The social brain in middle childhood: a neurobiological perspective on individual differences in social competence

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CHAPTER 6

General discussion

Summary

The main goal of this thesis was to investigate the behavioral and neural processes involved in social competence in middle childhood. First, I studied processes that contribute to social competence by looking into prosocial behavior and its associated neural mechanisms in children and young adults (**chapters 2, 3** and **4**). Further, I examined the association between structure of social brain regions and parent-reported prosocial behavior (**chapter 5**). Second, I studied processes that might negatively affect social competence by measuring neural responses to the experience of social exclusion (**chapters 3** and **4**). Finally, I estimated influences of genetics and environment on social competence and associated neural processes (**chapters 4** and **5**). In this final chapter of the thesis I first provide a summary of the main findings of these studies. A visual summary of the brain regions associated with prosocial behavior and social exclusion (see Figure 1). This section is followed by a general discussion, future directions and conclusions.

Social competence in adults

In **chapter 2**, I aimed to disentangle neural underpinnings for observing social exclusion and acting prosocially by employing a paradigm that allows for the investigation of both processes simultaneously. A sample of young adult females (*N* = 23; aged 18-19) played the Prosocial Cyberball Game (PCG; adapted from Riem et al. (2013)) during a MRI session. In this four-player ball tossing game, participants first played a fair block with three computerized players. During the fair situation all players received the ball an equal amount of times. Next participants played an unfair block, during which one of the players was excluded. This provided participants with the opportunity to compensate for the exclusion by tossing more balls to the excluded player and thereby show prosocial compensation behavior.

Behavioral findings indicated that participants tossed more balls to the excluded player compared to the two excluding players, thereby engaging in prosocial compensation behavior. Neuroimaging analyses revealed that tossing the ball to the excluded player was associated with in increased activity in bilateral insula, bilateral temporo-parietal junction

(TPJ) and bilateral nucleus accumbens (NAcc). In addition, participants showed neural activity in bilateral insula when observing exclusion. Together, these findings show that bilateral insula plays a role in both prosocial behavior and observing social exclusion, possibly indicating that both events are interpreted as meaningful events in a social context. Activation in social cognition and reward processing areas (e.g. TPJ and NAcc) was specific for prosocial behavior, thereby highlighting the dual role of other- (i.e. taking another's perspective) and self-oriented (i.e. experiencing a feeling of reward) motivations when engaging in prosocial behavior. With these findings as a starting point, I now turn to the three experimental studies conducted in middle childhood.

A test and replication study of social competence in childhood

I aimed to disentangle self- and other oriented concerns in middle childhood by studying prosocial behavior and concerns about experiencing social exclusion in **chapter 3**. A second aim of this study was to try and overcome some of the concerns raised about replicability of psychological experiments (Open Science, 2015), by using a replication and meta-analysis approach. In this study three middle childhood samples (aged 7-10) performed the PCG during a MRI session. Behavioral findings indicated that across all three samples children engage in prosocial compensation behavior in a situation of observed social exclusion. No significant activation in social brain regions was found in any of the three samples separately, nor in a meta-analysis. These findings demonstrate that children consistently show prosocial behavior towards an excluded player in a virtual ball tossing game, comparable to the findings in **chapter 2**. When investigating the experience of social exclusion, I found significant clusters of activation in the left orbitofrontal cortex (OFC) and occipital lobe in all three samples. During the experience of social inclusion, children showed increased activation in clusters spanning dorsal anterior cingulate cortex (dACC)/medial prefrontal cortex (mPFC), bilateral insula, ventral striatum and pre- and postcentral gyrus in all three samples. A meta-analysis indicated common activation of OFC for social exclusion, and activation of dACC and sections of the ventral striatum for social inclusion across the three samples. In sum, children show consistent neural reactions to the experience of social exclusion and inclusion in regions previously associated with perception management and reward processing, respectively. Underlying neural processes of prosocial behavior were less evident, possibly due to the large variation in prosocial behavior. This highlights the need for larger samples in research towards neural processes associated with prosocial behavior.

