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Me, My Friends, and I : a neuro-ecological perspective on adolescent prosocial development

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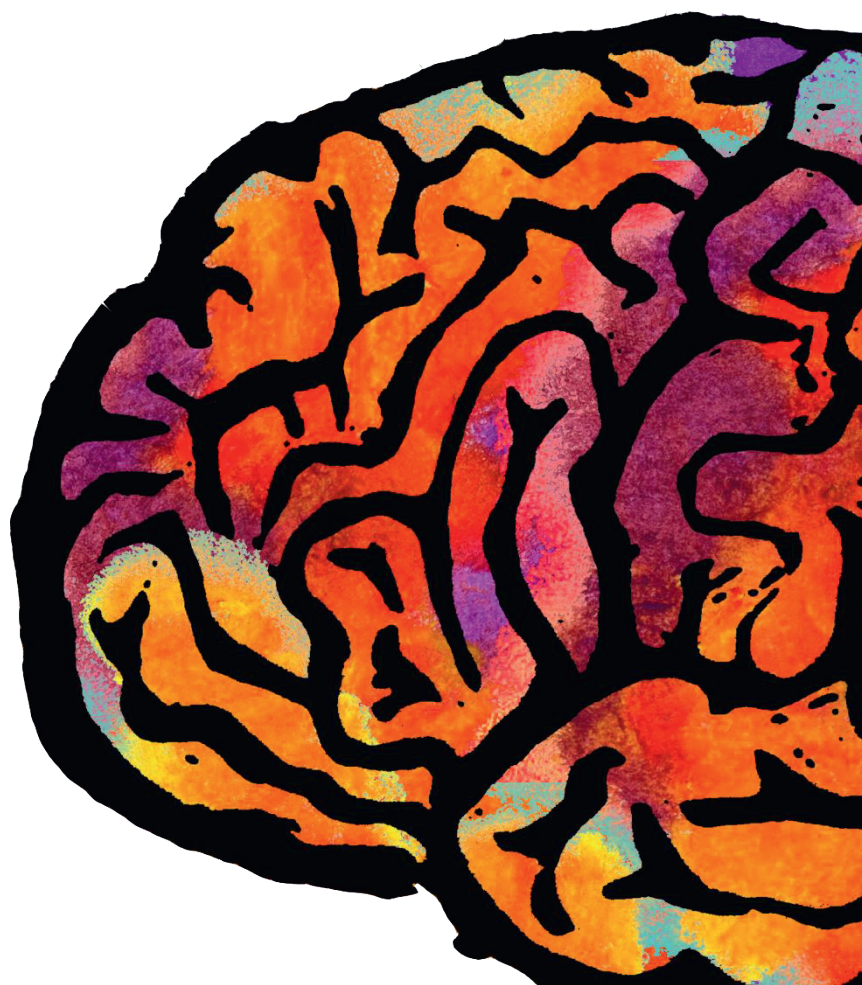


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CHAPTER 6

Summary and discussion

6.1 INTRODUCTION

This chapter summarizes and discusses the findings of the previous chapters and provides an integrative view on adolescent prosocial behavior and social brain development in the context of the peer system. First, summaries for all chapters are provided. Second, findings from different chapters are discussed vis-a-vis the existing literature to provide perspectives on 1) prosocial development in the peer context; 2) relational interconnectedness of individuals within the peer system; and 3) peer relationships and the developing social brain. Finally, the findings from the four studies will be embedded in the theoretical framework of neuro-ecological prosocial development that was proposed in first chapter.

6.2 GENERAL OVERVIEW OF FINDINGS

In **chapter 2**, I tested the development of equity preferences over the course of adolescence. Using four economic games I examined the preference for equity over non-costly, self-serving or more efficient distributions in a large sample ($N = 1216$) of pre- to late-adolescent boys and girls. Overall, adolescents prefer prosocial distributions, especially when these result in equity between players. Interestingly, with age adolescents are less willing to sacrifice their own benefit in order to achieve equity. Although this finding seems to indicate a decrease in prosociality with age, the willingness to let the other player receive more, instead of an equal division, increases. There were also interesting gender differences: boys have an increasingly stronger preference for efficiency with age, when compared to girls. Girls in turn continue to increasingly value equity over the course of adolescent development, instead of the decrease that boys show.

