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

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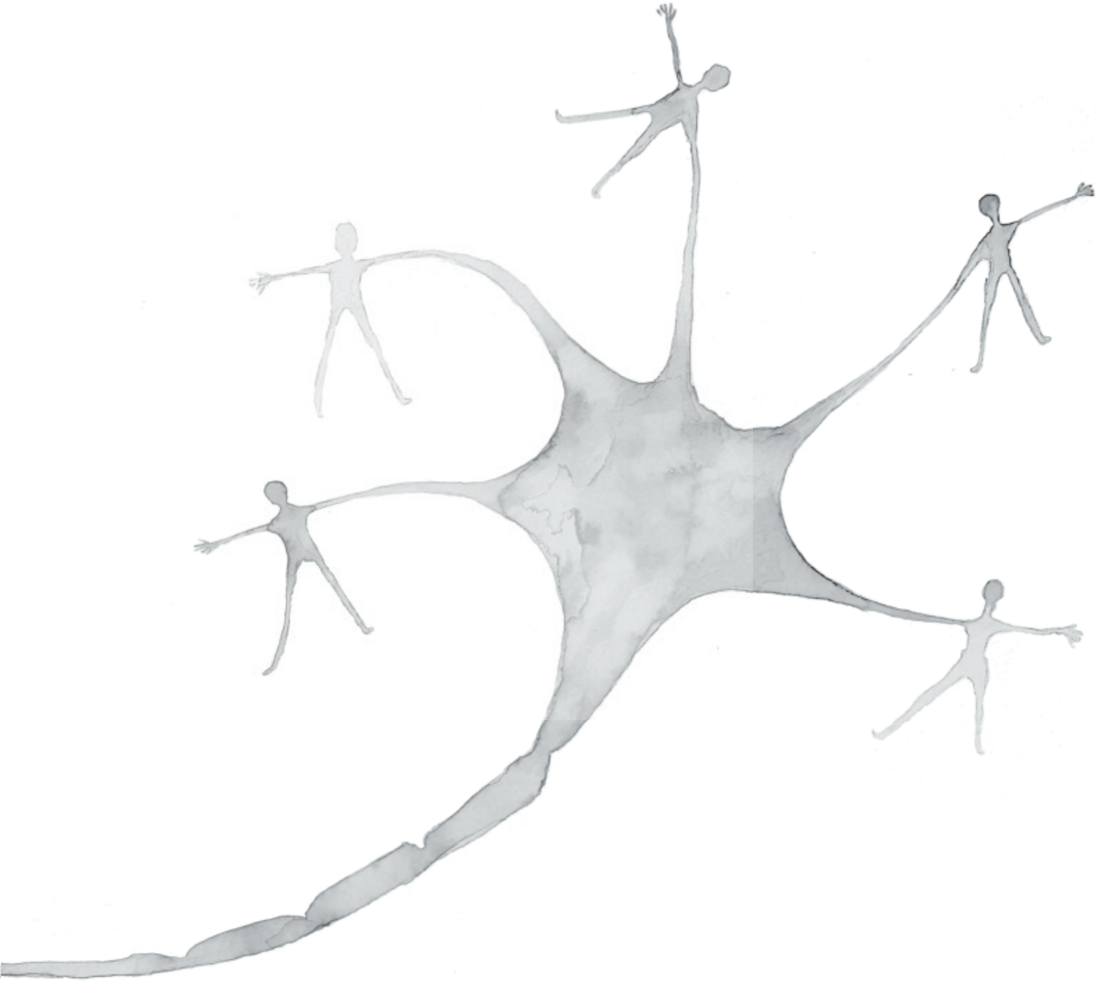
CHAPTER 1

General introduction



Introduction

A fundamental part of human development is the social relationship formed with other individuals. Numerous studies have indicated that people with a strong social network usually live longer, feel happier and are healthier than those who feel lonely (Goswami, 2012; Holt-Lunstad, Smith, & Layton, 2010; Reblin & Uchino, 2008; Smith & Christakis, 2008). In order to establish such a social network it is of key importance for children to develop social competence, or the ability to fulfill both others' and own needs in a social context (Rubin & Rose-Krasnor, 1992). Children can fulfill others' and their own needs by showing positive behavior such as helping another in distress (Eisenberg, Fabes, & Spinrad, 2006). However, if children are excluded from social interaction from an early age onwards, their own social needs are neglected and they might fail to develop the social competence that is necessary for social functioning later in life (Rubin, Bukowski, & Parker, 2006).