Heritability of social competence and brain function

To address the need for larger samples and to understand how genes and environment affect social competence, I studied the heritability of neural processes underlying prosocial behavior and social exclusion in **chapter 4**. In this experimental study a large middle childhood twin sample performed the PCG during a MRI session. Children showed prosocial compensation behavior towards a socially excluded player in the PCG, with neuroimaging findings revealing an increase in activity in the precuneus when participants behaved prosocially. An additional whole-brain regression analysis indicated that participants who demonstrated more prosocial behavior showed less insula activity when tossing to the excluded player. I interpreted these findings to indicate that prosocial compensation behavior in middle childhood is supported by underlying mentalizing processes (i.e. precuneus activity) as well as awareness of social norms (i.e. activity in bilateral insula). Both behavioral and neural findings were influenced by unique environmental factors and/or measurement error, possibly alluding to the strong influence of specific context on prosocial behavior. Regarding the experience of social exclusion, neuroimaging results showed increased activity in clusters spanning superior medial prefrontal cortex (smPFC)/inferior frontal gyrus (IFG) and subgenual ACC during social exclusion, and increased activity in a large cluster encompassing bilateral insula, bilateral putamen and dACC during social inclusion. Behavioral genetic analyses indicated that variance in neural activity in IFG and smPFC (during the experience of exclusion) was driven by a combination of genetic and unique environmental factors. Activity in other regions was best explained by unique environmental factors. In the current study unique environmental factors could not be separated from measurement error. In brief, this study showed that neural processes related to prosocial behavior and social inclusion might be more sensitive to environmental influences, as indicated by the influence of unique environmental factors and/or measurement error. Neural processing of social exclusion showed a small genetic effect in addition to unique environmental factors.

Heritability of prosocial behavior and brain structure

Turning to the association between social competence and brain structure, in **chapter 5** I studied whether similar genetic and environmental influences account for variance in structure of the social brain and prosocial behavior. I extracted measures of surface area and cortical thickness from four a-priori specified regions of interest (i.e. mPFC, TPJ, posterior superior temporal sulcus (pSTS) and precuneus) in the same middle childhood sample as described in **chapter 4**. Prosocial behavior was measured via parent-reported questionnaires. Findings from univariate behavioral genetic modelling showed substantial contributions of genetic factors to surface area of mPFC, pSTS and precuneus, whereas surface area of TPJ was influenced by both genetic and shared environmental factors. In contrast, cortical thickness of the precuneus was also largely driven by genetic factors, while cortical thickness of mPFC, pSTS and TPJ was influenced by both genetic and shared environmental factors. Finally, prosocial behavior and empathy were substantially influenced by genetic factors in addition to unique environmental factors. Bivariate genetic modelling showed a small overlap between genetic and unique environmental factors for cortical thickness of precuneus and empathy, indicating that some genetic and unique environmental factors account for lower cortical thickness of precuneus and higher levels of empathy. I also found a moderate overlap between genetic and unique environmental factors for prosocial behavior and empathy. Together these findings showed that both structure of the social brain and prosocial behavior are largely heritable, but that only a small amount of genetic factors overlap for brain structure and behavior.

