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GOT A
FRIEND IN ME?

Mapping the neural mechanisms
underlying social motivations
of adolescents and adults

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GOT A FRIEND IN ME?

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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

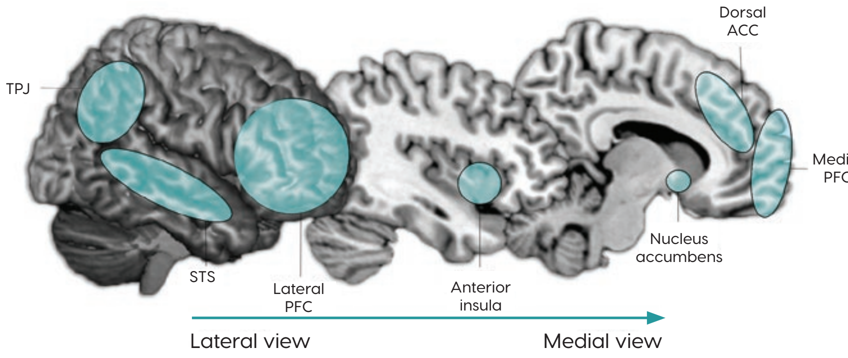

Figure 1. Brain regions implicated in social information processing and social decision-making.

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.


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CHAPTER TWO

Contributions of reward sensitivity to ventral striatum activity across adolescence and early adulthood

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Child Development, 89(3), 797-810.

ABSTRACT

It was examined how ventral striatum responses to rewards develop across adolescence and early adulthood and how individual differences in state- and trait-level reward sensitivity are related to these changes. Participants (aged 8-29 years) were tested across three waves separated by two years (693 fMRI scans) in an accelerated longitudinal design. The results confirmed an adolescent peak in reward-related ventral striatum, specifically nucleus accumbens, activity. In early to mid-adolescence, increases in reward activation were related to trait-level reward drive. In mid-adolescence to early adulthood decreases in reward activation were related to decreases in state-level hedonic reward pleasure. This study demonstrates that state- and trait-level reward sensitivity account for reward-related ventral striatum activity in different phases of adolescence and early adulthood.

INTRODUCTION

Adolescence has often been described as a period of exploration and novelty seeking (Hauser, Iannaccone, Walitza, Brandeis, & Brem, 2015). On the one hand, novelty seeking can lead to increased risk-taking behavior, which might have potentially damaging health consequences (Dahl, 2004). On the other hand, novelty seeking is an important aspect of normal explorative behavior with positive outcomes, such as seeking out new friendships (Telzer, 2016), and contributes to behavioral flexibility and greater learning (Crone & Dahl, 2012). An important factor that drives novelty seeking and explorative behavior in adolescence is reward sensitivity (Abler, Walter, Erk, Kammerer, & Spitzer, 2006; Demaree, DeDonno, Burns, & Erik Everhart, 2008; Hawes et al., 2017; Telzer, 2016; Van Duijvenvoorde, Peters, Braams, & Crone, 2016). Increases in reward sensitivity in adolescence have been explained in terms of asynchronous development of subcortical brain regions, including the ventral striatum and amygdala, relative to cortical brain regions (Casey, Galván, & Somerville, 2016; Ernst & Fudge, 2009). Prior studies have demonstrated that reward sensitivity is linked to ventral striatum activity in adolescence, but how reward sensitivity relates to neural activity patterns across adolescent development is not yet well understood (e.g., Braams, Van Duijvenvoorde, Peper, & Crone, 2015; Urošević, Collins, Muetzel, Lim, & Luciana, 2012). This three-wave longitudinal study set out to examine the relation between state- and trait-level reward sensitivity and neural activity in response to reward outcomes in the ventral striatum across adolescence.

Several recent studies have examined ventral striatum activity to rewards across developmental periods. In particular, the nucleus accumbens (NAcc) of the ventral striatum has been shown to be involved in reward processing across a variety of domains, such as gaining money, social status, or positive social feedback (Bhanji & Delgado, 2014; Izuma, Saito, & Sadato, 2008; Liu, Hairston, Schrier, & Fan, 2011; Sescousse, Caldú, Segura, & Dreher, 2013). Several empirical studies have demonstrated that the ventral striatum is more active in adolescents than in children and adults when receiving rewards in gambling tasks (Galvan et al., 2006; Van Leijenhorst et al., 2010b), with a peak in reward-related activity around age 16-17 years (Braams et al., 2015; Silverman, Jedd, & Luciana, 2015), although inconsistent findings have been reported as well (see review by Galvan, 2010). We aimed to confirm the adolescent peak in NAcc reward activation in a follow-up study of Braams et al. (2015), which included two data waves of the current study. We extended these analyses using three data waves and thereby examined the transition into young adulthood using a within-person design. We also sought to determine how state- and trait-level reward sensitivity levels related to increases in reward-related NAcc activity across early and mid-adolescence and declines in NAcc activity across late adolescence and early adulthood.

Several prior studies suggested that the NAcc plays an important role in adolescents' tendency to seek out rewarding and exciting experiences (Telzer, 2016; Van Duijvenvoorde et al., 2016). In previous studies it was shown that dopamine release from the ventral striatum, especially from the NAcc, is involved in the hedonic impact or the pleasure experienced in rewarding situations (Telzer, 2016; Wahlstrom, White, & Luciana, 2010). Hence, one type of behavioral reward sensitivity that may be involved in age-related changes in reward-related ventral striatum activation is the pleasure people experience when receiving rewards. This type of reward sensitivity was previously related to the actual rewards obtained (Telzer, 2016; Wahlstrom et al., 2010), and is therefore henceforth referred to as state-level reward sensitivity. Another type of reward sensitivity that may be associated with age-related changes in reward-related ventral striatum activation is individuals' general motivation to approach rewards (Carver & White, 1994). Increased ventral striatum activation to rewards has been associated with higher reward drive, that is the drive to pursue rewards or to achieve a goal (Braams et al., 2015), and more fun-seeking tendencies (Van Duijvenvoorde et al., 2014). In addition, a decline in NAcc volume in late adolescence, which is posed to be related to a lower density of synapses or less pruning, has been associated with a decrease in the tendency to approach rewards (Urošević et al., 2012). This type of reward sensitivity relates to someone's general tendency to seek out rewards and is henceforth referred to as trait-level reward sensitivity. In the current study, we examined how behavioral state- and trait-level reward sensitivity (i.e., pleasure derived from obtaining task-specific rewards and general desire to obtain rewards, respectively) contribute to fluctuations in NAcc reward-sensitivity.

We tested these questions using functional magnetic resonance imaging (fMRI) with an accelerated longitudinal design with three time points, each separated by two years. Results of the first and second time point of this study are reported in Braams et al. (2015) and Braams, Peters, Peper, Güroğlu, and Crone (2014). We acquired functional scans of NAcc responses to rewards versus losses when participants (8 to 29 years of age) played a gambling task that involved making a heads-or-tails guess with 50% chance of winning.

State-level reward sensitivity was measured using self-reports of how much participants enjoyed winning and losing in the fMRI task, and trait-level reward sensitivity was measured using the Behavioral Activation System (BAS) scale (Carver & White, 1994). There are currently no studies that have examined changes in ventral striatum reward sensitivity with a design including more than two time points (Braams et al., 2015; Lamm et al., 2014), and to our knowledge, no studies have focused on the decline in NAcc activity in early adulthood. On the basis of prior findings, we hypothesized that reward-related NAcc activation peaks in mid-adolescence (Braams et al., 2015; Silverman et al., 2015). We further expected a positive relation between NAcc activity and state-level reward sensitivity (i.e., pleasure from winning; Dohmen, Falk, Fliessbach, Sunde, & Weber, 2011) and trait-level reward sensitivity (i.e., general motivation to approach rewards; Simon et al., 2010). On the basis of prior studies, we specifically expected positive relations between the trait-level drive to pursue rewards and personal goals (measured with the BAS drive scale), and fun-seeking tendencies (measured with the BAS Fun Seeking scale; Braams et al., 2015; Van Duijvenvoorde et al., 2014). Specifically, we tested whether these two types of behavioral reward sensitivity measures accounted for the increase in NAcc response from early to mid-adolescence and the decrease in NAcc response from mid- to late adolescence and adulthood. As such, the findings will provide insights in the underlying mechanisms involved in age-related differences in explorative behaviors across adolescence and early adulthood.

METHOD

Participants

The current study is part of the Braintime longitudinal study, which has been conducted at Leiden University in 2011, 2013, and 2015. Data from the first and the second time points have been previously published (e.g., Braams, et al., 2014a; Braams, et al., 2014b; Braams et al., 2015). At the first time point (T1) we collected data of 299 participants (M_{Age} = 13.98 years, SD_{Age} = 3.68 years, $range_{Age}$ = 8.01 - 25.95 years; 153 females), at the second time point (T2) of 287 participants (M_{Age} = 15.84 years, SD_{Age} = 3.57 years, $range_{Age}$ = 9.92 - 26.61 years; 149 females), and at the third time point (T3) of 275 participants (M_{Age} = 17.91 years, SD_{Age} = 3.68 years, $range_{Age}$ = 11.94 - 28.72 years; 143 females). At T2 and T3 all participants who indicated to be willing to participate again were invited for participation. This meant that participants who did not participate at T2 could participate again at T3. At T2 and T3, 32 participants could not participate in the MRI session due to dental braces. From these participants, we obtained questionnaire measures (self-report BAS and pleasure from winning vs. losing, described below). Participants' estimated intelligence scores were obtained at T1 and T2 and these scores did not correlate with age (Braams et al., 2015). From all participants in our sample (N = 287), there were 235 (81.9%) participants with European parents and with at least three (out of four) European grandparents, and nine participants (3.1%) with European parents and with fewer than three European grandparents. The remaining participants (N = 27; 9.4%) were from diverse ethnic backgrounds, and from 16 participants (5.6%) data was missing.

There were 248 valid scans obtained for the analyses at T1, 226 valid scans at T2, and 219 scans at T3. Scans obtained at T2 and T3 of participants who had developed a neurological or psychiatric disorder at T2 and scans obtained at T3 of participants who had developed a disorder at T3 were excluded from the analyses. Table S1 provides a detailed overview of reasons for exclusion of the brain scans. We also excluded the self-report data from participants with neuropsychological disorders.

Across the three waves of the study, there were in total 12 participants who did not participate at T2 (4 females, 8 males) and 19 participants who did not participate at T3 (6 females, 13 males). Those who participated at T2 were significantly younger at T1 than those who did not participate at T2 (M_{age} = 13.8 and 15.6 respectively, $p < .01$), but there was no such effect when comparing those who participated at T3 and those who did not participate at T3 on age at T1 ($p = .08$). These two groups did not differ significantly on our outcome measures (described below): BAS drive (T2: $p = .50$, T3: $p = 1.00$), BAS fun seeking (T2: $p = .32$, T3: $p = .10$), BAS reward responsiveness (T2: $p = .40$, T3: $p = .88$), and pleasure from winning vs. losing (T2: $p = .46$, T3: $p = .16$).

Procedure

Participants were scanned three times with a two-year interval (Δ in years T1-T2: M = 1.99, SD = .10; Δ in years T2-T3: M = 2.02, SD = .09). All participants aged 18 years and older gave written consent for participation. Parents of participants under the age of 18 also provided their written consent and the under aged participants gave written assent. Before scanning, the participants were familiarized with the scanner environment using a mock scanner and practiced the fMRI task. Adult participants, participants 12-17 years of age, and participants under the age of 12 years received 60, 30, and 20€ respectively for their participation. Participants could win a small additional endowment of 3 to 6€ when playing the fMRI task. Participants younger than 18 years received 10€ for filling out the questionnaires, and adult participants received 15€.

FMRI Task

Participants played a heads-or-tails gambling game in which they guessed heads or tails on each trial (Figure S1 ;also see Braams et al., 2014a; Braams et al., 2014b; Braams et al., 2015). If they guessed correctly, they won coins, and if they guessed incorrectly they lost coins. Chances of winning were 50%. Participants were explained that the coins won in the task would translate to real money. See the Supplementary materials for a more detailed description of the task.

Pleasure from winning vs. losing

After the MRI session participants indicated how much pleasure they experienced when winning and losing coins during the task on an 11-point scale ranging from 0 (I did not like winning/losing at all) to 10 (I really liked winning/losing). For the analyses, we used difference scores (pleasure from winning vs. losing) to keep this measure consistent with the fMRI contrast (NAcc activation during winning > losing). At T1, these two questions were administered to all adolescents, but not adults. At T2 and T3 all participants filled out these questions.

Participants indicated pleasure from winning and losing on an 11-point scale ranging from 0 (I did not like winning/losing at all) to 10 (I really liked winning/losing). At T3, a sample of 28 participants received the same questions measuring pleasure with an 11-point scale (M_{Age} = 24.22, *SD* = .59, 17 females), but the majority of the participants received the questions on a 10-point scale (ranging from 1 to 10; 209 participants -105 females-, M_{Age} = 17.26, *SD* = 2.07) due to a program change. The results were similar with and without the group of 28 participants who received the questions with an 11-point scale at T3. Therefore only the results with the complete sample are reported.

Behavioral inhibition system/behavioral activation system

From the Behavioral Inhibition System/BAS scales, we used the BAS scales as a measure of reward sensitivity. The BAS scales contain 13 items and was administered to asses 3 different types of underlying motivations of behavior: positive responsiveness to rewards (i.e., the affective response to rewards; BAS reward responsiveness), a desire for new rewards and the tendency to seek out for rewards (BAS fun seeking), and the drive to obtain rewards or to achieve a goal (BAS drive; Carver & White, 1994). Participants indicated how well a statement described them on a 4-point scale ranging from 1 (*strongly agree*) to 4 (*strongly disagree*). The scores are recoded such that a higher score indicated a higher sensitivity to rewards. In the current study we were specifically interested in the BAS drive and BAS fun seeking subscales given prior evidence for their association with ventral striatum activation during adolescence (Braams et al., 2015; Van Duijvenvoorde et al., 2014). However, for completeness, we also included the BAS subscale reward responsiveness.

We also examined how BAS drive, BAS fun seeking, and BAS reward responsiveness correlated with pleasure from winning vs. losing within T1, T2, and T3 using partial correlation analyses controlling for age. These analyses show that at T1, pleasure from winning vs. losing correlated positively with BAS drive (r = .16, p = .01) and BAS reward responsiveness (r = .20, p < .01). At T2, pleasure from winning vs. losing correlated positively with BAS drive (r = .16, p = .01) and BAS fun seeking (r = .18, p < .01). At T3, pleasure from winning vs. losing correlated positively with BAS reward responsiveness (r = .16, p = .02). There were no significant correlations between pleasure from winning vs. losing with BAS fun seeking at T1, BAS reward responsiveness at T2, and BAS drive and BAS fun seeking at T3 (ps > .43).

MRI Data Acquisition

Scans were acquired with a 3T Philips Achieva MRI scanner. The scanning procedure included a (a) localizer scan, (b) Blood oxygenation level dependent (BOLD) T2* weighted gradient echo planar images (TR = 2.2 s, TE = 30 ms, sequential acquisition, 38 slices of 2.75 mm, field of view (FOV) = 220 mm x 220 mm x 114.7 mm), and a (c) anatomical 3D T1-weighted image (TR = 9.754 ms, TE = 4.59 ms, 8° flip angle, 140 slices, 0.875 mm x 0.875 mm x 1.2 mm, and FOV = 224.000 mm x 168.000 mm x 177.333 mm). Two functional runs were obtained at T1 and T2. At T3, one functional run was obtained in which all trials were presented in the same run. The first two volumes of the functional scans were discarded to allow for equilibration of T1 saturation effects.

FMRI Data Analysis

The data were analyzed using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/). Preprocessing steps of functional images included realignment, slice-time correction, and smoothing with a Gaussian filter of 6 mm full-width at half maximum. Functional and structural images were spatially normalized to T1 templates. Templates were based on the Montreal Neurological Institute 305 stereotactic space. Statistical analyses were performed using the general linear model in SPM8. Regressors were modeled as zero-duration events at feedback onset and convolved with a canonical hemodynamic response function.

In the current study, we investigated NAcc activation in the Win > Lose contrast when playing for self. We used an anatomical mask of the left and right NAcc thresholded at 40% from the Harvard-Oxford subcortical atlas, which included 28 (left NAcc) and 26 voxels (right NAcc). The MarsBar toolbox (Brett, Anton, Valabregue, & Poline, 2002) was used to extract the parameter estimates of the left and right NAcc for our analyses (also see Braams et al., 2015). We focused on the NAcc, because this region has been highlighted as a core region in the ventral striatum involved in reward processing (Braams et al., 2015; Telzer, 2016), and because we aimed to explain age-related changes in NAcc activity related to rewards reported in Braams et al. (2015).

Mixed-Model Building Procedure

We used a mixed models approach in R for our analyses (R Core Team, 2014) using the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2013). The first aim was to determine age-related patterns (linear, quadratic, or cubic) of NAcc activation, pleasure from winning vs. losing, and BAS subscale scores (BAS drive, BAS fun seeking, and BAS reward responsiveness). A linear relation between age and the outcome variable indicates an age-related increase or decrease. A quadratic relation between age and the outcome variables indicates a non-linear adolescent-specific U or inverted U-pattern. A cubic relation between age and the outcome variable indicates a non-linear adolescent emerging or declining pattern. We used the variables of interest as dependent variables in the models and added age as a polynomial predictor, and since the data were nested within subjects, we used a random intercept for subjects (also see Braams et al., 2015). All models were fitted following a formal model-fitting procedure (see also Braams et al., 2015), and we compared models with one degree of freedom difference. That is, we compared the null model (with a fixed and random intercept) with the linear model, the linear model with the quadratic model, and the cubic model with the quadratic model. We also investigated whether a main effect of sex or a sex x age interaction effect explained additional variance. Sex was dummy coded such that male participants were labeled as 1 and female participants as 0.

To test for the effects of individual differences in self-reported state- and trait-level reward sensitivity on NAcc activity, we investigated whether individual differences in BAS scores and pleasure from winning vs. losing were linearly associated with NAcc activity in separate multilevel models. We were specifically interested in testing whether these indices contributed differentially to the increase and decrease in NAcc activity across age. Therefore, the participants were separated in two age groups: adolescents younger than 16.0 years, and 16.0 years and older. The cut-off of 16 years of age is based on an estimation of the age where NAcc activation peaks in our data (at 15.3 and 15.1 years of age for the left and right NAcc respectively). For these analyses, we again started with a null model and then added the variable of interest as a linear predictor. In the next step, we compared this model with a model including both the variable of interest and age. We also tested whether a main effect of sex and an interaction effect between sex and the variable of interest explained additional variance. We used the Akaike Information Criterion (AIC; Akaike, 1974) to compare the model fits, and the log likelihood ratio to assess significance, but we also report the Bayesian Information Criterion (BIC; Schwarz, 1978). We reported the results with a significance threshold of $p < .05$. We also indicated which results survived a threshold corrected for multiple comparisons. We assessed these corrected thresholds using a method which accounts for dependency between different variables, e.g., when variables are components of the same psychological construct (http://www.quantitativeskills.com/sisa/calculations/bonfer.htm; Perneger, 1998; Sankoh, Huque, & Dubey, 1997).

We used a total of three constructs as independent variables: (a) NAcc activation, (b) the three BAS scales (drive, fun seeking, and reward responsiveness), and (c) pleasure from winning vs. losing. To correct for multiple comparisons, we adjusted the most commonly used significance threshold of .05. We first calculated an adjusted significance threshold for the first two constructs accounting for the mean correlation of the variables within constructs (i.e., mean correlation of left and right NAcc activity within T1, T2, and T3 of .79, and of the three BAS scales within T1, T2, and T3 of .35). The adjusted significance threshold for analyses with NAcc activity as the dependent variable was .043, and with one of the BAS scales as the dependent variable was .024. The threshold for analyses in which pleasure from winning vs. losing was used as a dependent variable was set to .05. Next we divided these adjusted significance thresholds by three (i.e., the number of constructs). The resulting adjusted significance thresholds corrected for multiple testing were (a) .014 when left or right NAcc activity was the dependent variable, (b) .008 when BAS drive, BAS fun seeking, or BAS reward responsiveness was the dependent variable, and (c) .017 when pleasure from winning vs. losing was the dependent variable.

RESULTS

Age-Related Patterns

For each measure (i.e., NAcc activation for winning > losing for the self, pleasure from winning vs. losing as state-level reward sensitivity, and BAS scores as trait-level reward sensitivity), we tested whether they showed a linear, quadratic, or cubic relation with age. We also tested whether sex explained additional variance. The intraclass correlations of these measures ranged from .21 to .61 (see Table 1). Information regarding the number of observations and participants' ages in the analyses is listed in Table 1. Furthermore, information regarding the model-fitting procedure (AIC and BIC values) is listed in Table 2, significance levels of the model comparisons are listed in Supplementary Table S2, and the statistical parameters of the best fitting models are listed in Table 3. A visual representation of the raw data can be found in Supplementary Figure S2.

Reward-related NAcc activation

The developmental pattern of left and right NAcc response to winning versus losing was best described by a quadratic relation ($p = .001$ [left], and $p < .001$ [right], remains significant after correction for multiple comparisons). As can be seen in Figure 1A, this relation indicates that reward-related NAcc activation peaks in mid-adolescence (at 15.3 and 15.1 years of age for the left and right NAcc respectively). There was no main effect of sex or an age x sex interaction effect.

State-level reward sensitivity: Pleasure from winning vs. losing

Self-reported pleasure from winning vs. losing coins showed a negative linear relation with age and there was a main effect of sex ($p < .001$, significant after correction for multiple comparisons). These results indicate that pleasure from winning vs. losing decreases across adolescence and males liked winning relatively more than losing compared to females (Figure 1B).

Trait-level reward sensitivity: BAS

The relation between BAS drive and age was best described by a cubic model with a main effect of sex and an age x sex interaction (p = .02, uncorrected for multiple comparisons; Figure 1C). Follow up analyses of the interaction effect showed a significant linear increase in BAS drive scores with age for females (linear age term: b = .12, SE = .05, p < .01, quadratic age term: p = .62., cubic age term: p = .72), and a cubic age effect on BAS drive for males (linear age term: p = .10, quadratic age term: b = .02, SE = .01, p = .02, cubic age term: b = .00, SE = .00, p < .01).

A cubic model best described the relation between age and BAS fun seeking (p < .01, uncorrected for multiple comparisons; Figure 1D). There was no effect of sex in this model. Finally, the cubic model with a main effect of sex best explained the relation between age and BAS reward responsiveness. Females scored higher on BAS reward responsiveness than males (Figure 1E).

Table 1. Descriptives for each measure

	N (females)			Age range (years)			ICC T1, T2, T3
Dependent variable	T1	T2	T3	T1	T2	T3	ICC (95% CI)
Left NAcc Win > Lose	248 (131)	226 (112)	219 (116)	8.41 - 25.96	9.92 - 26.36	11.94 - 28.46	0.30 (0.10 - 0.46)
Right NAcc Win > Lose	248 (131)	226 (112)	219 (116)	8.41 - 25.96	9.92 - 26.36	11.94 - 28.46	0.21 (-0.01 - 0.39)
Pleasure from Winning vs. Losing	260 (133)	241 (124)	224 (116)	8.01 - 17.91	9.92 - 26.36	11.94 - 28.46	0.65 (0.55 - 0.74)
BAS Drive	277 (145)	273 (141)	241 (130)	8.01 - 25.96	9.92 - 26.36	11.94 - 28.46	0.62 (0.53 - 0.70)
BAS Fun Seeking	277 (145)	273 (141)	241 (130)	8.01 - 25.96	9.92 - 26.36	11.94 - 28.46	0.60 (0.50 - 0.69)
BAS Reward Responsiveness	277 (145)	273 (141)	241 (130)	8.01 - 25.96	9.92 - 26.36	11.94 - 28.46	0.61 (0.51 - 0.69)

For each measure, number of observations, age range, and intraclass correlations (ICC) with 95% confidence interval (95% CI) at Time 1, Time 2, and Time 3.

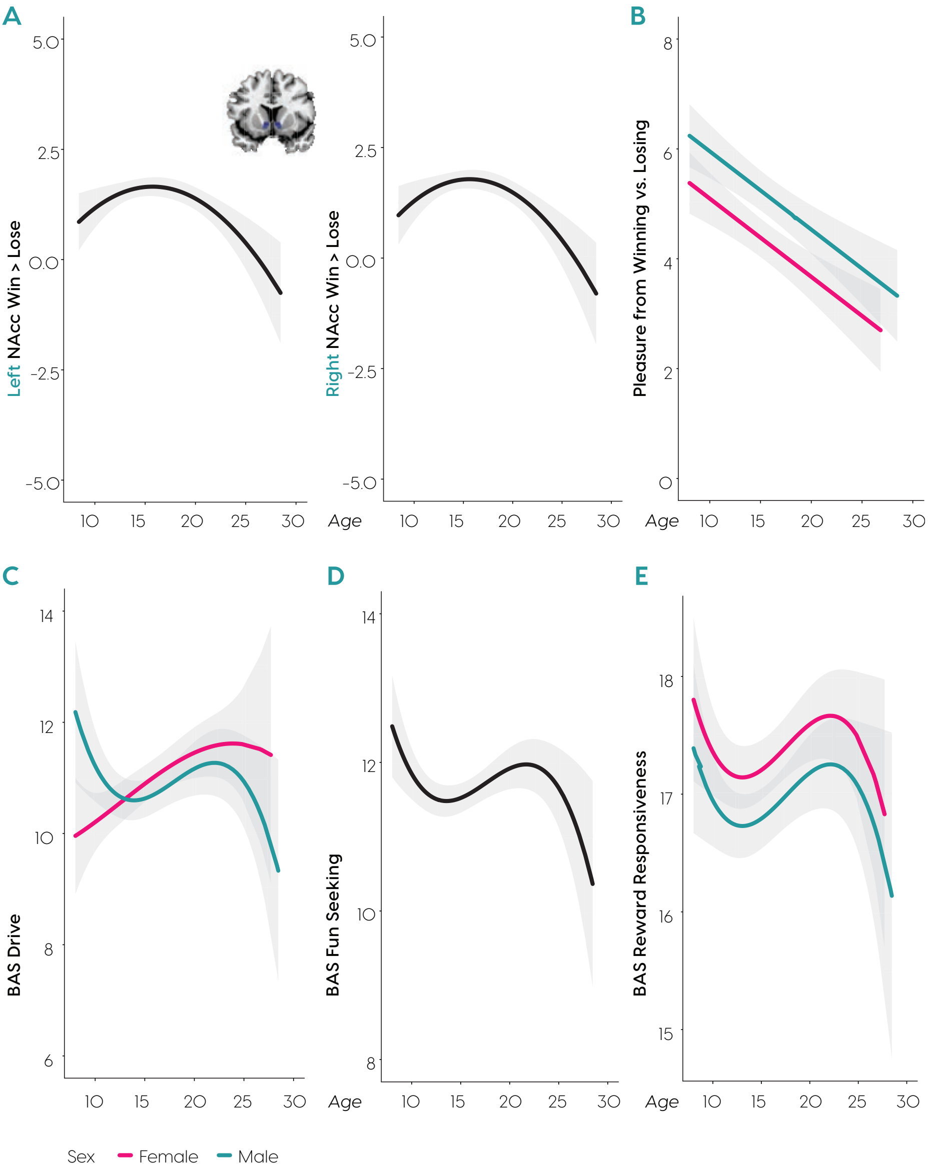

Figure 1. Development of (A) left and right NAcc activation during winning vs. losing, (B) self-reported pleasure from winning versus losing, (C) BAS drive, (D) BAS fun seeking, and (E) BAS reward responsiveness across development. *The smooth lines represent the predicted values and the light ribbon their 95%-confidence interval according to the best fitting model. Red and blue fitted lines indicate different age effects for males and females. A black fitted line indicates general age effects (no effects of sex).*

Table 2. AIC and BIC values for null, linear, quadratic, and cubic models

Model	**Null**		**Linear**	
Dependent variable	AIC	BIC	AIC	BIC
Left NAcc Win > Lose	3045	3059	3043	3062
Right NAcc Win > Lose	3098	3112	3096	3114
Pleasure from Winning vs. Losing	3519	3533	3500	3519
BAS Drive	3440	3454	3436	3454
BAS Fun Seeking	3174	3188	3176	3194
BAS Reward Responsiveness	3180	3194	3181	3200

The AIC and BIC values describe the relation with age and each of the measures reported.

Note. Preferred models are in bold.

Table 3. Statistical parameters for the best fitting models

Dependent variable	**Fixed effects**	***b***	***p***	**95% Confidence Interval ß**	
				Min	Max
Left NAcc Win > Lose	Intercept	1.65	< 0.001	1.43	1.87
	Age, 1	-0.01	0.62	-0.06	0.04
	Age, 2	-0.01	< 0.001	-0.02	-0.01
Right NAcc Win > Lose	Intercept	1.78	< 0.001	1.56	2.00
	Age, 1	-0.02	0.50	-0.06	0.03
	Age, 2	-0.02	< 0.001	-0.02	-0.01
Pleasure from Winning vs. Losing	Intercept	4.31	< 0.001	3.96	4.62
	Age, 1	-0.14	< 0.001	0.08	0.20
	Sex	0.87	< 0.001	0.36	1.36
BAS Drive	Intercept	10.99	< 0.001	10.66	11.31
	Age, 1	0.13	0.01	0.03	0.23
	Age, 2	0.00	0.61	-0.02	0.01
	Age, 3	0.00	0.72	0.00	0.00
	Sex	-0.31	0.20	-0.77	0.16
	Age, 1 x Sex	-0.04	0.54	-0.19	0.10

Quadratic		Cubic		If best fitting model has an effect of Sex			
AIC	BIC	AIC	BIC	Effect	Model	AIC	BIC
3035	3057	3037	3064	-	-	-	-
3086	3109	3088	3115	-	-	-	-
3500	3523	3502	3530	Main effect	Linear	3491	3514
				Interaction with Age	Linear	3493	3514
3437	3461	3435	3463	Main effect	Cubic	3436	3469
				Interaction with Age	Cubic	3434	3480
3177	3201	3169	3197	-	-	-	-
3183	3206	3178	3206	Main effect	Cubic	3174	3207
				Interaction with Age	Cubic	3177	3224

Table 3. Continued

Dependent variable	**Fixed effects**	***b***	***p***	**95% Confidence Interval ß**	
				Min	Max
BAS Drive *(continued)*	Age, 2 x Sex	0.02	0.05	-0.04	0.00
	Age, 3 x Sex	0.00	0.13	0.00	0.00
BAS Fun Seeking	Intercept	11.56	< 0.001	11.37	11.76
	Age, 1	0.07	0.02	0.01	0.13
	Age, 2	0.01	0.01	0.00	0.02
	Age, 3	0.00	< 0.01	0.00	0.00
BAS Reward Responsiveness	Intercept	17.25	< 0.001	17.00	17.50
	Age, 1	0.07	0.02	0.01	0.13
	Age, 2	0.01	0.07	0.00	0.02
	Age, 3	0.00	0.02	0.00	0.00
	Sex	-0.41	0.01	-0.74	-0.09

Statistical parameters (regression coefficient (b), significance level (p) and 95%-confidence interval for the bs) for the best fitting models testing the relation between age and each of the measures reported in the table.

Note. 'Age, 1' = Linear age terms, 'Age, 2' = quadratic terms, 'Age, 3'. = cubic terms.

Brain-Behavior Relations in Reward Sensitivity

Next, we tested the role of developmental differences in self-reported pleasure from winning vs. losing, and BAS subscales on NAcc activation in early to mid-adolescents (< 16 years of age) and mid-adolescents to young adults (≥ 16 years of age) separately. We used a model fitting procedure in which the linear term of the variable of interest was added before the linear term of age. Table S3, Table 4, and 5 give a detailed overview of the significance levels of the model comparisons, model fits (AIC and BIC values), and the statistical parameters of the best fitting models, respectively. Plots of the raw data can be found in Supplementary Figure S3.

Trait-level reward sensitivity (BAS scales) as predictors for NAcc activation

For the younger age group (early to mid-adolescents, < 16.0 years of age), the relation between left and right NAcc and BAS drive was best explained by a positive linear relation (*p* = .023 [left] and .020 [right], corrected significance threshold .014). There was no interaction with sex. These results show that participants who reported stronger BAS drive showed higher activity in NAcc for winning versus losing (Figure 2A). There was no such relation in the older age groups (> 16 years of age, mid-adolescence to adulthood). Furthermore, there were no relations between NAcc activation and the BAS fun seeking and BAS reward responsiveness subscale in either age group.

State-level reward sensitivity (pleasure from winning versus losing) as a predictor for NAcc activation

There was no relation between NAcc activation and pleasure from winning vs. losing in the younger age group (early to mid-adolescence). For mid- to late adolescents and young adults (≥ 16.0 years of age), the relation between left and right NAcc activation and pleasure from winning vs. losing was best explained by a positive linear relation (model: *p*s < .001, remain significant after correction for multiple comparisons; *b*s: *p* = .047 for left NAcc, uncorrected for multiple comparisons, and *p* = .0025 for right NAcc, significant after correction for multiple comparisons). Sex did not explain additional variance. Thus, in mid- to late adolescence and early adulthood, participants who reported less pleasure for winning money showed less NAcc activation for winning versus losing (Figure 2B).

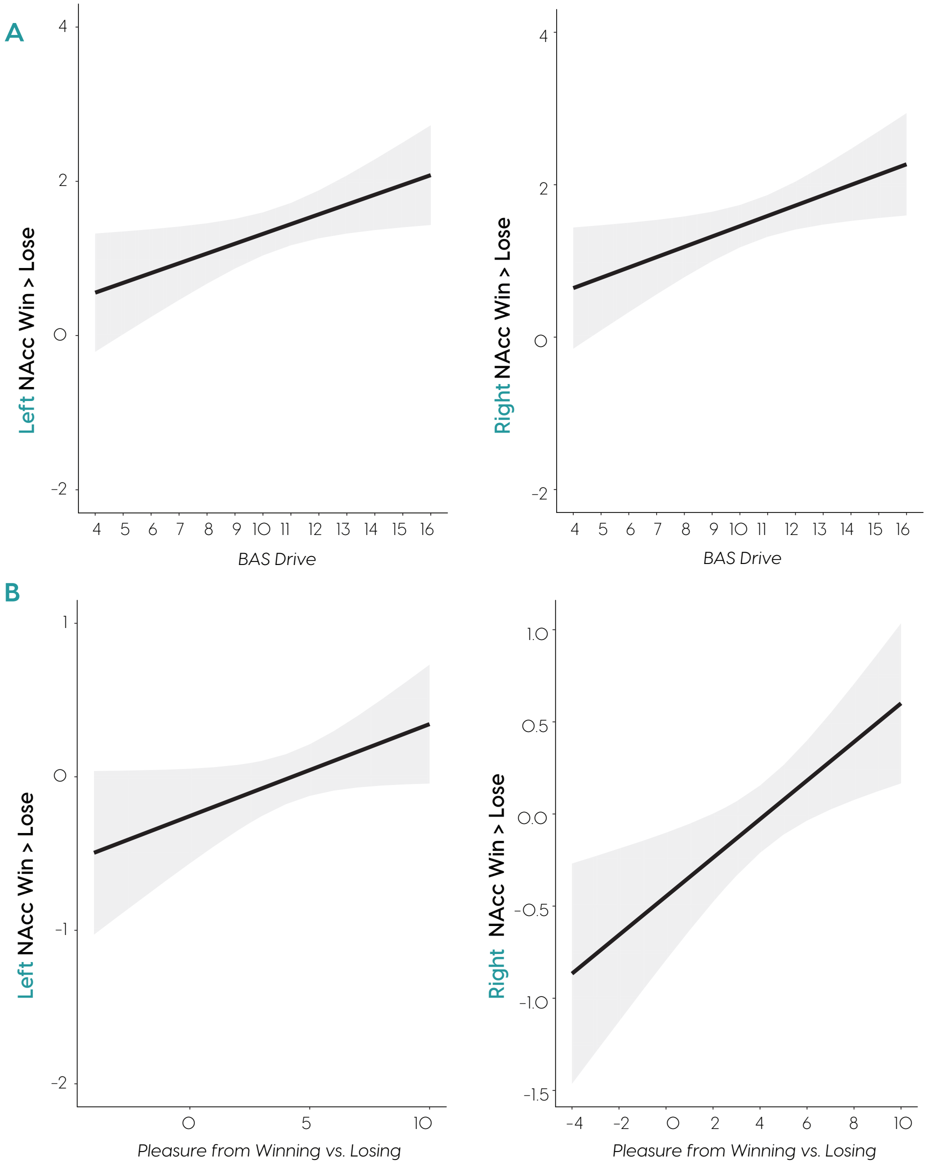

Figure 2. Relation between left and right NAcc activation during winning versus losing and (A) BAS drive scores from early to- mid adolescents, and (B) pleasure from winning vs. losing corrected for the main effect of age from mid- to late adolescents and young adults. *The smooth lines represent the predicted values and the light grey ribbon their 95%-confidence interval according to the best fitting model. A black fitted line indicates general age effects (no effects of sex).*

NAcc activation as a function of predictor x age group interaction

We also tested whether the strength of the relation between NAcc activation and individual differences in BAS drive, and pleasure from winning vs. losing was significantly different for the younger age group (< 16.0 years) and the older age group (≥ 16.0 years). We built separate models containing a main effect of the predictor of interest (BAS drive or pleasure from winning versus losing) and a predictor of interest x age group interaction term. The analyses revealed no significant interaction between age group and BAS drive, and age groups and pleasure from winning vs. losing (*ps* > .06). Possibly, the interaction was under powered to detect changing contributions over age. Therefore, effects per age group should not be interpreted as specific age effects.