The development of social competence is possible due to the specific wiring of the human brain, which has adapted to facilitate the need for social interaction (Dunbar & Shultz, 2007). It is thought that social competence, as well as the underlying neural processes, are a result of a constantly changing interplay between genes and environment (Ebstein, Israel, Chew, Zhong, & Knafo, 2010). Middle childhood (age 6-12) in particular is seen as a key period in the development of social competence (Del Giudice, Angeleri, & Manera, 2009). Therefore, it is important to better understand why some children in this developmental stage thrive socially, and how these individual differences are related to underlying neural processes.

The goal of this thesis is thus to examine the processes involved in social competence in middle childhood, using a combination of experimental paradigms and parent-report questionnaires. In addition to behavioral measures, I have used neuroimaging techniques in order to better understand underlying processes in social competence. Furthermore, I have used a behavioral genetics approach to unravel influences of genetics and environment on social competence and associated neural processes. In this first chapter, I start with an introduction of middle childhood as a key period in human social development. This is followed by a section on factors contributing to social competence, and a section on the brain regions that support social competence. Finally, I will highlight the additional value of heritability research in the understanding of social competence. The final section of this introduction describes how the individual chapters of this thesis contribute to a neurobiological perspective on social competence in middle childhood.

Middle childhood

Traditionally, middle childhood (age 6-12 years) has been seen as a period of relative tranquility in development. Middle childhood is preceded by early childhood (age 0-6 years), the developmental stage for obtaining basic skills including motor control, speech and initial academic performance, such as reading, writing, and simple mathematics (Siegler, Deloache, & Eisenberg, 2006). Directly after middle childhood follows adolescence (age 12-18 years), the period in life characterized by changes in individual exploration and identity development (Crone & Dahl, 2012), and increased independence from parents (Nelson, Jarcho, & Guyer, 2016).

Middle childhood provides the groundwork for the large-scale developments of adolescence and therefore forms a unique and crucial developmental stage. During middle childhood children still receive attention and care from their caregivers, but they also start to develop themselves as individual members of society by discovering their interests, likes and talents (Del Giudice, 2014; Erikson, 1994). In addition, children show a large increase in complex cognitive skills such as self-regulation (Del Giudice, 2014; Steinbeis, Singer, Fehr, & Haushofer, 2014), as well as an rising awareness of their own feelings and mental states (Mah & Ford-Jones, 2012). These personal developments go hand in hand with social developments such as an increased understanding of social norms and values, such as notions of fairness and morality (Jambon & Smetana, 2014; Piaget, 1932). Although younger children are aware of the existing social norms and values, it is not until middle childhood that these norms are internalized and enforced in the communication with others (McAuliffe, Blake, Steinbeis, & Warneken, 2017; Smith, Blake, & Harris, 2013). The combination of increased personal and social skills allows for an increase in social competence, along with a shift in peer interaction from merely playing together with peers to the formation of dyadic friendships that are often based on shared interests (Del Giudice et al., 2009). The social status derived from those friendships often carries over well into adulthood, thereby highlighting the importance of developing social competence at an early age.

Other- and self-oriented factors in social competence

Social competence

Following the definition by Rubin and Rose-Krasnor (1992) social competence should be seen as a two-pronged ability: a socially competent individual is able to understand both another individual's interests and needs, as well as their own interests and needs. From infancy onwards children are sensitive to each other's emotions (Decety & Jackson, 2004; Hoffman, 1987). However, additional affective and socio-cognitive skills are needed to actually understand another child's distress and act accordingly. Affective skills include emotion understanding (the ability to correctly label an emotion; Reschke, Walle, & Dukes, 2017) and empathy (the ability to feel the emotion another child is feeling; Eisenberg, Spinrad, & Knafo-Noam, 2015), whereas socio-cognitive skills include perspective taking (the ability to understand that another child's perception might differ from one's own perception; Penner & Finkelstein, 1998) and self-regulation (Steinbeis, 2018).