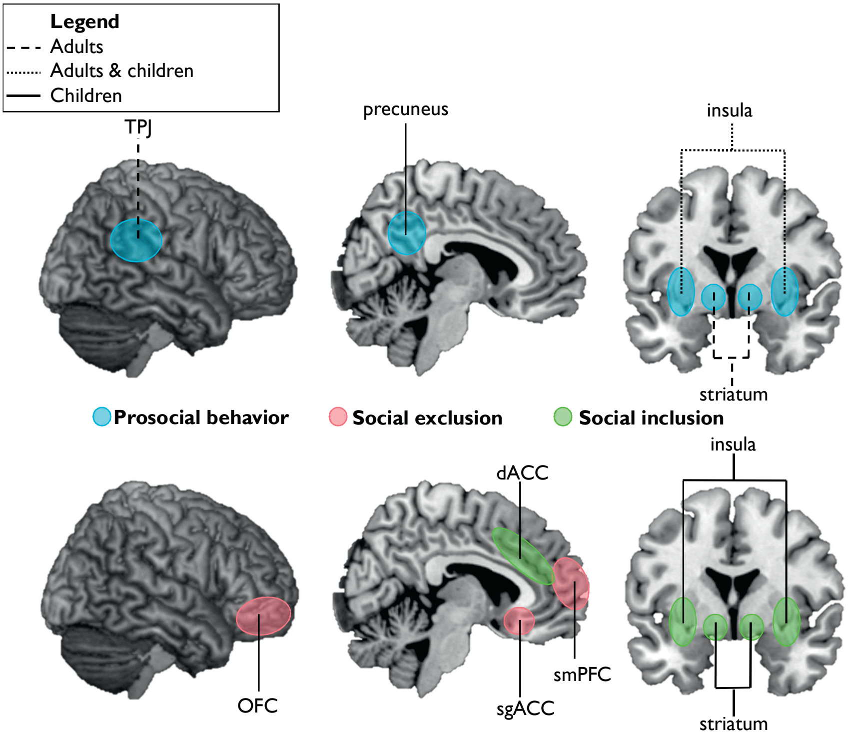

Figure 1. *Visual summary of findings with regard to functioning and structure of the social brain. Areas highlighted in blue were associated with prosocial behavior; temporo-parietal junction (TPJ), precuneus, insula and striatum. Areas highlighted in pink were associated with social exclusion; orbitofrontal cortex (OFC), subgenual anterior cingulate cortex (sgACC), superior medial prefrontal cortex (smPFC). Areas highlighted in green were associated with social inclusion; dorsal anterior cingulate cortex (dACC), insula, and striatum.*

General discussion

Neural signature of prosocial behavior

The studies that are part of this thesis can be summarized in a few main findings. First, I show that observing social exclusion results in prosocial compensation behavior in childhood (**chapters 3 and 4**) and adulthood (**chapter 2**). In other words, I found that participants adapted their behavior towards an unfamiliar player when that player was excluded. Brain regions that were activated during prosocial compensation behavior (e.g. TPJ in adults, precuneus in children) have previously been associated with the socio-cognitive processes of social competence (Blakemore, 2008), suggesting the presence of underlying mentalizing processes during the compensation of observed exclusion. Interestingly, neural structure of the precuneus was also associated with empathy (seen as a prerequisite for prosocial behavior; Eisenberg et al. (2015)) in middle childhood (as shown in **chapter 5**). More specifically, lower levels of cortical thickness of the precuneus was related to more empathic behavior. As maturation of the brain is characterized by cortical thinning (Mills et al., 2016; Wierenga et al., 2014), it is possible that higher levels of empathy reflect increased maturation of the social brain regions. However, the exact direction of this brain-behavior association needs to be determined in follow-up longitudinal studies.

In addition to neural regions involved in socio-cognitive processing, prosocial compensation behavior was also associated with brain regions associated with socio-affective processing. That is to say, in children I found that individuals who showed less prosocial behavior showed increased insula activity during prosocial behavior. Possibly, this neural activation signals an awareness of crossing social norms, as the insula has been shown to be involved in acting against social norms (Güroğlu et al., 2011). This might be particularly salient in middle childhood as this is the developmental stage of social norm internalization (Smith, Blake, & Harris, 2013). Furthermore, adults showed increased activity in the NAcc, a region associated with reward processing, during prosocial behavior. This finding fits with the hypothesis that prosocial behavior might be driven by expectations of a rewarding 'warm glow' after helping another individual (Harbaugh et al., 2007). As previous studies have shown that neural activity associated with reward processing (e.g. NAcc activity) continues to change across adolescence and adulthood (Nelson et al., 2016; Schreuders et al., 2018) it was surprising that there was no evidence in this thesis for reward related processes during prosocial behavior in childhood. It is possible that prosocial behavior might have different underlying motivations in childhood and adulthood, even when expressions of prosocial behavior do not necessarily differ across development (Do, McCormick, & Telzer, 2019). This might be a reflection of the distinct social goals to be achieved in various developmental stages (Nelson et al., 2016). Adults might be more motivated to pursue interpersonal goals (as mirrored in increased activity in NAcc; Mobbs et al. (2009)), whereas children might be more driven to follow social norms (McAuliffe et al., 2017).

