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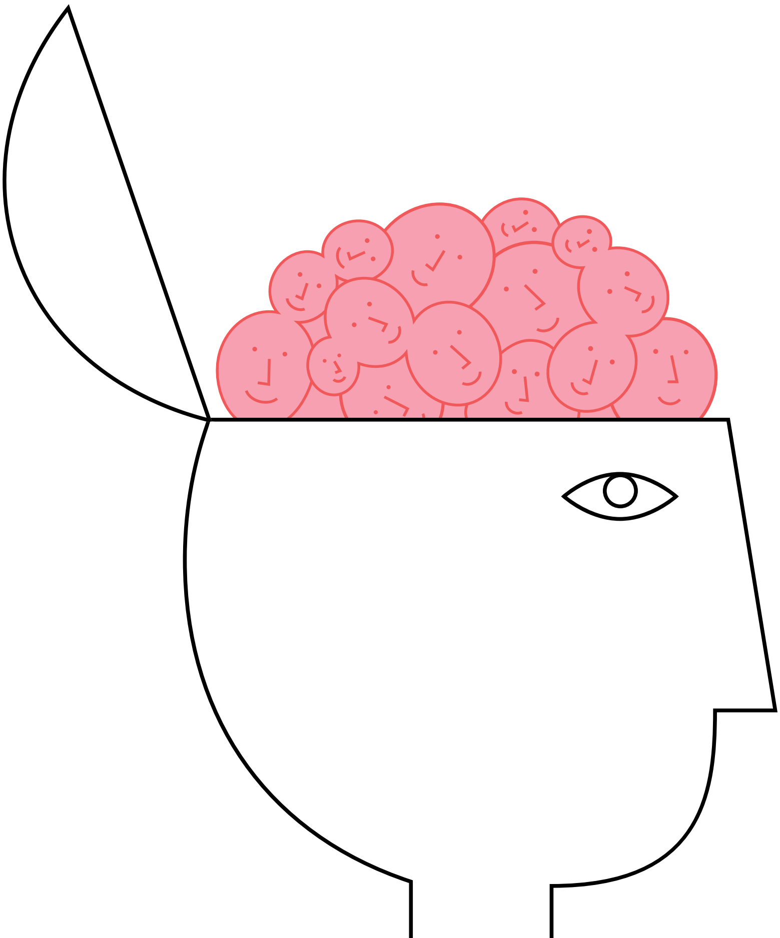
Title: Hanging out with the right crowd : behavioral and neuroimaging studies of peer influence on decision-making in adolescence
Issue Date: 2017-01-12

HANGING OUT WITH THE RIGHT CROWD

Behavioral and neuroimaging studies of peer influence on decision-making in adolescence

Jorien van Hoorn



Stellingen

Behorend bij de publieke verdediging van het proefschrift *"Hanging out with the right crowd"* door Jorien van Hoorn op 12 januari 2017.

1. De invloed van leeftijdgenoten in de adolescentie zorgt niet voor "kortsluiting" bij het nemen van risicovolle beslissingen (dit proefschrift)

2. Leeftijdgenoten beïnvloeden prosociaal gedrag. Prosociale leeftijdgenoten maken adolescenten meer prosociaal, terwijl antisociale leeftijdgenoten zorgen voor minder prosociaal gedrag (dit proefschrift)

3. Bij het nemen van een prosociale beslissing met leeftijdgenoten erbij zien we hersenactiviteit in het sociale brein, belangrijk bij het begrijpen van anderen, maar niet in het beloningssysteem. De aanwezigheid van leeftijdgenoten hoeft dus niet altijd belonend te zijn voor adolescenten (dit proefschrift)

4. Adolescenten met een autisme spectrum stoornis worden beïnvloed door leeftijdgenoten. Leeftijdgenoten zouden dus ingezet kunnen worden bij interventies om prosociaal gedrag te stimuleren (dit proefschrift)

5. Sociale context moet worden opgenomen in neuropsychologische modellen om risicogedrag te verklaren

6. *Peer influence* kan worden gedefinieerd als een socialisatieproces dat enerzijds leidt tot negatief risicogedrag en anderzijds tot positieve psychosociale uitkomsten

