Got a friend in me? Mapping the neural mechanisms underlying social motivations of adolescents and adults

Schreuders, E.

CHAPTER SIX

General discussion

THIS THESIS

In this thesis, I aimed to shed light on how reward sensitivity and peer relationship valence relate to (prosocial) drives. I examined how nucleus accumbens sensitivity to rewards for the self and for best friends related to reward-driven behavior and friendship stability across adolescence, respectively. I further examined brain activity patterns related to prosocial decision-making involving familiar friends and disliked peers in adults and adolescents. In this section, I first summarize the main findings of the studies I conducted. Next, a general discussion, suggestions for future directions, and conclusions follow. Here, I highlight the role of approach processes and prosocial actions in adolescent social development from a neuroscience perspective.

Nucleus Accumbens' Sensitivity to Rewards

The nucleus accumbens is a subcortical brain structure located in the ventral striatum and implicated in reward processing (Delgado, 2007). This brain region responds to various types rewards, for example money gained for the self and others, as well as gained social status or approval (Bhanji & Delgado, 2014; Izuma, Saito, & Sadato, 2008; Liu, Hairston, Schrier, & Fan, 2011; Sescousse, Caldú, Segura, & Dreher, 2013). The scientific literature shows that the nucleus accumbens responds to preferred outcomes, which is proposed to have motivating effects (Kringelbach & Berridge, 2016). In theoretical models, developmental changes in nucleus accumbens' reward sensitivity have been assigned an important role in age-related changes in reward-seeking behaviors across adolescence (Casey, 2015), such as exploration and novelty seeking, but also seeking out new friendships (Telzer et al., 2016). These are important behaviors that contribute to the developmental process of adopting mature, long-term goals (Crone & Dahl, 2012). As such, the nucleus accumbens has been hypothesized to play an important role in adolescent (social) development.

In the first part of this thesis I discussed a biannual three-wave longitudinal study on the development of reward-related nucleus accumbens activity from late childhood to early adulthood. With this study, I examined reward-related activity of the nucleus accumbens when participants (eight to twenty-nine years of age) played a heads-or-tails gambling game while functional brain images were acquired. During the experimental task, participants guessed which side of a coin would show after a coin flip. Participants gained a monetary reward when they guessed correctly, and lost monetary units when they guessed incorrectly. Chances of winning and losing were 50%. The outcome was determined by the computer. Participants could win or lose for themselves (chapter 2) and their best friend (chapter 3).

Nucleus accumbens activity in relation to reward-related drives across adolescence

Nucleus accumbens activity in response to rewards for the self has been previously found to be elevated in adolescents relative to children and adults (Galvan et al., 2006; Van Leijenhorst et al., 2010b). Although, nucleus accumbens activity has been posed to underlie reward-motivated behaviors such as exploration and seeking social acceptance (Telzer, 2016; Van Duijvenvoorde, Peters, Braams, & Crone, 2016), what drives developmental changes in activity across adolescence is not fully understood. In **chapter 2**, I examined changes in reward-related activity of the nucleus accumbens when winning relative to losing for the self, and how these developmental changes in nucleus accumbens activity across adolescence related to individual differences in (a) trait-level constructs of rewards sensitivity (e.g., a general drive to obtain desired goals) and (b) state-level responses to obtaining rewards (i.e., the pleasure experienced in response to winning).

First, the results confirmed an adolescent peak in nucleus accumbens reward activity, such that activity increased until mid-adolescence after which it decreased again until at least early adulthood (see, also Braams, Van Duijvenvoorde, Peper, & Crone, 2015). Second, I found that the motivation to pursue personal goals related to increases in nucleus accumbens activity from early to mid-adolescence. Third, I found that decreases in immediate reward pleasure related to decreases in nucleus accumbens reward activity from mid-adolescence to early adulthood. With this study, I showed that trait-level reward sensitivity in the form of the motivation to pursuit (long-term) goals and trait-level reward sensitivity in the form of (immediate) pleasure experienced in response to rewards contribute to nucleus accumbens reward sensitivity in different phases of adolescent development. These findings further extend prior findings by showing that nucleus accumbens responses to rewards continue to change until at least the late twenties.

