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

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CHAPTER ONE

General introduction

GOT A FRIEND IN ME?

The Scope of this Thesis

Humans have a strong need for social connections. Social connections provide social security and a feeling of social acceptance, and contribute to the development of identity and self-worth (Meeus, Oosterwegel, & Vollebergh, 2002). Whereas parents and caregivers remain an important source for security and support, peers emerge as social targets in adolescence to fulfill the need for social connections (Berndt, 1992; Helsen, Vollebergh, & Meeus, 2000). That is to say, peers more frequently provide company in adolescents' everyday lives, and friendships become more intimate and a source of emotional and social support (Buhrmester, 1990; McNelles & Connolly, 1999; Steinberg, 2005). Friendships are close peer relationships that are equal in nature, and provide a context in which essential social skills and an understanding of the social norms are adopted (Hartup, 1996). As these intimate peer relationships contribute to a feeling of social security, they may provide opportunities for exploration and novelty seeking. Exploration and novelty seeking are hypothesized to be crucial for adolescents to grow up to become independent and responsible adults (Crone & Dahl, 2012), who have acquired a good understanding of how to manage themselves, others, and their social relationships in society (Dahl, Allen, Wilbrecht, & Suleiman, 2018; Nelson, Jarcho, & Guyer, 2016).

Adolescence is the transition period from childhood to adulthood, and captures the period from the onset of puberty to the socially defined endpoint of maturity, which is adulthood (e.g., Dumontheil, 2016). It is a sensitive period for social changes and development, including a general increase in the motivation to build social bonds with peers and in the incorporation of context and others' perspectives into social decisions (Dumontheil, Apperly, & Blakemore, 2010; Nelson et al., 2016; Van den Bos, Westenberg, Van Dijk, & Crone, 2010). These developmental changes guide increases in adaptive social behaviors that are appropriate for the social context. For instance, when there is a motivation to build a social bond with others or to maintain a friendship, investment in the form of prosocial behavior may strengthen or foster continuation of such social relationships (Eisenberg, Fabes, Guthrie, & Reiser, 2000; Eisenberg, Fabes, & Spinrad, 2006), for example with giving, sharing, helping, and cooperating.

In this thesis I will discuss four studies that tap into processes that are involved in different aspects of the motivation to build or keep social bonds with peers. The processes I refer to (a) are reward-related, which are likely to have motivating effects, and (b) underlie prosocial actions, which are crucial for the continuation of social bonds. In the first part of this thesis, I addressed the question how, across adolescence and early adulthood, neural responses to rewards are related to developmental trajectories of reward sensitivity implicated in exploration and seeking out novel experiences (chapter 2) and the continuation and cessation of best friendships (chapter 3). In the second part of this thesis, I addressed the question how brain activity involved in prosocial behavior is related to positive and negative peer relationships in a group of adults (chapter 4) and adolescents (chapter 5).

Neurodevelopmental Changes Related to Social Development

Changing social orientation

Human's primary social interaction partners change across the life span. As such, human's social orientation changes across development, such that it adapts to changing social needs and circumstances (Nelson et al., 2016). In early developmental phases, the social focus is primarily directed at caregivers, which is followed by a gradual increase in peer-focused play. As children mature and make the transition into adolescence, there is an emerging shift in social focus toward the larger peer group. In late adolescence and early adulthood, a social interest into intimate and romantic relationships arises. Finally, social maturity is characterized by relatively stable social relationships, which can be directed at humans from multiple generations (e.g., offspring, family members, and friends).

The social brain

The social information processing network (SIPN) is a notorious model that aims to explain changes in social orientation in adolescence from a developmental neuroscience perspective (Nelson, Leibenluft, McClure, & Pine, 2005). The SIPN model poses involvement of three different nodes of clustered brain regions, which are widely considered to be involved in social processes, and are together often referred to as 'the social brain network' (Blakemore, 2008; see, Figure 1). The three nodes from the SIPN model develop at different paces, although fine-tuning and the assimilation of the separate brain areas continues across development (Nelson et al., 2016; Nelson et al., 2005). The SIPN model comprises (a) the detection node, which is involved in perceiving information as social, (b) the affective node, which is involved in assigning emotional significance to social information, and finally (c) the cognitive regulation node, which is involved in higher order social cognitive processes that are important for making deliberate social decisions, such as inferring others' mental states, regulating impulses, and behaving in a goal-directed manner.