7. Om te begrijpen wat leeftijdgenoten zo bijzonder maakt in de adolescentie moeten we meer onderzoek doen over de gehele ontwikkeling, van de kindertijd naar adolescentie tot in de volwassenheid

8. Samenwerking tussen experimenteel onderzoek en klinische praktijk kan zorgen voor beter onderzoek en interventies

9. We moeten risico's nemen om vooruitgang te boeken in de wetenschap (Gustavo Carlo)

10. "It always seems impossible until it's done" (Nelson Mandela)

Hanging out with the right crowd:
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Jorien van Hoorn

ISBN: 978-90-9030116-7
Cover design: Esther Jong
Graphic design: Ferdinand van Nispen | Citroenvlinder DTP&Vormgeving, *my*-thesis.nl
Printed by: GVO drukkers & vormgevers B.V. | Ponsen & Looijen, Ede, The Netherlands

The research described in this thesis was supported by the Netherlands Organization for Scientific Research (NWO Research Talent Grant 406-11-019 to Eveline Crone & Jorien van Hoorn).

Proefschrift

Ter verkrijging van
de graad van Doctor aan de Universiteit Leiden
op gezag van Rector Magnificus prof. mr. C.J.J.M. Stolker,
volgens besluit van het College voor Promoties
te verdedigen op donderdag 12 januari 2017
klokke 11:15 uur

door

Jorien van Hoorn
geboren te Vlaardingen
in 1988

Promotores

Prof. Dr. E.A. Crone
Prof. Dr. E. van Dijk
Prof. Dr. C. Rieffe

Promotiecommissie

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Dr. L. Krabbendam, Vrije Universiteit Amsterdam

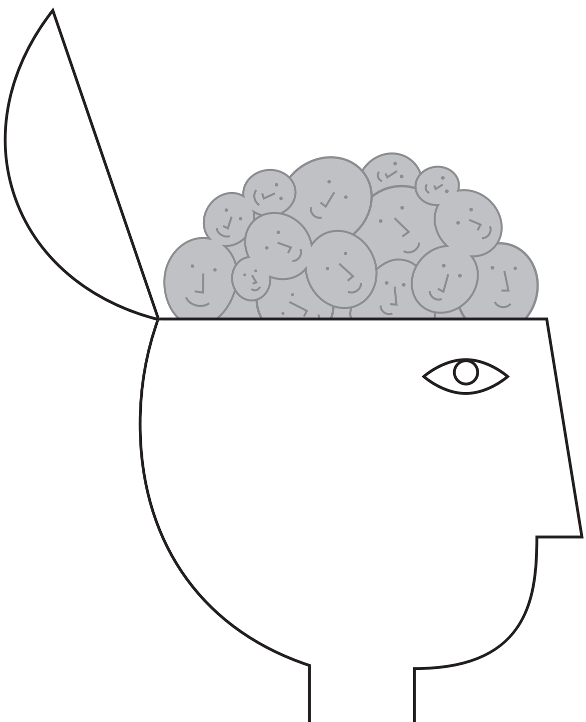
Voor mijn ouders

Table of contents

Chapter 1:

General introduction

This chapter is partly based on: Van Hoorn, J., Fuligni, A. J., Crone, E. A., & Galván, A. (2016). Peer influence effects on risk-taking and prosocial decision-making in adolescence: Insights from neuroimaging studies. *Current Opinion in Behavioral Sciences, 10,* 59-64.
doi: 10.1016/j.cobeha.2016.05.007



1. Scope of thesis

"Als je vrienden in de sloot springen, doe jij het dan ook?" (My Parents, ~2002)
"If your friends would jump in a ditch, then would you too?"

As my parents attempted to tell me more than a decade ago, the influence of peers is often associated with negative outcomes during the adolescent years. Were they right? Indeed, a vast literature indicates that health-compromising risky behaviors increase when adolescents are with their peers (reviewed in Albert, Chein, & Steinberg, 2013; Brechwald & Prinstein, 2011). These risky behaviors include, but are not limited to, drinking, speeding, gambling and smoking (Boyer, 2006). The increase in risky behaviors is associated with a 300% increase in morbidity and mortality rates, even though adolescents are physically in the healthiest phase of life (CDC, 2013). Therefore, it is crucial to further the understanding of the processes through which peers influence risky decision-making in adolescence.