Nucleus accumbens activity in relation to best friendship stability

As such, adolescence can be generally described as a period of heightened nucleus accumbens activity in response to rewards for the self. At the same time, adolescence is a period during which peers become important interaction partners in everyday live (e.g., Buhrmester, 1990). As the need for intimate peer relationships emerges in adolescence, friendships become increasingly supportive and stable (Poulin & Chan, 2010; Scholte, Van Lieshout, & Van Aken, 2001). Generally, the nucleus accumbens has been shown to respond to vicarious rewards for friends, but no age-related changes that mirror elevated reward sensitivity of the nucleus accumbens when rewards are gained for the self have been reported so far. Therefore, I examined in **chapter 3** whether adolescents with different types of best friendships, i.e., stable and unstable best friendships, showed different developmental trajectories of nucleus accumbens activity when participants won for their best friend in the heads-or-tails gambling game. Next, I examined whether participants reported different levels of the pleasure experienced when winning for their friend, perceived friendship quality (i.e., as reported by the participant, but not the friend), and perceived friendship closeness across adolescence. Finally, I examined whether nucleus accumbens activity could be linked to the pleasure experienced when winning for the best friend and friendship quality and closeness.

In order to distinguish between adolescents with stable and unstable best friendships, I included two groups of participants in this study: (a) individuals with stable best friendships, who named the same best friend at all three time points, and (b) individuals with unstable best friendships, who named a different best friend at each of the three time points.

I found that participants with stable best friendships showed a peak in reward activity in late adolescence, whereas participants with unstable best friendships showed no age-related changes. Differences in nucleus accumbens activity appeared most evident for the youngest adolescents, such that those adolescents with stable best friendships yielded *lower* levels of activity than adolescents with unstable best friendships. This indicates that young adolescents with a stable best friend were less sensitive to the reward for their friend than young adolescents with unstable best friends.

Next, I found that participants with stable and unstable best friendships did not report different levels of pleasure experienced when winning for their best friend. However, there was an effect of the stability of adolescents' friendships on friendship quality and closeness. There was an interaction between friendship stability and sex on positive friendship quality. Across all ages, males with stable best friendships reported higher levels of positive friendship quality than males with unstable best friendships. There was no such effect of friendship stability on friendship quality for females. Furthermore, there was an interaction between friendship stability and age on friendship closeness. Participants with unstable best friendships reported decreasing closeness with age, whereas there were no age-related changes in closeness for participants with stable best friendships. Overall, these results suggest that friendship stability does not modulate the hedonic impact of vicarious rewards, but that it modulates friendship characteristics.

Finally, I found that for participants with unstable best friendships, stronger nucleus accumbens activity related to stronger friendship closeness. No such relationship was found for participants with stable best friendships, and no relation was found between nucleus accumbens activity and friendship quality. These findings suggest that perceived closeness with unstable best friends is associated with vicarious reward-related nucleus accumbens activity, whereas friendship quality and the hedonic impact of the reward are not.

In conclusion, these findings show that adolescents with different types of best friendships (i.e., stable or unstable) show differential developmental patterns of nucleus accumbens activity when rewards are gained for a best friend. I also described how these patterns relate to the subjective pleasure experienced when gaining these rewards and friendship characteristics. By showing the role of adolescents' friendships on vicarious reward sensitivity, the current study contributes to our understanding of changing reward-related social motivations across adolescence.

Prosocial Actions Motivated by Relationship Valence of the Interaction Partner

In the studies described in chapter 2 and 3, participants passively processed the outcome of their guess in the heads-or-tails gambling game. That is, participants could not actively make the decision to gain or lose money for themselves or their best friend. In the studies presented in chapter 4 and 5, participants (adolescents and adults) actively decided whether they wanted to benefit themselves and/or others. This approach gives insights into brain activity responses underlying social decision-making.

