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

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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

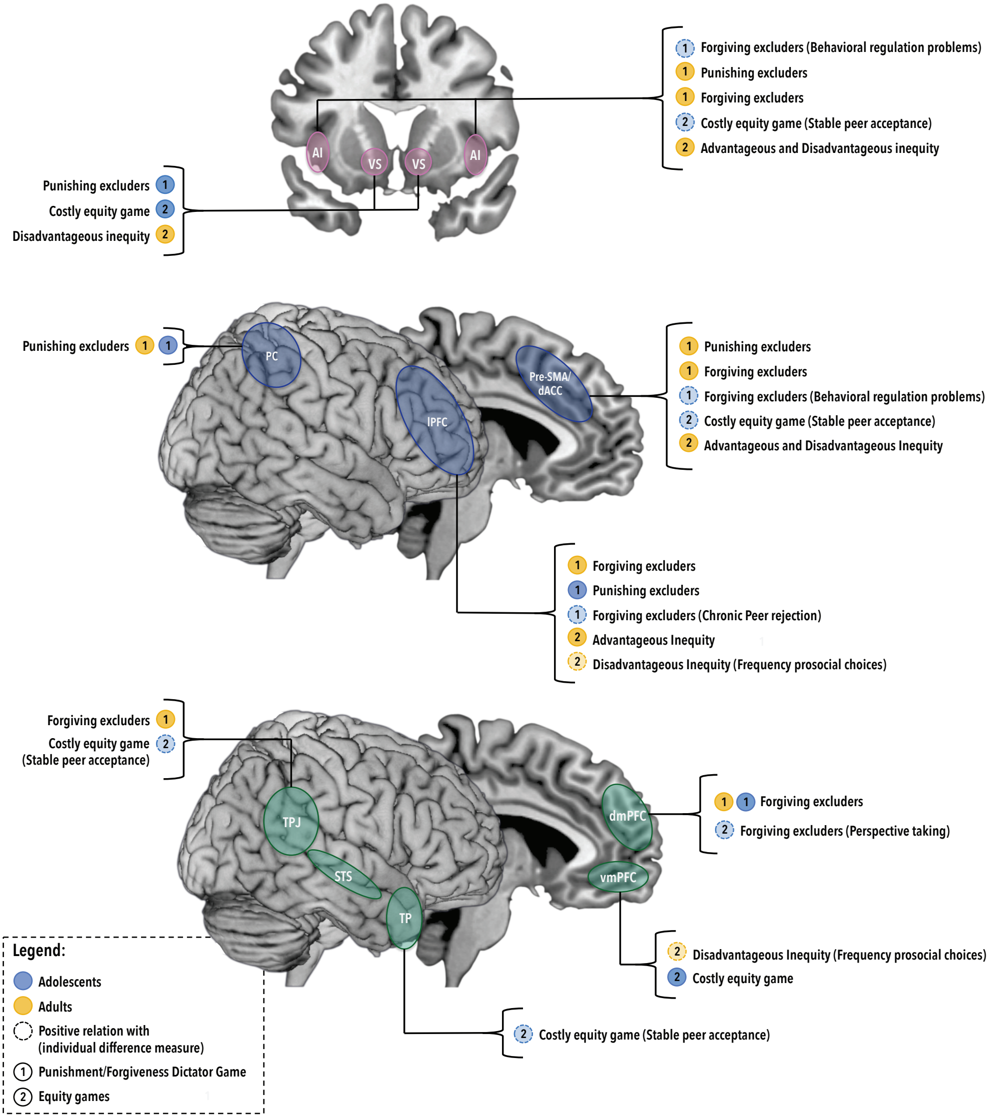

Figure 9.1 *Summary of the activations in three brain networks involved in social decision-making: basic affective network (pink), cognitive-regulatory network (blue) and mentalizing network (green). AI = anterior insula, VS = ventral striatum, PC = parietal cortex, lPFC = lateral Prefrontal Cortex, 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.