Recent research suggests that adolescents are not only negatively influenced by peers. Adolescence is also often defined as a window for adaptation and opportunity rather than solely as a period of vulnerability (Crone & Dahl, 2012). In line with this perspective, peer influence may also be protective against the increase in risk-taking or even lead to positive outcomes, such as adopting prosocial behaviors (Allen & Antonishak, 2008). These prosocial behaviors include sharing, helping and cooperation (Padilla-Walker & Carlo, 2014). To date the effect of peer influence on such adaptive psychosocial outcomes has received little attention in research. Some studies suggest that peers influence prosocial behavior in adolescence in a dyad (i.e., one-on-one) or larger groups (Barry & Wentzel, 2006; Berger & Rodkin, 2012). Hence, further investigation may shed light on peer influence as a constructive process for prosocial development and social adjustment learning.

This thesis attempts to fill these gaps in current knowledge about peer influence on decision-making. The goal is to investigate the effects of peer influence on risk-taking and prosocial behavior and to unravel its underlying neural processes in the typically developing brain. Moreover, it assesses the effects of peer influence in adolescents with autism spectrum disorders (ASD), a clinical population characterized by atypical social development (DSM-5, American Psychiatric Association, 2013). An increased understanding of how peers can potentially foster prosocial behavior is important given the many benefits associated with prosocial behavior, including healthy peer relationships, better health outcomes and academic accomplishment (reviewed in Lam, 2012).

In this chapter, I first provide an introduction about the social world of adolescence and peer influence more specifically. This behavioral background is followed by a section on developmental changes in the adolescent brain and neural correlates of peer influence. Finally, I extend the knowledge about social development in typically developing adolescents to atypical social development in autism.

2. The social world of adolescence

Adolescence is the developmental period between childhood and adulthood, marked by the onset of biological puberty while the endpoint is more culturally defined by reaching mature social goals (Cohen et al., 2016). Traditionally, the adolescent period is divided into three developmental phases: early adolescence (age 10-13 years), mid-adolescence (age 14-17 years) and late adolescence (age 18-early 20ies) (Steinberg, 2008). Late adolescence has also been termed "emerging adulthood" (until roughly 25 years of age), as reaching mature social goals tends to occur at a later age in modern Western society (Arnett, 2004). There is considerable debate within the field about these definitions and they are often used interchangeably (see Sawyer et al., 2012 for a comprehensive overview).

Adolescence is characterized by tremendous changes, with developmental tasks including identity development, exploration and gaining more independence from parents (Crone & Dahl, 2012). Besides the cascade of physical, social, and cognitive changes occurring during this period, adolescents also undergo major changes in the social world (Blakemore & Mills, 2014). The social focus transitions from peer-focused play behavior with the caregiver as a base to integration with larger peer groups (Nelson, Jarcho, & Guyer, 2016). This social reorientation brings about changes in motivation to obtain and maintain specific types of social experience. The need to be accepted by peers and social evaluation become highly salient (Blakemore & Mills, 2014; Somerville, 2013). More time is spent with peers than in childhood, both in terms of face-to-face contact and online through social media (Lam, McHale, & Crouter, 2014; Lenhart, 2015).

Moreover, qualitative changes in peer relationships emerge during adolescence (Brown, 2004). Dyadic peer relations start to become more complex, intimate and provide emotional support (Rubin, Bukowski, & Parker, 2006). Besides dyadic relationships, adolescents also become part of cliques (smaller groups based on friendship) and crowds (larger groups based on shared reputations, such as "alternatives") (Rubin et al., 2006). Nonetheless, peer relationships complement, rather than substitute, existing relationships with parents (Smetana et al., 2006). More specifically, parents and peers are thought to be active in different domains of adolescents' lives, with peers broadly influencing orientations to adolescent culture and parents remaining important for moral development and long-term decisions.