Relative to children, adolescents become increasingly flexible in their behavior during social interactions. Adolescents increasingly take into account the social context in which interactions with others take place (Güroğlu, Van den

Bos, & Crone, 2014; Meuwese, Crone, de Rooij, & Güroğlu, 2014). For example, in a behavioral study it was shown that, with age, adolescents increasingly differentiate between friends and disliked peers when deciding whether it is worth to behave in a prosocial manner (Güroğlu, Van den Bos, & Crone, 2014).

Prior neuroimaging studies on prosocial decision-making with peers have primarily focused on interactions with unfamiliar peers, and sometimes with friends (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Fareri & Delgado, 2014; Güroğlu et al., 2008; Lee & Harris, 2013). However, on a day-to-day basis we primarily interact with familiar peers. Consequently, the neural mechanisms underlying prosocial and non-prosocial (e.g., selfish) decisions involving familiar peers are understudied in adults as well as adolescents. I used an ecologically valid research design (i.e., with real-life interaction partners) to study prosocial and selfish decision-making with friends and disliked peers in both adults (chapter 4) and adolescents (fourteen years of age; chapter 5). I specifically examined the neural mechanism underlying prosocial and selfish decision-making involving friends and disliked peers.

Participants played an economic allocation game in which they distributed coins between themselves, friends, disliked peers, neutral peers, and unfamiliar peers. Friends were familiar classmates who were liked by the participant or were considered friends; disliked peers were disliked classmates; and neutral peers were classmates who were neither liked nor disliked by the participant. On every trial, participants could choose between a prosocial (i.e., benefiting the interaction partner) and a selfish distribution of coins (i.e., maximizing outcomes for the self or resulting in the smallest number of coins for the interaction partner as possible).

The neural mechanisms underlying social decisions in adults' social relationships

In **chapter 4** I examined prosocial behavior and its neural correlates in adults. First, I examined how behavior was affected by the relationship valence with the interaction partner. Second, I examined how individual differences in prosocial behavior related to brain activity when making social decisions involving friends relative to disliked peers. Third, I examined which brain regions were engaged in prosocial and selfish decision-making involving friends and disliked peers.

As expected, adults were most prosocial toward friends and least prosocial toward disliked peers, and were equally prosocial toward neutral and unfamiliar peers. Hence, adults were generally motivated to invest in friendships but not in relationships based on dislike. The results further showed that participants who were least prosocial toward friends yielded increased levels of activity in the anterior insula and the supplementary motor area (SMA), and participants who were most prosocial toward friends yielded decreased levels of activity in these brain regions. Prior studies have often point toward involvement of these brain regions in conflict monitoring and processing norm violations (Feng, Luo, & Krueger, 2015). The behavioral results from the current study and results from prior studies show that individuals generally behave in a prosocial manner toward friends (Newcomb & Bagwell, 1995). As such, there appears to be a general social norm that individuals are expected to act in a prosocial manner toward friends. In the current study, participants who did not act according to this social norm activated the anterior insula and SMA to a greater extent than individuals who did. This may point toward the interpretation that the anterior insula and the SMA may be implicated in signaling social norm violations.

I further found that prosocial decisions involving friends relative to disliked peers related to enhanced activity in brain regions including the posterior temporoparietal junction (TPJ), which extended to the inferior parietal lobule (IPL; pTPJ-IPL). Additionally, selfish decisions involving disliked peers relative to friends yielded activity in the superior temporal sulcus (STS). The STS and pTPJ-IPL are brain regions that are oftentimes reported to be involved in social decision-making, and have been particularly related to mentalizing processes (e.g., (Carter, Bowling, Reeck, & Huettel, 2012). Furthermore, the putamen was involved in both prosocial decision-making for friends (relative to disliked peers) and selfish decision-making for disliked peers (relative to friends). I interpreted involvement of the putamen in these social settings as playing a role in selecting an action that fits with the expectation whether the interaction partner will reciprocate prosocial actions (Delgado, Frank, & Phelps, 2005). Relatedly, another line of research shows that the putamen is implicated in habit formation and highlights its role in selecting an action that is most likely to result in a positive outcome (Brovelli, Nazarian, Meunier, Boussaoud, 2011; Schultz, Tremblay, & Hollerman, 2003). Together, the results presented in chapter 4 shed light on how neural processes underlying social decision-making are modulated by the relationship valence with the interaction partner in adults. Allied with prior findings, these results inform us on how established peer relationships are related to certain behavioral patterns, and how the neural processes underlying these behavioral patterns may be shaped according to past experiences with the interaction partner.

