft zelfs een causaal effect op de mate waarin een kind of adolescent geaccepteerd wordt door zijn/haar klasgenoten (Coie & Kupersmidt, 1983; Layous et al., 2012). Om inzicht te verkrijgen in verschillende mechanismen die betrokken zijn bij prosociaal gedrag, hebben we verschillende psychologische vermogens en hersenactiviteit gemeten tijdens het verdelen van geld tussen hezelf en een onbekende leeftijdsgenoot. Bij het ene kind kan een ogenschijnlijke egoïstische beslissing om al het geld te houden gepaard gaan met verhoogde activiteit in hersennetwerken die belangrijk zijn om je te verplaatsen in een ander of in netwerken die betrokken zijn bij de emotionele reactie op het schenden van een sociale norm. Een ander kind kan dezelfde beslissing nemen zonder zich te verplaatsen in een ander of zonder emotionele signalen te voelen bij het schenden van de sociale norm. De hypothese is dan dat bij het laatste kind deze netwerken in mindere mate geactiveerd worden dan bij kinderen die zich wel verplaatsen in een ander en ongemak voelen bij het schenden van een sociale norm. Zo kan het meten van hersenactiviteit inzicht bieden in verschillende sociaal-cognitieve en emotionele processen die ten grondslag liggen aan ogenschijnlijk vergelijkbaar egoïstisch of prosociaal gedrag.

Om een theoretisch kader te schetsen over de hersengebieden en de psychologische vermogens die belangrijk zijn voor het vertonen van prosociaal gedrag in verschillende fases van de ontwikkeling is in **Hoofdstuk 6** de relevante literatuur samengevat. Dit overzicht laat zien dat belang hechten aan het welzijn van een ander en een voorkeur voor eerlijke (gelijke) verdelingen van goederen al in de baby- en peutertijd zichtbaar is. Ondanks dat deze bouwstenen van prosociaal gedrag al zo vroeg in de ontwikkeling aanwezig zijn, wordt prosociaal gedrag gedurende de kindertijd en de adolescentie steeds complexer van aard en ook steeds geraffineerder ingezet. Deze veranderingen gaan gepaard met de ontwikkelende vermogens om je te kunnen verplaatsen in een ander en om (zelfzuchtige) impulsen te beheersen. Een overzicht van fMRI studies laat zien dat de toename in de complexiteit van prosociaal gedrag gepaard gaat met functionele veranderingen in neurale netwerken die betrokken zijn bij perspectief-nemen (TPJ en MPFC) en gedragsregulatie (dlPFC). Het neurale netwerk dat belangrijk is voor het detecteren van sociale normoverschrijdingen (ACC-insula netwerk) wordt in verschillende fasen van de ontwikkeling (kindertijd, adolescentie en volwassenheid) op een vergelijkbare manier geactiveerd. Deze studies ondersteunen de hypothese dat het herkennen van sociale normoverschrijdingen en bijbehorende hersenactiviteit al voor de adolescentie ontwikkelt. Ze laten ook zien dat het vermogen om te handelen volgens sociale normen als de situatie meer aandacht voor de ander vereist of wanneer deze meer controle behoeft nog volop in ontwikkeling is tijdens de adolescentie. **Hoofdstuk 6** bood ons de inzichten voor het opstellen van onze hypotheses over in welke neurale systemen we verschillen konden verwachten tussen geaccepteerde en afgewezen jongeren op het moment dat zij voor de keuze komen te staan of zij eerlijk willen delen met een ander.

In **Hoofdstuk 7** hebben we de neurale processen onderzocht die gepaard gaan met het kiezen voor een ongelijke verdeling van geld. Jongvolwassenen speelden drie verschillende economische spellen ('equity games') waarin zij geld mochten verdelen tussen zichzelf en een onbekende leeftijdsgenoot. In die spellen konden ze kiezen voor een eerlijke (beide spelers kregen evenveel) of oneerlijke (de ene speler kreeg meer dan de ander) verdeling. In deze spellen kon een oneerlijke verdeling soms in het eigen voordeel zijn of in het voordeel van de onbekende leeftijdsgenoot. Onze resultaten lieten zien dat in beide gevallen het schenden van de eerlijkheidsnorm (door voor de oneerlijke verdeling te kiezen) gepaard ging met activiteit in de dACC, AI en dlPFC – een neuraal netwerk dat al eerder is aangetoond belangrijk te zijn voor het herkennen van, en het reageren, op oneerlijke behandeling. Er werd ook hersenactiviteit gevonden die uniek was voor prosociale schendingen van de eerlijkheidsnorm. Wanneer deelnemers besloten om niet de eerlijkheidsnorm te volgen, maar te kiezen voor een ongelijke verdeling in het voordeel van een ander hadden zij een verhoogde activiteit in het ventrale striatum en de ventromediale prefrontale schors. Deze hersengebieden vormen een netwerk dat belangrijk is voor de representatie van beloningen en subjectieve waarde. Deze gebieden worden bijvoorbeeld ook actief bij het eten van iets lekkers, bij het zien van seksuele stimuli, en bij het ontvangen van geld. Deze resultaten legden de basis om verder te onderzoeken hoe acceptatie en afwijzing tijdens de kindertijd samenhangen met neurale processen tijdens eerlijk en oneerlijk delen.