Important brain areas assigned to the detection node are temporal cortical regions including the anterior temporal cortex, superior temporal sulcus (STS), temporoparietal junction (TPJ), and the fusiform face area (FFA). With regard to their role in basic social functions, brain areas from the detection node are the first to mature before the onset of puberty. The basic social functions of these brain regions are implicated in recognizing and processing social stimuli, biological motion, and faces. However, it should be noted that social functions of the STS, TPJ, and FFA continue to develop until at least late adolescence. Subcortical brain regions including the nucleus accumbens, amygdala, and hypothalamus, as well as the anterior insula and ventral prefrontal cortex are part of the affective node, and are implicated in processing socially valued signals. Maturation of the affective node appears to be linked to pubertal physiological processes. In addition, the affective node is posed to play an important role in the formation of brain circuits during sensitive organizational periods. Finally, the cognitive regulation node follows a protracted developmental trajectory until at least early adulthood and contains cortical brain regions in the lateral and medial prefrontal cortex. The cognitive regulation node serves to modulate emotional responses and to guide context appropriate social behavior. As brain regions from the affective node mature earlier in adolescence than brain regions from the cognitive regulation node, according to the SIPN model, adolescence might

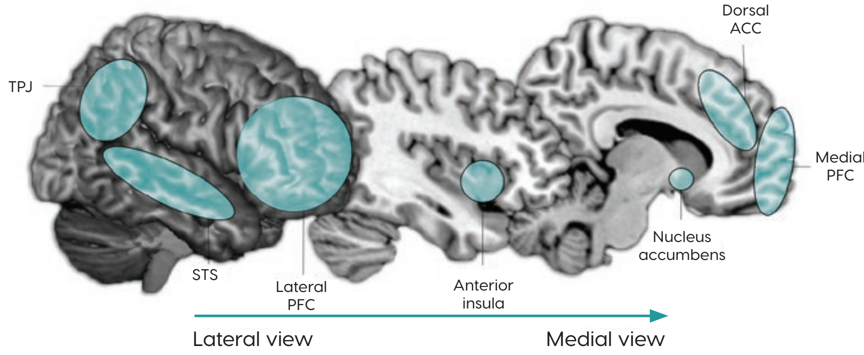

Figure 1. Brain regions implicated in social information processing and social decision-making.

be a sensitive period for changes in affective responses to social contexts. As such, sensitized affective brain responses to peer experiences are likely to affect adolescents' social development (see also Somerville, 2013).

Reward Sensitivity of the Ventral Striatum

Like the SIPN model, several other prevailing models have incorporated the hypothesis that certain brain systems develop at different paces, including the dual-systems model, the imbalance model, and the triadic model (Casey, 2015). These models highlight the nucleus accumbens, a subcortical region of the ventral striatum responsive to rewards (assigned to the affective node in the SIPN model), as a key region implicated in reward-seeking behaviors in adolescence. Like the SIPN model, these models hypothesize that subcortical and frontal regions develop in an asynchronous manner (Casey, Galván, & Somerville, 2016; Ernst & Fudge, 2009). In support of this hypothesis, the nucleus accumbens is found to be hyper-responsive to (often monetary) rewards gained for the self in adolescence (Braams, Van Duijvenvoorde, Peper, & Crone, 2015; Galvan et al., 2006; Van Leijenhorst et al., 2010b), although discrepancies have also been reported (Galvan, 2010).

The nucleus accumbens has not only been found to serve as a neural basis for processing rewards for the self, but also for social rewards in the form of social status, as well as vicarious rewards, i.e., rewards for others (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010; Wake & Izuma, 2017). Furthermore, nucleus accumbens responses elevate when similar others relative to dissimilar others, and friends relative to disliked others gain rewards (Braams et al., 2014a; Mobbs et al., 2009). These findings show that nucleus accumbens responses are dependent on the social context, such that the nucleus accumbens appears to be particularly responsive to preferred social events.

Together, a substantial number of studies highlighted the nucleus accumbens as a key region involved in affective processing, which may be especially sensitive to rewards in adolescence. The SIPN model poses that subcortical regions, including the nucleus accumbens, become especially sensitive to the peer environment in adolescence. Moreover, interplay between brain regions implicated in social information processing may influence (the development of) social behavior (Nelson et al., 2016). In the following sections of this chapter, I will introduce the studies presented in chapter 2 and 3 in which I examined how reward sensitivity of the nucleus accumbens is related to reward-related drives and friendship stability across adolescence, respectively. Furthermore, I will introduce the studies described in chapter 4 and 5 in which I examined the neural mechanisms underlying prosocial decision-making involving interaction partners of varying relationship valence in adults and adolescents, respectively.