The neural mechanisms underlying social decisions in adolescents' social relationships

In **chapter 5** I examined prosocial decision-making processes of adolescents of fourteen years of age, a developmental period during which peer relationships are relevant for the development of social skills and forming friendships (e.g., Aikins, Bierman, & Parker, 2005; Bukowski, Hoza, & Boivin, 1993; Parker et al., 2015). I examined how prosocial decision-making was affected by the relationship valence with friends, disliked peers, neutral peers, and unfamiliar peers. Next, I examined brain activity patterns underlying prosocial and selfish decisions toward friends and disliked peers. Finally, I explored whether individual differences in brain activity during prosocial decisions involving friends were associated with individual differences in social competence including friendship quality and empathy. .

The findings of this study show several commonalities with the study findings described in chapter 4. Similar to adults, adolescents behaved most prosocial toward friends and least toward disliked peers, and were equally prosocial toward neutral and unfamiliar peers. Furthermore, participants yielded activity in the superior parietal lobule (SPL; adjacent to the pTPJ-IPL) when making prosocial decisions for friends (relative to disliked peers as well as relative to unfamiliar and neutral peers). Finally, putamen activity was associated with prosocial decisions involving friends.

There were also some brain activity patterns that were unique for the adolescent sample. In contrast to the adult sample, social decisions involving disliked peers were not associated with significant brain activity. Furthermore, only in this adolescent sample, prosocial decisions involving friends yielded activity in the posterior middle temporal gyrus (pMTG; relative to disliked peers) and precentral gyrus (relative to unfamiliar and neutral peers).

The explorative analyses testing the relation between brain activity and social competence revealed that negative friendship quality related to putamen activity negatively, and that empathic personal distress related to SPL and precentral gyrus activity positively. These results together suggest that social competence may modulate engagement of brain regions involved in prosocial decision-making toward friends, such that better social competence may be associated with stronger activity.

GENERAL DISCUSSION

Together, the studies in this thesis present a number of findings that inform us on adolescent (social) development. With the longitudinal studies described in chapter 2 and 3 I show that nucleus accumbens activity in response to rewards for the self follows an inverted u-shaped developmental trajectory across adolescence (i.e., with an adolescent peak), and that a similar developmental pattern is found when adolescents gain rewards for stable, but not unstable, best friends. In chapter 2, I show that stronger nucleus accumbens activity in response to rewards for the self relates to a stronger motivation to pursue personally desired goals. In chapter 3, I show that from early to mid- and/or late adolescence nucleus accumbens activity in response to rewards for stable best friends increases. Together, these findings emphasize the involvement of changes in nucleus accumbens reward sensitivity from early to mid-adolescence in the motivation to pursue personally valued goals, including stable, perhaps more adult-like, friendships (Nelson, Jarcho, & Guyer, 2016; Poulin & Chan, 2010; Urošević, Collins, Muetzel, Lim, & Luciana, 2012; Van Duijvenvoorde et al., 2014). These results highlight adolescence as an important developmental period during which adolescents may adopt an identity with regards to what they want to achieve as well as with regards to others.

The findings discussed in chapter 2 and 3 highlight reward sensitivity as a fundamental factor for adolescent development. With age, adolescents become increasingly skilled to understand complex and abstract reward outcomes (Davey, Yücel, & Allen, 2008). Consequently, adolescents might value various types of rewards across development differently. For example, a recent study suggests that useful information becomes more valuable across adolescence as evidenced by the finding that explorative behaviors become strategic (i.e., with the goal to obtain information; Somerville et al., 2017). This type of explorative behavior may be especially important to achieving personally relevant goals. Building on the current findings, research should focus on examining the underlying processes of more complex reward-motivated behaviors in a social setting across adolescence. For example, what drives adolescents to be socially accepted by a friend or the larger peer group and does this drive change with age? All in all, to understand behavioral changes that take place in real-life, scientists should shift to a research approach that includes the examination of more complex, perhaps real-world explorative behaviors.