Table 4. AIC and BIC values for null, linear, quadratic, and cubic models

Dependent variable	**Left NAcc Win > Lose**					
Model	Null		Predictor		Predictor + Age	
Predictor	AIC	BIC	AIC	BIC	AIC	BIC
Early to Mid-Adolescents						
Pleasure from Winning vs. Losing	**1631**	**1643**	1631	1646	1633	1652
BAS Drive	1581	1593	**1578**	**1594**	1580	1599
BAS Fun Seeking	**1581**	**1593**	1580	1595	1581	1601
BAS Reward Responsiveness	**1581**	**1593**	1583	1598	1584	1603
Mid-Adolescents to Young Adults						
Pleasure from Winning vs. Losing	1201	1212	1195	1211	**1174**	**1193**
BAS Drive	1369	1380	1371	1386	**1352**	**1371**
BAS Fun Seeking	1369	1380	1370	1386	**1352**	**1371**
BAS Reward Responsiveness	1369	1380	1370	1385	**1352**	**1370**

Note. Preferred models are in ***bold.***

Right NAcc Win > Lose					
Null		Predictor		Predictor + Age	
AIC	BIC	AIC	BIC	AIC	BIC
1662	1674	1662	1677	1663	1683
1629	1641	1626	1641	1627	1647
1629	1641	1630	1646	1632	1651
1629	1641	1630	1646	1632	1651
1223	1234	1211	1226	1187	1205
1380	1391	1382	1397	1360	1379
1380	1391	1382	1397	1360	1379
1380	1391	1381	1396	1360	1379

Table 5. Statistical parameters for the best fitting models

		b	***p***	**95% Confidence Interval ß**	
	Fixed effects			Min	Max
Early to Mid-Adolescents					
Pleasure from Winning vs. Losing					
Left NAcc	Intercept	1.46	< 0.001	1.19	1.73
Right NAcc	Intercept	1.58	< 0.001	1.31	1.84
BAS Drive					
Left NAcc	Intercept	0.05	0.94	-1.14	1.24
	BAS Drive	0.13	0.02	0.02	0.24
Right NAcc	Intercept	0.10	0.87	-1.18	1.27
	BAS Drive	0.14	0.02	0.03	0.25
BAS Fun Seeking					
Left NAcc	Intercept	1.39	< 0.001	1.12	1.67
Right NAcc	Intercept	1.53	< 0.001	1.26	1.81
BAS Reward Responsiveness					
Left NAcc	Intercept	1.39	< 0.001	1.12	1.67
Right NAcc	Intercept	1.53	< 0.001	1.26	1.81
Mid-Adolescents to Young Adults					
Pleasure from Winning vs. Losing					
Left NAcc	Intercept	4.72	< 0.001	3.20	6.24
	Pleasure from Winning vs. Losing	0.08	0.05	0.00	0.15
	Age	-0.19	< 0.001	-0.26	-0.11
Right NAcc	Intercept	4.85	< 0.001	3.32	6.38
	Pleasure from Winning vs. Losing	0.12	< 0.01	0.04	0.20
	Age	-0.20	< 0.001	-0.27	-0.12

Statistical parameters (regression coefficient (b), significance level (p) and 95%-confidence interval for the bs) for the best fitting models testing the relation between Nacc activation and each of the measures reported in the table.

DISCUSSION

The goal of this three-wave accelerated longitudinal study was to test the developmental trajectory of reward-related NAcc activation across ages 8-29 years, and how behavioral state- and trait-level reward-sensitivity related to these changes. The results confirmed that NAcc activity to rewards peaks in mid-adolescence consistent with our previous findings based on data from the first two waves of the study reported by Braams et al. (2015). In addition, it was found that developmental differences in self-reported motivation to approach rewards (trait-level reward sensitivity), and the immediate pleasure from winning (state-level reward sensitivity) contributed to these changes. Below, we set out how these two different types of reward sensitivity explained NAcc activation in early to mid-adolescence and in mid-adolescence to early adulthood.

Consistent with previous studies, we found that NAcc activation during the receipt of a reward peaks in mid-adolescence (Braams et al., 2015; Galvan et al., 2006; Silverman et al., 2015; Telzer, 2016; Van Leijenhorst et al., 2010a). Our results demonstrate that mid-adolescents respond to a greater extent to rewards than children, early adolescents, late adolescents, and young adults, and extend previous findings by showing that this developmental trajectory continues until at least into the late twenties. It has previously been argued that adolescence is a time of stronger dopamine release, which may also contribute to the greater reward sensitivity in the NAcc in mid-adolescence (Wahlstrom et al., 2010). This study is the first to show results of NAcc activation during receipt of rewards measured at three time points, and the accelerated longitudinal design of the study precludes influence of cohort-effects (Crone & Elzinga, 2015; Ordaz, Foran, Velanova, & Luna, 2013).

Given that the peak of reward activation was predicted around the age of 16 years, we separately tested whether variance in NAcc activity could be explained between ages 8-16 years, and between ages 16-29 years by trait-level reward sensitivity as measured with the BAS scales (Urošević et al., 2012) and state-level reward sensitivity as measured with a scale assessing immediate pleasure from rewards (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). In younger adolescents (8-16 years of age), higher levels of a self-reported drive to pursue and achieve personal goals, i.e., trait-level reward sensitivity, were associated with stronger NAcc activity to rewards. This finding suggests that the rise in NAcc activity is stronger for adolescents with a higher motivation to obtain rewards (Simon et al., 2010), such as the drive to obtain rewards or the desire for rewards (Braams et al., 2015; Van Duijvenvoorde et al., 2014). Our finding suggests that higher NAcc responses to rewards may relate to the drive to seek out novel experiences. It should be noted that in the current study the relation between reward drive and NAcc activation was not significant after Bonferroni correction for multiple comparisons and should therefore be replicated in future studies. In addition, the longitudinal design allows for a better estimation of brain-behavior relations than cross-sectional studies, but does not allow for causal inferences, because patterns may coincide over time in relation to a third factor, such as changes in pubertal hormones (Braams et al., 2015; Forbes et al., 2010; Op de Macks et al., 2011). Nonetheless, the findings are consistent with prior studies (Braams et al., 2015; Urošević et al., 2012; Van Duijvenvoorde et al., 2014) and show that individual differences in reward drive are an important factor to investigate in future research.

Another important question for future research is to test *why* effects were specific for reward drive. No significant relation was found between NAcc activity and other forms of trait-level reward sensitivity measured in our study, such as fun-seeking tendencies (cf. Van Duijvenvoorde et al., 2014) and affective responses to rewards. Possibly, these forms of reward sensitivity are distinctly related to NAcc responses to rewards and, by extension, to novelty seeking behaviors. In addition, this implies that they are distinct constructs within trait-level reward sensitivity. However, to test this question of specificity of reward drive in more detail, it will be important to test relations with multiple reward types in future research.

A final question concerns the relation between neural responses to rewards and measures of state- and trait-level reward sensitivity between mid-adolescence and adulthood. In older adolescents and young adults (16-29 years of age), reducing levels of NAcc activity were associated with less reward pleasure experiences when receiving rewards in the task (i.e., state-level reward sensitivity). This suggests that the age-related decrease in state-level reward sensitivity can possibly be explained by a decrease in NAcc activation. This finding fits with previous findings showing that ventral striatum activation and dopamine release from the striatum were related to pleasure experienced during listening to music and during winning money in a simple estimation task (Dohmen et al., 2011; Salimpoor et al., 2011). The incentive in these types of simple reward tasks may be lower for late adolescents and young adults than early adolescents. Possibly, NAcc activity scales with the reduction in pleasure obtained when gaining rewards in a simple gambling task in adulthood.

This study also had several limitations that deserve attention. First, although we have often linked ventral striatum activation to explorative behaviors, we did not assess these behaviors in our study. Prior studies have found that increased self-reported risk propensity (Galvan, Hare, Voss, Glover, & Casey, 2007) and risky decision-making (Van Duijvenvoorde et al., 2014) are associated with increased reward-related ventral striatum activity. In future research, it will be important to include measures that represent real-life explorative behaviors. Second, we could not identify an interaction on NAcc activation between the self-report measures of state- and trait-level reward sensitivity measures and the two age groups. Therefore, we cannot conclude that the relations between NAcc activation and state- and trait-level reward sensitivity are significantly different between the two age groups. Third, in this study we contrasted NAcc activity for winning and losing. This manner of presenting the results does not allow for distinguishing whether NAcc activity was driven by wins or losses (Braams et al., 2015). Hence, the results should be interpreted as a relative difference, and future studies should include an appropriate baseline condition, for example, in which participants do not win or lose coins.

To conclude, in the current study we demonstrated that reward-related NAcc activation peaks in mid-adolescence and declines again in late adolescence and early adulthood. We show that the increase in NAcc activation to rewards in early to mid-adolescence is driven by developmental differences in a general (trait-level) drive to pursue personal goals. The decrease in NAcc activation in late adolescence and adulthood was related to a decrease in state-level hedonic reward ratings. A strength of this study was the use of longitudinal measurements, which are pivotal for understanding trajectories of change, given that these reduce cohort effects and provide more power for detecting change (Crone & Elzinga, 2015; Ordaz et al., 2013). Furthermore, longitudinal measurements are essential for testing how changes in neural activity co-vary with individual differences (Telzer, Fuligni, Lieberman, & Galván, 2013). Most studies on ventral striatum activity to date are based on cross-sectional studies, but there are some exceptions that are based on assessments from two time points (Braams et al., 2015; Lamm et al., 2014; Van Duijvenvoorde et al., 2014). Importantly, with the third time point included in the current study, we were not only able to study adolescence but also to capture the transition from late adolescence to early adulthood. Future longitudinal studies should further examine (a) how individual differences in NAcc sensitivity to rewards in adolescence relate to real-life explorative behaviors and future achievements, and (b) what motivates older adolescents and adults to obtain rewards and how this relates to NAcc reward responses. Importantly, future longitudinal studies should examine how rewards in different contexts, for example when participants gain rewards for others or play a more complex reward task, affect neural reward mechanisms and behavior across adolescence and early adulthood (Rosenbaum, Venkatraman, Steinberg, & Chein, 2017). Together, our findings set the stage for future research into unique contributions of motivational factors for the neural underpinnings of explorative behaviors, which might ultimately help adolescents and young adults to become successful adults.


3

CHAPTER THREE

Friendship stability in adolescence is associated with ventral striatum responses to vicarious rewards

This chapter is in preparation as:
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ABSTRACT

An important developmental task for adolescents is to form and maintain friendships. Stable best friendships are a unique form of friendships that are characterized by strong closeness and require great investment. Moreover, they become increasingly common across adolescence. Not surprisingly, adolescents yield reward-related neural responses in the nucleus accumbens (NAcc), a key reward region, when rewards are gained for friends. Enhanced reward-related activity of the NAcc may relate to motivations directed at friends.

Relative to childhood and adulthood, adolescence is a period of elevated NAcc activity when rewards are gained for the self. In contrast, no age-related changes that resemble this developmental trajectory when rewards are gained for friends have been reported so far. We use data from a three-wave biannual longitudinal study in which adolescents, ages eight to twenty-eight, played a gambling game in the MRI scanner during which they could win and lose money for their best friend. We differentiate between participants with stable (n = 48) and unstable friendships (n = 75). We tested whether these two groups of participants showed differential developmental trajectories of NAcc activity when gaining rewards for their friends. We show that participants with stable friendships showed a quadratic developmental trajectory of NAcc responses to rewards for best friends, whereas participants with unstable best friends showed no age-related changes. NAcc activity further varied with currently experienced friendship closeness for participants with unstable friendships. We conclude that friendship stability affects age-related changes in vicarious reward-related NAcc activity, and hypothesize that this may reflect changing social motivations across adolescence.

INTRODUCTION

Adolescence is a transitional period in development during which individuals learn to navigate in an increasing complex social world (Blakemore & Mills, 2014; Crone & Dahl, 2012). Friendships -unique relationships that are voluntary and equal in nature- become increasingly relevant in adolescence. Not surprisingly, adolescents yield reward-related neural responses in the nucleus accumbens (NAcc), a primary reward area, when vicarious rewards are gained for friends (Fareri, Niznikiewicz, Lee, & Delgado, 2012). Relative to childhood and adulthood, adolescence is a period of heightened reward sensitivity of the NAcc when rewards are gained for the self (Galvan et al., 2006; Schreuders et al., 2018a; Silverman, Jedd, & Luciana, 2015; Van Leijenhorst et al., 2010b), but no age-related changes in activity have been reported so far when winning for a friend (Braams & Crone, 2017). The question we addressed in the current study was whether different types of friendships affect the developmental trajectory of vicarious reward-related NAcc activity. Therefore, we conducted a longitudinal study and distinguished between adolescents with two different types of best friendships: stable and unstable best friendships. Adolescents with stable best friendships have the same best friend across time, whereas adolescents with unstable best friendships more often change best friends. We examined whether adolescents with stable and unstable best friendships showed different NAcc responsiveness across adolescent development when rewards are gained for best friends.

Reward-related responses of the NAcc have been studied extensively. Heightened activity in the NAcc when rewards are gained for the self in adolescence has been suggested to play an important role in motivating behaviors, such as pursuing personally valued goals and novelty seeking (Braams, Van Duijvenvoorde, Peper, & Crone, 2015; Schreuders et al., 2018a; Telzer, 2016; Van Duijvenvoorde, Peters, Braams, & Crone, 2016). Stronger NAcc responsiveness to rewards is shown to relate to a stronger hedonic impact (Galván & McGlennen, 2013; Schreuders et al., 2018a; Wahlstrom, White, & Luciana, 2010). The NAcc is also implicated in processing rewards in a social context. For example, the ventral striatum is involved in decisions to donate to charity (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010) especially while others are watching (Izuma, Saito, & Sadato, 2010), and when giving money to family (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010). There is also evidence that increased activity is observed when sharing gains with friends relative to unfamiliar others (Fareri et al., 2012), and when winning rewards for liked others (i.e., friends) relative to disliked others (Braams et al., 2014a; Mobbs et al., 2009). Braams and Crone (2017) examined adolescents' NAcc responses to winning for their mother and best friend using cross-sectional data from the current dataset. NAcc activity in response to rewards gained for mothers was heightened in mid-adolescence, echoing the developmental trajectory of NAcc sensitivity to rewards for the self. However, NAcc activity in response to rewards for friends did not change across adolescence. Together, prior findings show that developmental trajectories of reward sensitivity of the NAcc are dependent on the social setting, and on the social relationship with the beneficiary.

Friendships not only become more relevant for adolescents, they also become more intimate (Buhrmester, 1990; McNelles & Connolly, 1999) and socially supportive (Mahon & Yarcheski, 2017; Scholte, Van Lieshout, & Van Aken, 2001; Spithoven et al., 2017). As such, friendships provide opportunities for prosperous psychosocial development (Hartup, 1996). Best friendships are a unique form of friendships that are characterized by high relationship quality and high closeness between the two friends (Hartl, Laursen, & Cillessen, 2015; Marengo, Rabaglietti, & Tani, 2017). As friendships change through time in response to changing personal needs and circumstances, some best friendships dissolve. It has been reported that about fifty percent of adolescent best friendships are stable throughout one academic year (Branje, Frijns, Finkenauer, Engels, & Meeus, 2007; Değirmencioğlu, Urberg, Tolson, & Richard, 1998). Stable best friendships require more commitment and investment than unstable best friendships and are more common in adolescence than in childhood (Berndt & Hoyle, 1985; Branje et al., 2007). Taken together, stable best friendships appear to become more salient in adolescence than in childhood.

Here, we compared developmental trajectories of NAcc responses to rewards for best friends and the immediate pleasure experienced in adolescents with unstable versus stable best friendships, and how these relate to each other. In this three-wave biannual longitudinal study, participants of eight to twenty-eight years of age could win or lose money in a heads-or-tails guessing game. Based on prior findings we expected that NAcc activity would peak in adolescents more so in response to winning for stable best friends than unstable best friends (Fareri et al., 2012; Mobbs et al., 2009; Schreuders et al., 2018a). To also understand dynamic relations with changes in subjectively experienced pleasure from winning for friends, friendship quality, and friendship closeness, we tested whether these variables explained additional variance in NAcc activity.

METHOD

Participants

The current study is part of a larger, longitudinal study called Braintime, which has been conducted at Leiden University (e.g., see, Braams & Crone, 2017; Braams, Peters, Peper, Güroğlu, & Crone, 2014) and includes three waves separated by 2 years across a 5-year period. We collected data from 298 healthy, right-handed participants at the first time point (T1), 287 participants at the second time point (T2) and 274 participants at the third time point (T3), resulting in 205 participants that were included in each wave. From this sample, we identified two groups of participants: (a) individuals with a stable best friendship (n = 48), and (b) individuals with an unstable best friendship (n = 75). To identify these participants, they were asked to name their best friend at each time point. Participants with a stable best friendship named the *same* best friend at *each* time point, and participants with an unstable best friendship named a *different* best friend at *each* time point (i.e., the best friend at a particular time point was named only once). Sex was evenly distributed in both the stable and unstable friendship groups (χ^2 = .13, p = .36): there were 28 females with stable friendships (58.3%) and 40 females with unstable friendships (53.3%).

Participants in the resulting sample (N = 123) were aged 8.01 to 23.44 years at T1 (M_{age}= 14.11, SD = 3.26), 10.02 to 25.48 years at T2 (M_{age} = 16.10, SD = 3.28), and 11.95 to 27.54 years at T3 (M_{age}= 18.11, SD = 3.28). An independent two-sample t-test showed that participants with stable friendships were older than participants with unstable friendships (age at T1, stable friendships: M_{age} = 14.88 years, SD = 3.58; unstable friendships: M_{age} = 13.62, SD = 2.96; t (86.56) = -2.04, p = .05).

Vicarious Reward NAcc Activity

FMRI task

Functional scans were acquired while participants played a heads-or-tails gambling game in which they had to guess which side of a coin would show (as determined by the computer) by pressing a button with their right index or middle finger. Chances of winning on each trial were 50%. The participants started the game with 10 coins. If they guessed correctly they earned more coins and if they guessed incorrectly they lost coins (see Figure 1). Three different types of trials were included in the task to keep the participants engaged: trials on which participants could (a) win 3 or lose 3 coins, (b) win 5 or lose 3 coins, and (c) win 2 or lose 5 coins. Participants were instructed that the coins represented real money, which would be paid out at the end of the experiment. A trial started with a screen showing how many coins could be won or lost (4000 ms) followed by a fixation screen (1000 ms). Next, participants were shown a feedback screen, which revealed whether they won or lost coins (1500 ms). The trial ended with a jittered fixation screen (1000–13200 ms).

At T1 and T2, participants played 30 trials for themselves, 30 trials for their best friend, and 30 trials for another person (disliked peer at T1 and mother at T2). At T3, participants played 23 trials for themselves, and 22 trials for their best friend. In the current study, we examined NAcc activity during rewards for best friends (i.e., NAcc activity during winning versus losing for friends); therefore only trials when participants played for their best friends were included in the analyses.

From the 48 participants with *stable* best friendships, there were in total 135 valid scans that could be used for the analyses (41, 47, and 47 scans obtained at T1, T2, and T3, respectively). Most scans were lost due to excessive motion

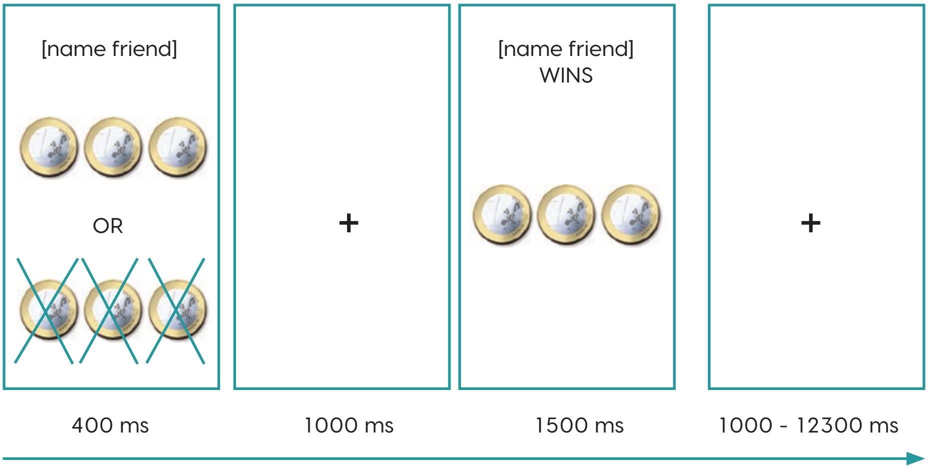


Figure 1. **Example of one trial of the fMRI task.** *Participants played a gambling task in which they could win or lose money for their best friend. On stimulus onset, a screen was presented to the participants showing how much they could win and lose. During the stimulus presentation, participants guessed heads or tails. After a fixation screen, participants received feedback with whether they won or lost for their friend. The trial ended with another fixation cross.*

(motion cut-off > 3 mm movement in any direction) by the participant (six at T2 and one at T3). At T1 one scan was excluded due to a hole in the functional mask and at T3 one scan was excluded due to technical problems with the fMRI task. From the 75 participants with *unstable* best friendships, there were in total 211 valid scans that could be used for the analyses (66, 72, and 73 scans obtained at T1, T2, and T3, respectively). Again, most scans were lost due to excessive motion of the participant during scanning: eight at T1, two at T2, and two at T3. One scan was lost due to technical difficulties with the fMRI task at T1 and one scan was excluded due to artifacts at T2.

MRI data acquisition

Scans were acquired with a 3T Philips Achieva MRI scanner. The scanning procedure included (a) a localizer scan, (b) Blood Oxygenation Level Dependent (BOLD) T2* weighted gradient echo planar images (TR = 2.2 s, TE = 30 ms, sequential acquisition, 38 slices of 2.75 mm, field of view (FOV) = 220 mm x 220 mm x 114.7 mm), and (c) an anatomical 3D T1-weighted image (TR = 9.754 ms, TE = 4.59 ms, 8° flip angle, 140 slices, 0.875 mm x 0.875 mm x 1.2 mm, and FOV = 224 mm x 168 mm x 177.3 mm). Two functional runs with 45 trials each were obtained at T1 and T2. At T3, one functional run was obtained in which all 45 trials were presented in the same run. The first two volumes of the functional runs were discarded to allow for equilibration of T1 saturation effects.

FMRI data analysis

The data were analyzed using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/). Preprocessing steps of functional images included realignment, slice-time correction, and smoothing using a Gaussian kernel of 6 mm full-width at half maximum. Functional and structural images were spatially normalized to T1 templates. Templates were based on the Montreal Neurological Institute 305 stereotactic space. Statistical analyses were performed using the general linear model in SPM8. Regressors were modeled as zero-duration events at feedback onset and convolved with a canonical hemodynamic response function.

We examined NAcc activity in the Win > Lose contrast when playing for the friend. We focused on the NAcc, because this region has been highlighted as a core region in the ventral striatum involved in reward processing (Braams et al., 2015; Telzer, 2016). We used anatomical masks of the left and right NAcc from the Harvard-Oxford subcortical atlas, thresholded at 40%. These anatomical masks included 28 voxels for the left NAcc and 26 voxels for the right NAcc. The MarsBar toolbox (Brett, Anton, Valabregue, & Poline, 2002) was used to extract the parameter estimates of the left and right NAcc for our analyses (left NAcc: Intraclass Correlation (ICC) = .13, 95%- Confidence Interval (CI) = [-0.30, .38]; for T1, T2, and T3, respectively, *M* = 1.13, 1.03, 0.67, *SD* = 3.09, 2.69, 1.35; right NAcc: ICC = -.40, 95%-CI = [-0.43, .26]; for T1, T2, and T3, respectively, *M* = 1.27, 1.30, 0.67, *SD* = 3.31, 2.80, 1.19). Two extreme outliers (> 3 *SD*s) of the right NAcc were winsorized (Tabachnick & Fidell, 2007). The brain contrasts within time points separately for the stable and unstable friendship groups are presented in the Supplementary materials.

Pleasure from Winning

After the MRI session, participants indicated how much pleasure they experienced after winning and losing for their best friend on an 11-point scale ranging from 0 (*not at all*) to 10 (*really liked winning/losing*). For the analyses we used difference scores (pleasure from winning-losing) to keep this measure consistent with the fMRI contrast (NAcc activity during winning > losing for the friend; Intraclass Correlation (ICC) = .59, 95%-CI = [0.45, 0.74)]; for T1, T2, and T3, respectively, *M* = 4.14, 3.73, 4.20 and *SD* = 3.26, 2.83. 2.33). At T1, T2, and T3, pleasure from winning *M* ranged from 7.34 to 7.67 (*SD*s = 1.35 to 1.87) and pleasure from losing *M* ranged from 3.19 to 3.60 (*SD*s = 1.37 to 2.19).

Friendship Quality Scale

At T1, T2, and T3, we measured the quality of the relationship with the best friend at each time point using the self-report friendship quality scale (FQS; adapted from (Bukowski, Hoza, & Boivin, 1994; Meuwese, Cillessen, & Güroğlu, 2017). Participants indicated on a 5-point scale how true each item was for them from 1 (*not true at all*) to 5 (*very true*). Positive friendship quality was measured with 13 questions assessing positive characteristics of the friendship, like providing support and showing affection (ICC = .73 95%-CI = [0.64, 0.81]; for T1, T2, and T3, respectively, *M* = 4.29, 4.35, 4.34 and *SD* = .49, .45, .36). Higher scores on this scale indicated higher levels of positive friendship quality. Negative friendship quality was measured with seven questions assessing negative characteristics of the friendship, including levels of conflict and power imbalance (ICC = .63, 95%-CI = [0.48, .74]; for T1, T2, and T3, respectively, *M* = 1.67, 1.70, 1.93 and *SD* = .56, .56, .40). Higher scores on this scale indicated higher levels of negative friendship quality.

Friendship Closeness

At T2 and T3, participants indicated how close they felt with their best friend using the Inclusion of Other in the Self (IOS) scale (Aron, Aron, & Smollan, 1992). The IOS scale is a pictorial measure of perceived closeness to others. Participants were instructed to select one picture (of seven in total) that best described the relationship with their best friend. Each of the seven pictures showed two circles: one representing the self and the other one their best friend. The circles in the pictures showed a gradual increase in overlap from picture 1 (*circles were not overlapping*) to 7 (*pictures almost entirely overlapping*). Thus, a higher proportion of overlap represents a higher level of perceived closeness with the best friend (ICC = .45, 95%-CI = [0.19, .63]; for T2 and T3, respectively, *M* = 5.19, 5.12, and *SD* = 1.26, 1.25). Correlations between the pleasure from winning, friendship quality, and friendship closeness are reported in the Supplementary materials.

Procedure

Participants aged 18 years and older gave written consent for their participation, participants aged 12 to 17 years gave written assent and their parents provided written consent, and parents from participants under the age of 12 gave written consent for their children's participation. Participants aged 18 years and older received 60€ for participation, participants between the ages of 12-17 received 30€, and participants under the age of 12 received 20€. Additionally, all participants could win a small endowment of 3 to 6€ for themselves, their best friend or another person when playing the fMRI task (Braams & Crone, 2017; Braams et al., 2014b). Furthermore, participants received 10 (when under the age of 18) or 15€ (when 18 years of age and older) for filling out additional questionnaires at home.

Before scanning, participants were familiarized with the scanner environment using a mock scanner. They also practiced the fMRI task, in which they could win or lose coins for their best friend. When the experimenter set up the practice run of the task (consisting of 6 trials) for the participants, the participants were asked for the name of their same-sex best friend. This name was used in the practice run as well as during the fMRItask such that participants saw the name of their best friend when playing for him/her.

Mixed-Model Building Procedure

We used a mixed models approach in R for our analyses (R Core Team, 2014) using the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2013). We conducted separate tests to examine the main effect of friendship stability and its interaction with age on left and right NAcc activity, pleasure from winning, friendship quality, and friendship closeness. We used the left and right NAcc activity, pleasure from winning, friendship quality, and friendship closeness as dependent variables in the models and added age as a polynomial predictor, and since the data were nested within subjects, we used a random intercept for subjects (also see Braams et al., 2015; Schreuders et al., 2018a). We tested for linear and quadratic patterns of age. A linear relation between age and the outcome variable would indicate an age-related increase or decrease. A quadratic relation between age and the outcome variables would indicate a non-linear U or inverted U-pattern. We first built a null model without any predictors, a model with only a linear term of age, and a model with both a linear and quadratic age terms. Regardless of whether these age terms were significant at this stage of the analyses, we kept them in the model during the model-building procedure to eventually be able to test for interactions between age and friendship stability (and/or sex). Second, we tested whether a main effect of sex and an interaction between age and sex explained additional variance above and beyond the linear and quadratic term of age. If sex explained additional variance to the model we included it in the follow-up models, and if sex did not explain additional variance it was excluded. Sex was dummy coded such that male participants were labeled as 1 and female participants as 0. Finally, we tested whether friendship stability explained additional variance in the form of a main effect, and an interaction with age or sex (if sex showed to improve the model fit in previous steps). Friendship stability was dummy coded such that individuals with stable best friendships were labeled as 1 and individuals with unstable best friendships as 0.

Furthermore, in separate models, we tested whether pleasure from winning, friendship quality, and friendship closeness explained additional variance in NAcc activity above and beyond age for participants with stable and unstable best friendships separately. We used the Akaike Information Criterion (AIC; Akaike, 1974) to compare the model fits, and the log likelihood ratio to assess significance. For transparency, we also report the Bayesian Information Criterion (BIC; Schwarz, 1978). We reported the results with a significance threshold of $p < .05$.

RESULTS

We first examined whether friendship stability modulated age-related changes of NAcc activity, pleasure from winning, friendship quality, and friendship closeness. The fit parameters (AIC & BIC) of the models we tested are listed in Table 1. The parameter estimates and significance of the best model are listed in Table 2. Plots of the raw data are presented in the Supplementary materials (Figure S2).

Does Friendship Stability Modulate Age-Related Changes of Vicarious Reward-Related NAcc Activity?

We conducted separate analyses for the left and right NAcc as outcome variables. We first tested whether sex improved the model fit above and beyond linear and quadratic terms of age. Since there was no main effect of sex or an interaction between age and sex on NAcc activity, sex was removed from the model (left NAcc: $ps > .31$; right NAcc: $ps > .08$). Next we tested whether friendship stability improved the model fit. Only a main effect of friendship stability did not improve the model fit (left NAcc: $p = .42$; right NAcc: $p = .97$). A model that was extended with a friendship stability x age interaction best explained the model (left NAcc: $p < .01$, random effects: $SD_{intercept} = .22$, $SD_{residual}=2.31$; right NAcc: $p < .01$, random effects: $SD_{intercept} = .00$, $SD_{residual}=2.40$, Figure 2A and 2B); there was an interaction between linear age and friendship stability, and between quadratic age and friendship stability (left NAcc: $ps = .01$; right NAcc: $ps < .01$ and $= .02$, respectively).

To further interrogate the significant interaction between age and friendship stability we performed post hoc tests. These tests revealed that in the stable best friendship group, there is a significant quadratic age effect on NAcc activity (left NAcc: random effects: $SD_{intercept} = .00$, $SD_{residual}=2.09$; fixed effects: [Intercept] $b = 1.68$, $SE = 0.23$, $p < .001$; [linear age] $p = 0.07$; [quadratic age] $b= -.04$, $SE = 0.01$, $p < .001$; right NAcc: random effects: $SD_{intercept} = .00$, $SD_{residual}=1.87$; fixed effects: [Intercept] $b = 1.42$, SE = 0.20, $p < .001$; [linear age] $p = 0.94$; [quadratic age] $b= -.02$, SE = 0.01, $p = .04$), whereas there was no significant relation between age and NAcc activity in the unstable best friendship group (*ps* of linear and quadratic age terms > .53 and > .12 for left and right NAcc, respectively).