3. Peer influence as a maladaptive and adaptive socialization process

From an early age a myriad of sources socialize children's behavior in line with the social norms of society, including parents, grandparents, peers, siblings, and even (social) media (books, TV, internet) (Bronfenbenner & Morris, 1998; Padilla-Walker & Carlo, 2014). *Peer pressure* is one of those socialization processes and can be defined as the direct pressure to adjust to opinions of the peer group (Brown et al., 2008). Although this definition is associated with a direct impact on behavior, more often peer influence is indirect. Indirect modes include modeling after valued peers and behavioral reinforcement. Throughout this thesis I make a distinction between peer feedback (i.e., active peer influence or encouragement) and peer presence (i.e., passive peer influence, also termed the "peer effect"). [1]

The theory to understanding peer influence used in the chapters of this thesis is referred to as *social norms approach* (Bandura, 1986; Cialdini & Trost, 1998). Through peer influence, adolescents learn injunctive social norms about appropriate behavior in the peer context, for example "I should drink beer" or "I should do well in school" (McDonald & Crandall, 2015). Most importantly, social norms and their reinforcement not only dictate behavior and attitudes (i.e., praise for drinking or doing well in school), but so does the perception of those norms (Berger, 2008). In the context of risk-taking behavior, it is thought that adolescents often overestimate the level of their peers' risk-taking behavior (Prinstein & Wang, 2005). If adolescents conform to each other's perceived rate of risk-taking, the result may be an interactive increase of risky behaviors.

3.1 Peer influence on risk taking behavior

Substantial epidemiological evidence shows that peers are a crucial factor in the increase of health-risk behaviors during adolescence, including car accidents, smoking

1 "Peers" can be defined as persons of the same age, status, or ability as another specified person (Oxford English Dictionary, 2016). In research peers have included a broad range of people, for instance best friends, members of the broader peer context (with or without peer nominations), and undefined peer groups of (unknown) others (Brown et al., 2008).

and drinking (Allen & Brown, 2008; Simons-Morton, & Farhat, 2010; Guo, Li, Wang, Cai & Duncan, 2015). The majority of experimental research corroborates these real-world trends, showing that peers increase risk-taking in various laboratory risk-taking tasks during adolescence (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005; Knoll, Magis-Weinberg, & Blakemore, 2015; MacLean, Geier, Henry, & Wilson, 2014; Munoz Centifanti, Modecki, MacLellan, & Gowling, 2014; Smith, Chein, & Steinberg, 2014). A few studies do report mixed findings (Haddad, Harrison, Norman, & Lau, 2014; Lourenco, Decker, Pedersen, Dellarco, & Casey, 2015). Collectively, these studies have tapped into explicit (i.e., known probabilities) and implicit risk (unknown probabilities), with tasks including computerized driving (Stoplight game), the Balloon analogue risk task (BART) and gambling/guessing tasks (Wheel of Fortune/Card Guessing Game/Treasure Chests).

In addition, some work has used the social norms approach in a driving simulator to mimic more ecologically valid driving conditions (Simons-Morton et al., 2011; Simons-Morton et al., 2014). Besides a general effect of peer presence, the authors reported that adolescents' risky driving increased more with a risk-accepting peer than with a risk-averse peer as driving companion. These findings show that social norms explain some of the variability in risk-taking behavior with peers. Yet, it is unclear how social norms from peer advice operate in settings that involve uncertainty of an outcome. In other words, are peer norms more influential when an adolescent makes a decision with a high degree of uncertainty? I will address this question in Chapter 2 of this thesis.

3.2 Peer influence on prosocial behavior

As previously noted, recent research suggests that peer influence may also facilitate learning and adaptive prosocial development. Within the domain of learning, peer presence during late adolescence is associated with more exploratory behavior and higher learning rates from positive as well as negative task feedback (Silva, Shulman, Chein, & Steinberg, 2015)."Prosocial behavior" is a multidimensional construct that can be defined as voluntary behavior to benefit another (Eisenberg, Fabes, & Spinrad, 2006). It encompasses a variety of behaviors, including sharing, interpersonal helping behavior, as well as cooperation that benefits one's group (Padilla-Walker & Carlo, 2014).[2] Studies that employed self-report