In **Hoofdstuk 8** wordt een studie beschreven waarin dit verder is onderzocht. Adolescenten met een geschiedenis van langdurige afwijzing en adolescenten met een geschiedenis van langdurige acceptatie speelden de equity games in een MRI scanner. Langdurig geaccepteerde adolescenten kozen vaker voor een gelijke verdeling van geld dan langdurig afgewezen adolescenten, maar alleen als dit henzelf geen geld kostte. Op het moment dat het geld kostte om eerlijk te delen werden er geen groepsverschillen gevonden. Er werden wel verschillen gevonden binnen de langdurige afgewezen groep. Om precies te zijn, langdurig afgewezen jongeren met lagere niveaus van perspectief-nemen gaven veel minder vaak geld weg dan afgewezen jongeren met hogere niveaus van perspectief-nemen. Perspectief-nemen bleek dus wederom een belangrijke voorspeller voor prosociaal gedrag. Tijdens het nemen van dit soort kostbare beslissingen over de verdeling van geld, vertoonde de langdurig geaccepteerde groep meer activiteit in netwerken in het brein die betrokken zijn bij perspectief-nemen (c.q. TPJ/pSTS en de temporale pool) en het detecteren van sociale normoverschrijdingen (c.q. pre-SMA en AI) dan de langdurig afgewezen groep. Uit eerder onderzoek weten we dat kinderen en jongeren die geaccepteerd zijn in hun klassen meer prosociaal gedrag vertonen en zich beter kunnen inleven in een ander (Caputi et al., 2012; Fink et al., 2014; Slaughter et al., 2002). De verschillen in activatie in deze twee neurale netwerken bieden een eerste kijk op de mechanismen die mogelijk ten grondslag liggen aan deze observaties.

Kritische bespiegeling

De verhoogde neurale reactiviteit op uitsluiting in de langdurig afgewezen adolescenten is in overeenstemming met literatuur die stelt dat langdurige blootstelling aan afwijzing leidt tot een overgevoeligheid voor afwijzing (Feldman & Downey, 1994; London et al., 2007). In het licht van dergelijk werk, zouden de verhoogde neurale reactiviteit op uitsluiting geïnterpreteerd kunnen worden als een *gevolg* van langdurige blootstelling aan afwijzing. Echter, wij hebben de hersenactiviteit tijdens uitsluiting slechts op één moment gemeten. Daarom weten we niet of de verhoogde neurale reactiviteit een gevolg is van langdurige afwijzing of dat deze al aanwezig was voordat deze jongeren voor het eerst naar de basisschool gingen en dus nog voordat zij werden afgewezen door hun klasgenoten. De verhoogde neurale reactiviteit zou net zo goed een mechanisme kunnen zijn dat een rol heeft gespeeld bij het verwerven van afwijzing. Het zou bijvoorbeeld een afspiegeling kunnen zijn van problemen in het reguleren van negatieve gevoelens zoals verdriet of woede. Kinderen die moeite hebben met het reguleren van negatieve gevoelens lopen een grotere kans op afwijzing dan kinderen die hun gevoelens goed onder controle kunnen houden (Spinrad et al., 2006; Eisenberg et al., 1997). Om meer inzicht te krijgen in deze vraag, is het belangrijk om longitudinale onderzoeksdesigns te gebruiken waarbij kinderen langdurig gevolgd worden en meerdere malen gescand worden. Met dergelijke designs is het mogelijk om te testen of de verhoogde neurale reactiviteit een bijproduct is van een afgewezen status of dat deze reactiviteit zich ontwikkelt ten gevolge van langdurige blootstelling aan afwijzing.