Prosocial behavior

Prosocial behavior is seen as a component of social competence that provides a foundation for positive and reciprocal relationships (Over, 2016; Steinbeis, Bernhardt, & Singer, 2012). It can be broadly defined as a voluntary act to help another individual (Eisenberg et al., 2006; El Mallah, 2019; Padilla-Walker & Carlo, 2014), such as helping someone in need or distress, sharing resources, cooperating or comforting. In addition, those who show more prosocial behavior also show more academic achievement (Caprara, Barbaranelli, Pastorelli, Bandura, & Zimbardo, 2000; Wentzel, 1993), less externalizing behavior (Padilla-Walker, Carlo, & Nielson, 2015) and a better sense of well-being (Eisenberg et al., 2015) thereby extending the benefits of prosocial behavior past the social environment. Early signs of prosocial behavior are already apparent when children are 18 months old (Warneken & Tomasello, 2006), but prosocial behavior continues to develop throughout childhood along with the development of affective and cognitive abilities (Steinbeis & Over, 2017). Displays of prosocial behavior vary across contexts (Carlo & Randall, 2002; Dunfield, Kuhlmeier, O'Connell, & Kelley, 2011), as one might be generous with donating money to charity, but be more hesitant in comforting a stranger. Moreover, the motivations underlying prosocial behavior are thought to vary from altruistic (with no regard for own benefit) to self-serving intentions (Eisenberg & Spinrad, 2014). In line with this diversity in behavior, it should be noted that the best practice for measuring prosocial behavior is sometimes debated and differs between researchers (see El Mallah (2019) for review). For example, some researchers prefer to focus on observable prosocial behavior (using observational or experimental measures; Fehr, Bernhard, & Rockenbach, 2008; Güroğlu, van den Bos, & Crone, 2014), whereas other researchers are more interested in the tendencies underlying prosocial behavior, regardless of the outcome being more beneficial for the actor or the recipient (using questionnaires; Knafo-Noam, Uzefovsky, Israel, Davidov, & Zahn-Waxler, 2015). In this thesis I have combined two measurement types in order to measure various aspects of prosocial behavior. In **chapters 2, 3** and **4** I used an experimental task to measure prosocial behavior in a specific situation of observed social exclusion, and in **chapter 5** I have used a parent-reported measure of prosocial behavior to investigate prosocial behavior towards different recipients and across contexts.

Social exclusion

In contrast to children who can increase their social competence in a supportive peer environment, children who already have a lower level of social competence might be excluded from the peer group (Rubin et al., 2006). Being socially excluded results in internalizing and externalizing problems (Ladd, 2006), and feelings of loneliness (Boivin, Hymel, & Bukowski, 1995; Cassidy & Asher, 1992). In the long term, social exclusion is linked to feelings of depression (Ladd & Troop-Gordon, 2003), decreased academic performance (DeRosier & Lloyd, 2010; Véronneau, Vitaro, Brendgen, Dishion, & Tremblay, 2010) and decreased overall well-being, again extending the results of peer group interaction far past the social environment. Often children who are rejected by their peers either internalize their feelings and hide their emotions, or they lash out, thus behaving against social norms and giving peers cause for further rejection (Ladd, 2006; Rubin et al., 2006).

This in turn leaves a rejected child with less possibilities to obtain the social competence that they so desperately need to connect better with their classmates. It might therefore not be surprising that children who were excluded in childhood are also more likely to be socially excluded later in life (Hardy, Bukowski, & Sippola, 2002).

Across the lifespan, being socially excluded is such a salient event that even a simple virtual ball-tossing game is enough to elicit feelings of exclusion. The Cyberball Game, designed by Williams, Cheung, and Choi (2000) has often been used to create a virtual situation of social exclusion, in order to better understand the psychological consequences of exclusion (Masten et al., 2009; Will, van Lier, Crone, & Güroğlu, 2016). In **chapters 3** and **4** I have used an adapted version of the Cyberball Game (based on Riem, Bakermans-Kranenburg, Huffmeijer, and van IJzendoorn (2013)) to examine responses to short-term social exclusion from a group of virtual players.