2 There is a distinction between prosocial behavior and altruism. *Altruism* can be defined as voluntary behavior *primarily motivated by other-concern*, with no gain for self (Hawley, 2014). Although cooperation to benefit one's group is not necessarily altruistic, it does represent an important dimension of prosocial behavior (Batson & Powell, 2003; Penner, Dovidio, Piliavin & Schroeder, 2005).

and hypothetical situations suggest links between peer influence and various prosocial outcomes throughout development (Barry & Wentzel, 2006; Berndt, 1979; Ellis & Zabartany, 2007; Wentzel, Filisetti, & Looney, 2007). Similarly, research that made use of social network analyses reports that children's friends influence prosocial behavior in dyads as well as the larger peer group (Berger & Rodkin, 2012; Logis, Rodkin, Gest, & Ahn, 2013; for a review on social network analyses see Veenstra, Dijkstra, Steglich, & van Zalk, 2013).

The type of prosocial behavior studied in this thesis is cooperation to benefit one's group, as measured by the public goods game (PGG) (Harbaugh & Krause, 2000; Ledyard, 1995). In this social dilemma, participants are asked to allocate tokens within a group of anonymous peers and given the opportunity to gain a monetary bonus as a group. They can decide to donate tokens to the public goods pot (cooperate – and receive the bonus as a group), but also keep part of the tokens for themselves (not cooperate). The advantage of using a social dilemma such as the PGG is that it provides the opportunity to measure quantifiable on-the-spot prosocial behavior in small peer groups. Cooperation to benefit one's group is especially interesting in adolescence, given that most peer interactions take place in groups after childhood (Rubin et al., 2006). In **Chapter 3**, I adapted a PGG to investigate whether manipulated prosocial and antisocial peer feedback influence prosocial behavior during adolescence.

Taken together, the peer influence literature suggests that adolescence is a time of particular sensitivity to social context, which may create an opportunity as well as vulnerability for development. With this background, I now focus on the continuing maturation of the brain that parallels these behavioral changes during adolescence.

4. Neurodevelopmental changes during adolescence

The advances in brain imaging techniques such as magnetic resonance imaging (MRI) in the past decades have made it possible to look under the hood of the adolescent brain. With MRI we can assess the development of brain structure (sMRI) and brain functioning (fMRI), i.e., which areas are engaged while performing a task. *Structural* MRI studies have shown consistent evidence that both grey matter (neurons) and white matter (connections between neurons) continue to develop until the early twenties. Grey matter volume and cortical thickness decrease at varying speeds for distinct brain regions, while white matter volume increases and shows changes in the organization of connections (Koolschijn & Crone, 2014; Lebel & Beaulieu, 2011; Mills & Tamnes, 2014; Tamnes, et al., 2013). Moreover, the

1

behavioral changes in adolescence are related to changes in brain *function* (Casey, 2015; Crone & Dahl, 2012; Nelson et al., 2016). The next section describes the functional brain regions implicated in risk-taking, prosocial behavior and peer influence.

4.1 Risk-taking and peer influence: enhanced motivational circuitry

Neuroimaging studies have the potential to elucidate the neural underpinnings of peer influence and risk-taking in the adolescent brain. One prominent theoretical framework that guided this research is the maturational imbalance model of adolescent risk-taking (Somerville, Jones, & Casey, 2010; Steinberg, 2008). This model posits that control systems in the developing brain show protracted maturation, while the motivational circuitry is hyperactive in adolescence.[3] The motivational circuitry consists of the interconnections between ventral striatum (VS), involved in learning and prediction of rewarding outcomes, and the amygdala, implicated in associative learning and determining emotional significance (Casey, 2015). The control system, comprising the prefrontal cortex and its interconnections, is implicated in reasoning and behavioral regulation.