Neural signature of social exclusion

The second main finding is that the neural responses to social exclusion in middle childhood are similar to neural responses in older individuals. That is to say, in **chapter 2** and **3** I found that children show increased activity in IFG, sgACC, smPFC and amygdala when they were briefly excluded from a virtual interaction. These patterns of activation are in line with earlier studies that investigated neural reactions to periods of social exclusion in adolescence and adults (Cacioppo et al., 2013; Rotge et al., 2015; Vijayakumar et al., 2017). The commonalities between earlier research and the findings from this thesis are striking given the differences between the set-up of paradigms used to investigate social exclusion. That is to say, in the current set of studies children were only excluded for short intervals (compared to longer periods) and their exclusion coincided with the exclusion from another player (instead of being the only excluded player in the game). The findings of a consistent neural response to short-term social exclusion across two studies therefore touches on the saliency of this negative social event. On a similar note, I found that being included in the virtual game resulted in increased activity in dACC, bilateral insula and striatum, regions that have previously been associated with appraisal and reward processing (Delgado, 2007; Shenhav et al., 2016). Earlier work on neural responses to receiving positive feedback revealed similar activation in dACC and insula (Achterberg et al., 2016; Dalgleish et al., 2017) as well as in striatal regions (Davey et al., 2010), suggesting that both explicit (i.e. positive feedback) and implicit (i.e. inclusion in a game) positive evaluation by peers is processed by regions in the social brain that play a role in affective processing.

Although it should be noted that the attribution of reward processing was derived via reverse inferencing, it is interesting to point out that reward processing in a social situation might play different roles for children and adults. That is to say, being included in the game results in activation of reward processing regions in children (**chapter 3** and **4**), whereas including someone else in the game resulted in reward related activity in adults (**chapter 2**). Speculatively, these findings might reflect a developmental shift in self- and other processing (Crone, 2013; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011): whereas children might experience feelings of reward for themselves but not for others, adults might have increased their socio-cognitive skills to the level of experiencing feelings of reward for vicarious inclusion (Braams et al., 2013).

To better understand how neural responses to social exclusion and inclusion interact with children's social competence, it is necessary to combine a neuroimaging approach with real-life measures of social functioning, such as sociometric measures. For example, even though the (Prosocial) Cyberball Game is a well-validated instrument that has been reliably used to measure the experience of social exclusion (Hartgerink, van Beest, Wicherts, & Williams, 2015; Vijayakumar et al., 2017), it is a reduction of the complexity and intricacies of the actual social environment. Using sociometry to quantify indicators of social competence such as friendship quality (Berndt, 2002) and social acceptance (for review see Gifford-Smith and Brownell (2003)), it would be possible to identify individuals with higher or lower social competence and to find out whether these individual differences are reflected in underlying neural responses to social exclusion.