Table 1. AIC and BIC values

		Left NAcc		Right NAcc		Pleasure ratings	
	df	AIC	BIC	AIC	BIC	AIC	BIC
Null	3	1586	1597	1606	1618	**1761**	**1773**
+ Linear Age (1)	4	1587	1602	1608	1623	1763	1778
+ Quadratic Age (2)	5	1584	1604	1608	1627	1764	1783
+ Main effect Sex	6	1585	1508	1607	1630	1763	1786
+ Interaction Age & Sex	8	1587	1618	1609	1640	1764	1795
Age (1 and 2) + Main effect Friendship stability[1]	6	1586	1609	1610	1633	1766	1789
+ Interaction Age (1&2) & Friendship stability	8	**1580**	**1611**	**1604**	**1635**	1767	1798

		Positive friendship quality		Negative friendship quality		Friendship closeness	
	df	AIC	BIC	AIC	BIC	AIC	BIC
Null	3	354	367	527	539	730	741
+ Linear Age (1)	4	354	369	519	535	731	744
+ Quadratic Age (2)	5	355	375	520	540	733	750
+ Main effect Sex	6	*316*	*339*	518	541	*728*	*748*
+ Interaction Age & Sex	8	315	346	522	553	730	757
Age (1&2) & Sex effects + Main effect Friendship stability	7	307	335	516	544	727	751
+ Interaction Sex and Friendship stability	8	**305**	**337**	518	549	729	756
+ Interaction Age (1&2) & Friendship stability	10	308	347	522	560	**724**	**758**

Preferred models are shown in ***bold*** *and effects of sex are shown in italics. Df = degrees of freedom.*

[1] *Sex did not improve the model fit and was removed from the model.*

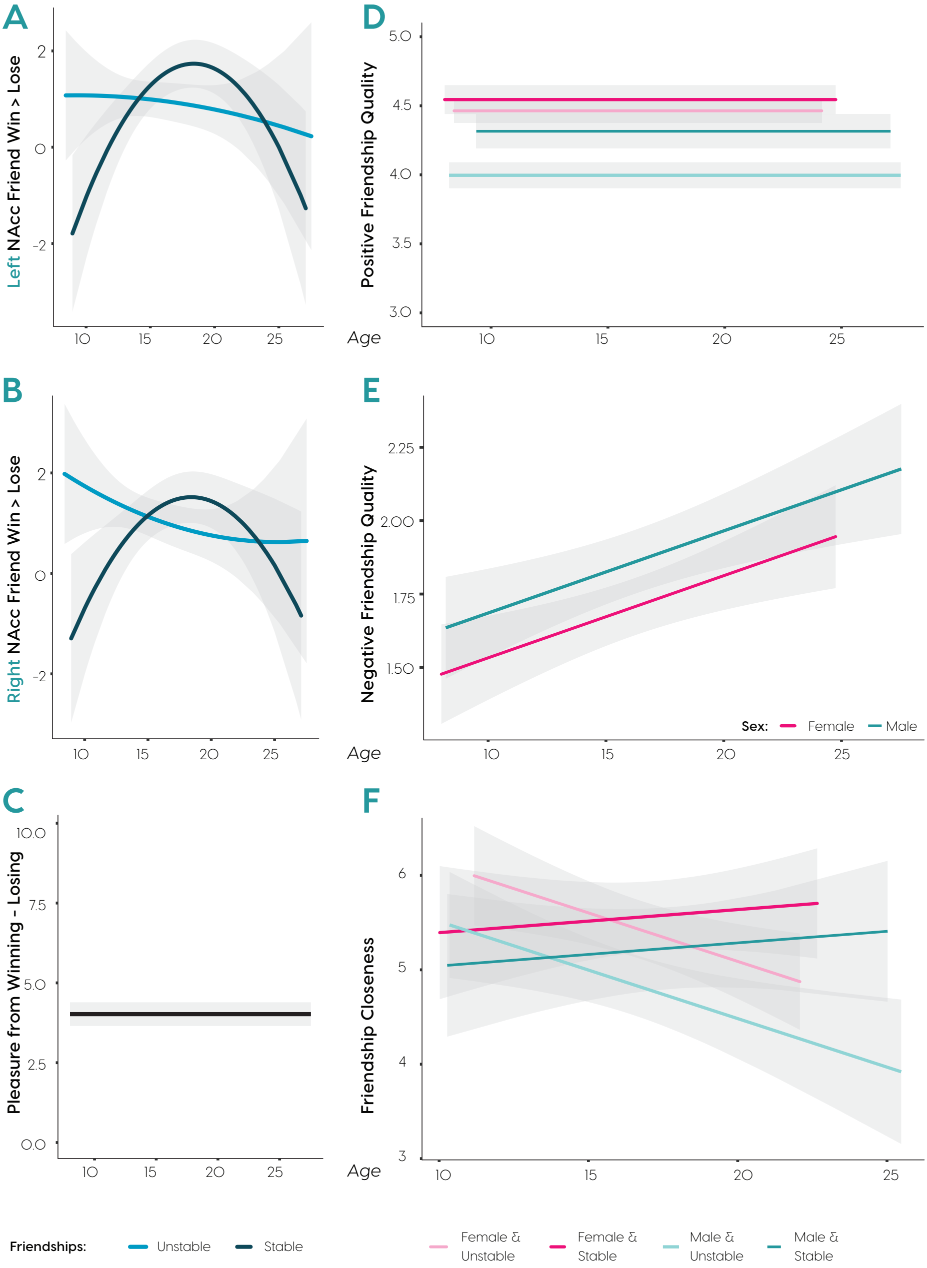


Figure 2. Age-related patterns and effects of sex and friendship *of A) left NAcc activity, B) right NAcc activity, and C) pleasure from winning, D) positive friendship quality, E) negative friendship quality, and F) friendship closeness.*

Does Friendship Stability Modulate Age-Related Changes of Vicarious Reward-Related Pleasure Ratings?

Next we tested whether participants with stable and unstable best friendships showed different developmental trajectories of pleasure experienced after winning minus losing. We first tested whether a main effect of sex and an interaction between sex and age improved the model fit for pleasure from winning (versus losing for the best friend) above and beyond linear and quadratic terms of age. These tests showed that there were no significant age-related changes in pleasure ratings (*ps* > .41) and there were no main effects of sex and interaction effects of sex with age (*ps* > .08). Next, sex was removed from the model, and we tested whether a main effect of friendship stability and an interaction between friendship stability and age significantly improved the model. The results showed that friendship stability did not affect developmental trajectories of pleasure ratings of winning for a best friend (model fits *ps* > .41; Random effects: $SD_{\text{intercept}}$ = 1.60, SD_{residual}=2.34), and there was no effect of friendship stability (model fits *ps* > .19, Figure 2C).

Does Friendship Stability Modulate Age-Related Changes of Friendship Quality?

We first built a model including an intercept, a linear term of age, and a quadratic term of age. Then we tested whether a main effect of sex and an interaction between sex and age improved the model fit for friendship quality. Positive friendship quality was best explained by a model including a main effect of sex (*p* < .001), and a sex x friendship stability interaction (*p* = .03; Random effects: $SD_{\text{intercept}}$ = .22, SD_{residual}=0.31; Figure 2D). There was no effect of age. Post hoc tests showed that there was a main effect of friendship stability for males (Random effects: $SD_{\text{intercept}}$ = .26, SD_{residual}= .32; Fixed effects: [intercept] *b* = 3.99, *SE* = .06, *p* = < .001; [friendship stability] *b* = 0.30, *SE* = .09, *p* < .01; [linear age] *p* = ns; [quadratic age] *p* = ns), such that males with stable best friendships reported higher positive friendship quality than males with unstable best friendships. There was no effect of friendship stability on positive friendship quality for females (Random effects: $SD_{\text{intercept}}$ = .18, SD_{residual}= .30; Fixed effects: [intercept] *b* = 4.49, *SE* = .04, *p* = < .001; [friendship stability] *p* = .15; [linear age] *p* = .83; [quadratic age] *p* = .10).

Table 2 Statistical parameters for the best fitting models

Dependent variable	Fixed effects	*b*	*SE*	*p*
Left NAcc Win > Lose	Intercept	0.95	0.2	< 0.001
	Age (1)	-0.04	0.05	0.46
	Age (2)	0.00	0.01	0.80
	Friendship stability	0.63	0.32	0.05
	Age (1) x Friendship stability	0.19	0.08	0.01
	Age (2) x Friendship stability	-0.04	0.01	0.01
Right NAcc Win > Lose	Intercept	1.00	0.21	< 0.001
	Age (1)	-0.09	0.05	0.10
	Age (2)	0.00	0.01	0.65
	Friendship stability	0.38	0.33	0.24
	Age (1) x Friendship stability	0.21	0.08	< 0.01
	Age (2) x Friendship stability	-0.04	0.02	0.02
Pleasure from winning	Intercept	4.11	0.22	< 0.001
	Age (1)	-0.10	0.05	0.80
	Age (2)	-0.01	0.01	0.41
Positive friendship quality	Intercept	4.47	0.05	< 0.001
	Age (1)	0.01	0.01	0.26
	Age (2)	0.00	0.00	0.64
	Sex	-0.47	0.07	< 0.001
	Friendship stability	0.08	0.07	0.29
	Sex x Friendship stability	0.23	0.11	0.03
Negative friendship quality	Intercept	1.69	0.05	< 0.001
	Age (1)	0.03	0.01	< 0.01
	Age (2)	0.00	0.00	0.34
	Sex	0.15	0.08	0.05
Friendship closeness	Intercept	5.33	0.17	< 0.001
	Age (1)	-0.11	0.04	< 0.01
	Age (2)	0.01	0.01	0.25
	Sex	-0.62	0.23	< 0.01
	Friendship stability	0.41	0.28	0.15
	Age (1) x Friendship stability	0.14	0.06	0.02
	Age (2) x Friendship stability	-0.03	0.01	0.05
	Sex x Friendship stability	0.25	0.37	0.50

Statistical parameters (regression coefficients (b), significance level (p) and standard errors (SE) for the bs) for the best fitting models testing the relation between age and each of the measures reported in the table. Age (1) = linear term of Age; Age (2) = quadratic term of Age.

Negative friendship quality was best explained by a linear term of age ($p <$ .01), and a main effect of sex (p = .0462; Random effects: $SD_{intercept}$ = .34, $SD_{residual}$=0.41). With increasing age, there was an increase in negative friendship quality and males reported higher levels of negative friendship quality (see Figure 2E). Friendship stability did not improve the model fit of the developmental trajectory of negative friendship quality (*ps* > .06).

Does Friendship Stability Modulate Age-Related Changes of Friendship Closeness?

Above and beyond a model with linear and quadratic age terms, a main effect of sex explained additional variance in friendship closeness (model fit: p < .01). Next we tested whether main effects of friendship stability and interaction effects with friendship stability improved the model fit. The final model included main effects of the linear age term (p < .01) and quadratic age term (p = *ns*), a main effect of sex (females > males; p < .01), a linear age x friendship stability interaction (p = .02), and a quadratic age x friendship stability interaction, which was significant at trend level (p = .05; Random effects: $SD_{intercept}$ = .59, $SD_{residual}$= 1.04). Post hoc tests revealed that there were no age-related changes in friendship closeness for participants with a stable best friendship (Random effects: $SD_{intercept}$ = .76, $SD_{residual}$= 1.04; Fixed effects: [intercept] b = 5.67, SE = .25 p = < .001; [linear age] p = .84; [quadratic age] p = .13; [sex] p = .27), and that friendship closeness decreased linearly with age for participants with an unstable best friendship (Random effects: $SD_{intercept}$ = .43, $SD_{residual}$= 1.05; Fixed effects: [intercept] b = 5.37, SE = .16, p < .001; [linear age] b = −.11, SE = .04, p < .01; [quadratic age] p = .25; [sex] b = −.62, SE = .24, p < .01; Figure 2F).

Are Pleasure Ratings, Friendship Quality, and Friendship Closeness Related to Vicarious Reward-Related NAcc Activity?

Finally, we examined whether pleasure from winning, friendship quality, and friendship closeness related to NAcc activity. We extracted residuals from the best fitting age models of pleasure from winning versus losing, friendship quality, and friendship closeness to correct for developmental and sex effects in this set of analyses. Furthermore, because our results showed differential age-related trajectories of NAcc activity when winning for a best friend for the stable and unstable friendship groups, we examined the role of pleasure from winning, friendship quality, and closeness on the development of NAcc activity separately for both groups of participants. For participants with stable best friendships, we examined whether a main effect of pleasure from winning versus losing, friendship quality, or closeness explained additional variance above and beyond the linear and quadratic age term. For participants with unstable best friendships, we added a main effect to a model without any age terms, since our results showed no significant age effects on NAcc activity in this group. We conducted separate analyses for each main effect we tested on NAcc activity (i.e., pleasure from winning, positive and negative friendship quality, and friendship closeness). Table 3 provides an overview of the AIC and BIC parameters for the models we tested.

Table 3. AIC and BIC values

	Left NAcc				**Right NAcc**			
	Best age model		+ Predictor		Best age model		+ Predictor	
Friendship type & predictor	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC
Stable best friendship								
Pleasure from winning	**581**	**596**	583	600	**578**	**592**	580	597
Positive friendship quality	**582**	**597**	584	601	**580**	**595**	581	599
Negative friendship quality	**582**	**597**	583	600	**580**	**595**	582	599
Friendship closeness	**366**	**379**	368	383	**367**	**379**	368	383
Unstable best friendship								
Pleasure from winning	**971**	**981**	973	986	**994**	**1005**	996	1009
Positive friendship quality	**965**	**975**	967	980	**990**	**1000**	992	1005
Negative friendship quality	**953**	**963**	951	965	**980**	**991**	979	993
Friendship closeness	587	596	**584**	**596**	598	607	**593**	**605**

*Preferred models are shown in **bold**.*

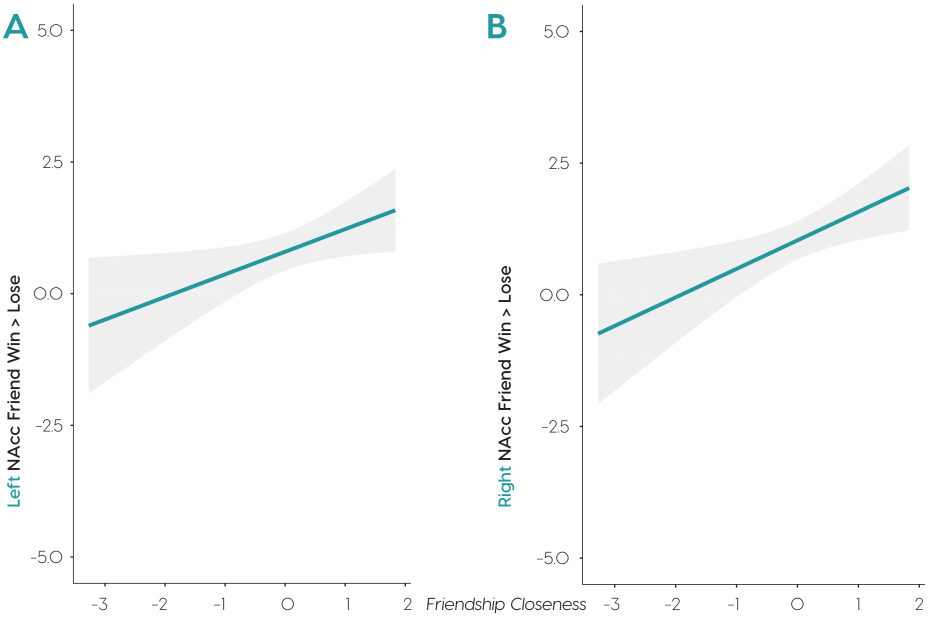


Figure 3. Relation between vicarious reward-related NAcc activity and friendship closeness in adolescents with unstable best friendships for A) the left NAcc, and B) the right NAcc.

Pleasure from winning

First, we examined whether ratings of pleasure after winning versus losing for a best friend related to NAcc activity. Pleasure from winning versus losing for a best friend was not related to NAcc activity for neither group of participants with stable (left NAcc: $p = .64$; right NAcc: $p = .98$) and unstable friendships (left NAcc: $p = .85$; right NAcc: $p = .45$).

Friendship quality

Second, we examined whether friendship quality related to NAcc activity. We conducted separate analyses with positive and friendship quality as a predictor. Neither positive nor negative friendship quality was related to NAcc activity for participants with stable (left NAcc: $p = .75$ and .20 for positive and negative friendship quality, respectively; right NAcc: $p = .37$, and .87 for positive and negative friendship quality, respectively) and unstable friendships (left NAcc: $p = .84$ and .07 for positive and negative friendship quality, respectively; right NAcc: $p = .77$ and .06 for positive and negative friendship quality, respectively).

Friendship closeness

Finally, we examined whether friendship closeness related to NAcc activity. Self-reported friendship closeness was not related to NAcc activity for participants with stable friendships (left NAcc: $p = .69$; right NAcc: $p = .55$). There was a significant positive linear relation between friendship closeness and NAcc activity for participants with unstable friendships (left NAcc: $p = .03$; right NAcc: $p < .01$), such that higher closeness was related to higher NAcc activity (left NAcc: Random effects: $SD_{intercept} = .55$, $SD_{residual} = 1.97$; Fixed effects: [intercept] $b_{intercept} = .80$, $SE = .18$, $p < .001$; [IOS residuals] $b = .43$, $SE = .19$, $p = .03$; right NAcc: Random effects: $SD_{intercept} = .58$, $SD_{residual} = 2.03$; Fixed effects: [intercept] $b_{intercept} = 1.03$, $SE = .19$, $p < .001$; [IOS residuals] $b = .54$, $SE = .20$, $p < .01$; see Figure 3 for the fitted relationship and Figure S3 for plot with the raw data).

DISCUSSION

In this study, we tested whether adolescents, between eight to twenty-eight years of age, with stable and unstable best friendships showed differential developmental trajectories of vicarious reward-related NAcc activity and the pleasure experienced after winning rewards for their best friend. We used a longitudinal design and distinguished between groups of adolescents with stable and unstable best friends over a trajectory of four years. When rewards for best friends were gained, adolescents with stable best friendships showed a quadratic trajectory of change in NAcc activity, whereas adolescents with unstable best friendships showed no age-related changes in their NAcc responses to winning for their best friend. Despite these neural differences in vicarious reward activity, the two groups of adolescents did not show different trajectories of change in the subjective pleasure experienced after gaining rewards for best friends. However, there was an effect of friendship stability on perceived positive friendship quality and closeness. Finally, for participants with unstable best friendships, stronger closeness related to stronger NAcc activity. In the following paragraphs we set out how friendship stability affected developmental trajectories of NAcc activity and how this related to the pleasure experienced, friendship quality, and friendship closeness.

Our finding that adolescents with stable best friendships yield greater NAcc activity when rewards are gained for best friends in mid- to late adolescence than early adolescence and adulthood, confirms our hypothesis that friendship stability modulates vicarious reward activity in the NAcc across development. The increase and decrease in vicarious reward activity in the NAcc across adolescence seems to resemble age-related changes of NAcc activity when rewards are gained for the self (Schreuders et al., 2018a). These findings extend prior findings of NAcc involvement in processing vicarious rewards for socially close others, by showing that friendship stability may affect developmental trajectories of NAcc activity when rewards are gained for best friends (Braams et al., 2014a; Mobbs et al., 2009).

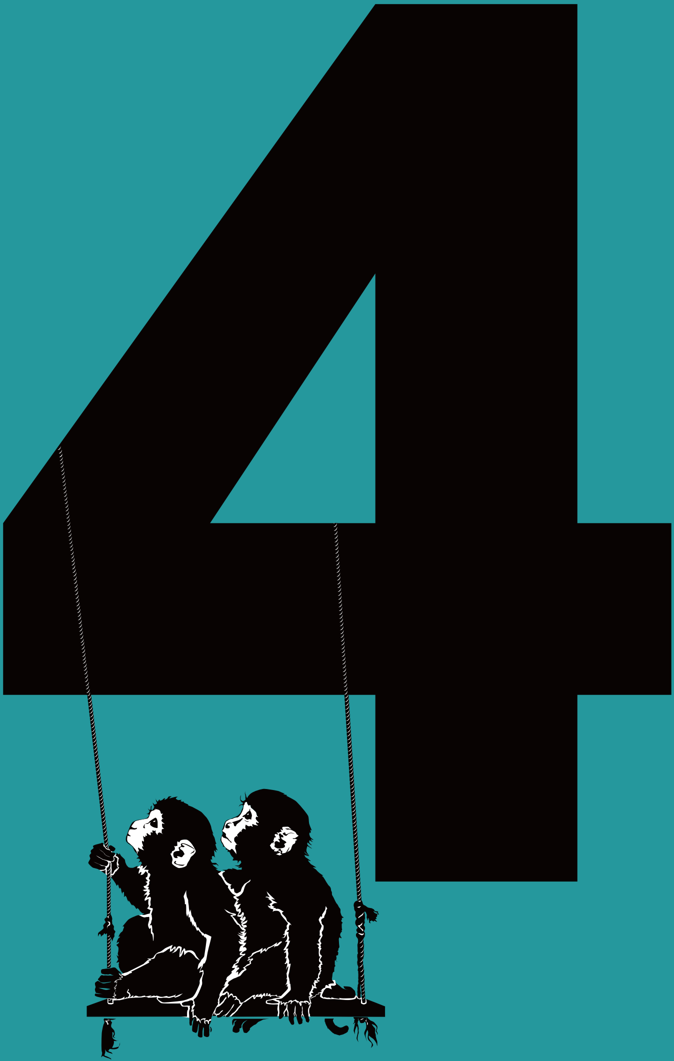
Interestingly, individual differences in vicarious NAcc activity when gaining rewards for a stable or unstable best friend appeared to be most pronounced in early adolescence. That is to say, the youngest adolescents from our sample with stable best friendships appeared to show lower NAcc activity in response to vicarious rewards for their best friend than participants with unstable best friendships. In mid- to late adolescence and early adulthood, participants with stable and unstable best friendships appear to show similar levels of vicarious reward-related NAcc activity. This finding may indicate that in early adolescence, rewards for best friends possibly have a lower rewarding impact in stable friendships than unstable friendships. This supports the notion that young adolescents are not yet as motivated to orient to stable friendships as older adolescents (Branje et al., 2007; Nelson, Jarcho, & Guyer, 2016). That is, in early adolescence there might be a higher social motivation to expand the friend network than building stable best friendships (Buhrmester, 1990; Nelson, Jarcho, & Guyer, 2016; Poulin & Chan, 2010). This interpretation should be further examined in future studies.

Whereas the hedonic impact of gaining rewards for best friends did not change across adolescence, and was not different for adolescents with stable and unstable best friendships, it was found that best friendship stability related to the development of friendship quality and closeness of the current best friendship. For both males and females, positive friendship quality did not change across adolescence. However, for males only, levels of positive friendship quality for adolescents with stable best friendships were higher than for adolescents with unstable best friendships. Furthermore, adolescents with stable and unstable best friendships showed differential developmental trajectories of friendship closeness. More specifically, adolescents with unstable best friendships reported weaker closeness with the best friend with age, whereas adolescents with stable best friendships reported stable levels of closeness. These findings together emphasize that adolescents with stable and unstable best friendships may differ across development in perceived friendship characteristics, but not in the subjective pleasure experienced after gaining rewards for friends (Poulin & Chan, 2010).

In a similar vein, whereas the subjective pleasure experienced after winning was not related to NAcc responses to vicarious rewards, we found that stronger closeness with the concurrent best friend related to higher NAcc activity in adolescents with unstable best friendships. Although we found no relation between NAcc activity and friendship quality, these findings may together suggest that vicarious reward NAcc activity does not reflect the degree of pleasure experienced when winning for best friends, but that there may be other underling processes are driving vicarious NAcc activity across adolescence, such as changing prosocial motivations (Braams & Crone, 2017).

Some limitations should be acknowledged. Although a strength of this study was that we used unrestricted nominations of same-sex best friends, we did not incorporate information about friendship duration (before the study started), whether unstable best friends were still part of a close peer network, and whether the best friendships were reciprocated (although the latter is challenging with unrestricted peer nominations and without direct access to a closed peer group). Future studies could benefit from including information about participants' peer network, including friends and romantic relationships (Laursen, 2017; Poulin & Chan, 2010). Furthermore, to measure NAcc reward sensitivity we used a Win > Lose contrast, which does not allow for distinguishing whether activity is driven by wins or losses, and therefore should be interpreted as a relative difference. Future studies should include a baseline *no win* or *no loss* condition.

To conclude, our findings support the hypothesis that the developmental trajectory of ventral striatum activity in response to vicarious rewards depends on relationship stability. This suggests that the ventral striatum may be involved in changing social motivations across adolescence and that stable best friendships become more desirable across adolescence.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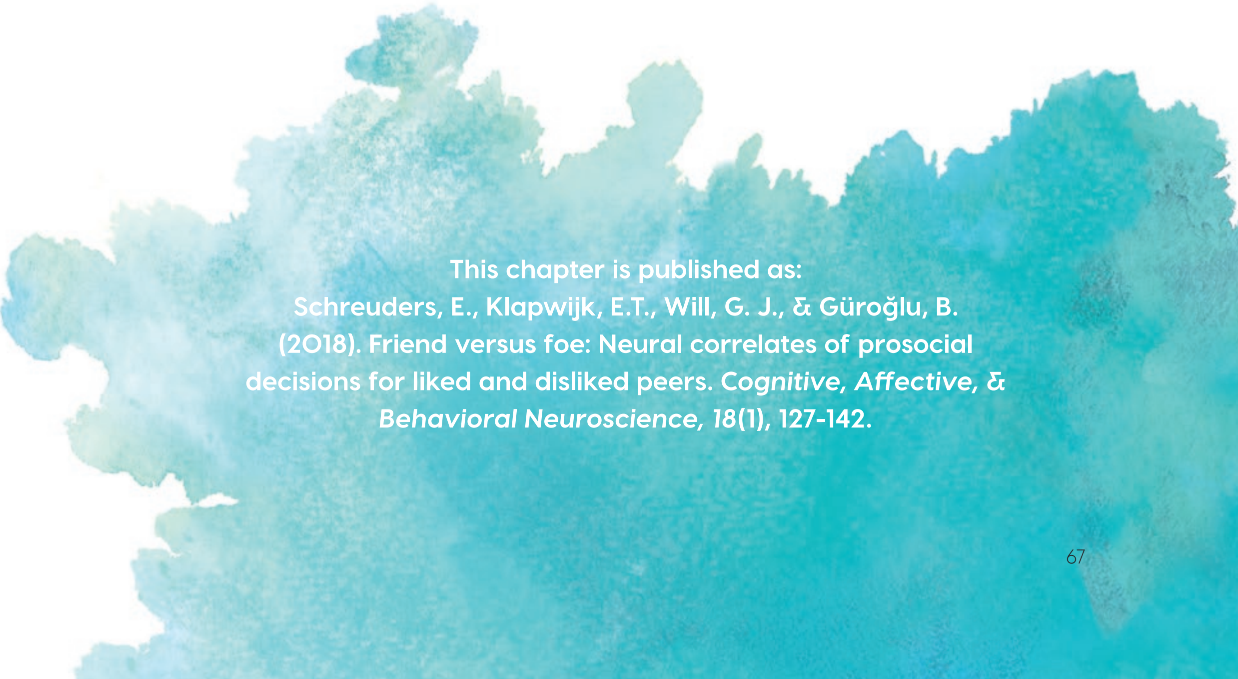
CHAPTER FOUR

Friend versus foe: Neural correlates of prosocial decisions for liked and disliked peers



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ABSTRACT

Although the majority of our social interactions are with people we know, few studies have investigated the neural correlates of sharing valuable resources with familiar others. Using an ecologically valid research paradigm, this functional magnetic resonance imaging study examined the neural correlates of prosocial and selfish behavior in interactions with real-life friends and disliked peers in young adults. Participants (*N* = 27) distributed coins between themselves and another person, where they could make selfish choices that maximized their own gains or prosocial choices that maximized outcomes of the other. Participants were more prosocial toward friends and more selfish toward disliked peers. Individual prosociality levels toward friends were associated negatively with supplementary motor area and anterior insula activity. Further preliminary analyses showed that prosocial decisions involving friends were associated with heightened activity in the bilateral posterior temporoparietal junction, and selfish decisions involving disliked peers were associated with heightened superior temporal sulcus activity, which are brain regions consistently shown to be involved in mentalizing and perspective taking in prior studies. Further, activation of the putamen was observed during prosocial choices involving friends and selfish choices involving disliked peers. These findings provide insights into the modulation of neural processes that underlie prosocial behavior as a function of a positive or negative relationship with the interaction partner.

INTRODUCTION

Throughout the day, we interact with all kinds of people, such as people we know and strangers. The majority of our interactions are most likely to involve liked others, such as friends, but sometimes they involve those we do not like. Friends provide support and company (Hartup, 1996), whereas relationships based on dislike are characterized by aggression, attempts to do harm, and avoidance (Card, 2007). It is therefore not surprising that individuals tend to behave in a more prosocial manner toward friends than toward disliked peers (Güroğlu, Van den Bos, & Crone, 2014). Moreover, prosocial behaviors that maximize outcomes for the other person are important for forming and maintaining friendships (Eisenberg, Fabes, & Spinrad, 2006; Fehr, Fischbacher, & Gächter, 2002), whereas nonprosocial or selfish behaviors that maximize outcomes for the self may weaken a relationship and may even provide a basis for relationships based on dislike. A better understanding of the neural mechanisms of decision-making in social interactions is crucial for understanding the formation and maintenance of personal relationships of positive and negative valence (Güroğlu, Van den Bos, & Crone, 2009b).

There is substantial amount of research on neural processes underpinning interactions with unfamiliar others (for review see Rilling & Sanfey, 2011), yet few neuroscientific studies have investigated social interactions involving familiar others, that is, others from real-life relationships. There are several neuroimaging studies in which decisions concerning friends were compared with those concerning unfamiliar others (Fareri, Chang, & Delgado, 2015; Fareri & Delgado, 2014). Especially, little is known about the underlying neural processes of social decisions involving *disliked peers*, even though it is as crucial to understand a disliked other's intentions and to act on them in social interactions as it is to understand friends. The majority of prior studies examining decision-making processes with different types of interaction partners have employed experimental manipulations to create positive or negative impressions about unfamiliar others (Bault, Pelloux, Fahrenfort, Ridderinkhof, & van Winden, 2015; Fahrenfort, Pelloux, Stallen, & Ridderinkhof, 2012; Fareri, Chang, & Delgado, 2012; Van den Bos, Van Dijk, & Crone, 2012). As informative as studies using manipulations of whether one feels positive or negative valence toward others are, the interactions with such unfamiliar others might not be as personally relevant for individuals as interactions with others from real-life relationships and are hence ecologically less valid. The goal of the current study was thus to investigate how real-life relationships with friends and disliked peers modulate prosocial behavior and the underlying neural processes during these social decisions.

Social Decision-Making and its Neural Correlates

Social interactions involve exchanges with others who might have different intentions and perspectives. People have to rely on inferences about others' intentions and perspectives in order to guide decision-making in these social interactions (V. K. Lee & Harris, 2013). Using economic allocation paradigms researchers have shown that in interactions with unfamiliar others individuals show concern not only for their own outcomes, but also for those of their interaction partner (Camerer, 2003; Will & Güroğlu, 2016). Thinking about other people's mental states, needs and intentions (i.e., mentalizing) and taking their perspectives into account contribute to the ability to feel concern for others (Batson, Eklund, Chermok, Hoyt, & Ortiz, 2007). These abilities have been consistently linked to activity in a brain network comprising the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), and superior temporal sulcus (STS; Blakemore, 2008; Frith & Frith, 2012).

Showing concern for others can be expressed by prosocial decisions that (also) benefit others. Prosocial decisions involve self-regulation in the form of controlling selfish impulses (Blake, Piovesan, Montinari, Warneken, & Gino, 2015; Eisenberg, Fabes, Guthrie, & Reiser, 2000; Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007; Steinbeis, Bernhardt, & Singer, 2012), mentalizing skills to shift the attention from the self to the needs and goals of others (e.g., Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011), and possibly a sense of reward (Declerck, Boone, & Emonds, 2013; Zaki & Mitchell, 2011). This is supported by evidence showing involvement of ventrolateral, dorsolateral, and dorsomedial prefrontal cortex (vlPFC, dlPFC, and dmPFC), the TPJ, and the striatum in making prosocial decisions. These are brain regions often implicated in higher order cognitive functions such as self-regulation (vlPFC and dlPFC; Coutlee & Huettel, 2012; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), social cognition (dmPFC and TPJ; Telzer et al., 2011; Waytz, Zaki, & Mitchell, 2012), and reward processing (striatum; Bhanji & Delgado, 2014; Fehr & Camerer, 2007; Izuma, Saito, & Sadato, 2008; Telzer, Fuligni, Lieberman, & Galván, 2013; Telzer et al., 2011).

Activity in the brain regions typically involved in social cognition, such as the mPFC, the STS, and the TPJ, have been shown to be modulated by the relationship valence with the interaction partner during social interactions. For example, TPJ and STS activation has been shown to increase during social interactions with familiar peers compared to unfamiliar others (Güroğlu et al., 2008). Moreover, the social tie with an unfamiliar peer, which develops during interactive social decisions, is shown to modulate activity in the posterior STS (pSTS) and TPJ (Bault et al., 2015; Fahrenfort et al., 2012). That is, lower levels of activation in pSTS and TPJ have been found in interactions with liked others (Bault et al., 2015) and higher levels of pSTS activation have been found when gaining money at the expense of others, but only after a social tie has been established (Fahrenfort et al., 2012). Along these lines, activation in pSTS has been suggested to be involved in keeping track of one's own and others' social decisions and their effect on the social interaction (Hampton, Bossaerts, & O'Doherty, 2008). Finally, mPFC activation has often been linked to the integration of (social) information in goal-directed behavior (Amodio & Frith, 2006; Bault, Joffily, Rustichini, & Coricelli, 2011; Bault et al., 2015; Euston, Gruber, & McNaughton, 2012), and its activation is shown to be heightened during decisions involving friends (Braams et al., 2014a; Fareri & Delgado, 2014; Güroğlu et al., 2008).

Interaction partners modulate not only brain activation during decision-making in social interactions but also during processing outcomes for others. Processing outcomes are often examined based on distribution of resources or on winning or losing resources (i.e., typically money). Both monetary gains for the self (Fareri et al., 2012; Fareri & Delgado, 2014) and others, such as charities (Kuss et al., 2013; Moll et al., 2006) and family members (Telzer et al., 2011), lead to enhanced activity in the striatum. Social rewards, such as having a good reputation or receiving approval, also lead to enhanced activity in the striatum (Bhanji & Delgado, 2014; Izuma et al., 2008; Jones et al., 2014). Interestingly, heightened striatum activity is associated with observing both monetary gains for friends (Braams et al., 2014a; Varnum, Shi, Chen, Qiu, & Han, 2014) and losses for *unfamiliar* disliked others (Braams et al., 2014a). In short, these prior studies show that whether one feels positive or negative valence toward interaction partners modulates activity in a set of brain regions implicated in socio-cognitive and emotional processing. The current study is different from these existing studies in that we examine (a) interactions with friends *and* familiar (i.e., real-life) disliked peers, and (b) active decision-making (i.e., prosocial and selfish decisions) instead of observing monetary outcomes without being able to actually influence them.

Not only the social context modulates social behavior and its underlying neural processes, but individual differences in prosociality may also affect neural processes during social interactions. In particular individual differences in social norms and preferences shape neural processes underlying social decision-making in varying social contexts. For example, studies on social exchanges with unfamiliar peers show that individual differences in prosocial behavior related to TPJ involvement when participants made donating decisions while being evaluated by peers (Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016) and that enhanced activity in dorsal anterior cingulate cortex (dACC), anterior insula, and dlPFC underlie violations of personal norms in prosocial and selfish decision-making (Güroğlu, Van den Bos, Rombouts, & Crone, 2010; Haruno, Kimura, & Frith, 2014; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009).

The Current Study

Based on evidence showing that interaction partners modulate prosocial behavior such that individuals are more prosocial toward close others and people they like than more distant and disliked others (Güroğlu et al., 2014), in this study we investigated whether and how activation of brain regions involved in higher order cognitive functions, mentalizing, and emotion processing are modulated by interaction partners and individual differences in prosociality during social decision-making. In this study, participants actively made prosocial or selfish decisions involving familiar peers who were their actual classmates in real life. By doing so, we aimed to investigate the role of personal relationships of positive (i.e., friends) and negative valence (i.e., disliked peers) in social decisions and the underlying neural circuitry.

To identify existing positive and negative relationships, we used a widely established sociometric nomination method (Cillessen & Bukowski, 2000). Using this method, we were able to identify friends and disliked peers in a group of college students. During the scanning session, participants distributed coins between themselves and another player by choosing one of two preset distributions of coins, where one option always involved a prosocial and the other a selfish distribution of coins. Prosocial distributions benefited the interaction partner irrespective of the costs attached to the decision (Eisenberg et al., 2006), and selfish distributions maximized the outcome of the participant or resulted in the smallest number of coins for the interaction partner possible.

We expected participants to make more prosocial decisions toward their friends than toward disliked peers (Güroğlu et al., 2014), and that individual differences in prosociality would relate to brain regions that are sensitive to personal social norms and preferences such as the dACC/SMA, the dlPFC, and TPJ (Güroğlu et al., 2010; Haruno et al., 2014; Van den Bos et al., 2009b; Van

Hoorn et al., 2016). We further expected interaction partners to modulate brain activation during decision-making in brain regions involved in social cognition (e.g., self and other preferences and anticipating on outcomes of social decisions), such as the TPJ and STS, the mPFC, and striatum. Specifically, we expected increased mPFC and striatum activity during decisions for friends since these regions have been consistently found to be involved in information processing during interactions with friends (Braams et al., 2014a; Fareri & Delgado, 2014; Güroğlu et al., 2008).