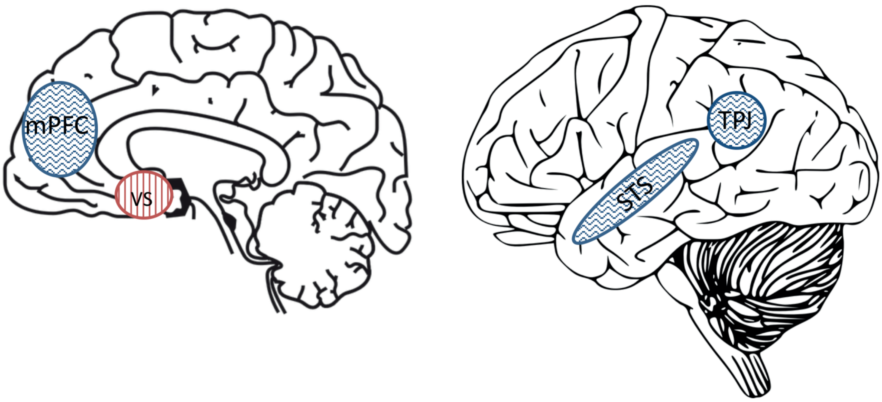


Figure 1. Brain regions previously implicated in risk-taking (indicated in red stripe pattern) and social information processing (indicated in blue zigzag pattern). Abbreviations: mPFC = medial prefrontal cortex, STS = superior temporal sulcus, TPJ = temporo-parietal junction, VS = ventral striatum.

3 Recently, there has been considerable debate in the field concerning the imbalance model, as it may be an oversimplification of the complex interplay between developing brain networks. For recent accounts, see Casey (2015), Pfeifer & Allen (2016), Shulman et al. (2016) and Telzer (2016).

Most work in the risk-taking domain has focused on reward-related processes in the VS. A large body of literature shows that VS activity in response to reward peaks during adolescence (Braams, van Duijvenvoorde, Peper, & Crone, 2015; Silverman, Jedd, & Luciana, 2015; Willoughby, Good, Adachi, Hamza, & Tavernier, 2014) and is linked to self-reported risk-taking behavior (Galván, Hare, Voss, Glover, & Casey, 2007; Telzer, Fuligni, Lieberman, & Galván, 2013). Research suggests that laboratory-based risk taking is also associated with enhanced VS activity, an effect that is exaggerated in the presence of peers (Chein et al., 2011) (VS, see Figure 1).

Chein and colleagues (2011) asked adolescents, young adults and adults to play a computerized risky driving task either alone or with a peer present. With peers present, risk-taking behavior increased in adolescents - but not (young) adults - and this was associated with enhanced activation in the VS and orbitofrontal cortex. This age-specific peak in reward-related activity is present even during a gambling task with no risk involved (Smith, Steinberg, Strang, & Chein, 2015), and thus occurs even outside the context of risky decision-making. These neuroimaging findings are consistent with peer effects in behavioral studies reporting that peer presence and influence are related to an increased preference for smaller immediate rewards over larger long-term rewards (O'Brien, Albert, Chein, & Steinberg, 2011; Gilman, Curran, Calderon, Stoeckel, & Evins, 2014; Weigard, Chein, Albert, Smith, & Steinberg, 2011). Taken together, these findings suggest that the presence of peers increases the motivational salience of rewards, likely motivating adolescents to seek out opportunities for reward (Chein et al., 2011; Smith et al., 2015).

4.2 Prosocial behavior and peer influence: enhanced social brain network

A second line of research shows that peer influence outside the context of risk-taking behavior is associated with heightened activation in a collection of areas sometimes called the social brain network (Cascio, Scholz, & Falk, 2015; Somerville et al., 2013; Welborn, Lieberman, Goldenberg, Fuligni, Galván, & Telzer, 2016). This network involved in thinking about the self and others is comprised of dorsal and ventral medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), and superior temporal sulcus (STS) (Blakemore, 2008; Blakemore & Mills, 2014; Frith & Frith, 2012) (see Figure 1). Although the broader medial PFC is implicated in social cognition, the peak in functional activity during adolescence is generally observed in dorsal medial PFC (Burnett, Sebastian, Cohen Kadosh, & Blakemore, 2011). These social brain areas are mostly distinct from the motivational circuitry and control systems described in the imbalance model and these two lines of research are typically described separately. As such, it is not well understood how the motivational circuitry and social brain areas interact in shaping the peer influence process.