The notion that in early adolescence individuals' social orientation is not yet directed at stable social relationships is in line with the findings presented in chapter 3. Here, I showed that young adolescents are more sensitive to rewards for unstable best friend than stable best friends (Nelson et al., 2016). This may suggest that young adolescents are more motivated to expand their friend network than to invest in one particular best friendship. All participants from the study in chapter 3 appear to be within a healthy range of social functioning, because all participants reported to have best friendships of overall good quality and strong closeness at all three measurement waves. Although chapter 3 provides a valuable starting point for understanding the role of friendship stability across development, whether stable friendships, unstable friendships, and other types of relationships are of varying developmental significance across adolescence is still an outstanding question. To answer this question, researchers should collect information on adolescents' peer network, romantic relationships, and relationships with family members. For instance, similar to the developmental trajectory of nucleus accumbens responses to rewards for stable best friends, Braams and Crone (2017) showed that when participants gained rewards for their mother, nucleus accumbens activity peaked in mid-adolescence. A direct comparison of nucleus accumbens responses to vicarious rewards for (stable and unstable) best friends and mothers, could answer the question whether these activity patterns are of a similar intensity across different ages and thus whether they relate to similar underlying processes. A next step would be to examine relations between vicarious neural reward sensitivity and social functioning and well-being. Comparing the contribution of different types of social relationships to social functioning and well-being will provide insights into the interplay of varying social factors across adolescent development (Bekkhus et al., 2016; Groh et al., 2014; Pallini, Baiocco, Schneider, Madigan, & Atkinson, 2014).

With the studies described in chapter 4 and 5 I made the first steps in examining the impact of familiar interaction partners of varying relationship valence on behavior in social interactions and the neural correlates. The results demonstrate that mid-adolescents as well as adults treat friends and disliked peers differently. This suggests that in mid-adolescence, adolescents are motivated to invest in friendships (by behaving a prosocial manner), but not in relationships based on dislike (by behaving in a more selfish manner). This behavioral pattern appears to persist into adulthood, although there might still be some protracted refinement of behavior with regards to the impact of the social context across development, such as the costs and the benefits of a social decision (Meuwese et al., 2014).

The overlap of neuroimaging results in chapter 4 and 5 suggest that there may be robust involvement of the (inferior or superior) parietal lobule and putamen when making prosocial decisions involving friends in both mid-adolescence and adulthood. There were also some differences in brain activity patterns between mid-adolescents and adults. Only adults yielded activity in the putamen and STS during selfish decisions for disliked peers, and only adolescents yielded activity in the pMTG and precentral gyrus when making prosocial decisions for friends. It should be tested in future studies whether these differences in activity patterns in adulthood and adolescence reflect developmental effects. This will inform us on how brain development relates to behavioral patterns in prosocial decision-making across development, and by extension how peer relationships become established. The next steps in this area of research include longitudinal studies that are focused on tracking engagement of brain regions implicated in prosocial decision-making involving familiar peers. The findings presented in chapter 4 and 5 highlight the IPL, STS, and putamen as well as the SMA and anterior insula as candidate regions. Together, these results pose that from at least mid-adolescence onward, the recruitment of certain brain regions during prosocial decisions for friends may be to some extent hard wired, whereas this may not yet be the case for social decisions involving disliked peers.

Furthermore, adults who made fewer prosocial decisions toward their friends yielded stronger activity in the anterior insula and SMA. Previous studies highlighted these brain regions as related to processing conflicts and norm violations (Feng et al., 2015). Speculatively, activity of the anterior insula and SMA may reflect a signal of conflict or norm violation for adults who do not adhere to a general social norm of being prosocial to friends. Future studies should examine whether involvement of the anterior insula and SMA during social decision-making with peers changes when individuals do not behave in a prosocial manner to friends. For example, changing (e.g., increasing) recruitment of these brain regions across adolescence may support the hypothesis that social norms of how to behave to friends (relative to others) become socialized and internalized across adolescence.