Heritability of social competence and associated neural processes

Finally, I investigated genetic and environmental influences on social competence and associated neural processes. Behavioral genetics analyses showed no influence of genetics or shared environment on prosocial behavior in a task-situation (**chapter 4)**, whereas parent-reported prosocial behavior was influenced by a combination of genetics and unique environment (**chapter 5)**. These findings are in line with earlier research on the heritability of prosocial behavior (Knafo-Noam et al., 2015; Knafo & Plomin, 2006). Together these findings might illustrate that general trait-like tendencies for prosocial behavior are more strongly driven by genetic factors. This notion fits with the theory that some individuals have a "prosocial personality" that accounts for prosocial behavior in multiple contexts (Eisenberg et al., 2014). As prosocial behavior also has been shown to be heavily influenced by contextual factors (Dunfield & Kuhlmeier, 2013; van Hoorn, van Dijk, Meuwese, Rieffe, & Crone, 2016; van Ijzendoorn, Bakermans-Kranenburg, Pannebakker, & Out, 2010) it is possible that state-like prosocial behavior is more strongly influenced by unique environmental factors.

The division of genetic and environmental influences on state- and trait-like prosocial behavior might be reflected in the neural correlates of prosocial behavior. In **chapter 4**, I showed that neural activity in the precuneus and bilateral insula during acts of prosocial behavior were best explained by unique environmental influences. In contrast, in **chapter 5** I found that surface area of social brain regions (mPFC, pSTS and precuneus) was strongly influenced by genetic factors. Cortical thickness was influenced by both genetic and shared environmental factors. Here brain activity can be seen as a state-like neural correlate, as it is relatively susceptible to temporary influences (e.g. sleep deprivation, see Krause et al. (2017)), whereas brain structure can be seen as a trait-like neural correlate that is stable across contexts and more strongly driven by genetic factors. This distinction is also evident in test-retest reliability research, with lower test-retest reliability estimates for brain function than for brain structure (Heckendorf, Bakermans-Kranenburg, van Ijzendoorn, & Huffmeijer, 2019; Herting, Gautam, Chen, Mezher, & Vetter, 2018; Madan & Kensinger, 2017). It is noteworthy that I also found a negative association between parent-reported empathy and cortical thickness of precuneus, which was in turn influenced by genetic and unique environmental factors. In fact, to a small extent overlapping genetic and environmental factors accounted for variance in empathy and brain structure. Although further research is necessary to confirm this hypothesis, it might be the case that the stable behavioral and neural correlates of prosocial behavior are at least partly driven by similar genetic factors.

With regard to the neural processes underlying social exclusion and inclusion, I found evidence of genetic influence on the processing of social exclusion in **chapter 4**. Specifically, behavioral genetic analyses revealed that activity in smPFC and IFG were partly driven by genetic factors. Activity in other regions associated with social exclusion, as well as in regions associated with social inclusion, showed predominant influences of unique environment. These findings might be interpreted to indicate that even though humans have a fundamental need to belong and to be included in a social context (Baumeister & Leary, 1995), individual reactions to social exclusion are strongly dependent on personal experiences (van Harmelen et al., 2014; van Schie et al., 2017) and therefore influenced by unique environmental factors. As a final note, when discussing outcomes of behavioral genetic analyses we should keep in mind that in the current statistical models unique environment cannot be distinguished from measurement error (Plomin, 2011). Although attempts have been made to disentangle these two factors (see for example Ge et al. (2017)), this should remain a point of focus for future studies.

Future directions

The findings presented in this thesis provide a starting point for future studies to address several exciting questions. In this next section I will first discuss the importance of measuring a broad concept of prosociality, followed by options to investigate specific windows in development. Finally, I will discuss the need for integrating multiple methods.

The concept of prosociality

In this thesis I showed that measuring prosocial behavior with an experimental paradigm or via parent-report resulted in very different estimates of genetic and environmental influences. This highlights the diversity in prosocial behaviors, and the methodological challenges involved in capturing this complex behavior (also see El Mallah (2019) for review). Although some studies have tried to integrate different components of prosocial behavior into a coherent construct (see for example (Knafo-Noam et al., 2015)) we are only beginning to understand how prosocial behavior is presented across contexts and how different motivations might increase prosocial in one situation, but decrease prosocial behavior in another situation. In the current set of studies the relationship between different measures of prosocial behavior was not investigated. Underlying motivations for prosocial behavior were also not taken into account, making it difficult to understand why individuals showed prosocial behavior in different contexts. To correctly assess prosocial behavior in an individual I suggest that multiple assessments (i.e. self-report, other-report, behavioral observation, experimental paradigm) are combined in order to measure prosocial behavior across contexts and recipients. In addition, future research should aim to identify underlying common factors in various prosocial behaviors, with options including empathy (Eisenberg et al., 2006) and self-regulation (Steinbeis & Crone, 2016). Together, these measurements might increase our understanding of the multidimensionality of prosocial behavior.