In conclusion, when weighing the benefits for themselves against the benefits for the other, older adolescents seem to increasingly incorporate the context into the decision-making and are less reliant on an equity norm. Especially boys are more driven by efficiency. This development appears during a phase in life with more demands of authority and responsibility over one's own social decisions. For older ad-

olescents, it is therefore fundamental to be able to rely on the ability to adapt to different social circumstances and a basic norm such as equity can no longer fulfill increasing environmental needs.

Being able to carefully weigh own benefits against benefits of the other is a necessary skill in the context of close relationships with non-kin others such as best friendships. Friendships are based on an equal balance of power and reciprocity (Asher, Parker, & Walker, 1996) and jealousy and imbalance within a friendship is related to peer adjustment difficulties (Parker, Low, Walker, & Gamm, 2005). In general, supportive friendships have been shown to be important for social development in the peer context (Berndt, 2002). In **chapter 3** I extended current knowledge on the role of friendship quality in social development by studying the longitudinal link between friendship quality and the morphology of brain regions that are essential in social development.

In this study, I first tested longitudinal developmental trajectories of gray matter volume, cortical thickness and surface area in social brain regions (mBA10, TPJ, pSTS) and were able to generally replicate earlier findings of Mills, Lalonde, Clasen, Giedd, and Blakemore (2014). Overall, the social brain continues to mature at least until early adulthood, showing different decreasing trajectories across measures and regions. Furthermore, I included the precuneus as social brain region of interest in my study and showed similar decreasing patterns in this region. There was no continued maturation across adolescence in the primary visual cortex, a control region that I selected to test for changes in a region where no change should be expected.

The main goal of this study was to longitudinally relate relationship quality experiences in best friendships to structural development of the social brain regions. Results revealed that changes in friendship quality are associated with accelerated maturation of surface area in the mBA10 (for older males only) and pSTS and in TPJ cortical thickness (for females only). Although caution is needed in inferring causal relationships, these findings nonetheless provide a first indication of the positive effects of close peer relationships on structural social brain development.

Dyadic friendships are embedded within a wider peer context. The links between functioning in the dyadic and group levels of peer relationships was investigated in **chapter 4**, where I also examined the mediating role of prosocial behavior in associations between peer status and friendship quality. In this study, I employed a multi-method design to capture and relate social functioning in different social contexts. Social functioning in the wider peer group (classroom) was measured using

peer nominations of social preference/likability and popularity and the 430 adolescents in 215 best friend dyads reported on their relationship quality using a questionnaire (FQS: Bukowski, Hoza, & Boivin, 1994). Furthermore, peer nominations of cooperation and helping behaviors, experimental measures (equity games also employed in chapter 2) and a self-report questionnaire on empathy were used in order to test for the mediating role of prosocial behavior and empathic skills.

Results revealed that in adolescence, friendship quality as reported by one member within the dyad is positively related to both social preference and popularity of the best friend. Mediation analyses confirmed that this link could be explained by the prosocial skills of the friend nominated as high in preference, yet not for the friend nominated as highly popular. This indicates that the advantage of prosocial skills and behavior in the peer context is limited and that other person characteristics or even status in itself are important in close relationships with popular friends. Yet overall, individual prosocial skills can support success in both the larger peer system and on the dyadic level of the close relationship. This interrelatedness of social functioning on individual, dyadic and group level supports the theory that relationships with peers function in a dynamic peer system.

Finally, in **chapter 5**, I addressed the self-serving and prosocial motivations underlying social status among peers. In this study, I examined associations between neural sensitivity in the Nucleus Accumbens (NAcc) during winning money for oneself and money for the best friend and likability among peers. Likability was measured using peer nominations of liking and disliking by peers in the school class.

Results showed that more activation in the NAcc during self-serving winning is related to more disliking and less liking by peers. This finding demonstrates that being motivated for outcomes that are self-serving can underlie behaviors that are related to less liking and more disliking by peers. Interestingly, no associations were found for NAcc activity during winning for the best friend. In addition, I tested the moderating role of behavior inhibition and activation and found that behavior activation amplified the link between NAcc responsivity during self-serving wins and disliking by peers. In other words, having a strong tendency to act upon impulses can serve as a mechanism as to which self-serving motivation is disclosed in the peer context.