Neural networks supporting social competence

In the last decades structural and functional magnetic resonance imaging (MRI) has been employed to further investigate underlying neural processes in social competence. Structural neuroimaging studies have shown that both grey matter (neurons) and white matter (connections between neurons) continue to increase from infancy throughout childhood. In adolescence, a large number of neurons are eliminated following the "use it or lose it" principle: important connections in the brain are kept to be refined and optimized, whereas redundant connections are discarded (Gogtay et al., 2004; Wierenga, Langen, Oranje, & Durston, 2014). This means that even though the brain has already reached its maximum volume at the start of middle childhood (Del Giudice, 2014), neural development continues until adulthood. In the investigation of social behavior, functional neuroimaging studies have consistently shown that a network of specific brain regions (known as the social brain) has developed to support the complex functions needed for human interaction (Blakemore, 2008; Frith & Frith, 2003). The social brain includes regions that are involved in both the socio-cognitive and affective processes of social competence (also see Figure 1).

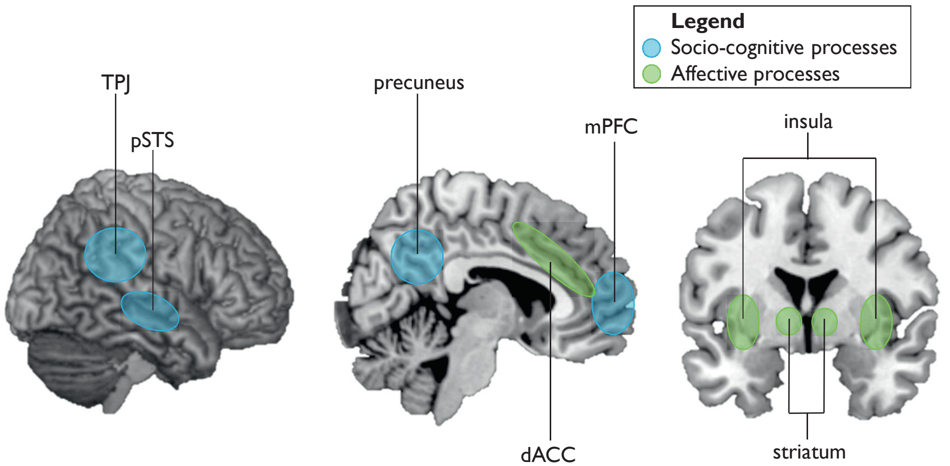


Figure 1. *Visualization of the social brain. Areas highlighted in blue are involved in socio-cognitive processes; temporo-parietal junction (TPJ), posterior superior temporal sulcus (pSTS), precuneus, and medial prefontal cortex (mPFC). Areas highlighted in green are involved in affective processes; dorsal anterior cingulate cortex (dACC), insula, and striatum. Figure adapted from Will and Güroğlu (2016).*

The socio-cognitive processes of social competence, including the ability to take someone else's perspective, are supported by regions such as the medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), posterior superior temporal sulcus (pSTS) and the precuneus (Blakemore, 2008). Specifically, the TPJ is thought to play a role in perspective taking (Carter & Huettel, 2013; Will, Crone, & Guroglu, 2015), whereas the pSTS is involved in the processing of general social information such as biological motion and speech (Frith & Frith, 2007; Frith & Frith, 2003; Van Overwalle & Baetens, 2009). The mPFC might be more involved in thinking about one's personal and others' mental states (Frith & Frith, 2007; Frith & Frith, 2003; Van Overwalle & Baetens, 2009). The role of the precuneus in social competence is less clear, as this region is both implicated in the retrieval of social information (Pfeifer, Lieberman, & Dapretto, 2007) as well as in empathic responding (Masten, Morelli, & Eisenberger, 2011). Together, these regions have been consistently shown to support prosocial behavior (Güroğlu, van den Bos, & Crone, 2009; Güroğlu, van den Bos, van Dijk, Rombouts, & Crone, 2011; Tousignant, Eugène, Sirois, & Jackson, 2017; Will et al., 2015).