METHOD

Participants

Participants were recruited from vocational universities that offer a 4-year bachelor's degree and have a fixed classroom structure. Students from 24 classrooms in five vocational universities (total *N* = 380) filled out a sociometric questionnaire and an MRI screening checklist. Only right-handed students without a history of psychiatric and neurological impairments were further contacted. Individuals were eligible to participate in the study if they nominated at least two classmates as friends and two classmates as disliked peers. One participant was excluded due to excessive movement in the MRI scanner (>3 mm). The remaining sample consisted of 27 participants (M_{age} = 21.25, *SD* = 2.93, 15 males).

Procedure

Before scanning, participants gave their written informed consent to participate, were familiarized with the scanner environment using a mock scanner, and practiced the fMRI task. They received €30 plus their earnings from the fMRI task.

Sociometric Nominations

The sociometric questionnaire was administered in the classroom (class size ranged between 17 and 33 students, *M* = 25.08, *SD* = 4.61). All students in the class were asked to (a) rate how much they like each of their classmates on a 5-point scale ranging from 1 (*not at all*) to 5 (*very much*), and (b) make five nominations among their classmates for the questions 'Who are your friends?' and 'Who do you like the least?' These ratings and nominations were used to determine three types of classmates: (a) *Friends* were nominated as friends and received a rating of 4 or 5, (b) *disliked peers* were nominated as least liked classmates and/or received a rating of 1 or 2, and (c) *neutral peers* were classmates receiving a rating of 3. These nominations were used to form the peer groups that the participant played the coin distribution game with (see fMRI task description). For each participant, we aimed to have two or three friends and two or three disliked peers. The majority (67.9%) of the friendships that we identified were based on mutual friendship nominations; in total 79.5% of the nominated friends reported to like the participant very much and for the remaining 20.5% of the friendships mutuality could not be determined due to missing sociometric data. Relationships based on dislike were more heterogeneous: Only 13% of these relationships were based on mutual dislike nominations; in total 23.2% of the disliked peers reported to dislike the participant or reported *not* to prefer to collaborate with the participant, 42% of the relationships were based on unilateral dislike and for the remaining 34.8% of the relationships mutuality could not be determined due to missing sociometric data.

FMRI Task Description

Peer groups

Participants were told that they would play a coin distribution game with other peers who were distributed into four groups. They were told that three of these four groups involve randomly chosen peers from their classroom (i.e., classmates) and that the fourth group consists of unfamiliar peers of same age who are also participants of the study. In reality, the group compositions were not random and were based on the sociometric questionnaire. Unique groups of peers were constructed for each participant based on their individual sociometric nominations and ratings. We aimed to have three peer names in the friend and the disliked peer groups; whenever this was not possible, participants were presented with two friend names (11.1%) and two disliked peer names (44.4%). Overall, we presented two groups with two peer names and two groups with 3 peer names to keep a balanced distribution across the four groups of peers.

Participants were told that on each trial they would see the group they would be distributing the coins with, and the names of the peers in that group, but that they would not exactly know with whom from that peer group they played on each trial. There were three reasons for this manner of presenting the players: (a) to prevent that participants could use strategies of how to distribute coins to different players, (b) to correct for slightly different personal relationships the participant might have with specific players within a group, and (c) to make the task more engaging such that participants did not have to make the same decision for the same player repeatedly. Participants were also told that the computer would keep track of exactly whom they are making a decision for.

In order to present the four groups of friends, disliked peers, neutral peers, and unfamiliar peers in a neutral manner to the participants, the groups were randomly assigned to one of the four vehicle symbols named train, bike, car, and boat (Figure 1A). The names of the group members were presented to the participants at the start of the scanning session (before scanning started). Participants were told that they were not required to memorize these names and that the names would be presented on the screen during each trial of the task.

At the end of the experiment, a free recall test was administered to see whether the participants could produce the names of the group members for each of the four groups of interaction partners. They were also asked about their attitude toward each group by writing down what they thought of the members of each group. This was done to check whether the manipulation of groups representing different kind of relationships was successful and to assess whether the participants paid attention to the task. Results of the manipulation checks are reported in the Results section.

Coin distributions

Participants played three modified dictator games (Fehr, Bernhard, & Rockenbach, 2008; Güroğlu, Will, & Crone, 2014), in which they distributed coins between themselves and another player. In each of the games participants were asked to choose one of two predetermined distributions of coins. Each game had one prosocial option and one selfish option: (a) In the advantageous competitive inequity (ACI) game participants could choose to keep one coin for themselves and give nothing to the other player (self/other: 1/0, selfish option), or to give one coin to the other player resulting in an equal distribution (1/1, prosocial option), and (b) in the self-maximizing inequity (SMI) game participants could choose to keep two coins for themselves (2/0, selfish option) or to share the two coins with the other person resulting in an equal distribution (1/1, prosocial option), and (c) in the disadvantageous prosocial inequity (DPI) game participants could equally divide two coins between themselves and the other player (1/1, selfish option) or give an additional coin to the other player (1/2, prosocial option). Prosocial choices in the three games were coded as 1 and selfish choices were coded as 0. We used these different types of prosocial choices (i.e., prosocial giving in the ACI game, prosocial sharing in the SMI game, and disadvantageous prosocial giving in the DPI game) to keep the participants engaged in the task (Figure 1B). Percentage of prosocial choices per interaction partner was calculated across games. It was explained that the computer kept track of the coin distributions and calculated everyone's earnings, which would be paid out at the end of all the trials. During the instructions, it was also emphasized that decisions had consequences for the participants as well as for the interaction partners. However, it was not explicitly specified how this would exactly be implemented; none of the participants had questions about this implementation. In reality, all participants got feedback at the end of the task that they had earned €2.

Task duration

The task consisted of 96 trials presented in a randomized order, in which participants engaged in 24 interactions with members of each group across a set of three allocation games. Each trial started with a jittered fixation cross (*M* = 1512.5 ms, min = 550 ms, max = 5500 ms; optimized with Opt-Seq2, surfer.nmr.mgh.harvard.edu/optseq/; Dale, 1999). This was followed by a screen with the group symbol and its members' names and the set of distributions they could choose from (see Figure 1C). Participants had 5000 ms to respond by a button press with their right index finger for the distribution on the left and with their right middle finger for the distribution on the right. The response of the participants was presented on the screen until 6000 ms. If they failed to respond within 5000 ms, a screen showing "Too late!" was presented for 1000 ms. The location of the equity option was counterbalanced across trials.

MRI Data Acquisition

MRI scans were acquired using a 3T Philips Achieva MRI scanner. The scanning procedure included a localizer scan, and T2* weighted gradient echo planar images (EPI; TR = 2.2 s, TE = 30 ms, descending and sequential acquisition, 38 slices of 2.75 mm, field of view [FOV] = 220 x 220 x 114.7 mm) were obtained during two functional runs. Each run consisted of 170 volumes and lasted approximately 6 minutes.

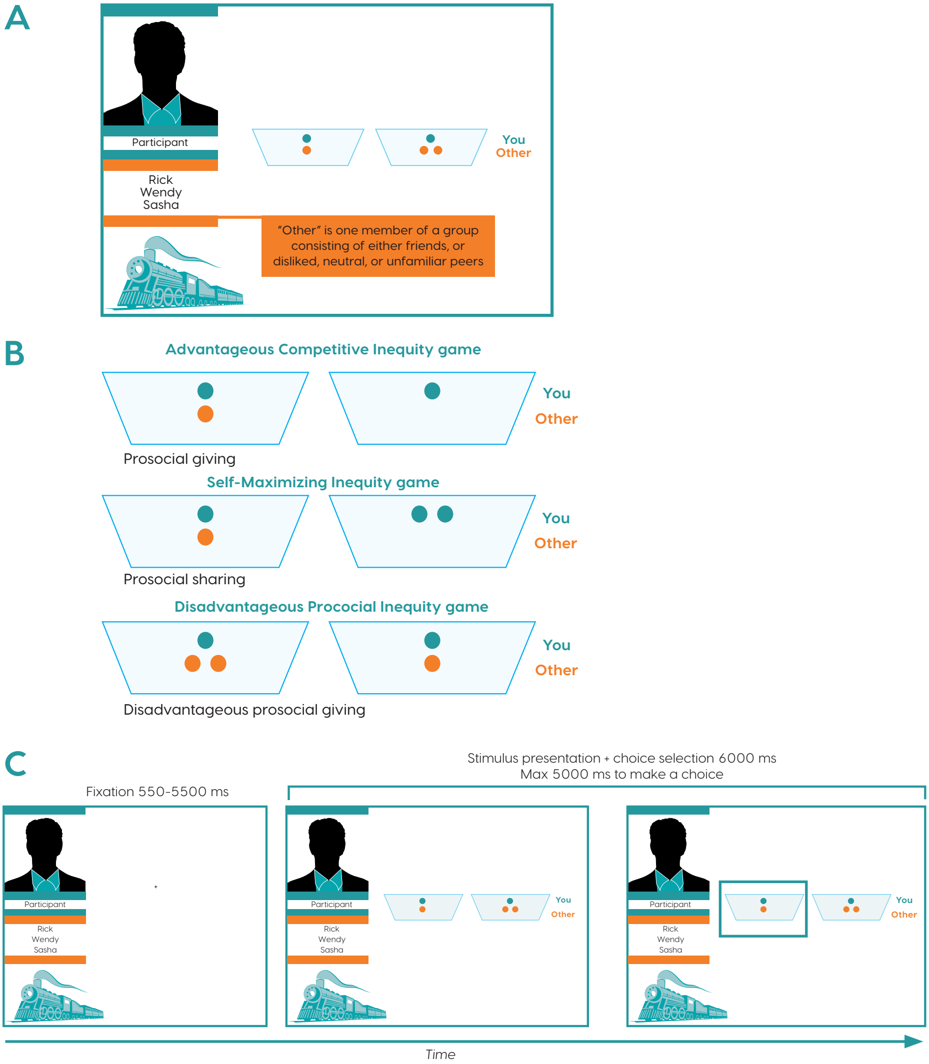


Figure 1. (A) Group member names were displayed on the screen. These three group members always belonged to the same peer category (i.e., friend, disliked peer, neutral peer, or unfamiliar peer). The interaction partner was one of these three group members. (B) There were three different preset coin distributions, always with a prosocial and a selfish option, depicted here on the left and right, respectively. (C) Example of a trial of the fMRI task. *After a fixation cross participants were presented with a screen showing the stimulus and with whom they were playing that trial. At stimulus onset, they could choose between the two options presented on the screen by pressing the corresponding button. A trial ended with selected choice indicated on the screen.*

FMRI Data Analysis

Image pre-processing and analyses were conducted using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/). The preprocessing steps of the functional images included realignment, slice-time correction (middle slice as reference), spatial normalization to EPI templates, and smoothing with a Gaussian filter of 8 mm full-width at half maximum. Regressors were modeled as zero-duration events (stick functions) time-locked to the stimulus onset and convolved with a canonical hemodynamic response function; stimulus onset was the moment participants were presented with the two distributions to choose from. Trials on which the participant failed to respond were modeled separately as covariate of no interest and were excluded from further analyses. The modeled events (players; i.e., friends, and disliked, neutral, and unfamiliar peers, and type of response; i.e., prosocial or selfish, per player) were used as regressors in a general linear model (GLM), along with a basic set of cosine functions that high-pass filtered the data (cutoff 120 seconds) and a covariate for session effects. Autocorrelations were estimated using an AR(1) model. The least-square parameter estimates of height of the best-fitting canonical HRF for each condition were used in the contrasts. No events for the button press were included in the GLM. For visualization purposes, mean beta estimates were extracted from whole brain clusters using the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002). Activity was averaged across the clusters derived from our whole brain analyses. All results are reported in Montreal Neurological Institute (MNI) 305 stereotactic space.

We examined the neural underpinnings of decision-making for friends and disliked peers by comparing (a) the two most "extreme" relationships, (i.e., friendships and relationships based on dislike), and by comparing (b) decisions involving friends and disliked peers with decisions involving peers with whom participants had no affective relationship, that is, the unfamiliar peers. For these comparisons we used the unfamiliar peers instead of the neutral peers because none of the participants was affiliated with the unfamiliar peer in any way, making these relationships more homogeneous across the participants. We report the contrasts with neutral peers in the Supplementary materials. See also Supplementary materials for whole brain contrasts of decision-making for different types of peers collapsed across behavior (i.e., the general Friend > Disliked Peer, Friend > Unfamiliar Peer, Disliked Peer > Friend, and Disliked Peer > Unfamiliar Peer contrasts).

To examine how prosocial tendencies to different types of interaction partners relate to the underlying neural process, we examined brain and behavior links with (a) percentage of prosocial choices for friends minus disliked peers as a regressor in the Friend > Disliked Peer whole brain *t*-contrast, (b) percentage prosocial choices for friends minus unfamiliar peers as a regressor in the Friend > Unfamiliar Peer whole brain *t*-contrast, and (c) percentage prosocial choices for disliked peers minus unfamiliar peers as a regressor in the Disliked Peer > Unfamiliar Peer whole brain *t*-contrast.

Next we conducted analyses in which we broke down the Friend > Disliked Peer, Friend > Unfamiliar Peer, Disliked Peer > Friend, and Disliked Peer > Unfamiliar Peer contrasts by behavior to examine the neural activation underlying prosocial and selfish choices in interactions with friends and disliked others. We did this by contrasting prosocial choices for friends with those for disliked peers (Friend Prosocial > Disliked Peer Prosocial) and unfamiliar peers (Friend Prosocial > Unfamiliar Peer Prosocial), and by contrasting prosocial choices for disliked peers with those for friends (Disliked Peer Prosocial > Friend Prosocial) and unfamiliar peers (Disliked Peer Prosocial > Unfamiliar Peer Prosocial). Similarly, we examined the contrasts for selfish choices, that is Friend Selfish > Disliked Peer Selfish, Disliked Peer Selfish > Friend Selfish, Friend Selfish > Unfamiliar Peer Selfish, and Disliked Peer Selfish > Unfamiliar Peer Selfish. In all these contrasts, we controlled for the percentage of the behavior of interest. For example, we controlled for the percentage of prosocial choices in the Friend Prosocial > Disliked Peer Prosocial contrast by first subtracting the percentage of prosocial choices for disliked peers from the percentage of prosocial choices for friends for each participant, and then by including these values as a covariate in the whole brain contrasts. We did the same thing for social decision-making with disliked peers.

Importantly, these analyses are considered preliminary because (a) the sample size in the analyses contrasting prosocial and selfish decisions might differ from the complete sample size of 27 participants due to participants who did not make the specific decision of interest and could thus not be included in a specific contrast, and (b) we did not exclude participants from the analyses based on a minimum number of responses in a specific contrast. The latter decision was made because (a) we wanted to make use of our full data set in our relatively small sample, and (b) participants with few trials in a specific contrast are also those who are consistent in their behavior toward different types of peers (e.g., by being consistently selfish toward disliked peers or prosocial toward friends) and thus of interest for our research questions. Figure 2 shows for each participant the percentage of prosocial choices made for friends, disliked peers, neutral peers, and unfamiliar peers. See also Table

S1 in the Supplementary materials for an overview of how many participants had more than zero, one, two, three, four, of five trials in the contrasts discussed in the Results section. To further check the robustness of these results we also report our results where we reran these analyses with a subset of the sample.

We considered the results significant using family-wise error (FWE) cluster-correction at $p < .005$ with a cluster-forming threshold of $p < .005$ (Woo, Krishnan, & Wager, 2014). We chose a threshold of $p < .005$ to avoid Type II errors (Lieberman & Cunningham, 2009). This correction method has greater sensitivity to weak and diffuse signals and is suitable for relatively small sample sizes ($N < 50$; Cremers, Wager, & Yarkoni, 2017; Woo et al., 2014).

RESULTS

Manipulation Check

Correct recall of the names of the interaction partners ("players") was high (M_{range}= 87% - 91%; SD_{range}= 20% - 30%). There were no significant differences in percentage correct recall of the names in the four groups, $F(2.23, 55.70) = .16$, $p = .87$, Greenhouse-Geisser corrected. Open-ended questions about how participants described the four groups were coded into a five-point scale ranging from 1 (*very negative*) to 5 (*very positive*). There were significant differences between attitudes to the familiar peers (i.e., friends, disliked peers, and neutral peers), $F(2, 46) = 125.66$, $p < .001$, $\eta_p^2 = .845$. Participants evaluated friends ($M = 4.58$, $SE = .10$) more positive than neutral peers ($M = 3.46$, $SE = .10$), which were also evaluated more positive than disliked peers ($M = 2.13$, $SE = .14$), all *ps* < .001. For the unfamiliar peers, 18 participants (66.7%) stated "these persons were unfamiliar"; eight (29.6%) participants described them as neutral ($M = 3.38$, $SD = .74$) and 1 participant (3.7%) was missing a description. This manipulation check confirmed that participants differentiated between the four groups regarding their relationship with the players in each group.

Behavioral Results

An examination of participants' individual response patterns in the fMRI task showed that they had strong preferences for prosocial or selfish choices depending on their interaction partner (see Figure 2 for a detailed overview of

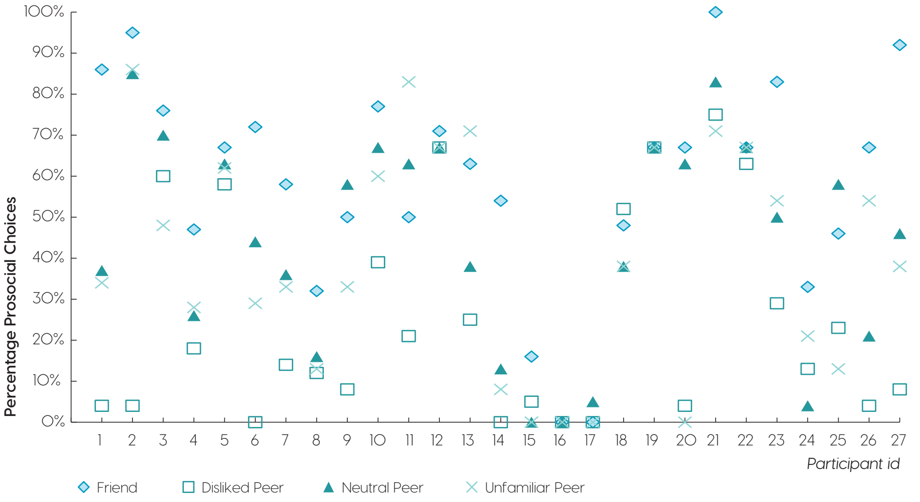


Figure 2. Percentage of prosocial choices separately for friends, disliked peers, neutral peers, and unfamiliar peers for each of the 27 participants.

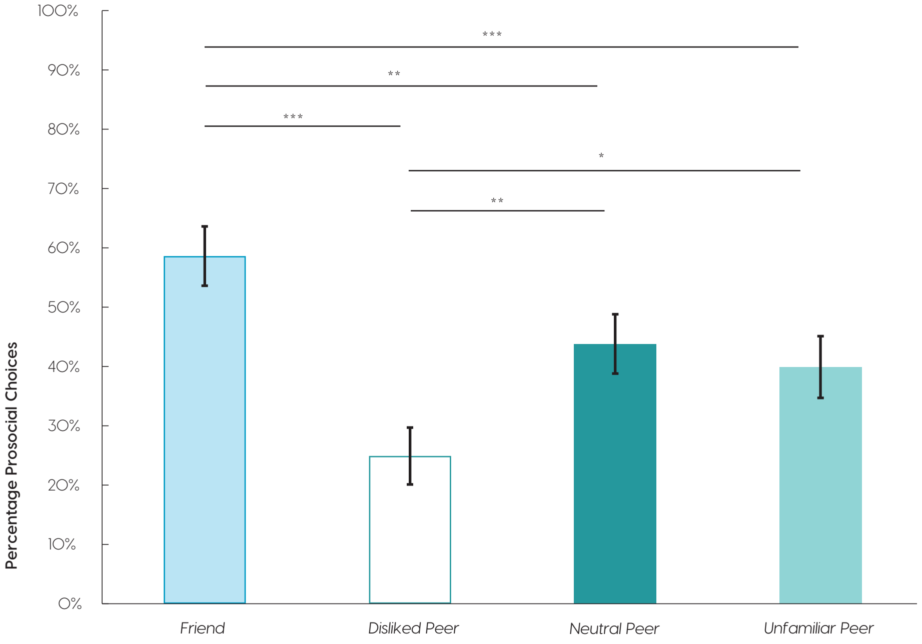


Figure 3. Mean frequency (%) and standard errors of prosocial choices per interaction partner. *Significant differences are indicated by an asterisk (*). *p < .05, ** p < .01, *** p < .001.*

frequencies at trial level). To examine whether participants' prosocial behavior was modulated by the interaction partner a repeated measures ANOVA was conducted with within-subject factor player (4 levels: friend, disliked peer, neutral peer, and unfamiliar peer) and the percentage of prosocial choices as the dependent variable. There was a significant main effect of player, $F(3, 78) = 20.487$, $p < .001$, $\eta_p^2 = .441$. Post hoc tests for this main effect showed that participants made significantly more prosocial choices when they were playing for friends (M = 59%) than for disliked peers (M = 25%, $p < .001$), neutral peers (M = 44%, $p < .01$) and unfamiliar peers (M = 40%, $p < .001$), and when playing for neutral peers and unfamiliar peers than for disliked peers, $p < .01$ and $p < .05$ respectively. Prosocial behavior toward unfamiliar and neutral peers did not differ significantly from one another, $p = 1$. These results demonstrate that participants were more prosocial toward friends and less prosocial toward disliked peers than toward other peers (Figure 3). There were no significant differences in response time for decisions for the players, $F(3, 78) = 2.548$, $p = .06$.

Neuroimaging Results

Links between individual differences in prosocial behavior and neural processes

In order to investigate brain and behavior links during interactions with friends and disliked peers separately, we included the difference scores of the percentage of prosocial choices for friends and disliked peers as a regressor in the Friend > Disliked Peer *t*-contrast (see Table 1). This revealed a negative correlation between the number of prosocial decisions for friends minus disliked peers and activity in the supplementary motor area (SMA) and right anterior insula (see Figure 4A). To inspect whether this negative relation was driven by individual differences in prosocial choices for friends or disliked peers, we plotted the mean parameter estimates against the percentage of prosocial choices for friends and disliked peers separately (Figure 4B). These plots show that the negative relation between percentage of prosocial choices for friends minus disliked peers and SMA and anterior insula activity is driven by prosocial interactions with friends: Correlation coefficients of the relation between the parameter estimates of the SMA and anterior insula of the Friend > Disliked Peer contrast and (a) the percentage of prosocial choices for friends are -.60 and -.62, respectively, and (b) the percentage of prosocial choices for disliked peers .27 and .15, respectively. These analyses did not yield any positive correlations.

Analyses using the difference scores of percentage of prosocial choices for friends minus unfamiliar peers as a regressor in the Friend > Unfamiliar Peer and the difference scores of percentage of prosocial choices for disliked peers and unfamiliar peers as a regressor in the Disliked Peer > Unfamiliar Peer *t*-contrasts did not result in any significant positive or negative relations with brain activity at our chosen threshold.

Table 1. Regions of neural activation

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Friend > Disliked peer						
Mean prosocial choices for friends-disliked peers as negative regressor						
Supplementary motor area (SMA)	-	511	4.10	-6	15	60
			3.87	15	9	60
			3.86	21	0	66
Anterior insula	R	171	4.05	36	12	-6
			3.40	51	15	-18
			2.86	30	21	12
Middle frontal gyrus	R	208	3.83	48	12	45
			3.58	36	12	45
			3.36	39	-18	39
Calcarine gyrus	R	126	3.67	15	-72	18
			3.45	24	-69	12
			3.34	18	-81	12
Precentral gyrus	L	149	3.48	-45	6	48
			3.38	-66	-27	30
			3.26	-42	-12	42
Lingual gyrus	L	142	3.42	-18	-63	-12
			3.22	-18	-69	12
			3.03	-24	-54	-9

Note. Analyses are conducted using FWE cluster-correction at p < .05 with a cluster-forming threshold of p < .005.

L = left, R = right.

Prosocial and selfish choices

Next, we examined neural activation patterns for specific behaviors (i.e., prosocial or selfish) separately for friends and disliked peers. Note that sample sizes for these results diverge from our total sample size of 27 due to participants who never make specific choices (e.g., prosocial choice for disliked peer).

Friends

We investigated neural activation during interactions with friends separately for prosocial and selfish choices. The Friend Prosocial > Disliked Peer Prosocial contrast (*n* = 23), controlling for the percentage of prosocial choices, resulted in activation in left putamen, and left inferior parietal lobule (IPL) and right IPL extending toward the angular gyrus (Figure 5A). These parietal brain regions have been previously labeled as subdivisions of the TPJ, and will be henceforth referred to as posterior TPJ (pTPJ)-IPL (Mars et al., 2012). The Friend Prosocial > Unfamiliar Peer Prosocial contrast (controlling for the percentage of prosocial choices, *n* = 23) yielded activation in a cluster containing the left IPL extending toward the superior parietal lobule (SPL), precuneus, and angular gyrus, and right IPL extending toward the angular gyrus. These regions are henceforth also referred to as pTPJ-IPL. The Friend Selfish > Disliked Peer Selfish and Friend Selfish > Unfamiliar Peer Selfish contrasts did not result in significant clusters of activation at our chosen threshold. See Table 2 for a detailed overview of the results.

Disliked peers

We conducted one sample *t*-tests to investigate neural activation for disliked peers during prosocial and selfish choices separately. The Disliked Peer Selfish > Friend Selfish contrast, controlling for percentage of Selfish choices (*n* = 26), yielded activation in the left middle temporal gyrus/STS, and right putamen (Figure 5B). The Disliked Peer Prosocial > Friend Prosocial, Disliked Peer Prosocial > Unfamiliar Peer Prosocial, and Disliked Peer Selfish > Unfamiliar Peer Selfish contrasts did not result in heightened brain activation. See Table 2 for a detailed overview of the results.

Robustness of results

To examine the robustness of these results, we reran these analyses where we excluded participants who only had 1 trial for a specific contrast. In the Friend Prosocial > Unfamiliar Peer Prosocial contrast we replicated enhanced activity in bilateral pTPJ-IPL.

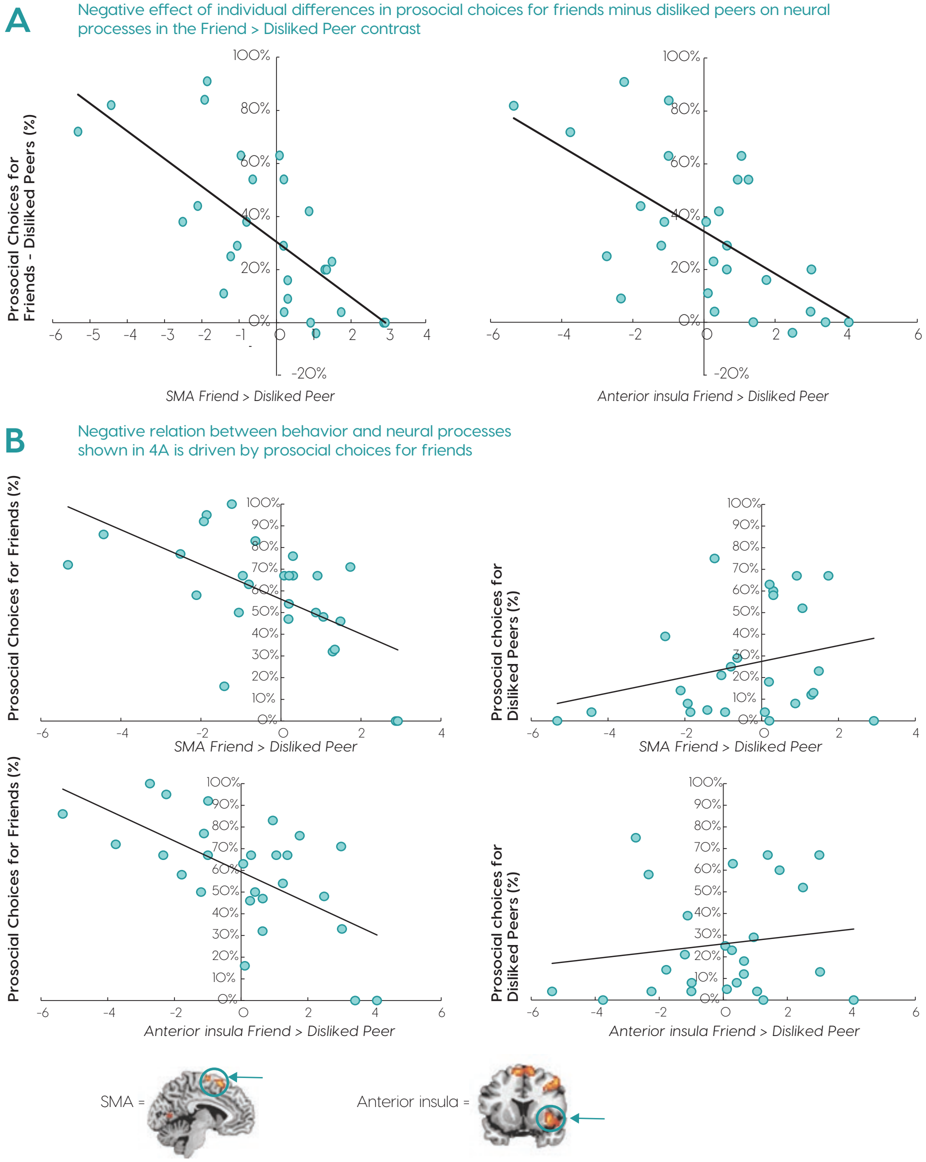


Figure 4. Links between individual differences in prosocial behavior and neural processes. *(A) Percentage of prosocial choices for friends minus disliked peers as a negative regressor in the whole brain contrast Friend > Disliked Peer resulted in right anterior insula (36, 12, -6) and SMA activation (-6, 15, 60). (B) Parameter estimates of the beta values of SMA and anterior insula from this contrast are plotted for percentage of prosocial choices for friends (left panel) and disliked peers (right panel) separately, showing that the negative relation between prosocial choices for friends minus disliked peers with SMA and anterior insula is driven by prosocial choices for friends.*

Table 2. Regions of neural activation

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Prosocial choices						
Friend > Disliked Peer						
Putamen	L	160	3.92	-30	-18	0
			3.77	-24	-9	-6
			3.50	-39	-15	-6
pTPJ-IPL	L	297	3.88	-48	-48	48
			3.49	-27	-57	42
			3.26	-36	-60	45
pTPJ-IPL	R	149	3.23	45	-57	45
			3.19	36	-72	51
			3.16	42	-51	39
Inferior frontal gyrus-Rolandic operculum	R	121	3.73	51	6	18
			3.55	48	-6	15
			3.31	36	0	18
Friend > Unfamiliar Peer						
pTPJ-IPL	L/R	594	3.86	9	-75	45
			3.55	-33	-69	42
			3.45	-42	-54	42
pTPJ-IPL	R	277	3.84	36	-69	45
			3.67	51	-42	54
			3.59	45	-54	57

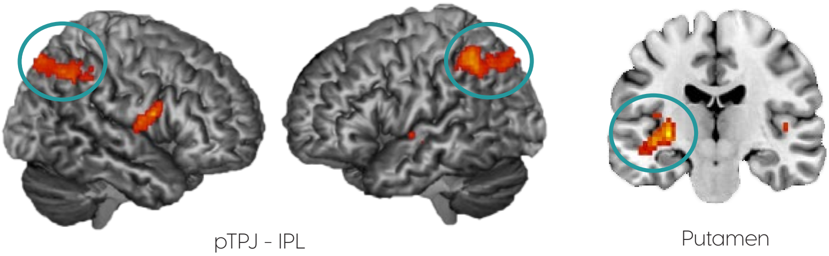
Table 2. Continued

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Selfish choices						
Disliked Peer > Friend						
Middle temporal gyrus-Superior Temporal Sulcus	L	487	4.63	-66	-36	0
			4.46	-66	-30	-6
			4.01	-57	-18	-15
Putamen		142	3.78	24	3	-6
			3.46	30	-3	-24
			3.40	27	-6	-12
Postcentral gyrus-Precentral gyrus		2081	4.58	45	-21	48
			4.38	-12	-27	60
			4.30	-48	9	51
Middle temporal gyrus	R	164	4.15	60	-63	0
			3.71	48	-60	6
			3.26	54	-57	12
Occipital gyrus	L	244	3.87	-15	-90	33
			3.26	-9	-78	15
			3.19	-30	-87	24
Lingual gyrus		423	3.79	24	-51	0
			3.70	12	-36	-3
			3.69	21	-60	15

Note. Analyses are conducted using FWE cluster-correction at p < .05 with a cluster-forming threshold of p < .005.

L = left, R = right.

A **Friend Prosocial > Disliked Peer Prosocial**



B **Disliked Peer Selfish > Friend Selfish**

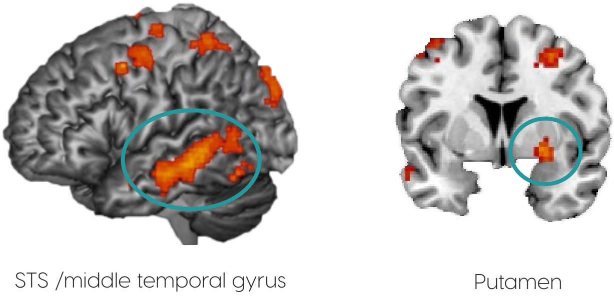


Figure 5. Whole brain *t*-contrasts

(A) Whole brain t-contrasts controlling for the percentage of prosocial choices for Friend Prosocial > Disliked peer Prosocial, which resulted in bilateral pTPJ-IPL (45, -57, 45; -48, -48, 48) and left putamen activation (-30, -18, 0), and (B) whole brain t-contrasts for Disliked Peer Selfish > Friend Selfish controlling for the percentage of selfish choices, resulted in activation in left STS/middle temporal gyrus (-66, -36, 0) and right putamen (24, 3, -6).

Enhanced activity in bilateral pTPJ-IPL in the Friend Prosocial > Disliked Peer Prosocial contrast was only replicated at an uncorrected threshold of $p < .005$. We did not replicate the enhanced putamen activity in the Friend Prosocial > Disliked Peer Prosocial contrast. In the Disliked Peer Selfish > Friend Selfish contrast we replicated the enhanced STS activity, but the enhanced putamen activity in the Disliked Peer Selfish > Friend Selfish contrast was only replicated at an uncorrected threshold of $p < .005$. Importantly, there were no outliers in the activation patterns in the original Friend Prosocial > Disliked Prosocial and Disliked Peer Selfish > Friend Selfish contrasts suggesting that differences stem from a decrease in statistical power (see Supplementary materials for more details).

DISCUSSION

This study examined the role of real-life relationships with peers during prosocial decisions and their neural correlates in young adults. Participants made more prosocial decisions in interactions with their friends and more selfish decisions (i.e., fewer prosocial decisions) in interactions with disliked peers. Our fMRI findings show that making fewer prosocial decisions for friends was associated with greater SMA and right anterior insula activity during interactions with friends versus disliked peers. We further show with preliminary analyses that putamen activity was elevated when participants made prosocial decisions involving friends and selfish decisions involving disliked peers. Prosocial decisions involving friends were also associated with heightened bilateral pTPJ-IPL activation, and selfish decisions involving disliked peers were associated with heightened STS activation.

When investigating individual differences in neural processes underlying prosocial behavior, we found a negative relation between the percentage of prosocial decisions for friends versus disliked peers and activation in SMA and anterior insula during interactions with friends relative to those with disliked peers. In other words, participants who were less prosocial toward their friends had higher activation in SMA and anterior insula during these interactions. In a prior study in which participants distributed coins between themselves and unfamiliar peers in a similar research paradigm, enhanced activity in the dACC and anterior insula was associated with inequity decisions, which could be either selfish or prosocial in nature (Güroğlu, Will, et al., 2014). The current study extends these results by showing that not acting in a prosocial manner toward friends yields similar neural responses as when distributing coins in an unequal manner with unfamiliar peers.