6.3 DEVELOPMENT OF PROSOCIAL BEHAVIOR IN ADOLESCENT PEER CONTEXT

Changes in social-affective and social-cognitive markers during adolescence could lead to an expectation of continued increases of prosociality. For example, previous work showing continued maturation during adolescence of the brain network that is related to social cognitive skills (Mills et al., 2014; chapter 3), increases in social cognitive skills (Dumontheil, Apperly, & Blakemore, 2010; Güroğlu, Van den Bos, & Crone, 2009), the strong need to be accepted by peers (Masten et al., 2009; Vanhalst, Luyckx, & Goossens, 2013) and the importance of prosocial behavior in peer status (Newcomb, Bukowski, & Pattee, 1993; Wolters, Knoors, Cillessen, & Verhoeven, 2013; chapter 4). More specifically, increased social skills could account for better understanding of the needs of others and thereby provide the necessary tools for prosocial behavior. The need for acceptance could serve as motivation to actually initiate prosocial actions. Also, significant rises between early and mid-childhood (Blake & McAuliffe, 2011; Fehr, Bernhard, & Rockenbach, 2008; Shaw & Olson, 2012) could lead to expectations of some continued increases in prosocial decision-making into adolescence. Yet, as chapter 2 shows, prosocial decision-making does not necessarily increase across adolescence.

Simultaneously, having less self-serving tendencies seems to be important for acceptance in the peer group (chapter 5). Furthermore, instead of a general prosocial preference, chapter 2 shows that adolescents increasingly incorporate contextual factors into their social decision-making and that this does not directly result in more prosocial decision-making. An alternative theory to expected general increases of prosociality would be that social adaptation in adolescence requires a more flexible and context-dependent recruitment of social skills and more selective prosocial decision-making. This theory is supported by studies on the development of cognitive flexibility in adolescence (Crone & Dahl, 2012). In addition, chapter 5 shows that a stronger tendency to act upon self-serving impulses (and thus showing limited cognitive control in decision-making) is related to lower likability among peers.

The ability to understand the perspective of others is not sufficient to elicit prosocial actions and should be driven by sufficient prosocial motivation to engage these skills to the benefit of the other (e.g. Decety, Chen, Harenski, & Kiehl, 2013).

Initially, infants appear to have an innate drive to act prosocially and even altruistically; later on, in early-to-mid-childhood, prosocial behaviors become less intuitive and more effortful (Shaw et al., 2013; Steinbeis, 2016). This decrease in intuitive prosociality and increase in competitiveness over resources could be a developmentally adaptive strategy for basic survival purposes, because children do not yet have the responsibility to care for others and are partly dependent on their own skills to get their share in order to survive (Charlesworth, 1996). Adolescence, as a transitional period with heightened reward-sensitivity in general (Braams, Van Duijvenvoorde, Peper, & Crone, 2015) and increased levels of sensitivity to social stimuli (for a review, see Foulkes & Blakemore, 2016) provides unique opportunities for further development of (pro)social skills: increased social reward sensitivity could serve as the drive for prosocial motivation (Telzer, 2016). This development in motivation (although dependent on social context) can considerably support communal goals, through supporting the skills to be able to weigh benefits for themselves and others. These skills are essential for cooperation in adult life (Burkart et al., 2014), when parental support has mostly disappeared

6.4 RELATIONAL INTERCONNECTEDNESS OF INDIVIDUALS WITHIN THE PEER SYSTEM

Chapter 4 reveals that social functioning in the peer group is related to best friendship quality. Previous family and peer relations research has shown that relationships within social systems can affect one another. For example in the case of the effect of marital dyad characteristics on the parent-child relationship (Erel & Burman, 1995), of the parent-child relationship on later friendships (Schneider, Atkinson, & Tardif, 2001), and the effect of sibling relationship features on best friendship quality (Bekkhuis et al., 2016). In these examples, one individual can transfer social interaction styles and affective traits from one dyadic relationship to the other. But even without the contribution of the same individual's characteristics to explain the association between the two dyads, the functioning of two "independent" dyadic relationships can be related, as for example with the effect of interparental conflict on best friendship quality of children (Kitzmann, & Cohen, 2003). Furthermore, besides

effects of social functioning between two dyads, wider group functioning is also related to dyadic functioning, as was shown in chapter 4. In this chapter, individual social success of an adolescent within a network of relationships, that is, the peer group, was related to dyadic best friendship quality of this adolescent. Finally, social climate in the peer system is related to the quality of dyadic relationships in this system (Way, & Greene, 2006; Way & Pahl, 2001).

Together, these studies emphasize the social interconnectedness of individuals in social functioning. This evidently justifies the use of the term “system”, when describing peer relationships on multiple levels (Bronfenbrenner, 1979). Chapter 3 shows that changes in friendship quality are related to increased maturation in social brain regions. Increased exposure to positive interactions with a significant peer (i.e., best friend) could be through which social brain regions mature over time. Another study found that more spontaneous mentalizing is related to a more mature cortex in the social brain of young adults (Rice & Redcay, 2015). Therefore, brain structure could be a mediator for the association between important social relationships and social competence outcomes.