In addition to socio-cognitive processes, the affective processes of social competence encompass processing of emotions. These affective processes are supported by regions such as the anterior insula (AI), dorsal anterior cingulate cortex (dACC), and the ventral striatum (VS). The anterior insula and dACC are particularly important for detecting salient events (Menon & Uddin, 2010; Seeley et al., 2007), and have been implicated in the processing of both positive and negative social events (Davey, Allen, Harrison, Dwyer, & Yucel, 2010; Eisenberger, Lieberman, & Williams, 2003). The ventral striatum on the other hand is seen as a reward center in the brain (Delgado, 2007; Lieberman & Eisenberger, 2009) and might therefore be more involved in positive social experiences such as voluntary sharing goods (Harbaugh, Mayr, & Burghart, 2007). Neuroimaging research has consistently shown that the experience of social exclusion is associated with increased neural activity in the AI and dACC (Cacioppo et al., 2013; Eisenberger et al., 2003; Masten et al., 2009; Rotge et al., 2015). Additionally, self-reported levels of distress have been shown to positively correlate to neural activity in AI and dACC, thereby further establishing the association between the negative experience of social exclusion and concurrent neural activity (Masten et al., 2009). Interestingly, observing social exclusion of someone else is associated with the same neural network as experiencing social exclusion (Masten, Eisenberger, Pfeifer, & Dapretto, 2010; Meyer et al., 2013)

In an investigation of brain structure it has been shown that regions in the social brain continue to develop well into adolescence (Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). This finding is accompanied by functional MRI studies showing that brain activity for social events is different across development. For example, the TPJ shows increasingly stronger activation during prosocial behavior over the course of development (Güroğlu et al., 2009, 2014; Güroğlu et al., 2011; Tousignant et al., 2017; Will et al., 2015). It is important to note that the relationship between brain and behavior is bidirectional: brain structure and function can be affected by social factors such as a lack of positive parenting (Belsky & de Haan, 2011) or a lack of positive peer experiences (Will et al., 2016), but in turn alterations in brain structure can also affect a child's social behavior (Beauchamp, Dooley, & Anderson, 2013). Given the importance of middle childhood for the development of social competence, it is credible that individual differences in social behavior in this particular developmental stage are reflected in function and structure of the social brain. In this thesis, I examined the association between prosocial behavior and brain function, as well as between social exclusion and brain function, in **chapters 2, 3** and **4** (studying both adult and middle childhood samples)**.** In the same middle childhood sample, I studied the association between prosocial behavior and brain structure in **chapter 5.**

Heritability of social brain and behavior

A method to investigate whether middle childhood is a particularly sensitive period in terms of social environmental influences is by assessing the heritability of social competence in this particular age range. That is, to assess whether variance in social competence can be best explained by genetic factors, environmental factors, or a combination of the two. In short, genetic factors usually consist of variations in single or multiple genes, whereas environmental factors can be divided into shared (e.g. parenting or home environment) or unique (i.e. specific for an individual child) factors (McLoughlin, Ronald, Kuntsi, Asherson, & Plomin, 2007; Plomin, DeFries, McClearn, & McGuffin, 2001).

Estimations of genetic and environmental influence can be made in twin samples, as those samples allow for a comparison of individuals with 100% shared genes (i.e. monozygotic (MZ) twins) and individuals with 50% shared genes (i.e. dizygotic (DZ) twins). In those comparisons, it is assumed that both MZ and DZ twins are raised together and therefore share the home environment to a similar extent. The finding of a high positive association between MZ twins than between DZ twins is an indication of a strong genetic influence. If MZ twins and DZ twins show equally high associations then the behavior is probably driven by shared environmental factors, due to the shared home environment for both MZ and DZ twins. If there is no association between either MZ or DZ twins, then the variance in behavior is probably driven by unique environmental factors or by measurement errors (Knafo-Noam, Vertsberger, & Israel, 2018).