In previous studies examining the neural correlates of social decision-making the anterior insula and dACC or SMA are often interpreted to be involved in detecting the violation of social norms and in resolving the motivational conflict (e.g., for a meta-analysis, see Feng, Luo, & Krueger, 2015). Likewise, activity in the dACC and anterior insula are also interpreted to be involved in personal norm violations, like when prosocial-oriented individuals act selfishly or self-oriented individuals act prosocially (Van den Bos et al., 2009b), or when individuals make decisions that are not consistent with the socially accepted responses in particular social contexts (Güroğlu et al., 2010). Hence, a possible mechanism that could be underlying the neural response in our participants is that they evaluate their behavior based on their norms when interacting with friends, that is, making a distribution that benefits the friend (i.e., prosocial decisions). It is important to note that the dACC or SMA and insula are implicated in a broad range of cognitive tasks including conflict monitoring, error detection, and processing pain (Bonini et al., 2014; Eisenberger & Lieberman, 2004; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011); however, such other plausible functions of these regions have been interpreted to be in line with their involvement in social norm violations (Feng et al., 2015; Montague & Lohrenz, 2007). One could pose that there is a general social norm to act in prosocial ways toward friends and that, speculatively, not acting according to this social norm could induce internal conflict.

Interestingly, individual differences in prosocial behavior toward friends relative to unfamiliar peers did not yield increased neural activity in interactions with friends compared with unfamiliar peers. Speculatively, the fact that we did not find similar brain and behavior links that may suggest a role of social norm violations in interactions with friends versus unfamiliar peers as in interactions with friends versus disliked peers may be due to differences in socio-emotional valences of the relationships with disliked and unfamiliar peers. Tentatively, results obtained from contrasts in which interactions with friends are compared to those with disliked peers may have a higher socio-emotional valence because one's behavior in these interactions may affect the relationship, whereas behavior in interactions with unfamiliar peers may not change the relationship because there is no prospect of future social interactions. Furthermore, one might also hold social norms such that one should be nice (i.e., prosocial in this context) to unfamiliar others, which is similar to expectancies for friends. In this respect, it is possible that disliked peers are more distinct from friends than unfamiliar peers are compared to friends. These hypotheses should be tested in future studies.

In the whole brain contrasts comparing prosocial decisions for friends with prosocial decisions for disliked peers, we found that prosocial interactions with friends involved higher activation of a posterior TPJ region extending toward the IPL (pTPJ-IPL), a subdivision of the TPJ previously found to be connected to the lateral prefrontal cortex (Mars et al., 2012). The pTPJ-IPL region has been shown to be involved in mentalizing processes, such as understanding intentionality and others' perspectives (Güroğlu, Van den Bos, Van Dijk, Rombouts, & Crone, 2011; Saxe, 2006; Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2011; Young, Dodell-Feder, & Saxe, 2010), but also with other cognitive tasks, such as attentional processing (Vossel, Geng, & Fink, 2014), adjusting to a new or changed context (Geng & Vossel, 2013), and memory processes (Anticevic, Repovs, Shulman, & Barch, 2010; Corbetta, Kincade, & Shulman, 2002; for a comprehensive review, see Cabeza, Ciaramelli, & Moscovitch, 2012). Interestingly, it has been argued that the TPJ is involved in integrating distinct streams of attentional and memory processes, which together contribute to processing social contexts (Carter & Huettel, 2013). Involvement of the pTPJ-IPL during prosocial decisions involving friends is consistent with prior studies showing its important role in social interactions (Carter, Bowling, Reeck, & Huettel, 2012; Halko, Hlushchuk, Hari, & Schürmann, 2009) and in prosocial decision-making (Van Hoorn et al., 2016). A recent study also shows its involvement in the regulation of social behavior, such that the pTPJ is suggested to facilitate prosocial behavior toward close others but not for distant others (Strombach et al., 2015). Given that pTPJ-IPL activation was enhanced for prosocial decisions for friends when compared to both disliked and unfamiliar peers, our results indicate that the pTPJ is recruited to a greater extent during prosocial interactions with liked and close others compared to distant others such as disliked or unfamiliar peers. Considering the resting-state connectivity of this region with the prefrontal cortex as previously reported by Mars et al. (2012), future research should investigate the connectivity patterns to better understand how this region might support social decision-making.

In the whole brain contrasts comparing selfish decisions for disliked peers with selfish decisions for friends, we found involvement of the STS during selfish interactions with disliked peers. The STS is involved in social information processing, such as in processing eye contact (Pelphrey, Viola, & McCarthy, 2004), attributing intentions to inanimate objects (S. M. Lee, Gao, & McCarthy, 2014), and understanding and sharing emotions (Paulus, Müller-Pinzler, Jansen, Gazzola, & Krach, 2014; Peelen, Atkinson, & Vuilleumier, 2010; Zaki, Weber, & Ochsner, 2012). Furthermore, the STS is involved in tracking whether expectations about a social response are matched (Hampton et al., 2008). These findings suggest that the STS is involved in mentalizing processes, which might be important for recognizing the type of social setting or dynamic in social settings. Our results are in line with prior studies showing that during social decisions STS activity is modulated by the social relationship with the interaction partner (Bault et al., 2015) and that STS activation is enhanced when gaining money at the expense of others (Fahrenfort et al., 2012). The role of the STS in social interactions with negative valence should be further investigated in future studies to test these interpretations.

The putamen was activated both during prosocial decisions for friends and selfish decisions for disliked peers. Prior studies have also implicated putamen activation in being positively evaluated by peers (Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010). Similarly, enhanced putamen activation during prosocial decisions has been suggested to be related to predicting and anticipating outcomes of social interactions with peers (Delgado, Frank, & Phelps, 2005). Interestingly, the current study showed that putamen activation was also greater during selfish decisions in interactions with disliked peers than in interactions with friends. In these interactions, the participant chose to decrease the outcomes for the disliked peers. Consistent with this finding, Takahashi et al. (2009) found that activation in the putamen was heightened when envied peers experienced misfortune. Corroborating prior findings, the putamen might be involved in the anticipation of expected pattern of behaviors in social interactions. It would be interesting to further investigate how this might fit with putamen's role within the striatum in social learning for example in relation to prediction errors.

Strengths, Limitations and Conclusions

The current study provides a valuable starting point for future research where ecological validity should be further increased by, for example, having liked and disliked peers present. An advantage of the current research paradigm is that we used sociometric nominations in a closed peer group of college students to identify different types of peer relationships. The current study design enabled us to examine the underlying processes of social decision-making in the real world in an ecologically valid manner. This provides potential insights in how existing relationships are maintained (Güroğlu et al., 2009b).

During the task, participants were explicitly instructed to remember that their decisions in the task would not only have monetary consequences for themselves but also for their interaction partners on each trial. Considering that the implementation of the payments for their interaction partners was not explicitly specified, it is plausible that (some) participants might have seen their decisions to be hypothetical. Nevertheless, the behavioral results we present here suggest that participants have taken the task seriously and differentiate between different groups of players as we have expected.

Our behavioral findings showed that the percentage of prosocial decisions differed significantly across the interaction partners, which made it difficult to dissociate effects of behavior and interaction partners. This is in line with prior findings that show that friendships typically involve more prosocial behavior than interactions with disliked others (Newcomb & Bagwell, 1995). Here we aimed to control for these behavioral differences by including the percentage of prosocial behavior as a covariate in our analyses. However, one might raise the question whether it is favorable to dissociate the percentage of prosocial behavior and the relationship with interaction partners, because the combination of factors might give better insights in the underlying processes involved than the two factors separately.

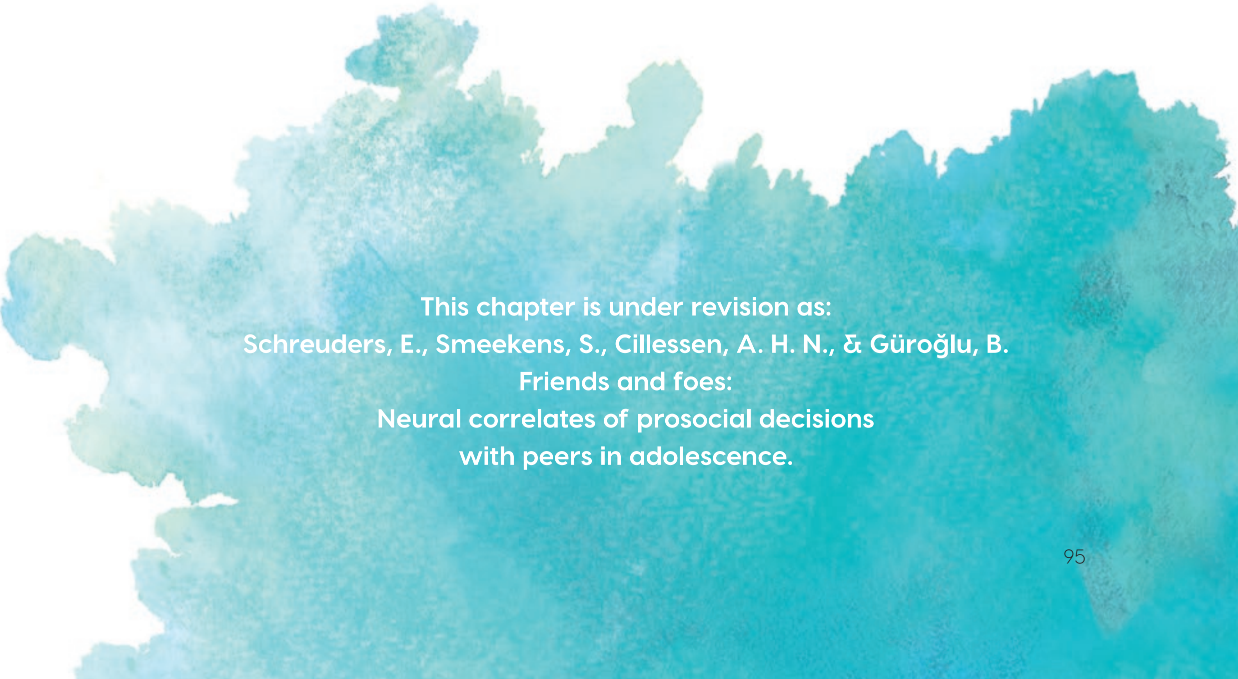
It should also be noted that our sample size was relatively small (*N* = 27) for analyses of interindividual differences. Therefore our results linking individual differences in the percentage of prosocial decisions should be interpreted with caution and replicated in future studies. Relatedly, in our analyses we did not exclude participants based on a minimum number of responses in a specific condition. By doing so we were able to use all the data of our relatively small sample, and we were not forced to create groups of participants with a specific type of social motivation (i.e., generally prosocial or selfish). In our study, participants were generally consistent in their behavior within a certain condition, which indicates that they did not make random choices in the fMRI task. Although this type of behavior is desired, because it reflects stable individual preferences (Güroğlu, Will, et al., 2014), it resulted in imbalanced whole brain contrasts for some of our analyses. We did not replicate all our fMRI findings obtained from imbalanced whole brain contrasts when we excluded participants with only one trial for these contrasts. This could be due to a power issue since our findings were not driven by outliers (see Figure S1 in the Supplementary materials). Nonetheless, the results from the analyses comparing prosocial and selfish decisions for friends and disliked peers should be interpreted with caution and replicated in future studies.

The current study was the first to use an ecologically valid experimental design to investigate neural correlates of prosocial and selfish decisions in interactions with different types of familiar peers, that is, friends and disliked peers. We demonstrate that the personal valence of the relationship with the interaction partner modulates behavior and neural activity in several brain regions typically involved in social cognition. These findings set the stage for future studies to further investigate how real-life relationships influence social cognition and to unravel the role of underlying neural processing in shaping the development of relationships of differing valence over time.

5

CHAPTER FIVE

Friends and foes: Neural correlates of prosocial decisions with peers in adolescence



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Neural correlates of prosocial decisions
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ABSTRACT

Adolescence is a critical period for social orientation to peers and for developing social skills in interactions with peers. In the current study we examined the neural correlates of prosocial decisions for friends and disliked peers, and their links with participants' friendship quality and empathy as indices of social competence. Participants' friends and disliked peers were identified using sociometric nominations. Mid-adolescents (M_{age} = 14.6; N = 50) distributed coins between themselves and another player in a set of allocation games where they could make prosocial or selfish decisions for their friends and disliked peers, as well as for neutral and unfamiliar peers. Participants made the most prosocial decisions for friends and the least prosocial decisions for disliked peers. Prosocial decisions for friends yielded activity in the putamen and posterior middle temporal gyrus (pMTG) when compared to prosocial decisions for disliked peers, and in the superior parietal lobule (SPL) and precentral gyrus when compared to prosocial decisions for unfamiliar peers. Selfish decisions for friends and decisions for disliked peers did not result in heightened neural activity. Explorative analyses to the relations between these neural activation patterns and measures of social competence revealed that putamen activity related negatively to negative friendship quality and that empathic personal distress related positively to SPL and precentral gyrus activity. Together, these findings illustrate that the SPL, precentral gyrus, pMTG and putamen may be involved in promoting the continuation of friendships, and that social competence may modulate these neural mechanisms.

INTRODUCTION

Adolescence is the transitional period from childhood to adulthood and is marked by significant social changes (Kilford, Garrett, & Blakemore, 2016; Roseth, Johnson, & Johnson, 2008). Compared to children, adolescents spend an increasing amount of their time with peers (Steinberg, 2005) and interactions with peers become increasingly salient for adolescents (Albert, Chein, & Steinberg, 2013; Berndt, 1992; Van Hoorn, Dijk, Meuwese, Rieffe, & Crone, 2014). Studies have shown that positive peer relationships, that is, relationships based on social preference or likeability, such as friendships, are associated with healthy adolescent development (e.g., Aikins, Bierman, & Parker, 2005; Bukowski, Hoza, & Boivin, 1993; Parker et al., 2015), while involvement in negative peer relationships, that is, relationships based on dislike, is moderately associated with maladaptive functioning (Abecassis, 2003; Card, 2010; Hartup, 2003; Murray-Close & Crick, 2006). Whereas the neural processes underlying interactions with unfamiliar peers have been investigated in numerous studies (for reviews, see Lee & Harris, 2013; Rilling & Sanfey, 2011), few studies have focused on the neural processes underlying interactions with familiar peers, such as friends and disliked peers. In the current study we examined the neural correlates of prosocial and selfish decisions made toward *familiar* peers, in particular, toward friends and disliked peers in mid-adolescence. We further explored the links between these neural patterns and social competence as indicated by best friendship quality and empathy.

Prosocial behavior, that is, voluntary actions intended to benefit others (Eisenberg, Fabes, & Spinrad, 2006), is important for forming and maintaining peer relationships (Fehr, Fischbacher, & Gächter, 2002; Markiewicz, Doyle, & Brendgen, 2001; Newcomb & Bagwell, 1995). Prosocial behavior has been shown to involve both self-regulation and mentalizing skills, which allow individuals to inhibit selfish impulses and orient toward others and attempt to understand their perspectives, intentions, and needs (Steinbeis & Crone, 2016; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011; Van den Bos, Westenberg, Van Dijk, & Crone, 2010). A study examining prosocial decision-making across the ages of eight and 18 has shown that adolescents become increasingly better in differentiating between their interaction partners with age (Güroğlu, Van den Bos, & Crone, 2014); from mid-adolescence onwards, participants made most prosocial decisions for friends and least prosocial decisions for disliked peers, showing that prosocial decisions become more context-dependent with age.

The developmental change in social skills across adolescence is reflected in the involvement of cognitive control and mentalizing brain areas in prosocial decisions, including the lateral prefontral cortex (lPFC), and the temporoparietal junction (TPJ), the superior temporal sulcus (STS), and the medial prefrontal cortex (mPFC; Masten, Morelli, & Eisenberger, 2011; Steinbeis & Crone, 2016; Telzer et al., 2011; Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). Developmental fMRI studies showed an age-related increase in activation patterns of these regulatory and mentalizing brain regions across adolescence (Güroğlu, Van den Bos, & Crone, 2009a; Steinbeis, Bernhardt, & Singer, 2012; Van den Bos et al., 2010). The TPJ and STS are both brain regions involved in mentalizing-related processes (Blakemore, 2008; Frith & Frith, 2012) and are suggested to be involved in social tie formation during repeated interactions with unfamiliar peers (Bault, Pelloux, Fahrenfort, Ridderinkhof, & van Winden, 2015). The mPFC, a brain region important for integrating information in order to determine future behavior (Amodio & Frith, 2006; Euston, Gruber, & McNaughton, 2012), is possibly crucial for selecting actions in relation to one's own goals and the goals of others in interactions (Bault, Joffily, Rustichini, & Coricelli, 2011; Bault et al., 2015). Importantly, activation of these brain regions involved in social decision-making has been shown to be modulated by interaction partners. For example, the mPFC and ventral striatum are activated to a greater extent during interactions with friends relative to other peers (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Fareri & Delgado, 2014; Güroğlu et al., 2008). Interestingly, losing money for *unfamiliar* disliked peers relative to winning money is found to be associated with increased ventral striatum activation (Braams et al., 2014b).

The aim of the current study was to make the first steps in understanding the neural activation patterns underlying social behaviors toward peers in a period that is highly significant for social development, that is, adolescence. To do so, we examined how real-life social contexts affect decision-making and associated neural processes, and how these are related to indices of social competence. We used a set of economic allocation games to examine the neural correlates of prosocial decisions involving real-life friends, disliked and neutral peers, and unfamiliar peers. In these paradigms, participants chose between dichotomous sets of coin distributions where one involved a prosocial distribution (i.e., benefiting the interaction partner) and the other involved a selfish distribution (i.e., resulting in a better outcome for the participant either in the form of having more coins than the other player or not allowing the other player have more coins than oneself; Schreuders, Klapwijk, Will, & Güroğlu, 2018). In line with previous behavioral findings from an adolescent sample, we hypothesized that adolescents would be more prosocial toward friends than neutral or unfamiliar peers and least prosocial toward disliked peers (Güroğlu, et al., 2014). In a recent fMRI study we examined the neural basis of prosocial decision-making in young adults using the same experimental paradigm as in the current study. Our findings in adults showed that posterior regions of the TPJ and the putamen were implicated in prosocial decision-making in interactions with friends and that the STS and putamen were implicated in selfish decision-making in interactions with familiar disliked peers (Schreuders et al., 2018b). Based on these prior findings, we expected similar increased activation patterns including the posterior TPJ (pTPJ)-inferior parietal lobe (IPL) and putamen activity during prosocial choices for friends, and STS and putamen activity during selfish choices for disliked peers.

In the current study, we also explored relations between individual differences in best friendship quality and empathy skills, as proxies of social competence, and neural activation patterns during prosocial and selfish decisions for friends and disliked peers. Social competence is posed to promote positive social interactions and relationships. For example, in prior studies it is demonstrated that best friendship quality is associated positively with prosocial tendencies (Markiewicz et al., 2001), and that higher empathy levels are associated with a better ability to resolve peer relational conflicts (De Wied, Branje, & Meeus, 2007). Furthermore, neuroimaging studies showed that empathy levels modulated neural responses to observing a peer being excluded and the tendency to send comforting messages to the excluded peer (Masten, Eisenberger, Pfeifer, Colich, & Dapretto, 2013; Masten, Eisenberger, Pfeifer, & Dapretto, 2010). In the current study, we explored whether empathy levels and best friendship quality shape underlying neural processes during decision-making in peer interactions. Based on prior findings on the role of friendship quality and empathic abilities in social behavior and functioning, we expected to find that better friendship quality and higher empathic skills would enhance neural activation patterns that underlie prosocial decision-making with friends.

METHOD

Participants

The current study was part of the 8th data collection wave of the Nijmegen Longitudinal Study on Infant and Child Development (NLS; for more detailed information on the prior waves of the longitudinal study, see Niermann et al., 2015; Smeekens, Riksen-Walraven, & van Bakel, 2007; Tyborowska, Volman, Smeekens, Toni, & Roelofs, 2016). All participants who declared to be willing to continue participation during the 7th wave (*n* = 108) were approached for participation in the current fMRI study. Healthy and right-handed participants who reported no contra-indications for fMRI and without a history of psychiatric and neurological impairments were considered eligible for participation (*n* = 58). Seven adolescents who were eligible for participation did not participate due to technical or logistic problems, and one participant was excluded from the analyses due to excessive movement during scanning (> 2.8 mm). This resulted in a sample of 50 mid-adolescents (M_{age} = 14.56, *SD* = .13, 29 males).

Procedure

Before scanning, participants and parents gave written informed consent for participation. The participants were familiarized with the scanner environment using a mock scanner and practiced the fMRI task. Participants and parents also filled out a battery of questionnaires. Participants received €30 in gift cards and a small additional endowment of €2 earned with the fMRI task, and their parents received a small gift for participation. The local medical research ethics committee approved the study.

Measures

Social competence

Friendship quality

Positive and negative best friendship quality was measured with an adapted parent-report version of the friendship quality scale (FQS; adapted from Bukowski, Hoza, & Boivin, 1994). This scale contained 5-point scale items measuring how true each items was for the relationships of the child with their best friend with 1 (*not true at all*) to 5 (*very true*). Parents also had the option to reply with "*I do not know*", considering that they may not be able to have insights to answer all questions regarding the relationship of their children with their best friend; this response was coded also as 'missing'. Positive friendship quality was measured with 13 questions assessing positive and supportive characteristics of the friendship (*M* = 4.23, *SD* = 0.56), with higher scores indicating higher positive friendship quality. Negative friendship quality was measured with seven questions assessing negative characteristics of the friendship (*M* = 1.69, *SD* = 0.56), with higher scores indicating higher negative friendship quality. Here, we report data from participants with at least 75% valid responses (i.e., not including the "*I do not know*" option and a missing response); that is, participants with at least 10 (*n* = 37) and 6 (*n* = 41) valid responses for the positive and negative FQS, respectively, were included. For 43 participants we had valid positive *and/or* negative FQS scores. For 21 participants (48.8%), the best friend for whom the FQS was filled out by the parent was also one of the three friends named in the fMRI task (see fMRI task description for details). The FQS scales were reliable: mean inter-item correlations within these scales were .362 and .438 for positive and negative FQS, respectively.

Empathy

Empathy was assessed with the self-report Interpersonal Reactivity Index (IRI; Davis, 1983). Participants indicated on 5-point scale whether a statement was 1 (*not true*) to 5 (*true*) for them. We used three six-item subscales to measure empathy. Concern for others was measured with the empathic concern (EC) subscale (*M* = 3.36, *SD* = 0.56), the tendency to take others' perspective was assessed with the perspective taking (PT) subscale (*M* = 3.40, *SD* = 0.57), and finally, to what extent participants get overwhelmed by others' emotions was assessed with the personal distress (PD) subscale (*M* = 2.29, *SD* = 0.59). We did not include the fantasy subscale in which empathic responses toward fictional characters is assessed, because we were interested in empathic responses in real-life social settings. The EC, PT, and PD subscales were reliable (Cronbach's alphas were .679, .657, and .741, respectively) and mean inter-item correlations ranged from .235 to .263.

FMRI task description

Peer groups

Prior to the scanning day, participants were asked to provide a list of the names of their current classmates and fill out a sociometric questionnaire. Within this questionnaire participants were asked to nominate 5 classmates as their friends and indicate which 5 classmates they liked the least. Participants were also asked to rate how much they liked each classmate on a 5-point scale ranging from 1 (*not at all*) to 5 (*very much*). These ratings and nominations were used to determine three types of peers: a) *friends*: classmates who were nominated by the participant as a friend and received a rating of 4 or 5, b) *disliked peers*: classmates who were nominated by the participant as a least liked and/or received a rating of 1 or 2, c) *neutral peers*: classmates who received a rating of 3. Participants played the fMRI task with these three groups of familiar peers plus a fourth group of *unfamiliar peers*, who were told to be other same age participants of the study. The groups of unfamiliar and neutral peers were included in the task as control conditions.

Each group (i.e., friends, disliked peers, neutral peers, and unfamiliar peers) consisted of two or three players. Participants were told that they would play each trial of the fMRI task with one person from these four groups of players (i.e., that they would distribute coins between themselves and a peer). Importantly, they were told that three groups of familiar peers consisted of randomly chosen classmates. To present the four peer groups in a neutral manner to the participants, the groups were randomly assigned to one of four vehicle symbols named train, bike, car, and boat (Figure 1A). At the end of the experiment, participants were asked to recall the names of all the group members and to indicate their attitude toward each group. This was done in order to check whether the manipulation of the group members representing a specific type of relationship was successful and whether participants paid attention to the task (see the Results section for the manipulation checks). In the instructions, it was emphasized that participants' decisions had consequences for themselves as well as for their interaction partners. However, it was not specified how this would be implemented. None of the participants had questions regarding this point during the instructions.

Coin distributions

In the scanner, participants played the role of the allocator in a set of three modified dictator games (Fehr, Bernhard, & Rockenbach, 2008; Güroğlu, Will, & Crone, 2014), in which they distributed coins between themselves and another player by choosing one of two preset distributions. Each set of distributions entailed an equity option in which coins were evenly distributed with one coin for the self and one coin for the other player (i.e., 1/1 distribution). The alternative inequity distribution varied across the three games: the alternative distribution for (a) the *advantageous competitive inequity* (ACI) game entailed one coin for the self and zero coins for the other player (i.e., 1/0 distribution); (b) the *self-maximizing inequity* (SMI) game entailed two coins for the self and zero coins for the other player (i.e., 2/0 distribution); and (c) the *disadvantageous prosocial inequity* (DPI) game entailed one coin for the self and two coins for the other player (i.e., 1/2 distribution). Prosocial choices in each of the three games, that is, 1/1 distribution in the ACI ("prosocial giving") and SMI ("prosocial sharing") games, and the 1/2 distribution in the DPI game ("disadvantageous prosocial giving"),

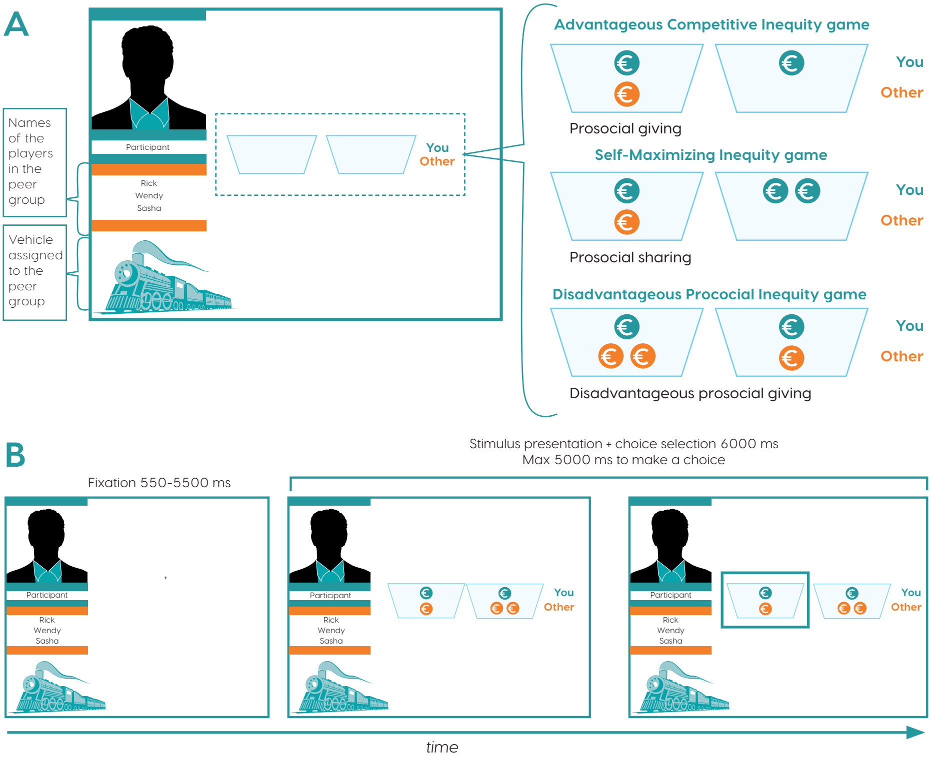


Figure 1. *(A) Names of players in each group were displayed in the left bottom panel of the screen. These three group members always belonged to the same peer category. The interaction partner was one of these players. The peer groups in the task were randomly assigned to a vehicle, which was displayed in the left bottom panel of the screen. There were three different preset coin distributions, always with a prosocial and a selfish option, depicted here on the left and right, respecively. (B) Example trial of the fMRI task. After a fixation cross participants were presented with a screen showing the stimulus and with whom they were playing that trial. At stimulus onset, they could choose between the two options presented on the screen. A trial ended with selected choice indicated on the screen.*

were coded as 1; selfish choices, that is, 2/0 distribution in the SMI game, the 1/0 distribution in the ACI game, and the 1/1 distribution in the DPI game, were coded as 0. The percentage of prosocial choices per interaction partner was calculated across games. We used three different types of games to keep the participants engaged in the task. Prosocial choices always benefited the interaction partner, whereas selfish choices maximized the outcome for the self (Figure 1A).

Task duration

The fMRI task included 96 trials presented in a randomized order. Participants engaged in 24 social decisions for members of each of the four groups (i.e., friends, disliked peers, neutral peers, and unfamiliar peers) across three allocation games (i.e., 8 trials per game). Each trial started with a jittered fixation cross (*M* = 1512.5 ms, min = 550 ms, max = 5500 ms: optimized with Opt-Seq2, surfer.nmr.mgh.harvard.edu/optseq/; Dale, 1999), and was followed by a screen presenting the two sets of coin distributions participants could choose from; this screen also displayed the group symbol along with the names of the group members for that trial. Participants had to respond to the trial within 5000 ms. The option selected by the participants was encircled in red for 1000 ms (Figure 1B). If they failed to respond within 5000 ms, a screen showing "Too late!" was presented for 1000 ms. It was explained that the computer selected a random number of trials to calculate their earnings which would be paid out at the end of the experiment. In reality, all participants were paid €2. See Schreuders et al. (2018b) for details on the same experimental paradigm and task design.

MRI Data Acquisition

MRI scanning was performed with a 3T Siemens Tim Trio scanner. The scanning procedure included (a) a localizer scan, (b) Blood oxygenation level dependent (BOLD) T2* weighted gradient echo planar images (EPI; TR = 2.00 s, TE = 30 ms, 80° flip angle, 38 axial, sequential acquisition, slice thickness = 2.8 mm, field of view (FOV) = 220 mm, and (c) high resolution anatomical T1-weighted MP-RAGE sequence image (TR= 2300 ms, TE= 3.03 ms, 8° flip angle, 192 sagittal slices, FOV= 256 mm, slice thickness = 1.00). Two functional scans were obtained that lasted approximately 6 minutes and 190 dynamics each.

FMRI Data Analysis

SPM8 software was used for the image preprocessing and analyses (http://www.fil.ion.ucl.ac.uk/spm/). The functional images were preprocessed using slice-time correction (middle slice as reference), realignment, spatial normalization, and smoothing with a Gaussian filter of 8 mm full-width at half maximum. Functional images were spatially normalized to T1 templates, functional images of one participant were spatially normalized to EPI templates. Regressors were modeled as zero-duration events at stimulus onset and convolved with a hemodynamic response function (HRF). Stimulus onset was the moment participants were presented with the two distributions to choose from. Trials on which the participant failed to respond were modeled separately as covariate of no interest and were excluded from further analyses. The modeled events were used as regressors in a general linear model (GLM), along with a basic set of cosine functions that high-pass filtered the data (cutoff 120 seconds) and a covariate for session effects. Autocorrelations were estimated using an autoregressive model order of 1. Additional analyses revealed that participants' response times on stimuli did not affect the results. The results are reported in Montreal Neurological Institute (MNI) 305 stereotactic space. Image pre-processing and analyses were conducted using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/).

In all neuroimaging analyses, we controlled for the frequency of prosocial choices to minimize its effect as a confounder variable, because the frequency of prosocial choices differed significantly between friends, disliked peers, and unfamiliar peers (see behavioral results). We controlled for the frequency of prosocial choices by calculating a difference score of prosocial choices for each participant (e.g., in the Friend Prosocial > Disliked Peer Prosocial contrast: [proportion prosocial choices for friends]$_i$-[proportion prosocial choices for disliked peers]$_{i,}$, where *i* represents a participant), and then we included these values as a covariate in the whole brain contrasts.

We examined the neural correlates for friends and disliked peers for prosocial and selfish choices by comparing decisions for friends with decisions for disliked peers (as a comparison between the two most "extreme" relationships) and by comparing decisions for friends and disliked peers with decisions for unfamiliar peers (who form a similar control condition for all participants). For brevity purposes, we report neuroimaging results involving the neutral peer in the Supplementary materials (Table S1; Figure S1). Please note that, participants who did not make any prosocial or selfish choices for one of the interaction partners in the contrasts could not be included in the *t*-tests. Therefore, the sample size in these tests occasionally differed from the complete sample size of 50 participants. The whole brain contrasts examining interactions with friends and disliked peers irrespective of choice were not the main focus of this chapter and are therefore also reported in the Supplementary materials (Table S1; Figure S2). In addition, we report analyses in the Supplementary materials where we reran these analyses with a subset of the sample consisting of participants with a minimum number of trials per condition to test the robustness of the results (Table S2 and Table S3).

Finally, in order to examine links between the neural correlates of prosocial and selfish choices and social competence, we extracted parameters of region of interests (ROIs) based on the whole brain *t*-contrasts using the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002). In all fMRI analyses, we used an family-wise-error (FWE) cluster-correction at $p < .05$, with a cluster-forming threshold of $p < .001$ (Woo, Krishnan, & Wager, 2014). We explored correlations between neural activation during prosocial choices for friends and disliked peers and indices of social competence. Since sample sizes of these correlation analyses differ from the total sample of 50 participants, we consider these analyses to be explorative and preliminary.

RESULTS

Manipulation Check

Correct recall of the names was high for friends, disliked peers, and neutral peers (*M* range 87%-99%, *SD* range 6%-32%), with recall – as expected – being lowest for unfamiliar peers (*M* = 43%, *SD* = 37%) and differing significantly from correct name recall for the other three groups, $F(1.99, 87.43) = 42.85$, $p < .001$, Greenhouse-Geisser corrected. Open-ended questions about participants' opinion of the four peer groups were coded into a 5-point scale ranging from 1 (*very negative*; e.g., "I do not like these people", or "these kids are arrogant") to 5 (*very positive*; e.g., "These people are my friends", or "I like these people the best"). Participants' opinion of the groups with familiar peers (i.e., friends, neutral peers, and disliked peers) differed significantly from one another, $F(2, 78) = 123.93$, $p < .001$. As expected, participants rated friends more positively (*M* = 4.68, *SE* = .08) than neutral peers (*M* = 3.35, *SE* = .12), who were also rated more positively than disliked peers ($M = 2.28$, $SE = .14$), all $ps < .001$. Regarding the unfamiliar peers, 4 participants (8%) rated this group as neutral (as was indicated by scores of 3 points), 2 participants (4%) as positive (as indicated by scores of 4 and 5 points), and 44 participants (88%) indicated that they could not evaluate this group of peers because they did not know them. Together, these results indicate that participants viewed the relationship with the different group members as intended.

Behavioral Results

Social competence

Correlation analyses showed that positive and negative friendship quality scores were not significantly correlated, $p =.09$. Scores on the EC subscale were correlated positively with scores on the PT and PD subscales, *Spearman's* $\rho = .32$, $p < .05$ and $\rho = .59$, $p < .001$, respectively. There was no correlation between PT and PD scores, $p = .09$. Positive FQS scores and PT were positively correlated, *Spearman's* $\rho = .36$, $p < .05$. There were no other significant correlations between the IRI and FQS subscales, $ps > .240$.