With evidence for social learning occurring in all levels of the peer system, multilevel interventions targeted to increase positive interactions in a malfunctioning peer system should be advised. Yet, due to the interrelatedness of social functioning in the system, highly effective interventions on a single level could indirectly support functioning at other levels of the peer system. For example, one study shows that after an intervention of performing prosocial acts towards recipients of choice (peers or non-peers), peer acceptance increased for these adolescents (Layous, Nelson, Oberle, Schonert-Reichl, & Lyubomirsky, 2012). As I show in chapter 4, being liked by peers is related to friendship quality in a dyadic relationship and both levels of peer functioning are related to prosocial behavior. Prompting prosocial behavior in adolescents in general could therefore possibly impact multiple levels of peer functioning. It is important to note that the term “system” also implies bidirectionality of prosocial influence. For an individual adolescent, being accepted in a peer group with a prosocial climate could as well increase prosocial behaviors of this individual.

6.5 PEER RELATIONSHIPS AND THE DEVELOPING SOCIAL BRAIN

The impact of the social environment on brain development has been examined before, and quality of social interactions between parents and young children have been found to be related to gray matter development (Benetti et al., 2010; Kok et al., 2015; Whittle et al., 2014). The site of impact in most of these studies was early brain development, while in the study in chapter 3 changes in friendship quality during adolescence were related to accelerated changes in structural social brain development. Furthermore, instead of a role of primary caretakers in brain development, I focused on best friendships. Adolescent social reorientation theory (Nelson, Jarcho, & Guyer, 2016; Nelson, Leibenluft, McClure, & Pine, 2005) states that in adolescence attention shifts away from parents to peers. The findings in chapter 3 support that at least the most close peer relationship can be developmentally relevant in adolescence, through a positive effect on social brain maturation.

Positive relationships provide an opportunity to practice social skills and can thereby lead to an increase in prosocial motivation. Observing someone close such as a best friend experience positive emotions as a result of a prosocial act can already be very rewarding (Mobbs et al., 2009). In addition, acting prosocial is generally well received by recipients and often reciprocated in relationships (Laursen & Hartup, 2002). A loop of reciprocated prosocial actions could arise: friend A does something nice for friend B, and friend B reciprocates by doing something nice for friend A, which in turn reciprocates and the cycle continues. Anticipation of observing positive emotions in a friend and anticipation of reciprocated prosocial actions could underlie prosocial motivation, mediated by reward-related neural processing. Increased levels of prosocial motivation could possibly increase the recruitment of brain regions that are used during the execution of social skills.

It should be noted that I did not find a direct link between prosocial motivation and likability among peers in chapter 5 (for various possible reasons, as discussed in this chapter). Lower motivation towards self-serving rewards seems to be related to higher likability. This suggests that the dimension of self-other orientations as reflected in neural responses to rewards is related to successful social functioning in the peer context. In other words, being motivated for own gain comes often

at the cost of benefits for others (also see chapter 2) and this self-serving motivational tendency is not well regarded among peers. Whether other types of prosocial motivation in the peer context, other than the operationalization that was used here, are related to social success among peers remains unclear and should be investigated.

Prosocial motivation as possible mediator between positive social interactions and increased social functioning requires an explanatory mechanism on a neural level. Across development, neural connections that are being used frequently strengthen and connections that are redundant are being pruned (Stiles & Jernigan, 2010). It is possible that increased neural prosocial motivation due to positive interactions increases recruitment of interconnected social brain regions and thereby strengthens synaptic connections in the social brain network. This in turn can result in cortical changes in the social brain regions. Increases in strength of *global* connections could decrease the thickness of the cortex (Jeon, Mishra, Ouyang, Chen, & Huang, 2015) and synaptic pruning due to increases in efficiency in *local* structural connectivity could result in decreases in surface area. As of yet, the latter has not been supported by evidence and remains speculative.