Using this method, studies have shown that half of the variance across the whole range of human behavior can be explained by genetics (Polderman et al., 2015). More specifically for factors underlying social competence, it has been shown that up to half of the variance in prosocial behavior and empathy could be attributed to genetic factors, with the remainder of the variance best explained by shared and unique environmental factors (Gregory, Light-Hausermann, Rijsdijk, & Eley, 2009; Knafo-Noam et al., 2015; Knafo et al., 2009; Melchers, Montag, Reuter, Spinath, & Hahn, 2016). Corresponding to heritability estimates of behavior, it has been found that different measures of brain structure are also strongly driven by genetic factors (Ma et al., 2016; Panizzon et al., 2009; Peper, Brouwer, Boomsma, Kahn, & Hulshoff Pol, 2007; Teeuw et al., 2018), although heritability estimates of brain functioning in social contexts have not been investigated in detail.

It is important to note that the relative influence of genes and environment on behavior and brain is not constant throughout development (Davis, Haworth, & Plomin, 2009; Lenroot & Giedd, 2008). For example, research has indicated that for both prosocial behavior and brain structure genetic factors become increasingly more influential as children grow older (Knafo & Plomin, 2006; Lenroot & Giedd, 2008). Moreover, heritability estimates differ for different components in prosocial behavior (Knafo-Noam et al., 2015). In this thesis I studied heritability of prosocial behavior and social exclusion in an experimental paradigm, along with associated brain function, in **chapter 4**. In **chapter 5** I investigated heritability of parent-reported prosocial behavior and its association with brain structure.

Outline of this thesis

In this thesis I report the results from four empirical studies that I have conducted to investigate individual differences in reactions to the social environment, using an experimental paradigm, parent-report questionnaires, and functional and structural neuroimaging. A graphical outline of the concepts and measurements discussed in the four subsequent chapters is shown in Figure 2.

In **chapter 2** the results of an fMRI version of a four-player Prosocial Cyberball Game (PCG) in adults are presented. Using an experimentally induced situation of observed exclusion, I aimed to disentangle neural responses during prosocial behavior from neural responses to observed social exclusion. This adult study was used as a starting point for the next chapters. In **chapter 3** the PCG was validated as a fMRI paradigm in middle childhood. Here I examined behavioral and neural responses to observed social exclusion, as well as neural responses to experienced social exclusion. I employed a test-replication design and meta-analytic approach to investigate behavioral and neural responses across three samples (all 7-10 years old). In **chapter 4** I combined neuroimaging and behavioral genetics in a large middle childhood sample, to investigate contributions of genes and environment on the behavioral and neural responses to the PCG. In **chapter 5** I extend the investigation of heritability of prosocial behavior and neural correlates in the same middle childhood sample, by describing unique and shared influences of genes and environment on parent-reported prosocial behavior and structural measures of social brain regions (i.e. mPFC, TPJ, pSTS, precuneus). Finally, in **chapter 6** I summarize and discuss the findings of the empirical chapters and provide an overview of the implications of these findings.

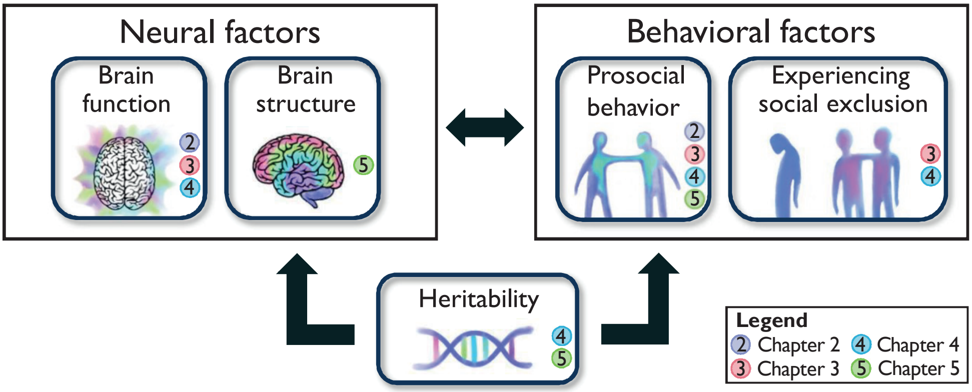


Figure 2. *Visualization of the relationship between behavioral, neural and heritability factors in social competence presented in the current thesis.*