FMRI task

Figure 2 depicts for each participant the percentage of prosocial choices made for friends, disliked peers, neutral peers, and unfamiliar peers. As can be seen in Figure 2, participants' changed their individual preferences for prosocial and selfish choices depending on their interaction partner. To examine the participants' number of prosocial choices involving different players, a repeated measures ANOVA was conducted with "player" as the within-subject factor indicating the relationship with the interaction partner (4 levels: friend, disliked peer, neutral peer, and unfamiliar peer) and the percentage of prosocial choices as the dependent variable. Prosocial behavior was significantly modulated by player, $F(1, 49) = 22.89$, $p < .001$. Participants made more prosocial choices for friends ($M = 78$ %, $SE = 3\%$) than for disliked peers ($M = 42\%$, $SE = 4\%$), neutral peers ($M = 57\%$, $SE = 4\%$), and unfamiliar peers ($M = 55\%$, $SE = 4\%$), all $ps < .001$. Participants also made more prosocial choices for neutral and unfamiliar peers than for disliked peers, $p < .01$ and $p < .001$, respectively. These behavioral results show that participants made most prosocial decisions for friends and the least prosocial decisions for disliked peers (see Figure 3).

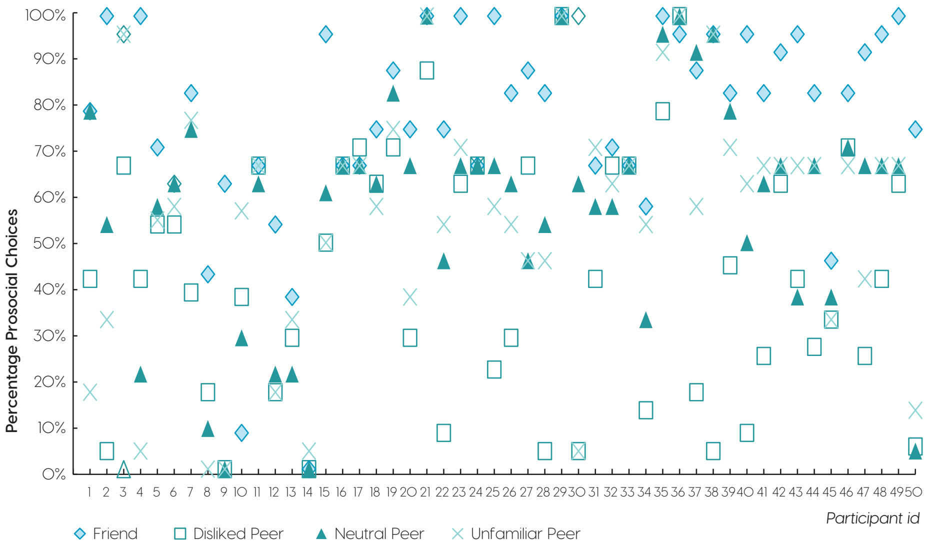


Figure 2. Percentage prosocial choices separately for friends, disliked peers, neutral peers, and unfamiliar peers for each of the 50 participants.

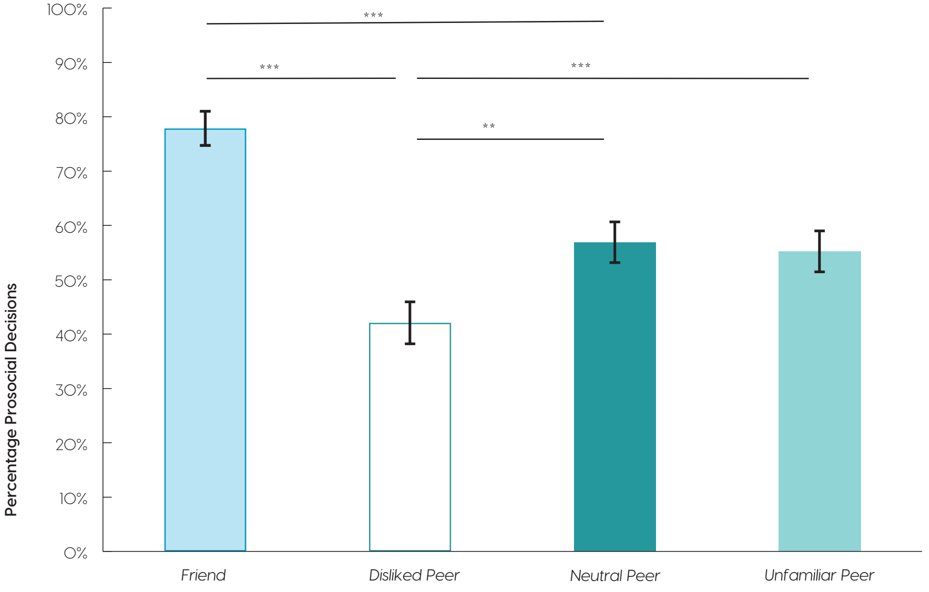


Figure 3. Mean frequency (%) and standard errors of prosocial choices per interaction partner. _Significant differences are indicated by an asterisk (*). *p < .05, **p < .01, ***p < .001._

Neuroimaging Results

Prosocial choices for friends

First, we investigated neural activation patterns during prosocial choices for friends versus for disliked peers where we controlled for the frequency of prosocial choices. The whole brain Friend Prosocial > Disliked Peer Prosocial one sample *t*-test (*n* = 48) yielded activation in brain regions including right putamen, right posterior middle temporal gyrus (pMTG), and scattered clusters of superior parietal lobule (SPL) activity (Figure 4A). Next, we examined the Friend Prosocial > Unfamiliar Peer Prosocial whole brain *t*-test (*n* = 47), which yielded activation in regions including bilateral SPL, and left precentral gyrus (Figure 4B). A complete list of activations can be found in Table 1; activations involved in the *t*-contrast of Unfamiliar Peer Prosocial > Friend Prosocial can be found in the Supplementary materials.

Selfish choices for friends

In a similar fashion, we examined neural activation patterns during selfish choices for friends. The Friend Selfish > Disliked Peer Selfish (*n* = 40) and Friend Selfish > Unfamiliar Peer Selfish (*n* = 40) *t*-tests did not result in any significant neural responses. Activations involved in the reverse *t*-contrast of Friend Selfish > Unfamiliar Peer Selfish can be found in the Supplementary materials.

Prosocial choices for disliked peers

The Disliked Peer Prosocial > Friend Prosocial (*n* = 48), and Disliked Peer Prosocial > Unfamiliar Peer Prosocial (*n* = 47) *t*-tests did not result in significant heightened brain activation. Reverse *t*-contrast of Disliked Peer Prosocial > Unfamiliar Peer Prosocial can be found in the Supplementary materials (Table S1).

Selfish choices for disliked peers

The Disliked Peer Selfish > Friend Selfish (*n* = 40), and the Disliked Peer Selfish > Unfamiliar Peer Selfish (*n* = 47) *t*-tests did not yield significant brain activity. Reverse *t*-contrast of Disliked Peer Selfish > Unfamiliar Peer Selfish can be found in the Supplementary materials.

Links with social competence

Finally, we explored Pearson's correlations between neural activation during prosocial choices for friends and social competence as assessed by friendship quality (i.e., positive and negative FQS) and empathy (i.e., IRI subscales EC, PD, and PT). We used the ROI parameter estimates from the putamen and pMTG from the Friend Prosocial > Disliked Peer *t*-contrast and left and right SPL and left precentral gyrus from the Friend Prosocial > Unfamiliar Peer Prosocial *t*-contrast.

For ROIs from the Friend Prosocial > Disliked Peer Prosocial contrast, there was a significant negative correlation between putamen activity and negative FQS (r = -.33, p =.04, n = 40; Figure 4A). There were no other significant correlations between the parameter estimates and positive and negative FQS (*ps* > .55, *ns* between 35 and 40) and IRI subscales EC, PD, and PT (*ps* > .130, n = 39). For ROIs from the Friend Prosocial > Unfamiliar Peer Prosocial contrast (n = 38), there was a positive correlation between PD and activity in left SPL (r = .40, p =.01), right SPL (r = .44, p < .01), and left precentral gyrus (r = .32, p < .05; Figure 4B). There were no significant correlations with EC and PT (*ps* > .21, n = 38) and positive and negative FQS (*ps* > .17, *ns* between 34 and 38).

DISCUSSION

In this study, we examined the neural correlates of prosocial and selfish decisions in interactions with friends and disliked peers in mid-adolescents. The behavioral results confirmed prior findings that participants made most prosocial decisions for their friends and were least prosocial toward disliked peers (Güroğlu, et al., 2014; Schreuders et al., 2018b). The neuroimaging results showed that prosocial decisions for friends yield distinct neural activation patterns when prosocial decisions for friends are contrasted with prosocial decisions for disliked peers (putamen and pMTG) and unfamiliar peers (precentral gyrus and the SPL). Selfish decisions for friends and both prosocial and selfish decisions for disliked peers were not related to any heightened brain activation patterns. We further explored links between social competence measures and brain activity from the regions that were found for prosocial decisions for friends. This revealed that lower parent-reported negative best friendship quality related to greater putamen activity during prosocial decisions for friends relative to prosocial decisions for disliked peers, and that higher levels of self-reported empathic personal distress related to higher levels of bilateral SPL and precentral gyrus for prosocial decisions for friends relative to prosocial decisions for unfamiliar peers.

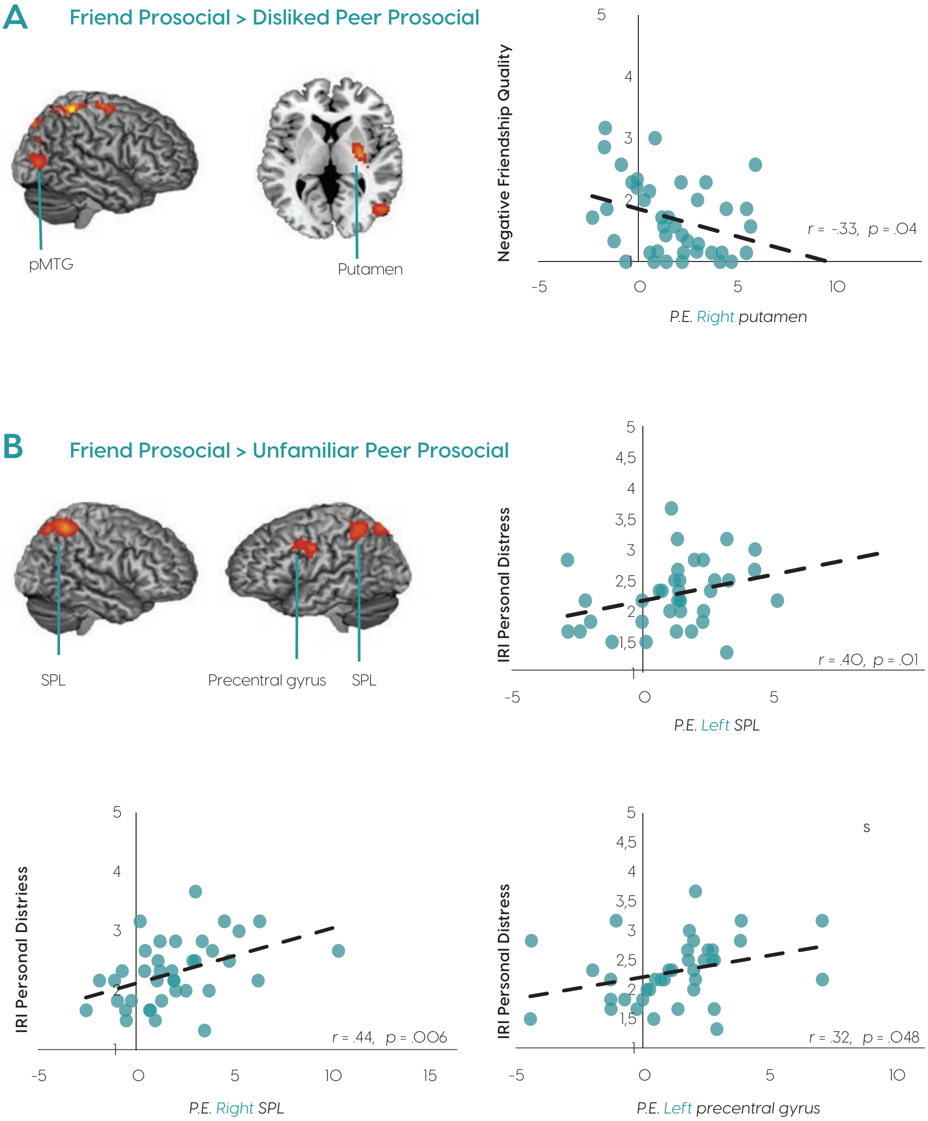


Figure 4. Whole brain contrasts controlling for the frequency of prosocial behavior for (A) Friend Prosocial > Disliked Peer Prosocial with activation in putamen (28, -11, 4) and the pMTG (50, -73, 6), and (B) Friend Prosocial > Unfamiliar Peer Prosocial with activation in bilateral SPL (42, -50, 57; -51, -50, 54) and left precentral gyrus (-48, -3, 37). *Scatterplots show significant correlations between parameter estimates (P. E.) of regions of interest (ROIs) and social competence measures friendship quality and empathy. pMTG = posterior middle temporal gyrus, SPL = superior parietal lobule.*

Table 1. Anatomical labels of regions of neural activation

Brain Region	L/R	Voxels	z	MNI coordinates		
				x	y	z
Friend Prosocial > Disliked Peer Prosocial						
Putamen	R	127	4.35	28	-11	4
Insula			3.89	42	-14	-8
Insula			3.87	36	-17	-2
Postcentral gyrus	L/R	1344	5.20	28	-42	62
Superior parietal lobule			5.07	16	-53	62
Superior parietal lobule			4.75	-20	-59	62
Precentral gyrus	R	118	4.18	28	-14	65
Middle temporal gyrus	R	199	4.04	50	-73	6
Angular gyrus			3.41	47	-73	32
Middle occipital gyrus			3.35	42	-73	23
Friend Prosocial > Unfamiliar Peer Prosocial						
Superior parietal lobule	R	281	4.91	42	-50	57
Superior parietal lobule			3.93	30	-67	57
Inferior parietal lobule			3.34	36	-48	46
Superior parietal lobule	L	154	4.05	-20	-76	57
Middle occipital gyrus			3.70	-28	-73	34
Inferior parietal lobule			3.67	-26	-67	43
Inferior parietal lobule	L	228	4.04	-51	-50	54
-			3.75	-34	-45	29
Inferior parietal lobule			3.48	-42	-39	37
Precentral gyrus	L	152	4.01	-48	-3	37
Precentral gyrus			3.68	-48	8	43
Precentral gyrus			3.65	-45	0	29

Anatomical labels of regions of neural activation for friends during prosocial choices whole brain contrasts controlled for frequency of prosocial choices. Unindented regions are the peak cluster, and indented regions are subclusters.

Note. Analyses are conducted at the threshold of $p < .001$ *FWE cluster-extent based corrected.*

L = left, R = right.

Friends

Similar to our findings in Schreuders et al. (2018b), although more superior in the current study, activity in the SPL was associated with prosocial decisions for friends when compared to unfamiliar peers, and there was less pronounced scattered SPL activity when compared to disliked peers. Together, these findings suggest that the lateral parietal cortex is involved in prosocial interactions with close others versus more emotionally distant others. Other studies also found parietal regions in the vicinity of the TPJ involved in various social tasks, including adjusting prosocial behavior depending on the social distance of the other (Strombach et al., 2015), social decision-making in the larger peer group (e.g., Van Hoorn et al., 2016), attentional processes (e.g., Vossel, Geng, & Fink, 2014), and integration of distinct cognitive processes to guide social decision-making (Carter, Bowling, Reeck, & Huettel, 2012).

In contrast to our prior study in young adults (Schreuders et al., 2018b), the comparison between prosocial choices for friends and for unfamiliar and neutral peers (see Supplementary materials) revealed precentral gyrus activation. The precentral gyrus is known to be involved in sensorimotor functions (Cooke & Graziano, 2004; Yousry et al., 1997). Although the precentral gyrus is reported in prior studies on social interactions (e.g., Cartmell, Chun, & Vickery, 2014; Lee & Harris, 2013), its role during social decision-making is still unclear.

In our prior study with adults, we found enhanced putamen activity during prosocial decisions for friends compared to disliked peers (Schreuders et al., 2018b). The current study extends these results by showing that the putamen is also underlying prosocial interactions with friends in mid-adolescence. The putamen is found to be involved in making choices that are most likely to result in a reward or positive outcomes (Balleine, Delgado, & Hikosaka, 2007; Haruno & Kawato, 2006), and in predicting and anticipating on the outcome of prosocial decisions involving peers (Delgado, Frank, & Phelps, 2005). We further found enhanced pMTG activity during prosocial decisions involving friends compared with prosocial decisions with disliked peers. In previous studies on social cognition, acitivity in the pMTG was linked to lower-order social cognitive functions like perceiving biological motion, but is hypothesized to play a supporting role in higher order functions involved in mentalizing (Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005). Corroborating prior findings, our results may suggest that the putamen and the pMTG play an important role during the decision-making process in indicating behavior that is consistent with the (positive) relationship valence, which might have significant implications for promoting the continuation of social relationships like friendships (Schreuders et al., 2018b).

Similar to our findings in young adults, the putamen was also not involved in prosocial decisions for friends when compared to unfamiliar peers in mid-adolescence, suggesting that difference in relationship valence might play an important role in putamen activation (Schreuders et al., 2018b). Our manipulation check showed that adolescents rated friendships most positive and disliked peer relationships most negative; similarly, our behavioral results showed that adolescents are most prosocial toward friends and least prosocial toward disliked peers. As such, unfamiliar peers are likely to be more similar to friends than relationships based on dislike. Putamen might possibly be also involved in prosocial decisions for unfamiliar peers to a certain extent, whereas it distinguishes most between relationships of most positive (i.e., friendships) and most negative (i.e., disliked peers) valence.

Our preliminary analyses on the role of social competence in decision-making suggest that social competence may modulate activation patterns underlying prosocial decisions for friends. Participants with lower levels of negative friendship quality, that is, friendships that were to a lesser extent characterized with conflict and power imbalance, yielded enhanced putamen activity when making prosocial decisions for friends compared with making prosocial decisions for disliked peers. Interestingly, this relation was observed for negative friendship quality in a contrast including disliked peers (i.e., a negative peer relationship), which may suggest that effects of negative friendship characteristics may be particularly salient in this context.

Furthermore, greater empathy levels regarding personal distress, that is, getting overwhelmed by others' emotions, were associated with enhanced activity in bilateral SPL and the precentral gyrus during prosocial decisions for friends relative to prosocial decisions for unfamiliar peers. These findings suggest that when compared to prosocial interactions with unaffiliated peers, individual differences in personal distress in response to others' emotional expressions may affect how prosocial decisions for friends are made. Personal distress is often described as a self-oriented reaction to others' emotions (Davis, 1983) that is suggested to relate to maladaptive empathic reactions (Rieffe & Camodeca, 2016). Nevertheless, feelings of empathic personal distress are also found to relate to less bullying (Rieffe & Camodeca, 2016), and to a greater social sensitivity, which is important to interpret social information (Cliffordson, 2002). As the participants from the current study show relatively low to moderate levels of general personal distress, one could perhaps argue that a moderate level of empathic distress may contribute to prosocial tendencies during interactions with friends.

Although future studies should further study the role of social competence in decision-making involving friends, our findings support the idea that social competence and positive peer interactions are linked (Hartup, 1996; Wentzel, 1998), and contribute to our understanding of work previously introduced reporting links between best friendship quality and empathy with interactions with peers (De Wied et al., 2007; Markiewicz et al., 2001; Masten et al., 2013; Masten et al., 2010; Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007). Together, our findings suggest that a greater orientation toward others is associated with greater involvement of neural mechanism underlying decisions that benefit friends.

Foes

It has been shown that adolescents perceive disliked peers as aggressive and not prosocial (French, Jansen, & Pidada, 2002; LaFontana & Cillessen, 2002), which could explain why adolescents made least prosocial choices in interactions with them in the current study. Individuals might presume that prosocial behavior toward disliked peers is not likely to benefit them later on, which makes prosocial decisions for disliked peers not necessarily worth the investment, especially if they are paired with costs for the self. Despite significant differences in the frequency of prosocial choices for disliked peers compared to friends and unfamiliar peers, prosocial decisions for disliked peers were not associated with any significant heightened neural activation compared to other types of peers. Investigating interactions with disliked peers in an experimental fMRI paradigm is challenging, and studies on this topic are therefore scarce. In our prior study, we employed a similar design where we investigated neural activation patterns of decision-making in interactions with friends and disliked peers in a sample of young adults (Schreuders et al., 2018b). In the current study we did not find heightened putamen and STS activity during selfish decisions for disliked peers compared with friends. This discrepancy may suggest developmental differences in the neural underpinnings of decision-making in interactions with disliked peers, but this should be tested explicitly in future studies. Another possible explanation for our lack of heightened neural activation for disliked peers might be that relationships with disliked peers are more diverse than friendships. It has been suggested that negative relationships with disliked peers are based on highly varying reasons and processes that might trigger dislike between individuals (Abecassis, 2003; Abecassis, Hartup, Haselager, Scholte, & Van Lieshout, 2002). Further, it is possible that in the current study not all disliked peers were strongly disliked but that they were relatively least liked compared to other classmates. Although different types and degrees of dislike might elicit similar behavior (i.e., fewer prosocial choices), the underlying reasons and neural mechanisms might be diverse, yielding it difficult to detect consistent neural activation patterns that underlie the same selfish behavior.

Limitations and Concluding Remarks

Based on the current paradigm, it was challenging to completely dissociate effects of interaction partners and behavior in the neural activation patterns. As our behavioral findings clearly show, prosocial decisions are dependent on the interaction partner. Even though we controlled for frequency of behavior in our contrasts of neuroimaging data, it can be discussed to what extent these results present a full dissociation of the role of interaction partners and behavior, as these are intertwined with each other. To our knowledge, the current study is the first to examine decision-making in the context of diverse real-life relationships with peers in adolescence. However, the social decisions in the fMRI task could be perceived as being hypothetical because the interaction partners were not present during the scanning session. To make the paradigm more ecologically valid, future studies might consider including the presence of real-life peers in the experiment paradigm. It should be acknowledged that having familiar disliked peers present during testing is a particularly challenging endeavor.

Furthermore, to be better able to interpret the functional neural correlates of prosocial decisions involving friends, we report preliminary findings linking individual differences in brain activity to social competence measures. A strength of this study is that we used parent- and self-report measures of social functioning (friendship quality and empathy, respectively). To draw more reliable conclusions, future studies should examine relations between social competence and brain activity using active decision-making paradigms that mirror natural peer interactions. Finally, in our study, participants were generally consistent in their behavior, which indicates they did not make random choices in the fMRI task. Although this is desired, it resulted in an imbalanced distribution in our whole brain contrasts. We did not exclude participants based on a minimum number of prosocial responses in a specific condition, because participants with few trials in a particular contrast are also those who behave consistently according to their social motivation (e.g., making many prosocial decisions for friends and few prosocial decisions for disliked peers), but additional analyses in which we excluded participants based on their number of prosocial responses confirmed that the neuroimaging results were generally robust (see Supplementary materials).

In conclusion, this study was the first to examine neural correlates of prosocial decisions in interactions with real-life friends and disliked peers in mid-adolescence. We showed that the relationship with the interaction partner modulates adolescents' prosocial behavior toward peers. Whereas prosocial interactions with friends were related to enhanced activation in brain regions speculatively involved in promoting the continuation friendships, social interactions with disliked peers did not yield enhanced neural activation in any brain regions. Furthermore, we showed that adolescents' social competence further modulate the underlying neural mechanisms of prosocial interactions with friends. Opportunities to develop social skills are particularly important in adolescence, which is a critical period for social reorientation and social learning (Steinberg, 2005; Van den Bos et al., 2010). The current study highlights the significance of prosocial interactions with friends in mid-adolescence, and of including different types of (real-life) interaction partners in experimental designs.


6

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

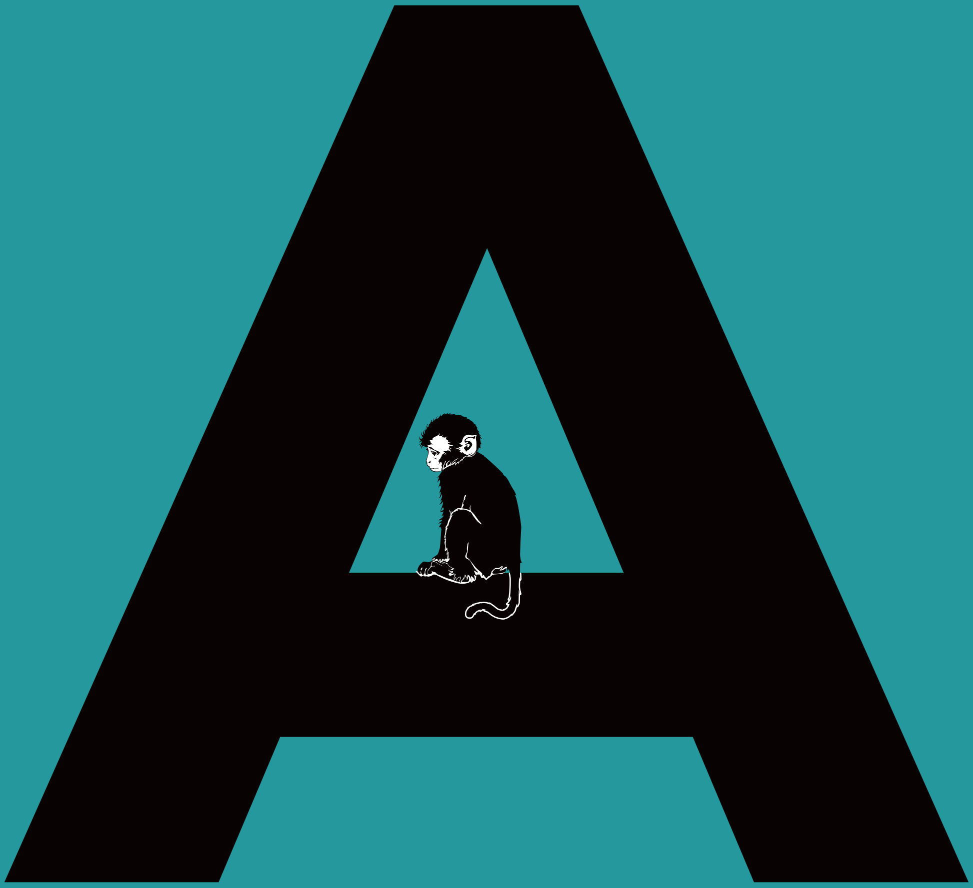
Together, prosocial motivations and behavior contribute to other-regarding social developmental goals, including strengthening social relationships and improving social skills. However, more self-regarding developmental goals, such as establishing one's social status within a social network, may also 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

Nederlandse samenvatting

INTRODUCTIE

Dit proefschrift

Mensen hebben een sterke behoefte aan sociale relaties en vinden het belangrijk ergens bij te horen. De adolescentie, een ontwikkelingsperiode waarin een kind opgroeit tot volwassene (ongeveer van acht tot begin twintig jaar), is een unieke fase voor de sociale ontwikkeling. Leeftijdsgenoten worden bijvoorbeeld steeds belangrijkere sociale partners tijdens de adolescentie. Zo gaan vrienden een andere rol spelen: Vrienden geven meer sociale en emotionele steun in het dagelijks leven en vriendschappen worden intiemer. Door met vrienden om te gaan, leren jongeren belangrijke sociale vaardigheden en sociale normen (Hartup, 1996). Daarnaast hoort exploreren zoals het uitproberen van nieuwe dingen ook bij de adolescentie. Wellicht voelen jongeren zich vrijer om grenzen te verleggen in het bijzijn van vrienden, omdat zij een gevoel van bescherming geven. Dit helpt jongeren om op te groeien tot onafhankelijke, verantwoordelijke volwassenen die zich goed kunnen redden in de huidige samenleving (Crone & Dahl. 2012; Dahl, Allen, Wilbrecht, & Suleiman, 2018; Nelson, Jarcho, & Guyer, 2016).

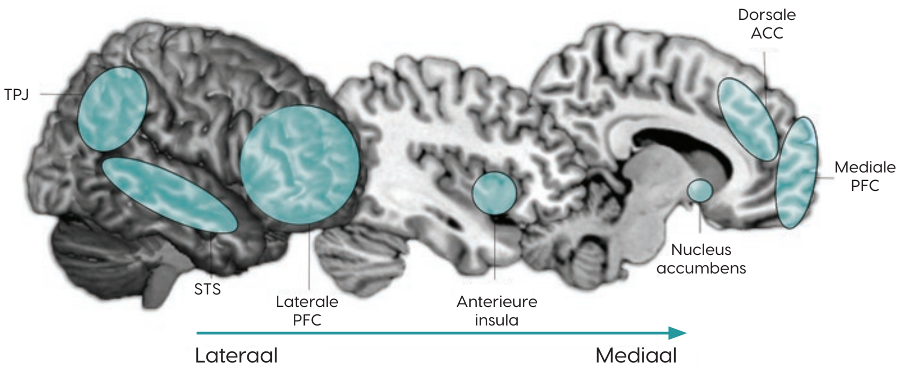
In dit proefschrift beschrijf ik vier empirische onderzoeken waarmee ik processen heb onderzocht die de motivatie om een sociale band op te bouwen of te onderhouden met leeftijdsgenoten reflecteren. Ik heb gekeken naar processen die gerelateerd zijn aan (a) het verwerken van beloningen (die een motiverend effect kunnen hebben) en (b) prosociaal gedrag (een belangrijke investering in een relatie). In het eerste deel van dit proefschrift onderzoek ik hoe een neurale gevoeligheid voor beloningen samenhangt met de motivatie om te exploreren (hoofdstuk 2) en het voortzetten en afkappen van een beste vriendschap (d.w.z. vriendschapsstabiliteit; hoofdstuk 3). In het tweede gedeelte van dit proefschrift onderzoek ik hoe hersenactiviteit gerelateerd aan prosociaal gedrag samenhangt met positieve en negatieve relaties met leeftijdsgenoten bij volwassenen (hoofdstuk 4) en jongeren (hoofdstuk 5).

Beloningsgevoeligheid

De hersenen zijn nog volop in ontwikkeling in de adolescentie. Uit de wetenschappelijke literatuur wordt duidelijk dat jongeren ontvankelijk zijn voor (sociaal-)emotionele prikkels doordat niet alle hersengebieden op hetzelfde tempo ontwikkelen (Casey, 2015; Nelson et al., 2016). Zo wordt de nucleus accumbens (een subcorticale kern gelegen in het ventraal striatum) vaak aangewezen als een belangrijk hersengebied voor het verwerken van beloningen voor jezelf en anderen. Als iets als belonend wordt ervaren, kan dat gedrag motiveren en aansturen. Onderzoek heeft aangetoond dat de nucleus accumbens van jongeren ontvankelijker is voor beloningen (zoals het winnen van geld in een spelletje) dan die van kinderen en volwassenen (Braams, Van Duijvenvoorde, Peper, & Crone, 2015; Galvan et al., 2006; Van Leijenhorst et al., 2010b). Deze verhoogde neurale ontvankelijkheid voor beloningen zou kunnen verklaren waarom jongeren meer gaan exploreren in de adolescentie en waarom vrienden een grote invloed hebben op het gedrag van jongeren (e.g., Crone & Dahl, 2012; Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016).

Prosociaal Gedrag

Jongeren worden steeds vaardiger in het aanpassen van hun gedrag aan de sociale context gedurende de adolescentie. Jongeren worden bijvoorbeeld steeds beter in het begrijpen van de intenties van anderen en kunnen daardoor beter weloverwogen beslissingen nemen tijdens sociale interacties



Figuur 1. Hersengebieden die betrokken zijn bij het verwerken van sociale informatie en bij het maken van sociale beslissingen.

(Güroğlu et al., 2014; Meuwese et al., 2014; Overgaauw, Güroğlu, & Crone, 2012). Als je je bijvoorbeeld in een situatie bevindt die je wilt gebruiken om een relatie te versterken of onderhouden, kun je iemand op een prosociale manier benaderen. Hoe je dat doet is afhankelijk van waar de ander op dat moment behoefte aan heeft. Je kan bijvoorbeeld iemand helpen, iets geven, met die persoon iets te delen of samenwerken.

Je prosociaal opstellen naar iemand kan gemotiveerd worden door verschillende factoren, zoals (a) een sociale beloning (zoals het verhogen van je sociale status, het krijgen van goedkeuring van anderen, of een zogenaamd "warm gevoel"), (b) een extrinsiek motief (een "voor wat hoort wat"-strategie, of het nastreven van een gezamenlijk doel), (c) sociale normen en verwachtingen en (d) een belangstelling voor (het welbevinden van) de ander in kwestie (Declerck, Boone, & Emonds, 2013; Luo, 2018; Zaki & Mitchell, 2011). Er wordt vaak een aantal hersengebieden genoemd dat betrokken is bij prosociaal gedrag, waaronder gebieden die betrokken zijn bij (a) het verwerken van affectieve informatie (het striatum [waaronder de nucleus accubmens], de amygdala, en de anterieure insula), (b) het beheersen van affectieve reacties (d.w.z. cognitieve controle; de laterale prefrontale cortex [LPFC], en de anterieure cingulate cortex [ACC]) en (c) sociale cognitie, zoals kunnen inschatten wat anderen nodig hebben (de mediale prefrontale cortex [mPFC], de superieure temporale sulcus [STS] en de temporale pariëtale junctie [TPJ]; Blakemore, 2008; Nelson et al., 2016). Figuur 1 geeft een overzicht van deze verschillende hersengebieden.

In het volgende gedeelte van dit hoofdstuk bespreek ik eerst de methode en resultaten van hoofdstuk 2 en 3 over beloningsgevoeligheid en daarna die van hoofdstuk 4 en 5 over prosociaal gedrag naar bekende anderen. Ik sluit dit hoofdstuk af met een algemene discussie, suggesties voor vervolgonderzoek en conclusies.

METHODE EN RESULTATEN

Reactiviteit van de Nucleus Accumbens op Beloningen gedurende de Adolescentie

Tijdens de adolescentie vinden er zowel sociale als gedragsveranderingen plaats. Veranderingen in onder andere een neurale beloningsgevoeligheid lijken hier een belangrijke rol in te spelen. Om veranderingen in de adolescentie beter te begrijpen, is het belangrijk om een grote groep jongeren (van verschillende leeftijden) meerdere keren te onderzoeken. Een longitudinaal onderzoek is dus nodig om goed de ontwikkeling in kaart te brengen.

Om te onderzoeken hoe de beloningsgevoeligheid van de nucleus accumbens verandert gedurende de adolescentie en hoe dit samenhangt met exploratief gedrag en vriendschapsstabiliteit, heb ik dezelfde deelnemers (tussen de acht en 26 jaar bij de eerste meting) drie keer (om het jaar) uitgenodigd om mee te doen aan een onderzoek. Tijdens hun bezoek aan het lab speelden de deelnemers een simpel goktaakje terwijl ze gescand werden in een *Magnetic Resonance Imaging* (MRI)-scanner. Tijdens de goktaak, werd het opgooien van een muntstuk gesimuleerd. De deelnemers moesten een aantal keer raden of de munt op "kop" of op "munt" terecht zou komen. Als ze goed gokten wonnen de deelnemers en als ze fout gokten verloren de deelnemers geld. Zij hadden steeds 50% kans om te winnen. In het taakje, speelden de deelnemers rondes voor zichzelf en wonnen of ze verloren ze dus geld voor zichzelf. In **hoofdstuk 2** heb ik gekeken naar de activiteit van de nucleus accumbens als de deelnemers wonnen versus als ze verloren voor zichzelf.

De deelnemers hebben ook rondes voor hun huidige beste vriend gespeeld waarbij ze geld wonnen of verloren voor hun beste vriend. Er is dus een groep deelnemers die drie keer (d.w.z. op ieder meetmoment) voor dezelfde beste vriend heeft gespeeld. Daarnaast is er ook een groep die drie keer voor een andere beste vriend heeft gespeeld. De eerste groep deelnemers heeft dus een *stabiele* beste vriendschap en de tweede groep een *instabiele* beste vriendschap. In **hoofdstuk 3** heb ik gekeken naar het effect van vriendschapsstabiliteit op de activiteit van de nucleus accumbens als de deelnemers wonnen versus als ze verloren voor hun beste vriend.