Developmental windows

The set of studies discussed in this thesis were cross-sectional. Although findings from childhood and adulthood could be compared, the current set of studies did not allow for the exploration of developmental trajectories. For example, it is not possible to draw conclusions about the direction of the brain-behavior relationship (i.e. does neural activity predict prosocial behavior). In order to fully understand the developmental importance of middle childhood it is therefore necessary to investigate the transition from middle childhood into adolescence using longitudinal designs. Adolescence has often been highlighted as a period of tremendous changes, in personal identity as well as in social behavior (Blakemore & Mills, 2014; Crone & Dahl, 2012). Many studies on adolescence now include 9-10 year olds as a younger control group, but pubertal hormonal changes might already have started in that age range (Dorn & Biro, 2011). Instead I propose that children as young as 6-8 years old (i.e. prior to or coinciding with the hormonal preparations for puberty known as adrenarche; Campbell, 2011) should be included in order to fully capture the transition from middle childhood into adolescence on both a behavioral and neural level. Longitudinal designs can also shed a light on the continued importance of achieving social competence in childhood, by investigating how socially competent children become socially competent adolescents, and what external factors might influence individual's trajectories. Information gathered through these studies, aided by longitudinal behavior genetics designs, might tell us which developmental period is the most sensitive for environmental influences, so intervention programs and trainings can be devised accordingly.

Integrating methodologies

Finally, future research should focus on increasing the integration of various measurements to further our understanding of complex constructs such as social competence. For example, although many studies have investigated the link between brain function and social behavior, the link between brain structure and social competence has not been investigated as extensively. For example, findings from this thesis showed that prosocial behavior results in increased activity of the precuneus, and that higher empathy is associated with lower cortical thickness, but I did not investigate the association between brain functioning and brain structure. Therefore the current set of studies cannot provide an answer to the question whether lower or higher cortical thickness is also associated with different levels of neural activity. If we want to increase our understanding of how the brain-behavior relationship actually works, multi-modal studies combining functional and structural neuroimaging and links to real-life social behavior are necessary (for example see Morishima, Schunk, Bruhin, Ruff, and Fehr (2012); Will, Crone, van Lier, and Güroğlu (2016)). This will also allow us to translate findings from more fundamental research (as described in this thesis) to practical implications for society.

Conclusions

This thesis focused on the heritability of behavioral and neural processes involved in social competence in middle childhood. I investigated how individuals fulfill *others'* and their *own social needs* by studying behavior as well as the structure and functioning of the social brain (Blakemore, 2008). This thesis builds upon the existing literature by demonstrating that children and adults take *others' needs* into account by showing prosocial behavior as a response to observed social exclusion. Additionally, I demonstrated that focusing on *others'* and *own needs* was associated with an integrated set of brain regions involved in socio-cognitive and affective processing. Although extensive neuroimaging research revealed that the structure of the social brain continues to develop from childhood into adulthood (Blakemore, 2008, 2012; Mills et al., 2014) I now show that the functional architecture underlying social competence is already well established in middle childhood. Results on heritability of social competence help us to understand that individual differences in prosocial tendencies and brain structure might be partly influenced by genetic factors, but that neural and behavioral responses in a specific social context are largely shaped by an individual's experiences in the (social) environment. By providing a neurobiological perspective this thesis has highlighted middle childhood as a window of opportunity to increase social competence through training or intervention, and to possibly serve as the starting point for establishing and maintaining of positive social relationships across the lifespan.