6.6 A NEURO-ECOLOGICAL MODEL OF ADOLESCENT PROSOCIAL DEVELOPMENT

The evidence provided by this thesis and previous studies supports a model that highlights interactions between the peer context, individual prosocial functioning and brain development. In this neuro-ecological model of prosocial development, the morphology of social brain regions develops in interaction with social experiences. Positive experiences could be responsible for the motivation that is necessary for the recruitment of regions that support social cognition skills and thereby facilitate prosocial behavior. Longitudinal changes in the social brain network could be the result of long-term recruitment of this network. In turn, under the condition of sufficient levels of prosocial motivation, maturation of the social brain network could support prosocial behaviors. Adolescent prosocial motivation is likely dependent on the peer context in which prosocial behaviors are selectively carried out, for example

in favor of close peers such as best friends or in a way that could increase peer likability. Finally, when these prosocial behaviors sort out positive effects on social interactions with peers, the end result is a model of typical prosocial development within the peer system that is characterized by stable levels of positive experiences and increasing levels of social skills over development.

6.7 LIMITATIONS AND FUTURE DIRECTIONS

An important limitation of this thesis is that I discuss the findings assuming a process of social influence between individuals and relationships, yet I did not directly measure influence. Relationship dynamics, such as power imbalance, could change the direction of social influence, regardless of relationship quality. In the friendship quality measure, power imbalance was measured as part of negative friendship quality, whereas higher levels of imbalance do not exclude positive relationship characteristics to be present as well. Combined with high levels of positive friendship quality and high levels of prosocial behavior in one dyad member some imbalance can result in more prosocial influence on the other member. Experimental tasks measuring social influence should be employed in peer relations research, in order to further disentangle the dynamics of one individual's prosocial influence on another's. For example, Van Hoorn, Van Dijk, Güroğlu, and Crone (2016) used an inventive adaptation of an economic game to test for prosocial peer influence and to investigate the neural correlates of this peer influence. Their results showed that peer presence increases prosocial behavior and simultaneously enhances activation of social brain regions, further highlighting the importance of considering the peer context in research on prosocial development.

Prosocial motivation is not only essential in all prosocial behavior, but in adolescence it seems to be even more meaningful because of elevated reward sensitivity in the peer context (Foulkes & Blakemore, 2016). In this thesis prosocial motivation was measured using self-reports in chapter 4 and using NAcc activation during vicarious winning in chapter 5. Further conceptualizing this construct is a fruitful avenue for future research on prosocial behavior. Using imaging techniques to assess reward-processing in the brain, related to prosocial cues and in order to measure

prosocial motivation, remains an elegant method, yet the validity of different modalities of prosocial neural processing should be tested.

Although the causality of the relationship between friendship quality and brain development remains unconfirmed, future research should disentangle whether it is the pole of a lack of a positive relationship that is related to decelerated development or whether it is the pole of high levels of friendship quality that allows for a developmental advantage. Structural (social) brain development of adolescents who have been chronically excluded by peers should be compared to adolescents who have been accepted by peers and this second group should also be compared to adolescents that have chronically had high levels of exposure to positive peer interactions. Whether it is the high lack of positive peer interactions or an abundance of positive interactions that can impact brain development has important practical implications for therapeutic interventions. Furthermore, this perspective aids constructing ecological theories on social brain development: is the adolescent social brain expectant of certain environmental circumstances and would a deficiency in adolescence result in atypical brain development (as seems to be the case in early brain development: Benetti et al., 2010; Kok et al., 2015; Whittle et al., 2014)? Or would a socially rich environment solely provide an advantage in brain development over typically developing adolescents?

In this thesis, I emphasize the importance of social relationships for prosocial functioning. Yet, in chapter 2, participants interacted with anonymous peers, in order to assess their equity preferences, independent of relational characteristics with real-life peers. In for example studies such as Powers, Somerville, Kelley, and Heatherton, (2016), Güroğlu, Will, and Klapwijk (2013), Chein, Albert, O'Brien, Uckert, and Steinberg (2011), Braams and colleagues (2014), and in the study of chapter 5, social agents were friends or the peer group. Future studies should continue to use interaction partners with whom the participants have a relationship (see Güroğlu et al., 2013). Especially brain development research could benefit from ecologically valid social interactions. That this approach can bring along challenges beyond practical impediments of bringing one or more peers to the lab, of for example construct validity and reliability, is demonstrated in chapter 5. Here, winning money for the best friend real prosocial motivation relationships differ in valence for each individual and relationship appreciation can vary from day-to-day.

6.8 CONCLUSION

The study of adolescent prosocial development should adopt an approach of integral interconnectedness between biological units within the peer system. Nonetheless, individualist traditions put restrictions of biological boundaries on theories of social development. There is still a lot to be learned about the brain in development from views on social relations in non-industrialized cultures. As the Zulu say: “*you are who you are relative to the other*”.