Reactiviteit van de nucleus accumbens op beloningen voor jezelf

In **hoofdstuk 2** wordt de hypothese bevestigt dat beloningsgevoeligheid van de nucleus accumbens hoger is bij adolescenten dan bij kinderen en volwassenen (zie ook Braams et al., 2014b). Als de deelnemers wonnen in het goktaakje (vergeleken met als ze verloren) leek de activiteit van de nucleus accumbens bij deelnemers tussen ongeveer de acht en zestien jaar toe te nemen en daarna bij deelnemers tot minstens 29 jaar weer af te nemen. De toename tot de midden-adolescentie hing samen met een sterkere motivatie om een persoonlijk doel na te streven. De afname van de midden-adolescentie tot de jongvolwassenheid hing samen met hoe de deelnemers het winnen in de goktaak ervaarden, namelijk met een afname in hoe leuk ze het vonden om te winnen. Deze resultaten laten zien dat een vorm van beloningsgevoeligheid die meer in je aard lijkt te zitten (hoe hard ben je bereid ergens voor te werken) en een vorm die meer op de situatie gericht is (hoe leuk je het vindt om te winnen tijdens de taak) samenhangen met veranderingen in reactiviteit van de nucleus accumbens op beloningen. Daarnaast laten deze bevindingen zien dat deze veranderingen plaatsvinden tot minstens eind twintig.

Reactiviteit van de nucleus accumbens op beloningen voor je beste vriend(in)

De adolescentie kan dus beschreven worden als een periode van een verhoogde reactiviteit van de nucleus accumens op beloningen voor jezelf. In **hoofdstuk 3** heb ik veranderingen in activiteit van de nucleus accumbens als reactie op beloningen voor de beste vriend(in) onderzocht. Ik laat zien dat activiteit van de nucleus accumbens gedurende de adolescentie wel verandert tijdens het winnen in het goktaakje voor een stabiele beste vriend, maar niet voor instabiele beste vrienden. Over het algemeen was de activiteit van de nucleus accumbens voor deelnemers met een stabiele beste vriendschap het hoogste in de midden-late adolescentie. Daarnaast leken de verschillen in activiteit tussen deelnemers met stabiele en onstabiele vriendschappen het grootste bij de jongere deelnemers: De reactiviteit van de nucleus accumbens op beloningen voor de beste vriend was *lager* bij deelnemers met stabiele vriendschappen dan deelnemers met instabiele vriendschappen. Jonge adolescenten waren dus minder gevoelig voor beloningen voor hun stabiele beste vriend dan jonge adolescenten met een instabiele beste vriend.

Ik heb met dit onderzoek ook laten zien dat vriendschapsstabiliteit geen invloed had op de hedonistische ervaring tijdens de taak. Deelnemers met stabiele en instabiele beste vriendschappen rapporteerden het even leuk te vinden om te winnen voor hun beste vriend. Vriendschapsstabiliteit had wel invloed op de vriendschapskwaliteit en –intimiteit. Mannelijke deelnemers van alle leeftijden rapporteerden een hogere positieve vriendschapskwaliteit met stabiele beste vrienden dan met instabiele beste vrienden. Dit effect was er niet voor de vrouwelijke deelnemers. Daarnaast bleek dat, voor zowel voor mannen als vrouwen, de vriendschapsintimiteit met instabiele beste vrienden met leeftijd afnam, terwijl dit niet het geval was voor de vriendschapsintimiteit met stabiele beste vrienden. Ten slotte, hing sterkere activiteit van de nucleus accumbens samen met een intiemere vriendschap voor deelnemers met instabiele beste vrienden. Samen laten deze resultaten dus zien dat (a) vriendschapsstabiliteit niet de hedonistische ervaring van beloningen voor beste vrienden beïnvloedt, maar wel vriendschapskarakteristieken en (b) vriendschapsintimiteit samenhangt met reactiviteit van de nucleus accumbens op beloningen voor instabiele beste vrienden.

Prosociaal Gedrag tijdens Interacties met Leeftijdsgenoten die Je Kent

Er is al veel onderzoek gedaan naar hoe mensen beslissingen maken in een sociale interactie met mensen die ze *niet* kennen (Lee & Harris, 2013), maar er is maar weinig onderzoek gedaan naar de neurale mechanismes die ten grondslag liggen aan sociale beslissingen in interacties met bekende anderen. Om zoveel mogelijk het echte leven na te bootsen, heb ik onderzocht welke hersengebieden betrokken zijn bij het maken van prosociale beslissingen in interacties met leeftijdsgenoten die je kent, waaronder vrienden en anderen die je niet aardig vindt in een groep volwassenen in **hoofdstuk 4** en een groep jongeren van 14 jaar in **hoofdstuk 5**.

Tijdens deze onderzoeken, speelden de deelnemers een spel waarbij ze muntjes moesten verdelen tussen zichzelf en iemand anders. "De ander" was een vriend, iemand die ze niet aardig vonden (een "onaardige ander"), een bekende "neutrale ander", of een onbekende ander. De deelnemers konden steeds kiezen tussen twee verdelingen van muntjes: één verdeling was altijd *prosociaal* en de ander altijd *egoïstisch*. De prosociale verdeling was altijd de verdeling die het gunstigste was voor de andere persoon en de egoïstische verdeling was altijd de verdeling die het gunstigste was de deelnemer zelf en/of het minst gunstig was voor de ander.

Sociale interacties met bekende anderen (volwassenen)

Ik laat in **hoofdstuk 4** zien dat volwassenen prosocialere keuzes maakten als ze munten verdeelden tussen zichzelf en een vriend dan als ze munten verdeelden tussen zichzelf en een onaardige ander. Zoals verwacht waren volwassenen dus meer bereid om te investeren in een vriendschap dan in een relatie met iemand die ze niet aardig vinden. De resultaten lieten verder zien dat deelnemers die zich het minst prosociaal naar hun vrienden opstelden de *supplementary motor area* (SMA) en de anterieure insula meer activeerden als ze munten verdeelden tussen zichzelf en hun vriend (versus de onaardige ander) dan deelnemers die zich juist wel prosociaal opstelden naar hun vrienden. Deze hersengebieden staan erom bekend dat ze actief worden als er een normschending wordt gedetecteerd en men zich in een conflictueuze situatie bevindt (Feng, Luo, & Krueger, 2015). Aangezien zowel dit als eerder onderzoek laat zien dat mensen zich over het algemeen prosociaal gedragen naar vrienden (Newcomb & Bagwell, 1995), lijkt er een sociale norm te zijn die dit voorschrijft. De deelnemers van dit onderzoek die zich niet volgens deze norm gedroegen activeerden de SMA en anterieure insula meer dan deelnemers die dat wel deden. Dit zou dus kunnen betekenen dat activiteit van deze hersengebieden ook samenhing met het schenden van een sociale norm in mijn onderzoek.

Verder wezen de resultaten uit dat prosociale beslissingen voor vrienden (versus voor onaardige anderen) samenhingen met activiteit in bepaalde hersengebieden, waaronder een gebied wat de posterieure temporopariëtale junctie (pTPJ) en de inferieure pariëtale *lobule* (IPL; pTPJ-IPL) beslaat. Egoïstische keuzes naar onaardige anderen toe (versus naar vrienden toe) hing samen met activiteit in de STS. De pTPJ-IPL en de STS zijn hersengebieden die veelal betrokken zijn bij het maken van sociale beslissingen, vooral als het gaat om *mentalizing* (d.w.z. nadenken over het perspectief van anderen en hun intenties; Carter, Bowling, Reeck, & Huettel, 2012).

Daarnaast was er ook een belangrijke rol voor het putamen weggelegd tijdens het maken van prosociale beslissingen tijdens interacties met vrienden (versus onaardige anderen) en egoïstische beslissingen tijdens interacties met onaardige anderen (versus vrienden). De rol van het putamen in deze sociale situaties heb ik geïnterpreteerd als belangrijk voor het selecteren van een actie (hier: het maken van een beslissing over het verdelen van de munten) die bij de verwachting past of de interactiepartner een prosociale keuze op dezelfde manier beantwoordt. Samen laten de resultaten van dit onderzoek zien welke gedrags- en neurale patronen horen bij bestaande relaties met leeftijdsgenoten.

Sociale interacties met bekende anderen (adolescenten)

In **hoofdstuk 5**, heb ik onderzocht welke processen ten grondslag liggen aan sociale beslissingen met bekende anderen bij jongeren van 14 jaar, een leeftijd waarop sociale vaardigheden nog volop in ontwikkeling zijn en nieuwe vriendschappen worden gevormd (Aikins, Bierman, & Parker, 2005; Bukowski, Hoza, & Boivin, 1993; Parker et al., 2015). De resultaten van dit onderzoek laten onder andere overeenkomsten zien met het onderzoek met volwassenen (hoofdstuk 4). Zo maakten de jongeren de meeste prosociale beslissingen wanneer ze munten verdeelden tussen zichzelf en vrienden en de minste prosociale beslissingen wanneer ze munten verdeelden tussen zichzelf en onaardige anderen. Ook was de superieure pariëtale *lobule* (SPL; gelegen naast de pTPJ-IPL) actiever tijdens het maken van prosociale beslissingen voor vrienden (versus onaardige anderen en versus onbekende anderen). Daarnaast was er ook verhoogde activiteit in het putamen tijdens het maken van prosociale beslissingen voor vrienden. De deelnemers lieten geen significante verandering van hersenactiviteit zien tijdens het verdelen van munten tussen zichzelf en onaardige anderen. Verder hing het maken van prosociale beslissingen voor vrienden nog samen met activiteit in de posterieure midden-temporale gyrus (pMTG; versus onaardige anderen) en de precentrale gyrus (versus onbekende anderen en versus neutrale anderen).

Met exploratieve analyses heb ik getoetst of de activatiepatronen die ik heb gevonden samenhingen met individuele verschillen in sociale competentie. De resultaten van de analyses lieten zien dat (a) jongeren die een negatieve vriendschapskwaliteit rapporteerden met hun beste vriend(in) het putamen minder activeerden en dat (b) jongeren die tot op een zeker hoogte rapporteerden emotioneel en empathisch te reageren op gespannen sociale situaties de SPL en precentrale gyrus meer activeerden. Deze resultaten laten samen zien dat sociale competentie een modererende rol kan hebben op de mate dat hersengebieden actief worden tijdens het maken van prosociale beslissingen voor vrienden. In andere woorden, hoe sociaal competenter de persoon, des te sterker de activiteit in deze hersengebieden.

ALGEMENE DISCUSSIE

Samen laten de onderzoeken uit dit proefschrift een aantal bevindingen zien die ons meer vertellen over de (sociale) ontwikkeling van adolescenten. Hoofdstuk 2 en 3 laten zien dat, tijdens de adolescentie, reactiviteit van de nucleus accumbens op beloningen veranderingen ondergaat die gerelateerd zijn aan de motivatie om persoonlijke doelen na te streven, waaronder misschien ook stabiele vriendschappen (Nelson et al., 2016; Poulin & Chan, 2010; Urošević, Collins, Muetzel, Lim, & Luciana, 2012; Van Duijvenvoorde et al., 2014). De adolescentie kan dus gezien worden als een belangrijke periode om persoonlijke doelen na te streven en je sociale netwerk in te richten, met een belangrijke onderliggende rol voor beloningsgevoeligheid (van de nucleus accumbens).

De resultaten die ik beschrijf in hoofdstuk 3 laten zien dat jonge adolescenten gevoeliger zijn voor beloningen die ze ontvangen voor instabiele dan voor stabiele beste vrienden. Met de bevindingen van andere onderzoeken in het achterhoofd, suggereert deze bevinding dat jonge adolescenten een sterkere motivatie hebben om hun sociale netwerk uit te breiden dan te investeren in één hechte vriendschap (Nelson, Jarcho, & Guyer, 2016). Een open vraag is nog steeds in hoeverre (en wat voor) verschillende sociale partners in de adolescentie invloed hebben op de ontwikkeling van de adolescent. Hoe verschilt bijvoorbeeld de invloed van vrienden van familieleden (zoals broers, zussen, neefjes en nichtjes, maar ook ouders) en klasgenoten op het (sociaal) welbevinden van de adolescent (Bekkhus et al., 2016; Groh et al., 2014; Pallini, Baiocco, Schneider, Madigan, & Atkinson, 2014)? Er ligt dus nog een belangrijke taak voor wetenschappers om te onderzoeken hoe sociale veranderingen plaatsvinden in het echte leven. Vervolgonderzoeken kunnen voortbouwen op de bevindingen uit dit proefschrift en processen onderzoeken die ten grondslag liggen aan complexere motivaties (bijvoorbeeld gedreven door beloningen) van adolescenten in een sociale setting.

In hoofdstuk 4 en 5 heb ik de neurale mechanismes onderzocht die ten grondslag liggen aan prosociale en egoïstische interacties met bekende leeftijdsgenoten, waaronder vrienden en onaardige anderen bij volwassenen en adolescenten. Uit de resultaten wordt duidelijk dat vrienden en onaardige anderen door volwassenen en adolescenten op een vergelijkbare manier worden behandeld, ook al wordt het beslissingsproces tijdens sociale interacties met leeftijd waarschijnlijk nog wel geraffineerder (d.w.z. meer in lijn met de sociale context; Meuwese et al., 2014). Over het algemeen kan er worden gezegd dat zowel volwassenen als adolescenten meer bereid zijn te investeren in een vriendschap (door zich prosociaal naar vrienden te gedragen) dan in een relatie met een onaardige ander.

Daarnaast lijken er zowel overeenkomsten als verschillen te zijn tussen volwassenen en adolescenten in de hersenactiviteit tijdens interacties met vrienden en onaardige anderen. Om beter te begrijpen hoe relaties met leeftijdsgenoten tot stand komen en hoe sociale normen geleerd en eigen gemaakt worden, moet (longitudinaal) vervolgonderzoek uitwijzen of deze overeenkomsten en verschillen ook ontwikkelingseffecten reflecteren. De bevindingen die ik beschrijf in hoofdstuk 4 en 5 geven wetenschappers een richtlijn om hersengebieden te selecteren die geschikt zijn te onderzoeken in vervolgonderzoek, zoals zowel de IPL, STS, het putamen als de SMA en anterieure insula.

VERVOLGONDERZOEK

Samen dragen prosociale motivaties en prosociaal gedrag bij aan het bereiken van sociale doelen, zoals het versterken van sociale relaties en het verbeteren van sociale vaardigheden. Tegelijkertijd kan een persoonlijk doel, zoals het verhogen van je eigen sociale status, ook invloed op sociaal gedrag hebben (Rodkin, Ryan, Jamison, & Wilson, 2013). Het is bijvoorbeeld belangrijk om te investeren in relaties met leeftijdsgenoten als je je eigen sociale status wilt verhogen. Het is immers niet mogelijk om dit zonder steun van anderen te bereiken. Zo zou de suggestie uit hoofdstuk 3 dat jonge adolescenten een minder sterke oriëntatie hebben naar stabiele vrienden maar wellicht een sterkere oriëntatie naar hun sociale netwerk een meer zelf-georiënteerde motivatie kunnen weerspiegelen. Daarnaast laat ik in hoofdstuk 4 en 5 zien dat jongeren en volwassenen beide geneigd zijn zich prosociaal op te stellen naar vrienden maar egoïstisch naar onaardige anderen. De balans tussen ander- en zelf-georiënteerde motivaties kan dus afhankelijk zijn van leeftijd en de sociale context. Er moet worden onderzocht hoe (de balans tussen) zelf- en ander-georiënteerde motivaties in verschillende contexten de sociale ontwikkeling beïnvloeden. Om de onderliggende processen hiervan te begrijpen, kunnen wetenschappers functionele connectiviteit tussen subcorticale hersengebieden die belangrijk zijn voor het verwerken van beloningen (zoals de nucleus accumbens) en corticale hersengebieden die belangrijk zijn voor het begrijpen van andermans intenties en perspectief (zoals de laterale temporale en pariëtale cortex) onderzoeken.

Ook is het van belang om verder te onderzoeken wat voor verschillende gevoelige periodes er binnen de adolescentie zijn voor de sociale ontwikkeling (Dahl, Allen, Wilbrecht, & Suleiman, 2018). Zo lijkt de invloed van de groep van leeftijdsgenoten het grootst in de vroege adolescentie, terwijl intieme vriendschappen juist later in de adolescentie belangrijker worden (Poulin & Chan, 2010; Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). Wetenschappelijk onderzoek laat zien dat positieve ervaringen met leeftijdsgenoten een belangrijke voorspeller is voor de weerbaarheid voor sociale stress en welbevinden (Masten, Telzer, Fuligni, Lieberman, & Eisenberger, 2012; Qualter, Brown, Munn, & Rotenberg, 2010). Het is dus niet zo gek dat het opbouwen van een sociaal netwerk met goede vrienden als één van de belangrijkste taken van jongeren wordt gezien. In dit proefschrift onderstreep ik een aantal belangrijke factoren die hieraan bijdraagt: prosociaal gedrag, sociale competentie en processen gestuurd door beloningen.

CONCLUSIES

Dit proefschrift markeert de adolescentie als een belangrijke periode voor het nastreven van persoonlijke doelen (hoofdstuk 2) en sociale ontwikkeling met betrekking tot interacties met verschillende bekende leeftijdsgenoten (hoofdstuk 3, 4, en 5). Ik heb besproken hoe verschillende hersengebieden betrokken zijn bij de sociale ontwikkeling en dat sociale interacties met leeftijdsgenoten, vrienden in het bijzonder, bijdragen aan een socialisatieproces met mogelijke effecten die doorklinken later in de ontwikkeling. Sociale motivaties beïnvloeden sociale beslissingen die weer invloed hebben op sociale relaties. Ten slotte biedt dit proefschrift vanuit een neurowetenschappelijk perspectief een veelomvattend overzicht van processen die invloed hebben op de motivatie om een sociale band op te bouwen of te onderhouden met leeftijdsgenoten; of in andere woorden, of er *een vriend in mij schuilt*.

Supplementary materials

CHAPTER 2

FMRI Task

Participants played a heads-or-tails gambling game in which they could win or lose coins (Figure S1; also see Braams, Güroğlu, et al., 2014; Braams, Peters, et al., 2014; Braams et al., 2015). Participants started the game with 10 coins. On each trial, participants made a guess for heads or tails by pressing a button with their right index or middle finger. They won if the computer matched their response and lost if the computer did not match their response. Chances of winning on each trial were thus 50%. The first trial screen (4000 ms) showed how many coins they could win or lose. To keep the participants engaged in the task, three different types of distributions of coins were included: trials on which participants could win 3 or lose 3 coins, win 5 or lose 3 coins, and win 2 or lose 5 coins. A fixation screen followed the trial screen (1000 ms), and a feedback screen (1500 ms) followed the fixation screen and showed the outcome of the gambling decision. Trials ended with a jittered fixation screen (1000 – 13200 ms). Participants were instructed that the coins won in this task would translate to actual money, which would be paid out at the end of the experiment. In reality, all participants were randomly paid 4, 5, or 6 euros at T1 and T2, and they were paid 3 euros at T3. At T1 and T2 participants played 30 trials for themselves, 30 trials for their best friends, and 30 trials for another person. At T3, participants played 23 trials for themselves and 22 trials for their best friend. The aim of the current study was to investigate nucleus accumbens activation during rewards for the self; therefore only trials when participants played for themselves are included in the current analyses. It should be noted that there were fewer trials at T3 which was not accounted for in the analyses. We included all available data for the self condition (i.e., when participants played for themselves) from each time point.

Table S1. Number of scans obtained at T1, T2, and T3

Time point	Total	valid scans for analyses	scans excluded due to excessive motion (> 3mm)	scans excluded for other reasons[1]
T1	299	248	36	15
T2	255	226	10	19
T3	243	219	4	20

[1] *Other reasons to exclude scans than excessive motion were technical problems or artifacts, not finishing the task, reporting of a neurological or psychiatric disorder.*

Table S2. . Significance levels model comparisons testing the relation with age

Model	1 vs. 0	2 vs. 1	3 vs. 2	4 vs. Best model	5 vs. 4
Dependent variable					
Left NAcc Win > Lose	0.07	**0.001**	0.70	0.07	0.82
Right NAcc Win > Lose	0.03	**< 0.001**	0.97	0.58	0.83
Pleasure from Winning vs. osing	< 0.001	0.14	0.93	**< 0.001**	0.50
BAS Drive	0.02	0.58	0.03	0.57	**0.02**
BAS Fun Seeking	0.83	0.54	**< 0.01**	0.70	0.28
BAS Reward Responsiveness	0.36	0.65	0.01	**0.01**	0.39

[1] *Note. O = Null model, 1 = Linear model 2 = Quadratic model, 3 = Cubic model, 4 = Best model + Main effect Sex, 5 = 4 + Sex x Age interaction.*

[2] *Note. Preferred models are in **bold**.*

Table S3. Significance levels model comparisons testing the relation with NAcc activation

Predictor	Left NAcc Win > Lose				Right NAcc Win > Lose			
	Model 1 vs. 0	Model 2 vs. 1	3 vs. Best model	Model 4 vs. 3	Model 1 vs. 0	Model 2 vs. 1	3 vs. Best model	Model 4 vs. 3
Early to Mid adolescents								
Pleasure from Winning vs. Losing	0.16	0.58	-	-	0.10	0.48	-	-
BAS Drive	**0.03**	0.55	0.16	0.09	**0.02**	0.73	0.84	0.41
BAS Fun Seeking	0.07	0.42	-	-	0.39	0.63	-	-
BAS Reward Responsiveness	0.37	0.45	-	-	0.38	0.62	-	-
Mid-Adolescents to Young Adults								
Pleasure from Winning vs. Losing	< 0.01	**< 0.001**	0.60	0.46	< 0.001	**< 0.001**	0.60	0.99
BAS Drive	0.96	**< 0.001**	0.19	0.88	0.96	**< 0.001**	0.28	0.85
BAS Fun Seeking	0.73	**< 0.001**	0.17	0.70	0.68	**< 0.001**	0.24	0.73
BAS Reward Responsiveness	0.50	**< 0.001**	0.13	0.70	0.35	**< 0.001**	0.17	0.68

[1] *Note. 0 = Null model, 1 = model with Predictor, 2 = model with Predictor + Age, 3 = Best model + main effect Sex, 4 = 3 + Sex x Predictor interaction.*

[2] *Note. Preferred models are in* ***bold****.*

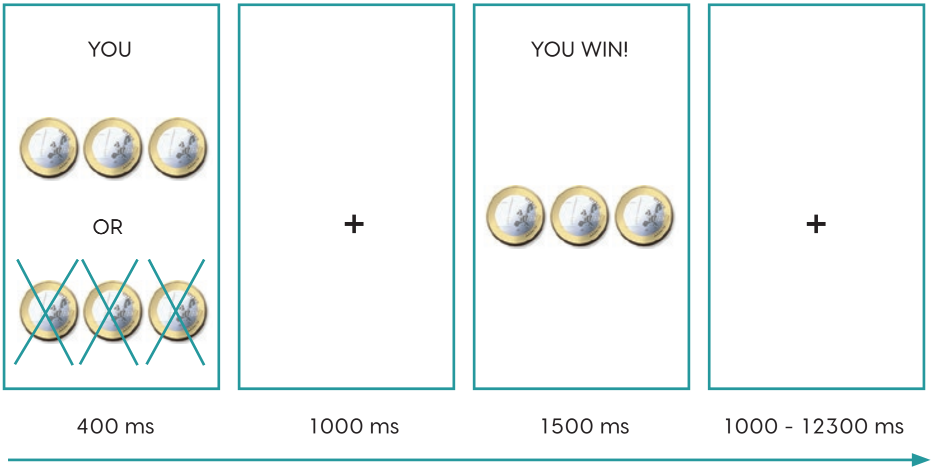


Figure S1. Example of one trial of the fMRI task.

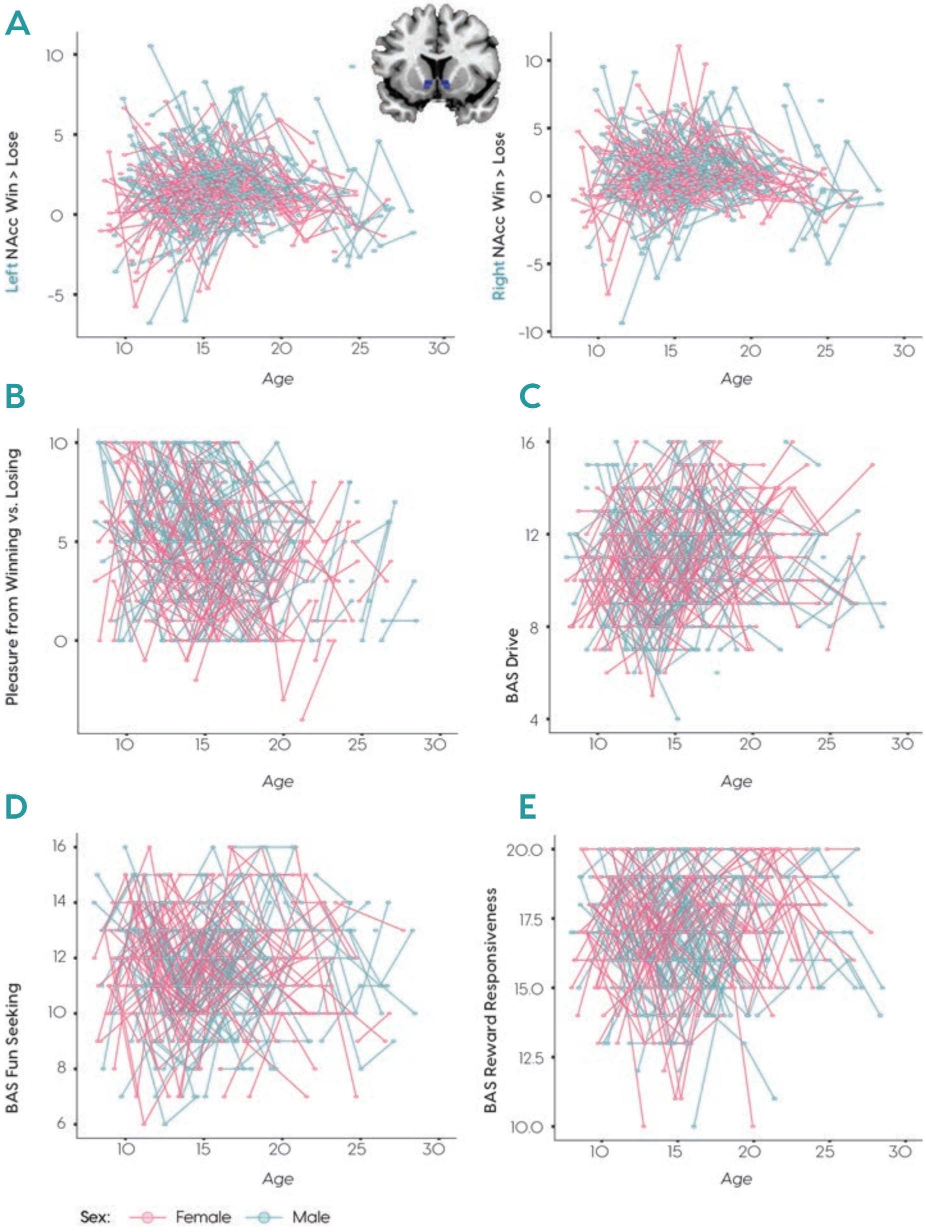
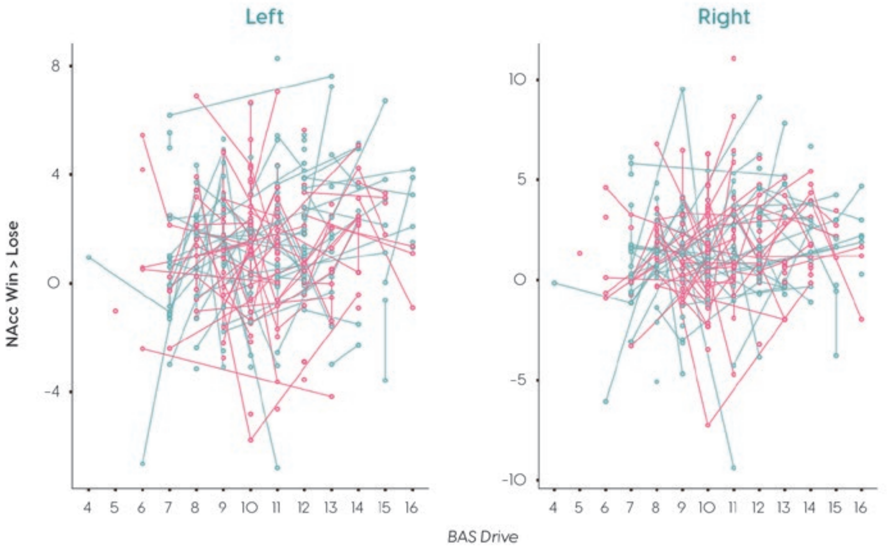


Figure S2. Raw data of (A) left and right NAcc activation during winning vs. losing, (B) self-reported pleasure from winning versus losing, (C) BAS drive, (D) BAS fun seeking, and (E) BAS reward responsiveness across development. *The connected points represent the participants, red for females and blue for males.*

A Early to mid-adolescents



B Mid-adolescents to young adults

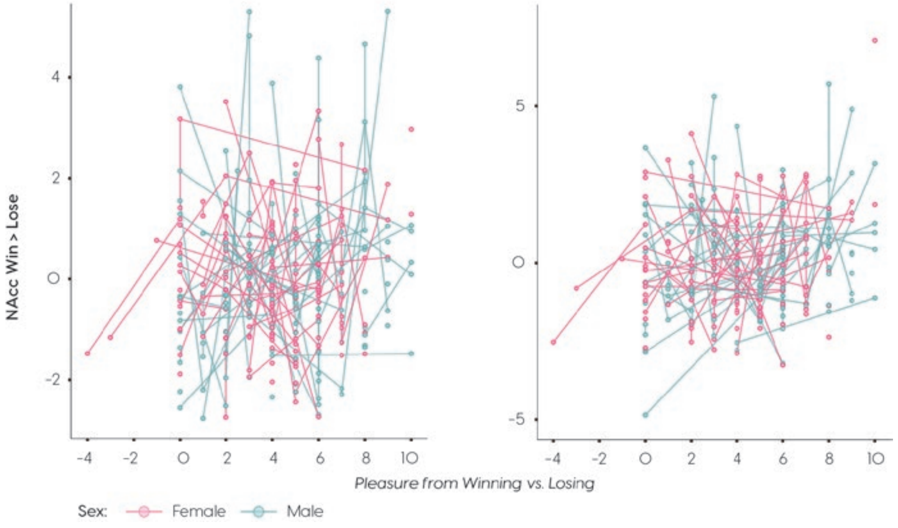


Figure S3. Raw data of the relation between left and right NAcc activation during winning versus losing and (A) BAS drive scores from early to mid-adolescent males and females, and (B) pleasure from winning vs. losing corrected for the main effect of age from mid- to late adolescents and young adult males and females. *The connected points represent the participants, red for females and blue for males.*

CHAPTER 3

Whole Brain Analysis:
Winning versus Losing for Best Friend

We examined which brain regions showed significantly increased activation during winning > losing for a best friend with a whole brain analysis of variance (ANOVA) with three factors: type of friendship (2 levels: stable and unstable), feedback (2 levels: winning or losing for friend), and time point (3 levels: T1, T2, and T3). We examined main effects of and interactions with feedback and friendship type. As expected, there was a main effect of feedback in the ventral striatum showing higher activity during winning than losing for the friend (Figure S1; Table S1). There were no effects of friendship type, and no interactions.

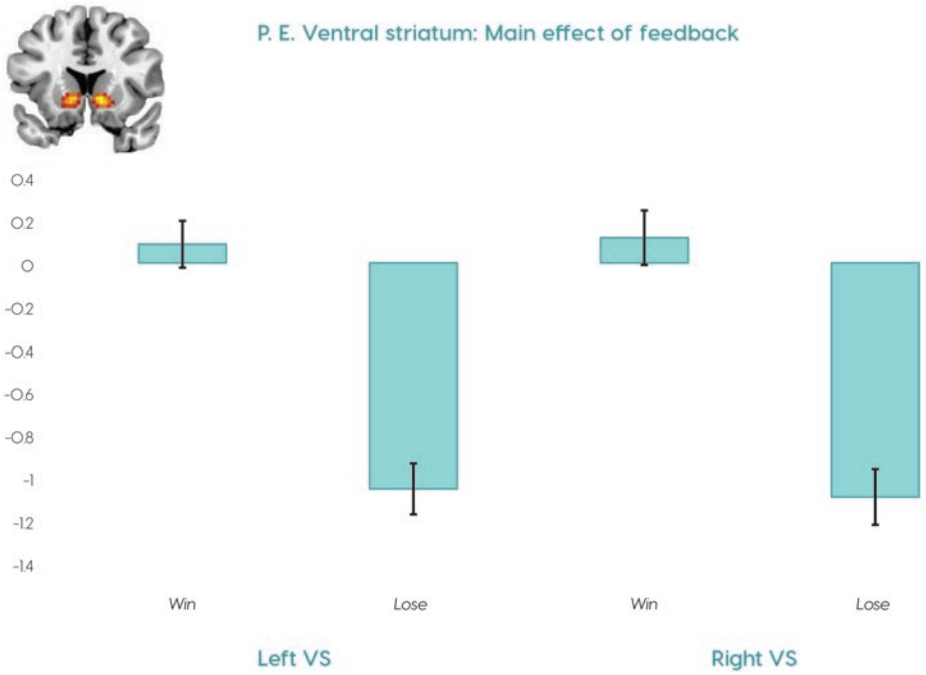


Figure S1. Main effect of feedback when playing for friends within a 2 [win or lose] x 2 [stable or unstable best friendship] x 3 [T1, T2, or T3] whole brain ANOVA. *P.E. = Parameter estimates, VS = Ventral striatum.*

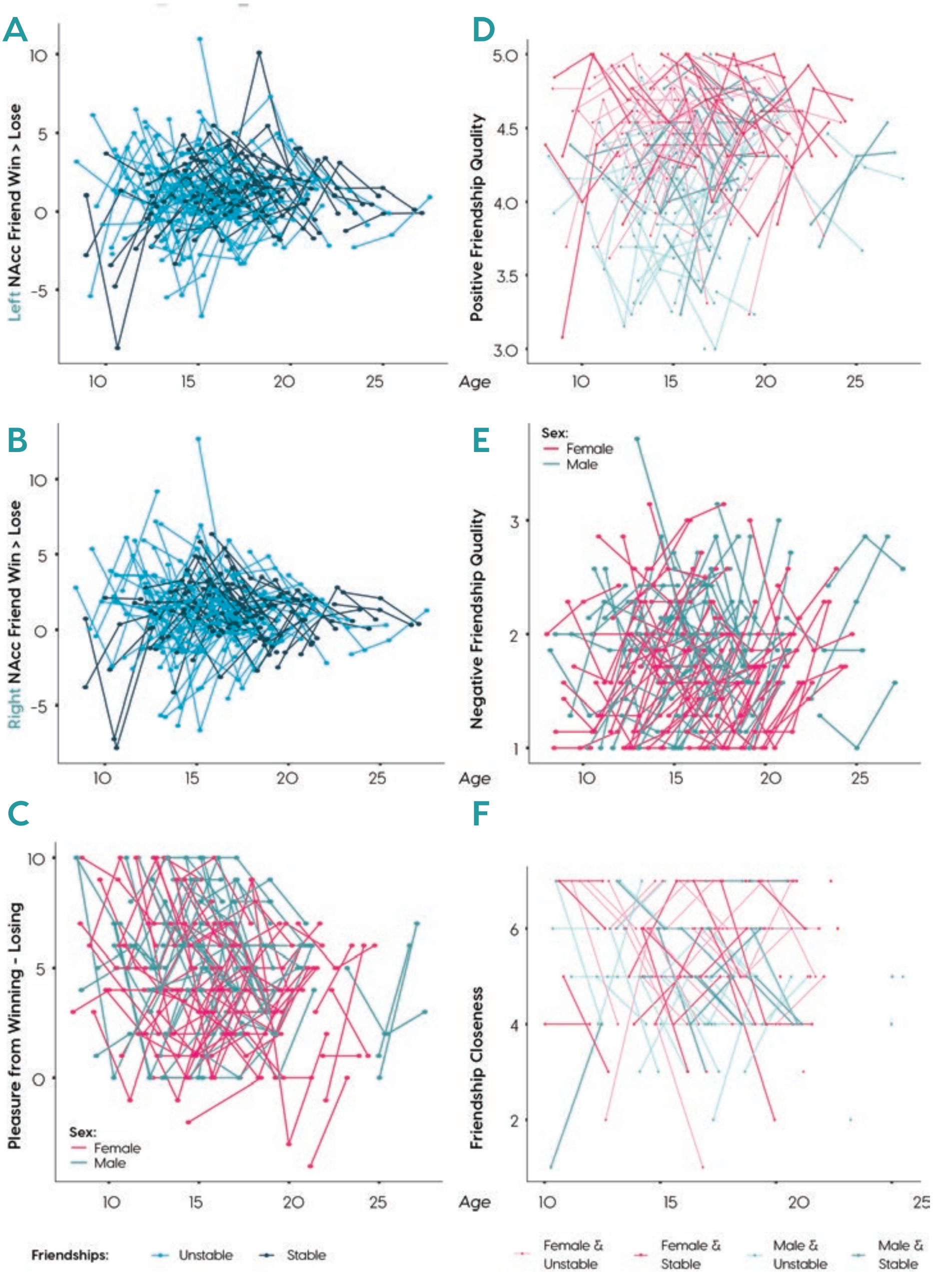


Figure S2. Raw data of the age-related patterns and effects of sex and friendship. *A) left NAcc activity, B) right NAcc activity, and C) pleasure from winning, D) positive friendship quality, E) negative friendship quality, and F) friendship closeness.*

Correlations between Pleasure from Winning, Friendship Quality, and Closeness

Partial correlation analyses were conducted to examine relations between positive and negative friendship quality, friendship closeness, and pleasure from winning within time points corrected for age (Table S2). At T1 positive and negative friendship quality correlated negatively ($p < .001$). There were no significant correlations at T1 for pleasure from winning and friendship quality ($ps > .23$). At T2, positive friendship quality correlated negatively with negative friendship quality ($p < .001$) and positively with pleasure from winning ($p < .01$). Furthermore, friendship closeness correlated negatively with negative friendship quality ($p < .001$) and positively with positive friendship quality ($p < .001$). There were no significant correlations at T2 between pleasure from winning and negative friendship quality and friendship closeness ($ps > .23$). At T3, pleasure from winning correlated positively with positive friendship quality ($p < .01$) and friendship closeness ($p = .01$). Friendship closeness further correlated positively with positive friendship quality ($p < .001$). Correlations of negative friendship quality with pleasure from winning, and of negative friendship quality with positive friendship quality and friendship closeness were not significant ($ps > .32$).