Basic peer evaluation elicits uniquely heightened mPFC activation and physiological arousal in adolescents relative to children or adults, even without performing a laboratory task (Somerville et al., 2013). Furthermore, one study investigated the neural correlates of influence from peers and parents on artwork ratings in adolescence (Welborn et al., 2016). Influence from both peers and parents elicited activity in a more extensive network of brain regions, including mPFC and TPJ (mentalizing), vmPFC (reward-related processing) and vlPFC (self-control). Thus, peer and parental influence in the context of this relatively neutral task seem to share the same underlying networks in adolescence (Welborn et al., 2016). Collectively, these studies point to the recruitment of mPFC and other (social) brain areas in peer and parent influence, which is consistent with previous studies in adults that also revealed an important role for mPFC in social influence (Cascio et al., 2015; Izuma, 2013).

Prosocial decision-making during adolescence has been previously linked to activity in both the social brain network (e.g. taking the perspective of others) and reward-related regions (possibly reflecting the rewarding nature of prosocial behavior) (Crone, 2013; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010; Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2011). The social brain and reward-related regions have connections to the control circuits such as dlPFC, to control selfish or self-oriented decisions (Casey, 2015). Taken together, these studies suggest that peers may influence prosocial decision-making by triggering regions of the social brain network that have been shown to be implicated in prosocial behavior. To fully understand the underlying processes of peer influence, it is vital to extend neuroimaging studies from risk-taking to the domain of prosocial behavior. I examine the neural correlates of prosocial peer influence on donations in the public goods game in **Chapter 4.** Next, I turn from understanding peer influence in typically developing adolescents to those with atypical social development in autism spectrum disorders.

5. Peer influence in adolescents with autism

For adolescents with autism spectrum disorders (ASD), understanding the social world is often a daily struggle (Lai, Lombardo, & Baron-Cohen, 2014; Travis & Sigman, 1998). This neurodevelopmental disorder is characterized by challenges in social communication and interaction (DSM-5, American Psychiatric Association, 2015) and often goes hand in hand with few reciprocal friendships, as well as difficulty in peer relationships (Orsmond, Kraus,

& Seltzer, 2004; Müller, Schuler & Yates, 2008). Yet, in typically developing adolescents we know that the peer context is an important socialization context (Allen & Antonishak, 2008; Padilla-Walker & Carlo, 2014; Nelson et al., 2016). Surprisingly, it is unknown to what extent adolescents with ASD are influenced by their peers. Given the atypical social development and suggested attenuated social motivation in autism (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012), it may be that adolescents with ASD show diminished sensitivity to peer influence.

Some work has investigated topics related to peer influence, such as conformity and social reputation management. One study adapted the classical Asch paradigm, in which participants are asked which of three sample lines is similar to a stimulus line, while a group of confederates provides the incorrect answer most of the time (Asch, 1956). In the adapted version for children age nine to eleven, the lines were adjusted to more concrete objects such as snakes (Yafai, Verrier, & Reidy, 2014). The experimenter informed participants what the "majority of people said", again incorrect most of the time. Findings indicated that children with ASD conformed less to the opinions of others than TD children. Similarly, adults with ASD seem less sensitive to social reputation. For example, ASD adults do not show an increase in charitable donations when others observe them, whereas TD adults donate more in the presence of others than alone (Izuma et al., 2011). In **Chapter 5**, I investigate whether adolescents with and without autism are influenced by peer feedback on prosocial decisions. It is important to increase our understanding of this aspect of social behavior in adolescents with ASD.

6. Outline of thesis

This thesis reports the results from four studies that I have conducted using behavioral experimental paradigms and functional MRI to investigate peer influence on decision-making during adolescence – in typically developing adolescents and those with autism.