Reward-Related Drives

Rewards for the self

To understand adolescent development in relation to peer relationships, a fundamental understanding of the neural mechanisms underlying adolescents' drives provides complementary insights. Adolescence is typically characterized by increases in the motivation to explore and push boundaries (Crone & Dahl, 2012). This increasing motivation is an important aspect of normative development, and is posed to contribute to a flexible mind that facilitates learning and the motivation to seek out new friendships (Hauser, Iannaccone, Walitza, Brandeis, & Brem, 2015; McCormick & Telzer, 2017; Telzer, 2016). These motivational changes coincide with developmental changes in neural reward sensitivity of the nucleus accumbens in adolescence. As such, changes in nucleus accumbens reward sensitivity may relate to changes in motivated behaviors, which may contribute to the developmental process of adopting adult-like motivations and values. I examined how developmental changes in reward-related nucleus accumbens responses related to motivations to explore and achieve personal goals and to what extent rewards are valued in chapter 2.

Rewards for friends

Reward sensitivity of the nucleus accumbens may also play a prominent role in the emerging social orientation toward friends in adolescence. Friendships become more stable across adolescence (Berndt & Hoyle, 1985; Branje, Frijns, Finkenauer, Engels, & Meeus, 2007), and to maintain or form stable friendships, a motivation to commit to the relationship is crucial. Nucleus accumbens' responsiveness to rewarding social events may motivate engagement in future positive peer interactions (e.g., Mobbs et al., 2009). As such, reward-related nucleus accumbens responses to friends may contribute to committed, stable friendships. In this thesis, I examined whether adolescents with stable and unstable best friendships showed different developmental trajectories of nucleus accumbens responsiveness to rewards for best friends in chapter 3.

Studying developmental trajectories

All in all, the scientific literature demonstrates that there are several social and behavioral changes across development (Casey, 2015; Nelson et al., 2016). Studying reward sensitivity using a neuroscience perspective aids to understand why these social and behavioral changes occur in adolescence. Furthermore, to better understand developmental changes within a wide developmental period, such as from childhood to adulthood, testing the same participants (from a wide age span) on multiple occasions becomes inevitable. In other words, empirical neuroimaging studies with a longitudinal design are pivotal to reliably explain developmental trajectories across adolescence. Therefore, in this thesis, I studied developmental changes in participants, ages eight to twenty-nine, who were invited for participation three times every other year. In this sample, I studied developmental trajectories of reward-related nucleus accumbens activity in relation to reward-related behavioral drives and friendship stability to get a better understanding of adolescent development.

Peer Relationship Valence

Real-life peer interactions

On a typical day, we interact with all kinds of people. These social interactions are likely to involve others that we value positively, such as friends, a liked colleague or classmate. On other occasions, however, social interactions may involve unfamiliar or disliked others. Friendships and peer relationships based on dislike have different characteristics, such that friendships are often based on some form of similarity and compatibility, whereas relationships based on dislike are often characterized by aggression and attempts to do harm (Abecassis, 2003; Card, 2007; Laursen, 2017). In general, prosocial actions contribute to the formation and maintenance of positive social connections like friendships, (Eisenberg et al., 2006; Fehr, Fischbacher, & Gächter, 2002), whereas selfish actions might weaken a social connection and potentially provide the basis for a relationship based on dislike. It should therefore come as no surprise that individuals tend to behave in a more prosocial manner toward friends than toward disliked peers (Güroğlu, Van den Bos, & Crone, 2014).

Prosocial behavior

Social behavior becomes more sophisticated throughout adolescence. For example, social decisions become increasingly dependent on the interaction partner, the costs attached, and relative outcomes (Güroğlu et al., 2014;

Meuwese et al., 2014; Overgaauw, Güroğlu, & Crone, 2012). In other words, adolescents become increasingly better in understanding other people's perspectives and intentions, and in making more regulated, deliberate decisions depending on the social context. In line with this observation and the SIPN model, involvement of brain regions underlying the process of making (pro-) social decisions also changes across adolescence (e.g., Crone, 2013; Güroğlu, Van den Bos, & Crone, 2009a; Nelson et al., 2016).