Table S1. Whole brain ANOVA

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Ventral striatum	R	89	6.82	12	15	-3
	L	102	6.50	-9	15	-3
			5.83	-18	6	-9

Note. Family-wise error correction, $p < .05$, $k \geq 10$.

L = left, R = right.

Table S2. Correlation matrix

	Pleasure from winning	Negative friendship quality	Positive friendship quality
T1			
Pleasure from winning	-		
Negative friendship quality	-.11	-	
Positive friendship quality	.11	**-.36*****	-
Friendship closeness	n/a	n/a	n/a
T2			
Pleasure from winning	-		
Negative friendship quality	-.12	-	
Positive friendship quality	**.25****	**-.42*****	-
Friendship closeness	.07	**-.27*****	**.50*****
T3			
Pleasure from winning	-		
Negative friendship quality	-.01	-	
Positive friendship quality	**.26****	.10	-
Friendship closeness	**.24***	.01	**.53*****

Table shows Pearson's r. Significant coefficients are in bold, *p < .05, **, p < .01, *** p < .001.
Note. Friendship closeness at T1 is not available (n/a).

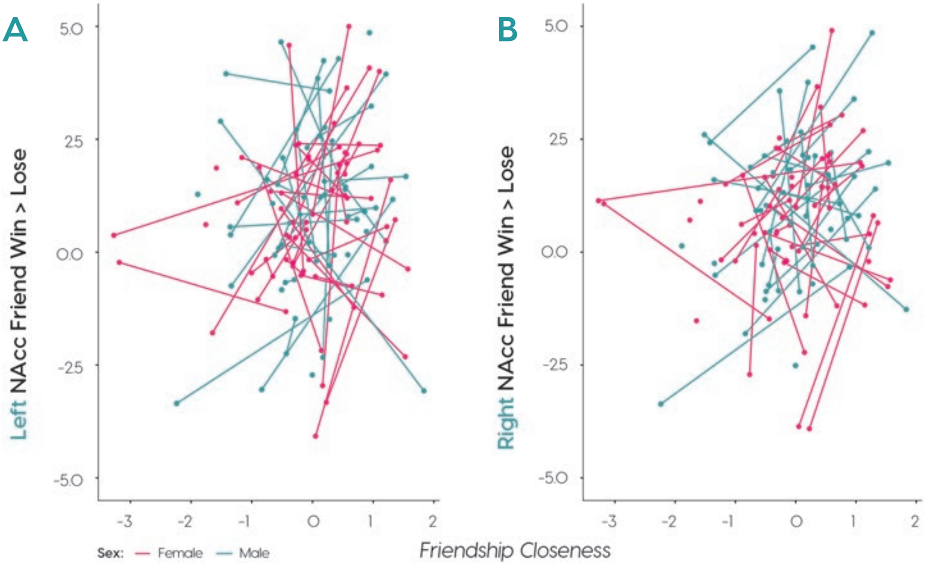


Figure S3. Raw data of the relation between vicarious reward-related NAcc activity and friendship closeness in adolescents with unstable best friendships. *A) the left NAcc, B) right NAcc.*

CHAPTER 4

Distribution of Behavior and Parameter Estimates

We did not exclude participants based on a minimum number of responses in a specific condition in the analyses. Table S1 provides an overview of how many participants had more than 0-5 trials in the contrasts discussed in the results section of chapter 4. To examine the robustness of our findings, we reran the whole brain contrasts Friend Prosocial > Disliked Peer Prosocial, Friend Prosocial > Unfamiliar Peer Prosocial, and Disliked Peer Selfish > Friend Selfish in which we excluded participants with only one trial. These results are described in chapter 4. In Figure S1 we show the distribution of parameter estimates from the clusters obtained in the Friend Prosocial > Disliked Peer Prosocial and Disliked Peer Selfish > Friend Selfish *t*-contrasts for each of the 27 participants. Importantly, Figure S1 shows that there were no outliers that could have driven our findings where all participants are included.

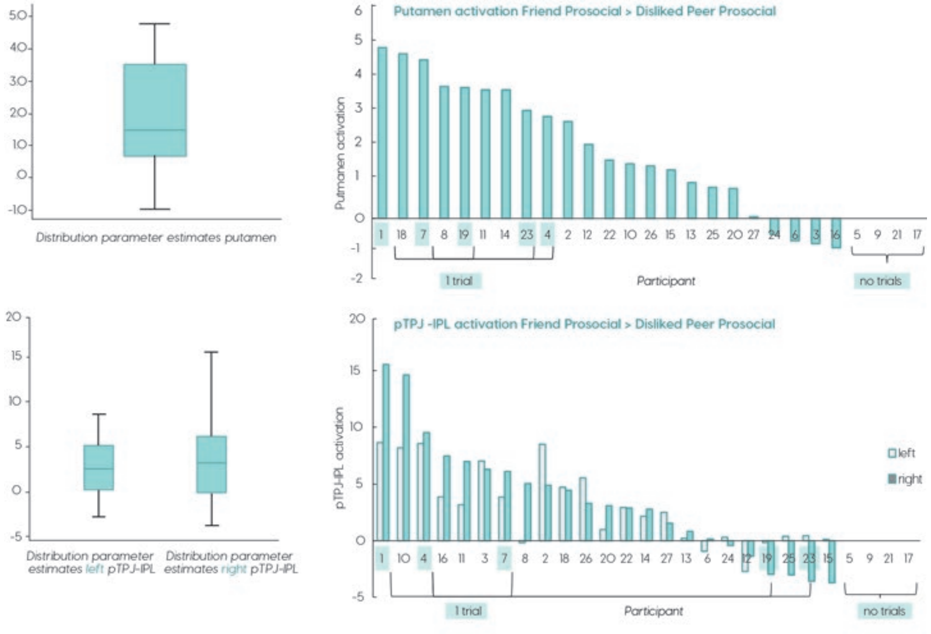
Table S1. Number of participants with more than 0-5 trials

	n > 0	*n* > 1	*n* > 2	*n* > 3	*n* > 4	*n* > 5
Friend Prosocial > Disliked Peer Prosocial	23	18	17	14	14	11
Friend Prosocial > Unfamiliar Peer Prosocial	23	23	22	20	19	19
Disliked Peer Selfish > Friend Selfish	26	24	23	22	21	20

Brain Regions of Activation during Interactions with Friends and Disliked Peers

First, we examined the neural underpinnings of decision-making for friends and disliked peers regardless of behavior. The whole brain one sample *t*-test of Friend > Disliked Peer (controlling for the frequency of prosocial behavior) did not yield significant clusters of brain activation. The Friend > Unfamiliar Peer contrast resulted in activation in the right inferior parietal lobule (IPL) extending towards the angular gyrus, and left IPL extending towards the superior parietal lobule. These brain regions are referred to as pTPJ-IPL. The whole brain *t*-contrasts of Disliked Peer > Friend, Disliked Peer > Unfamiliar Peer, Friend >

Friend Prosocial > Disliked Peer Prosocial



Disliked Peer Selfish > Friend Selfish

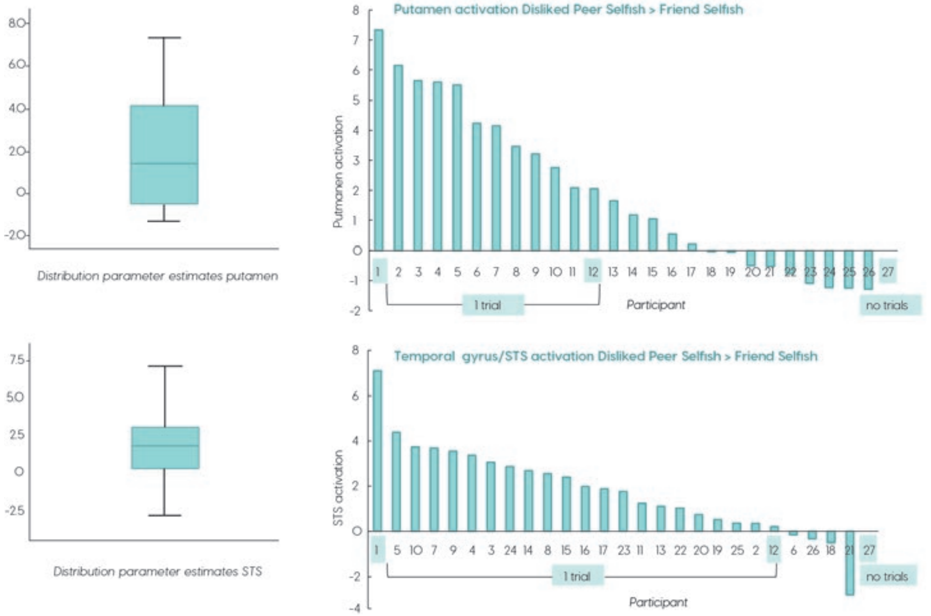


Figure S1. Distribution of activation clusters from the Friend Prosocial > Disliked Peer Prosocial and Disliked Peer Selfish > Friend Selfish t-contrasts for each of the 27 participants.

Neutral Peer, and Disliked Peer > Neutral Peer did not result in significant clusters of activity. The fact that there were no differences in neural activation for friends and disliked peers in the Friend > Disliked Peer and the reverse contrast were unexpected. Together with the results showing neural differences in the Friend Prosocial > Disliked Peer Prosocial and Disliked Peer Selfish > Friend Selfish contrasts, our findings suggest that at the neural level it is not the valence of the relationship with the interaction partner per se that affects the underlying neural processes differently, but rather the specific behavior for that interaction partner.

Next, we examined the neural correlates of prosocial and selfish decisions during interactions with friends and disliked peers. The whole brain one sample *t*-test for prosocial decisions for friends compared to neutral peers (Friend Prosocial > Neutral Peer Prosocial) controlled for the frequency of prosocial choices yielded heightened activation in the left inferior frontal gyrus ($n = 24$). The Friend Selfish > Neutral Peer Selfish contrast did not result in significant neural activation. The Disliked Peer Prosocial > Neutral Peer Prosocial, and Disliked Peer Selfish > Neutral Peer Selfish also did not yield significant increased brain activation.

Brain Regions of Activation during Decisions for Neutral Peers

We examined the neural correlates of decision making for neutral peers regardless of behavior. The Neutral Peer > Friend and Neutral Peer > Disliked peer *t*-contrasts did not yield significant activation clusters.

Next, we examined the neural correlates of prosocial and selfish decisions during interactions with neutral peers. The Neutral Peer Selfish > Friend Selfish contrast yielded activation in the left amygdala extending towards the temporal pole ($n = 26$). The Neutral Peer Prosocial > Friend Prosocial, Neutral Peer Prosocial > Disliked Peer Prosocial, and Neutral Peer Selfish > Disliked Peer Selfish contrasts did not yield significant heightened neural activation.

Table S2. Regions of neural activation

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Friend > Unfamiliar Peer						
pTPJ-IPL	R	399	4.26	30	-54	36
			3.9	42	-60	51
			3.37	42	-54	39
pTPJ-IPL	L	196	3.77	-48	-51	42
			3.36	-24	-54	42
			2.97	-36	-39	33
Dorsal anterior cingulate cortex	-	269	4.24	-12	30	36
			4.19	18	33	21
			4	-21	36	27
Lateral prefontal cortex	L	150	4.14	-33	45	-9
			3.67	-18	57	-3
			3.47	-24	45	-3
Prosocial choices						
Friend > Neutral Peer						
Inferior frontal gyrus	L	149	4.48	-54	15	6
			3.02	-54	27	0
Selfish choices						
Neutral Peer > Friend						
Amygdala - Fusiform gyrus - Temporal pole	L	205	3.9	-24	-3	-24
			3.79	-30	0	-33
			3.54	-36	9	-33

Note. Analyses are conducted using FWE cluster-correction at p < .05 with a cluster-forming threshold of p < .005.

Brain Regions of Activation during Decisions for Unfamiliar Peers

We examined the neural underpinnings of decision-making for unfamiliar peers regardless of behavior. The Unfamiliar Peer > Disliked Peer contrast showed activation in the dorsal anterior cingulate cortex and the left lateral prefrontal cortex. The Unfamiliar Peer > Friend did not yield significant activation clusters.

Next, we conducted *t*-tests to examine neural activation for unfamiliar peers during prosocial and selfish choices. The Unfamiliar Peer Prosocial > Friend Prosocial, Unfamiliar Peer Prosocial > Disliked Peer Prosocial, Unfamiliar Peer Selfish > Friend Selfish, Unfamiliar Peer Selfish > Disliked Peer Selfish contrasts did not yield significant heightened brain activation for unfamiliar peers. Table S2 provides a summary of all the results.

Brain and Behavior Links for Friends and Disliked Peers versus Neutral Peers

The percentage of prosocial choices for friends minus neutral peers in the Friend > Neutral Peer contrast did not result in any significant or positive relations with brain activity. To investigate the brain and behavior links during interactions with disliked peers, we included the difference scores of the percentage of prosocial choices for disliked peers minus neutral peers as a regressor in the Disliked Peer > Neutral Peer *t*-contrast. This showed a negative correlation between the frequency of prosocial choices for disliked peers minus neutral peers and an activation cluster in the left inferior frontal gyrus. Correlation coefficients indicated that this negative relation was driven by individual differences in prosocial choices for disliked peers rather than for neutral peers (correlation coefficients of the relation between the parameter estimates of the interior frontal gyrus and the percentage of prosocial choices for disliked peers and neutral peers separately were -.57 and .O8, respectively). This analysis did not yield a positive correlation between brain and behavior links for disliked peers versus neutral peers. Table S3 provides a detailed overview of these results.

Table S3. Regions of neural activation

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Disliked Peer > Neutral Peer						
Inferior frontal gyrus	L	119	4.33	-54	9	18
			3.13	-54	0	21
			2.92	-51	30	18

Mean prosocial choices for disliked peers-neutral peers as negative regressor.

Note. Analyses are conducted using FWE cluster-correction at p < .05 with a cluster-forming threshold of p < .005.

CHAPTER 5

In the Supplementary materials we report results in which decisions for friends and disliked peers are contrasted with neutral peers. We further show results for contrasts that are collapsed by choice, and that were aimed to examine decision-making for neutral and unfamiliar peers. Table S1 lists these neuroimaging results.

Additionally, Table S2 and Table S3 provide an overview of the number of participants and the neuroimaging results of the analyses we conducted to test the robustness of the results for the Friend Prosocial > Disliked Peer Prosocial, Friend Prosocial > Unfamiliar Peer Prosocial, and Friend Prosocial > Neutral Peer Prosocial contrasts. We tested whether the neuroimaging results were similar as the results reported in chapter 5 when only participants were included with more than 1, 2, 3, and 4 prosocial responses in the conditions from the contrast. Overall, these additional analyses yielded similar results.

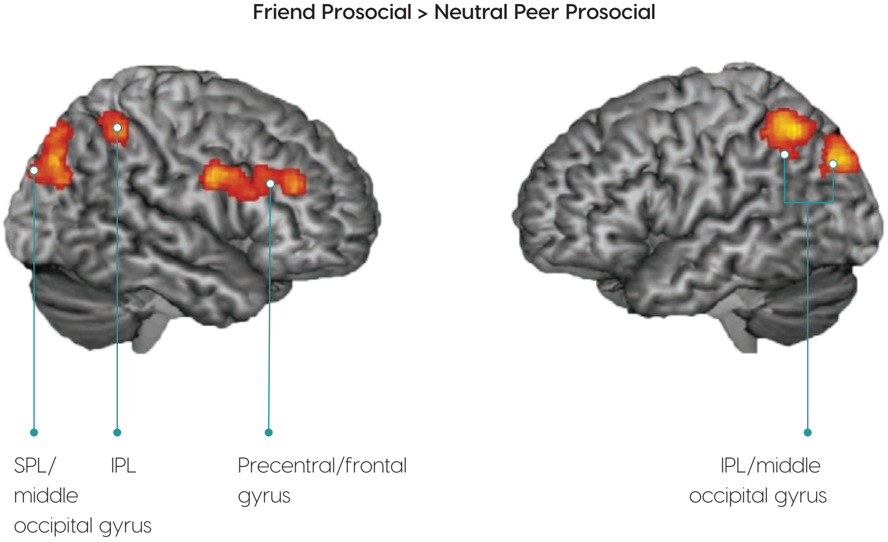


Figure S1. **Whole brain contrast controlling for the frequency of prosocial behavior for Friend Prosocial > Neutral Peer Prosocial.** *Right SPL/middle occipital gyrus (33, -76, 34), right IPL (42, -45, 51), right precentral/frontal gyrus (47, 3, 32), and left IPL/middle occipital gyrus (-3, -78, 37). SPL = superior parietal lobule, IPL = inferior parietal lobule.*

Neuroimaging Results for Social Decisions for Friends and Disliked Peers versus Neutral Peers (Collapsed over Choice)

Decision-making with friends

First, we examined the Friend Prosocial > Neutral Peer Prosocial (*n* = 47) contrast (controlled for the proportion of prosocial choices), which resulted in increased activation in right precentral-frontal gyrus, and bilateral clusters in inferior parietal lobule (IPL)-middle occipital gyrus (Figure S1).

Next, we investigated neural activation patterns in interactions with friends and disliked peers irrespective of choice and controlled for the frequency of prosocial choices (*n* = 50). The whole brain one-sample *t*-test of Friend > Disliked Peer revealed activation in left IPL extending toward the angular gyrus, and activation in the middle cingulate cortex, and the postcentral gyrus (Figure S2A). The Friend > Unfamiliar Peer *t*-test resulted in activation in the left IPL, the right SPL, the right middle frontal gyrus, left precentral gyrus, and the superior medial prefrontal gyrus (Figure S2B). The whole brain one sample t-test for decision-making for friends compared to neutral peers (Friend > Neutral Peer) yielded heightened activation in the left IPL, right SPL, and bilateral inferior frontal gyrus (IFG; Figure S2C). Table S1 provides a detailed list with the results.

Decision-making with disliked peers

The Disliked Peer > Friend, Disliked Peer > Unfamiliar Peer, Disliked Peer > Neutral Peer, Disliked Peer Prosocial > Neutral Peer Prosocial, and Disliked Peer Selfish > Neutral Peer Selfish did not yield significant increased brain activation at our chosen threshold.

Table S1. Anatomical labels of neural activation

Brain Region	L/R	Voxels	z	MNI coordinates		
				x	y	z
Friend Prosocial > Neutral Peer Prosocial						
Middle occipital gyrus	L	436	4.40	-34	-78	37
Inferior parietal lobule			4.40	-40	-53	51
Middle occipital gyrus			3.82	-34	-67	29
Middle occipital gyrus	R	196	4.16	33	-76	34
Superior parietal lobule			3.72	25	-78	48
Middle occipital gyrus			3.60	33	-87	29
Inferior parietal lobule	R	116	3.76	42	-45	51
Inferior parietal lobule			3.72	33	-48	46
-			3.56	28	-45	40
Precentral gyrus	R	261	4.38	47	3	32
Middle frontal gyrus			4.05	39	39	26
Inferior frontal gyrus			3.57	61	22	23
Friend > Disliked Peer						
Inferior parietal cortex	L	156	4.20	-31	-87	37
Inferior parietal cortex			3.61	-45	-78	32
Angular gyrus			3.41	-42	-53	29
Postcentral gyrus	R	108	4.03	28	-42	68
Precentral gyrus			3.45	28	-28	71
Middle cingulate cortex	-	242	4.6	-12	0	40
-			3.89	-23	11	40
SMA			3.88	2	-11	60
Middle cingulate cortex	-	173	3.87	-6	-28	43
Middle cingulate cortex			3.78	-3	-42	43
Paracentral lobule			3.63	-9	-34	51

Table S1. Continued

Brain Region	L/R	Voxels	z	MNI coordinates		
				x	y	z
Friend > Unfamiliar Peer						
Middle frontal gyrus	R	124	4.34	47	53	6
Middle frontal gyrus	R	149	3.72	47	36	37
Middle frontal gyrus			3.63	47	48	26
Inferior frontal gyrus			3.59	42	31	26
Superior medial (prefrontal) cortex	-	94	3.71	5	62	20
Superior medial (prefrontal) gyrus			3.51	-3	48	32
Superior medial (prefrontal) gyrus			3.38	-12	42	34
Precentral gyrus	L	528	4.85	-51	0	37
Middle frontal gyrus			3.67	-28	6	51
Precentral gyrus			3.56	-34	-6	57
-	R	421	4.62	30	-50	43
Superior parietal lobule			4.35	39	-56	54
Superior parietal lobule			4.09	53	-39	60
Inferior parietal lobule	L	500	4.26	-42	-56	57
Superior parietal lobule			4.06	-20	-70	54
-			4.01	-54	-50	54
-			3.49	-48	-50	48
Friend > Neutral Peer						
Inferior frontal gyrus	R	137	4.33	50	42	-5
Middle orbital gyrus			3.50	39	50	-10
Inferior frontal gyrus	L	124	3.80	-51	45	6
Inferior frontal gyrus			3.80	-48	39	-2
-	R	256	4.13	30	-48	43
Superior parietal lobule			3.85	33	-70	48

Table S1. Continued

Brain Region	L/R	Voxels	z	MNI coordinates		
				x	y	z
Friend > Neutral Peer (continued)						
Middle occipital gyrus			3.59	33	-76	32
Inferior parietal lobule	L	233	3.96	-34	-59	51
Inferior parietal lobule			3.49	-48	-50	48
Unfamiliar Peer Prosocial > Disliked Peer Prosocial						
Middle temporal gyrus	L	90	4.74	-62	-8	-10
Superior temporal gyrus			4.51	-59	-11	1
Postcentral gyrus	R	100	4.19	36	-22	48
Postcentral gyrus			3.91	44	-25	57
Postcentral gyrus			3.50	47	-20	48
Neutral Peer Selfish > Friend Selfish						
Precuneus	-	357	3.88	11	-67	29
Cuneus			3.68	-12	-73	20
Cuneus			3.51	-12	-76	32
Precentral gyrus	L	111	3.43	-40	-20	57
Precentral gyrus			3.40	-31	-28	57
Postcentral gyrus			3.32	-48	-31	54
Neutral Peer Selfish > Disliked Peer Selfish						
Calcarine gyrus	L	99	4.57	-12	-56	9
Cuneus			3.33	-9	-67	26

Anatomical labels of neural activity from whole brain contrasts for (prosocial and selfish) choices for friends, neutral peers, and unfamiliar peers. Unindented regions are the peak cluster, and indented regions are subclusters. L = left, R = right.

Note. Analyses are conducted at the threshold of p < .001 FWE cluster-extent based corrected.

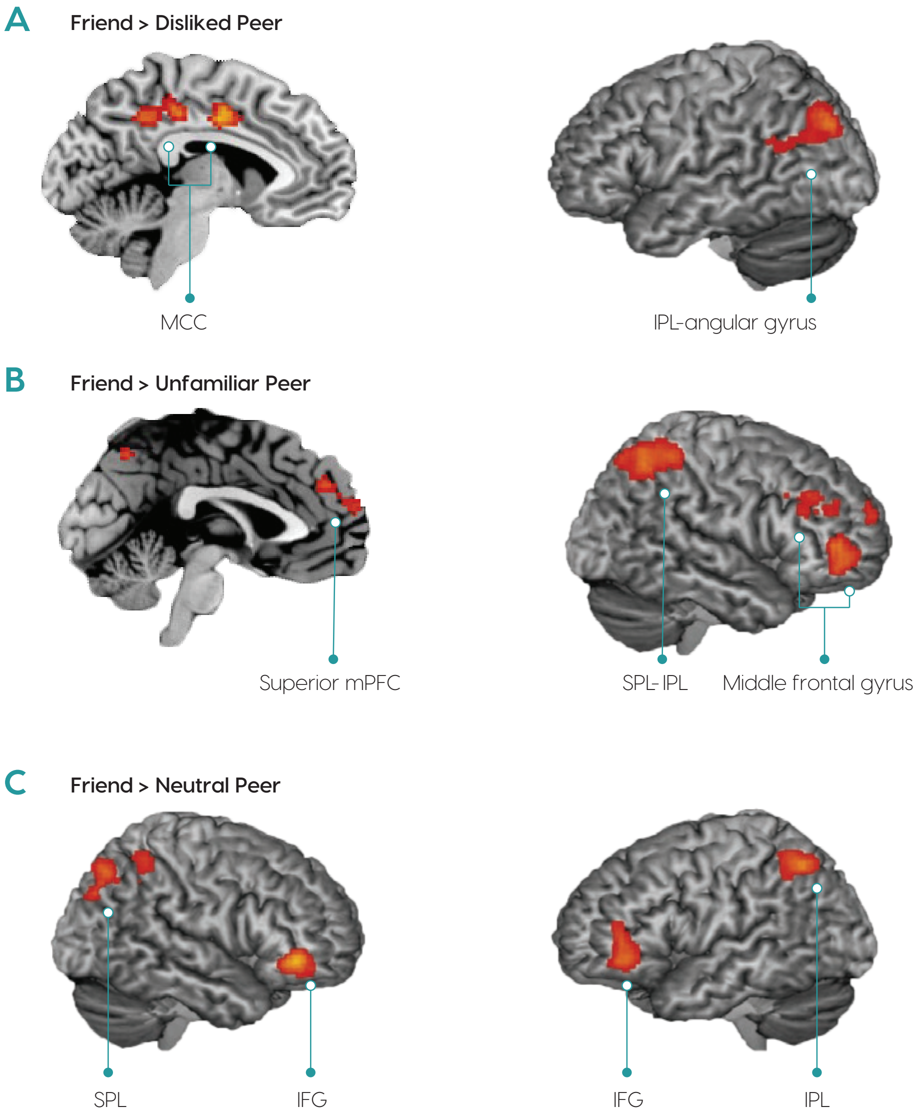


Figure S2. Whole brain contrasts controlling for the frequency of prosocial behavior of (A) Friend > Disliked Peer, (B) Friend > Unfamiliar Peer, and (C) Friend > Neutral Peer contrasts. *(A) resulted in activation in MCC (-12, 0, 40; -6, -28, 43) the IPL-angular gyrus (-31, -87, 37), (B) resulted in activation in superior mPFC (5, 62, 20), middle frontal gyrus (47, 36, 37; 47, 53, 6), and (C) resulted in activation in the right SPL (30, -48,43), right IFG (50,42, -5), left IFG (-51, 45, 6), and left IPL (-34, -59, 51). MCC = middle cingulate cortex, IPL = inferior parietal lobule, SPL = superior parietal lobule, mPFC = medial prefontal cortex, IFG = inferior frontal gyrus.*

Neuroimaging Results for Decisions for Neutral Peers and Unfamiliar Peers versus Friends and Disliked Peers

Collapsed over choice

The Neutral Peer > Friend, and the Neutral Peer > Disliked Peer did not yield significant increased brain activation. The Unfamiliar Peer > Friend and Unfamiliar Peer > Disliked Peer did not yield significant heightened brain activation for unfamiliar peers (all *n*s = 50).

Prosocial choices

The Neutral Peer Prosocial > Friend Prosocial (*n* = 47), Neutral Peer Prosocial > Disliked Peer Prosocial (*n* = 47), and Unfamiliar Peer Prosocial > Friend Prosocial (*n* = 47) did not yield significant clusters of brain activity. The Unfamiliar Peer Prosocial > Disliked Peer Prosocial (*n* = 47) whole brain *t*-test (controlled for the frequency of prosocial choices) yielded activation in the right postcentral gyrus and the middle temporal -superior temporal gyrus (Table S1).

Selfish choices

The Neutral Peer Selfish > Friend Selfish (*n* = 40) resulted in (pre)cuneus and precentral gyrus activity. The Neutral Peer Selfish > Disliked Peer selfish (*n* = 47) resulted in activity in the cuneus-calcarine gyrus (Table S1). The Unfamiliar Peer Selfish > Friend Selfish (*n* = 40) and Unfamiliar Peer Selfish > Disliked Peer Selfish (*n* = 47) *t*-tests did not yield heightened brain activation.

Robustness Neuroimaging Results during Prosocial Choices for Friends

We tested the robustness of the results from the Friend Prosocial > Disliked Peer Prosocial, Friend Prosocial > Unfamiliar Peer Prosocial, and Friend Prosocial > Neutral Peer Prosocial contrasts reported in chapter 5. We reran the analyses 4 more times where we only included participants with more than 1, 2, 3, and 4 prosocial responses, respectively, in the conditions contrasted. As can be seen in Table S2, most participants were lost in the Friend Prosocial > Disliked Peer Prosocial contrast as compared with the Friend Prosocial > Unfamiliar Peer Prosocial and Friend Prosocial > Neutral Peer Prosocial contrasts when only including participants with more than 1, 2, 3, or 4 prosocial responses for friends or disliked peers. This can be expected, since on average participants made least prosocial choices for disliked peers.

Table S2. Number of participants

	***n* participants**		
n trials	Friend Prosocial > Disliked Peer Prosocial	Friend Prosocial > Unfamiliar Peer Prosocial	Friend Prosocial > Neutral Peer Prosocial
> 1	43	45	46
> 2	40	44	44
> 3	39	43	44
> 4	36	41	44

The additional tests confirmed the activation of the putamen in the Friend Prosocial > Disliked Peer Prosocial contrast when only participants with more than 1, 2 and 3 prosocial responses for friends and disliked peers were included; enhanced putamen activity was not found when only participants were included with more than 4 prosocial choices in both conditions.

For the Friend Prosocial > Unfamiliar Peer Prosocial contrast heightened activity in the SPL was obtained in all analyses (i.e., when analyses were rerun including only participants with more than 1, 2, 3 and 4 trials in both conditions). Precentral gyrus activity was replicated only when participants were included with more than 4 responses in both conditions, but not in the other reanalyses. Finally, for the Friend Prosocial > Neutral Peer Prosocial contrast, the left IPL and right middle occipital gyrus-SPL activation patterns were replicated in all 4 reanalyses, but right precentral-middle frontal gyrus and right IPL activity were not. To briefly report these results, the analyses including only participants with more than 3 or 4 prosocial responses in the conditions of interest are reported in Table S3.

Table S3. Testing robustness of prosocial choices for friend versus other peer contrasts*

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
> *3 responses*						
Friend Prosocial > Disliked Peer Prosocial						
Middle cingulate cortex	L	450	5.03	-12	0	40
Postcentral gyrus			4.50	30	-42	65
Superior parietal lobule			4.22	16	-53	62
Pallidum	R	112	4.53	28	-8	1
Putamen			3.72	33	-20	1
Insula			3.42	42	-11	-13
Friend Prosocial > Unfamiliar Peer Prosocial						
Superior parietal lobule	R	121	4.28	42	-50	57
Superior parietal lobule			3.44	28	-67	51
> *4 responses*						
Friend Prosocial > Disliked Peer Prosocial						
Postcentral gyrus	R	106	4.19	28	-45	65
Superior parietal lobule			3.84	16	-53	62
Friend Prosocial > Unfamiliar Peer Prosocial						
Precentral gyrus	L	124	4.46	-48	0	37
-			3.58	-28	-3	40
Superior parietal lobule	R	150	4.22	39	-50	57
Superior parietal lobule			3.60	28	-67	51
Inferior parietal lobule			3.51	36	-48	46
Superior parietal lobule	L	126	3.88	-23	-70	57
Inferior parietal lobule			3.50	-26	-67	43
Superior occipital gyrus			3.19	-23	-84	46
> *3-4 responses*						

Table S3. Continued

Brain Region	**L/R**	**Voxels**	**z**	**MNI coordinates**		
				x	y	z
Friend Prosocial > Neutral Peer Prosocial						
Middle occipital gyrus	R	122	4.06	33	-76	32
Middle occipital gyrus			3.75	33	-87	29
Superior parietal lobule			3.30	28	-76	48
Inferior parietal lobule	L	115	3.98	-40	-53	54

Note. Analyses are conducted at the threshold of $p < .001$ *FWE cluster-extent based corrected. L = left, R = right.*

** contrasts including only participants with more than 3 or 4 trials in each condition. Unindented regions are the peak cluster, and indented regions are subclusters.*

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CURRICULUM VITAE

Elisabeth (Lisa) Schreuders was born on 4 November 1990 in 's-Gravenhage, The Netherlands. After graduating from high school (Dalton Den Haag) in 2009, Lisa obtained her Bachelor of Science in Psychology in 2012 and her (Research) Master of Science in Cognitive Neuroscience in 2014 at Leiden University. Lisa started her PhD project in the Brain and Development Research Center at Leiden University in January 2015 under joint supervision of Prof. Dr. Berna Güroğlu and Prof. Dr. Eveline Crone. During her PhD, Lisa studied links between peer relationships and adolescent brain development. After completion of her PhD research, Lisa started working as a postdoctoral researcher in the Department of Developmental Psychology at Tilburg University. As a postdoctoral researcher she continues studying how peer relationships contribute to adolescent development from a neuroscience perspective.