The interpretations of the findings presented in chapter 4 and 5 highlight adolescence as a sensitive period for social development, in which social habits and norms may be learned through interactions with different types of peers (Steinberg, 2005; Van den Bos, Westenberg, Van Dijk, & Crone, 2010). One may hypothesize that the adoption of social habits may help adolescents to adapt their behavior to the social context such that it has advantageous outcomes for themselves. For example, adolescents may learn who is likely to reciprocate prosocial actions through repeated social interactions. Eventually, these learned habits may become more internalized such that they become part of a general social norm. Future studies may formally test this hypothesis.

FUTURE DIRECTIONS

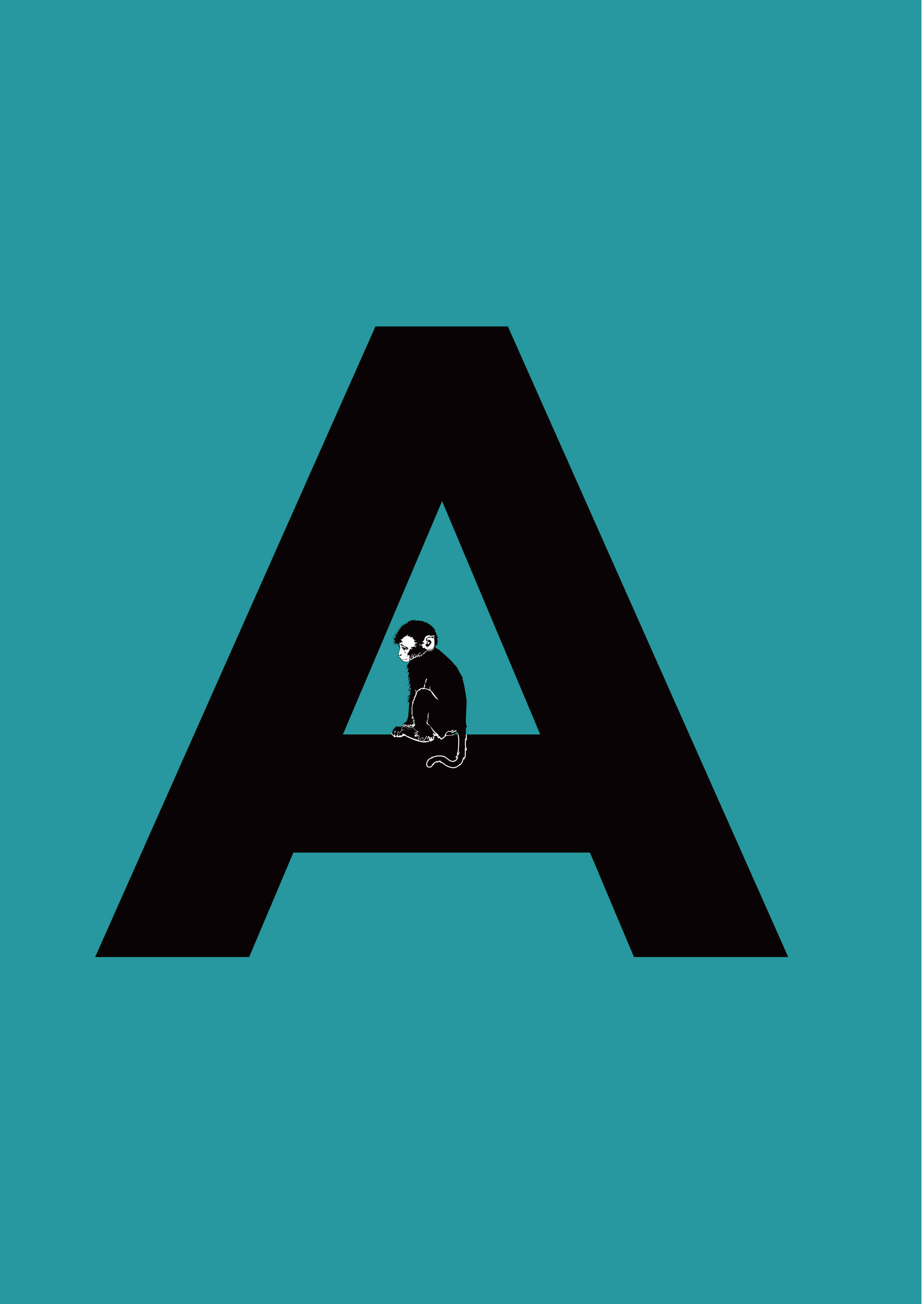
Together, prosocial motivations and behavior contribute to other-regarding social developmental goals, including strengthening social relationships and improving social skills. However, more self-regarding developmental goals, such as establishing one's social status within a social network, may also motivate the decision whether it is worth investing in a relationship (Rodkin, Ryan, Jamison, & Wilson, 2013). For example, in chapter 2, nucleus accumbens sensitivity to rewards for the self are related to the motivation to pursue personally valued goals in early to mid-adolescence. In a similar vein, in chapter 3, I showed that young adolescents might be less oriented toward stable best friendships than unstable best friendships (as reflected by lower vicarious reward sensitivity), perhaps to create opportunities to connect with others. Tentatively, a weaker orientation toward stable best friendships may be related to a self-regarding social goal to establish one's social status in a larger peer group. The balance between self- and other-regarding social motivations may vary across different contexts. In chapter 4 and 5, I showed that mid-adolescents and adults generally behaved in a prosocial manner toward friends, whereas they avoided acting in a prosocial manner toward disliked peers. This suggests that self-regarding motivations might outweigh other-regarding motivations in interactions with disliked peers but not friends. Future studies should examine how (the balance between) other- and self-regarding motivations across different contexts contribute to social development. In addition, to understand the underlying motivational processes involved in interactions, researchers could examine functional connectivity between subcortical regions implicated in reward-processing (such as the nucleus accumbens) and cortical regions implicated in mentalizing (such as lateral temporal and parietal brain regions).