Prosocial decisions might be motivated by social rewards (e.g., social status or approval, or a so-called "warm glow"); extrinsic incentives (e.g., a "tit for tat" strategy, or a common goal); social norms and expectations; and a concern for others (Declerck, Boone, & Emonds, 2013; Luo, 2018; Zaki & Mitchell, 2011). Accordingly, prosocial behavior is related to an interplay of brain regions involved in (a) processing affective information (the striatum, amygdala, and anterior insula), which is important for assigning emotional significance to a social interaction, for example to determine if something is rewarding or should be avoided, (b) controlling affective responses (i.e., cognitive control; the lateral prefrontal cortex [LPFC], and the anterior cingulate cortex [ACC]), which is important for showing goal-directed behavior and suppressing impulses that stem from selfish desires, and (c) social cognition (the medial prefrontal cortex [mPFC], the STS, and the TPJ), such as shifting the focus from the self to the goals and needs of others (this is referred to as mentalizing) and processing the social context (see also Figure 1).

Generally, involvement of neural processes underlying social decision-making (e.g., when deciding whether to behave in a prosocial manner) is dependent on the social context. For example, decisions to accept or reject a proposed distribution of resources in a psychological experiment in which social interactions are simulated require the ability to infer the interaction partner's intentions and mental states. This related to increased activity in the TPJ and the dorsal lPFC (Güroğlu, Van den Bos, Rombouts, & Crone, 2010; Güroğlu, Van den Bos, Van Dijk, Rombouts, & Crone, 2011). Furthermore, social decisions when being watched or evaluated by peers relative to deciding alone yields heightened activity in brain regions involved in social cognitive processes, including the mPFC, TPJ, and STS (Somerville, 2013; Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). In addition, processing social contexts involving familiar peers relative to unfamiliar peers are associated with increased activity in the striatum, lPFC, mPFC, STS, and TPJ (Güroğlu et al., 2008). Also individual differences in prosocial behavior affect involvement of brain activity underlying social decision-making. For example, individuals who tend to invest more in a public good yield more TPJ activity, and when individuals do not behave according to their personal social norms (which can be either prosocial or selfish), they yield increased activity in the dorsal ACC and anterior insula (Güroğlu et al., 2010; Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2009). Although it should be noted that engagement of these brain regions undergo developmental changes (e.g., as described by the SIPN model), these studies together show that the social context modulates engagement of brain regions that are involved in affective, cognitive control, and social cognitive processes.

Ecologically valid research paradigm to study social decision-making

Even though neuroimaging studies have extensively studied social decision-making with unfamiliar peers (Lee & Harris, 2013), little is known about the neural mechanisms underlying social decisions during interactions with friends and disliked peers, and how they compare to each other. Neuroimaging studies using an ecologically valid research paradigm (e.g., by including friends as well as familiar disliked peers in the experimental design) are important to achieve a better understanding of neural processes underlying social decisions. In this thesis, I studied how neural processes underlying social interactions are modulated by different types of interaction partners, including familiar friends and disliked peers, in adults in chapter 4, and adolescents in chapter 5.

Outline of this Thesis

In this thesis I will discuss four studies that tap into reward-related and relationship-valence-related motivations of adolescents and adults. Together, these studies aim to examine how reward and social decision-making processes are modulated by developmental periods and contexts. I aim to provide insights into how these processes contribute to social development using a neuroscience perspective.

First, I will discuss results from a longitudinal study on the development of reward-related nucleus accumbens activity in response to rewards for the self (chapter 2) and rewards for stable and unstable best friends (chapter 3) across adolescence. The nucleus accumbens is a good candidate region to examine changes in motivation processes across adolescence, because of its inherent implications in reward processing. With the study presented in **chapter 2**, I aimed to examine how the drive to obtain personal goals and the immediate pleasure experienced in response to rewards for the self relate to changes in reward-related nucleus accumbens activity across adolescence.

In **chapter 3**, I studied nucleus accumbens activity in response to rewards for stable and unstable best friends. More specifically, I aimed to examine whether adolescents with unstable and stable best friendships show different nucleus accumbens responses when gaining rewards for best friends across adolescence, and how these neural responses relate to the hedonic impact of rewards, and perceived friendship characteristics, including friendship quality and closeness.

Next, I will discuss the neural mechanisms underlying prosocial decision-making toward familiar friends and disliked peers in a sample of young adults (chapter 4) and adolescents (chapter 5). Prosocial decision-making requires the ability to understand others' perspectives and to inhibit selfish impulses, and the motivation to respond to others' needs. In **chapter 4**, I aimed to study how interactions with familiar friends and disliked peers modulated prosocial behavior and the underlying neural processes in adulthood. Similarly, in **chapter 5**, I examined brain activity patterns related to prosocial decision-making involving real-life friends and disliked peers. In addition, I explored how these are brain activity patterns related to individual differences in social competence in middle adolescence. Finally, in **chapter 6** I summarize and discuss the findings of the empirical studies.