Een tweede stap voor vervolgonderzoek is: verder onderzoek doen naar de relatie tussen hersenactiviteit enerzijds en gevoelens, gedachten en gedrag die acceptatie en afwijzing beïnvloeden anderzijds. De gevonden verhoogde activiteit in een 'cognitieve controle-netwerk' in het brein tijdens vergeving bij de langdurig afgewezen jongeren duidt erop dat een groter beroep op cognitieve controle een mogelijke rol speelt in de beteugeling van impulsieve reacties op uitsluiting. Maar om welke controle-vaardigheden gaat het hier? Het netwerk is immers betrokken bij een scala aan 'executieve functies' zoals inhibitie, switchen en het reguleren van emoties (Crone & Dahl, 2012). Om beter te begrijpen wat de verschillen in activatie van dit controle-netwerk betekenen, kunnen in de toekomst verschillende executieve functies gemeten worden. Vervolgens kunnen deze functies gerelateerd worden aan activiteit in de controle-netwerken in het brein en individuele verschillen in prosociaal gedrag en sociale status. De uitkomsten van zulke onderzoeken kunnen op den duur bijdragen aan interventiestudies waarbij getest kan worden of het trainen van executieve functies positieve effecten heeft op acceptatie door klasgenoten. Een andere veelbelovende benadering die meer inzicht kan geven in de relatie tussen hersenprocessen en de cognitieve processen die zij representeren is een computationele benadering van hersenfunctie (Chang & Sanfey, 2011; Chang et al, 2011). Door gebruik te maken van wiskundige modellen wordt het mogelijk om de specifieke "berekeningen" die populaties van hersencellen samen uitvoeren beter te begrijpen. Computationele modellen kunnen ons helpen om problemen in de omgang met leeftijdsgenoten beter te begrijpen door inzicht te bieden in de neurale systemen die onderliggend zijn aan die problemen.

Conclusies en toekomstperspectief

Dit proefschrift toont aan dat een neurowetenschappelijke benadering waardevolle inzichten biedt in de emotionele, regulerende en sociaal-cognitieve processen die ten grondslag liggen aan gedragingen die een rol spelen in het ontstaan en in stand houden van afwijzing en acceptatie door leeftijdsgenoten. Zo tonen de studies in dit proefschrift aan dat langdurige afwijzing tijdens de kindertijd gepaard gaat met een verhoogde “neurale gevoeligheid” voor uitsluiting tijdens de adolescentie. Langdurige afwijzing in de klas hangt ook samen met een verhoogde activiteit in controle-netwerken in het brein tijdens vergeving van pestkoppen en verminderde activiteit in ‘sociale cognitie’ netwerken tijdens prosociale keuzes. Tenslotte, laat ons onderzoek zien dat het vermogen om je in een ander te verplaatsen belangrijk is voor een reeks van prosociale gedragingen zoals: het vergeven van uitsluiters, een buitengesloten leeftijdsgenoot te helpen en eerlijk delen met een onbekende leeftijdsgenoot.

Dit proefschrift laat zien dat de integratie van een neurowetenschappelijke en traditionele ‘peer relaties’ methoden ons dichter bij antwoorden kan brengen op kernvragen in zowel de neurowetenschappen als de studie naar sociale relaties in groepen kinderen en jongeren. Wij moedigen 'peer-onderzoekers' en hersenwetenschappers aan om de handen in een te slaan om samen een theoretisch kader te ontwikkelen waarin sociale- en hersenontwikkeling begrepen kan worden als het product van biologische rijpingsprocessen en (sociale) ervaringen die elkaar voortdurend vormen. Toekomstige projecten waarin op meerdere momenten tijdens de ontwikkeling scans gemaakt worden van de hersenen van kinderen kunnen ons meer leren over de relatie tussen hersenontwikkeling en de sociale ontwikkeling op de lange termijn. Uiteindelijk zal een neurowetenschappelijk perspectief op acceptatie en afwijzing handvatten kunnen bieden voor interventies die gericht zijn op het helpen van jongeren die kampen met psychische problemen of problemen op school door een gebrek aan acceptatie door leeftijdsgenoten.

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CURRICULUM VITAE

Gerardus Johannes (Geert-Jan) Will was born on April 13th 1986 in Gouda, the Netherlands. After graduating from secondary school (Gymnasium at De Goudse Waarden in Gouda) in 2004, he went to Utrecht University to study psychology and neuroscience. He received a BSc in Psychology in 2008 and an MSc in Neuroscience and Cognition (cum laude) in 2011. During his master's, Geert-Jan investigated the role of testosterone in social decision-making together with Jack van Honk and David Terburg. For his second research internship, Geert-Jan went to Harvard University where he learned many things about the science of morality (and many things about the morality of science). At Harvard, he conducted studies on peer influence and moral decision-making and he assisted in studies on the development of the sense of fairness. He started with a PhD project at the Institute of Psychology at Leiden University in 2011. Under the supervision of Dr. Berna Güroğlu and Prof. dr. Eveline Crone, he explored the neural and psychological processes associated with peer group acceptance and rejection in childhood and adolescence. The results of his doctoral work are described in this dissertation. In 2015, Geert-Jan moved to London to work as a postdoctoral research associate in Prof. dr. Ray Dolan's 'Cognition, Emotion & Psychiatric Disorders' group at the Wellcome Trust Centre for Neuroimaging at University College London.

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