There also lies an opportunity for developmental neuroscience to (further) examine whether there are certain sensitive periods within adolescence for social influences on social functioning and well-being (Dahl, Allen, Wilbrecht, &

Suleiman, 2018). For example, sensitivity to prosocial norms from the larger peer group may be most pronounced in early adolescence (Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016), whereas stable and more intimate friendships become more important interaction partners later in adolescence (e.g., Poulin & Chan, 2010), and perhaps by extension greater influencers of behavior. There is also a vast amount of research that highlights positive peer experiences as beneficial for future well-being. Friendships are shown to contribute to future mental health as well as a desensitization to negative peer experiences including social exclusion (Masten, Telzer, Fuligni, Lieberman, & Eisenberger, 2012; Qualter, Brown, Munn, & Rotenberg, 2010). It is therefore not surprising that establishing a social network containing supportive peer relationships, especially friendships, is often emphasized as one of the most important developmental tasks of adolescents. The present thesis alludes to an important role of prosocial behavior, social competence, and reward-related approach processes in this developmental task. Studying the relation between individual differences in social competence and social networks across development using a neuroscience perspective may contribute to a thorough understanding of adolescence as a sensitive period for peer influences on social functioning and well-being.

CONCLUSIONS

This thesis highlights adolescence as a sensitive period for pursuing personal goals (chapter 2) and social development through interactions with different familiar peers (chapter 3, 4, and 5). I discussed involvement of brain regions responsive to rewards and social settings in social development. I propose that social interactions with peers, friends in particular, may serve as a socialization process with possible long lasting effects into adulthood. Self- and other-regarding motivations may drive social decisions that may affect social relationships. In conclusion, using a neuroscience perspective, this thesis provides a comprehensive overview of processes that are involved in different aspects of the motivation to build or keep social bonds with peers; or in other words, whether you *got a friend in me*.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ADDENDUM

Nederlandse samenvatting

Supplementary materials

References

List of publications

Curriculum vitae