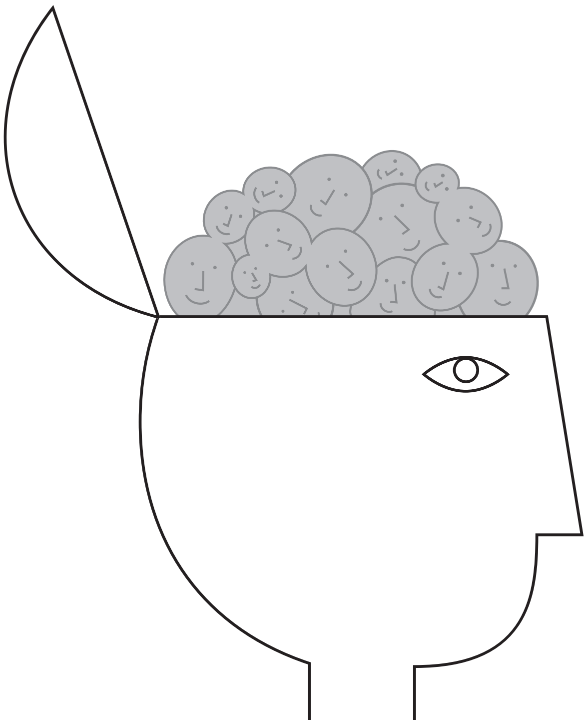
In **Chapter 2** I present a novel experimental paradigm called the Guess Gambling Game to examine peer feedback on risk-taking in adolescence. This task disentangles the influence of peers on the ability to make a rational guess and a gamble with poker chips (i.e., risk-taking). The goal was to investigate whether peer feedback was more influential when adolescents take a gamble associated with a highly uncertain outcome, in comparison to more certain outcomes. In **Chapter 3** I describe another new experimental paradigm, the peers Public Goods Game (PGG), which I used to examine peer feedback on prosocial behavior. This task distinguishes between effects of peer presence, prosocial and antisocial peer feedback on prosocial behavior; and was validated in a large sample of adolescents between twelve and sixteen years old.

In **Chapter 4** I describe an fMRI study in which I used a scanner-proof version of the peers PGG from Chapter 3 in two adolescent age groups (twelve-thirteen year olds and fifteen-sixteen year olds). Here, I was specifically interested in the neural correlates underlying peer presence and *prosocial* peer influence (that is, I did not include the antisocial condition). To increase ecological validity of the task even more, peers during the PGG were adolescent actors whom participants met before the start of the study. In **Chapter 5** I applied the PGG in a large sample of adolescents with and without ASD in order to investigate prosocial and antisocial peer influence in those characterized by atypical social development. Finally, **Chapter 6** summarizes the results of the empirical chapters and provides an overall discussion of the findings and its implications.

Chapter 2:

Peer influence on risk-taking behavior

This chapter is published as: Van Hoorn, J., Crone, E. A., & Van Leijenhorst, L. (2016).
Hanging out with the right crowd: Peer influence on risk-taking behavior in adolescence.
Journal of Research on Adolescence. doi: 10.1111/jora.12265



Abstract

Peer influence plays a key role in the increase of risk-taking behavior during adolescence. However, its underlying processes are not fully understood. This study examined the effects of social norms, conveyed through peer advice, on risk-taking behavior in 15-to-17 year-old adolescents ($N = 76$). Participants played a card-guessing task alone and with online peer advice. Results showed that risk-taking increased in the presence of peers. The results further showed that adolescents took into account the uncertainty associated with gambles, as well as the social norms conveyed by peers. Our findings suggest that peers are most influential in uncertain situations and demonstrate the value of a social norms approach in examining the processes underlying peer effects.

1. Introduction

If all your friends jumped off a cliff, then would you? Parents who worry about the negative influence of peers frequently pose this question to their adolescent son or daughter and expect the answer to be 'no.' It is not surprising that parents are concerned about the influence of friends on their child's engagement in risk-taking behaviors. The rates of these behaviors, such as substance abuse, risky driving, or gambling, increase in adolescence (Boyer, 2006). In addition, risk-taking behavior is more likely to occur when in the presence of peers than when alone (Albert, Chein, & Steinberg, 2013; Dishion & Tipsord, 2011).

A large body of literature has consistently demonstrated that peers increase risk-taking behavior in the laboratory (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005; Haddad, Harrison, Norman, & Lau, 2014; Knoll, Magis-Weinberg, Speekenbrink, & Blakemore, 2015; Munoz Centifanti, Modecki, MacLellan, & Gowling, 2014; Simons-Morton et al., 2014; Smith, Chein, & Steinberg, 2014; but see Lourenco et al., 2015) and in daily life (Simons-Morton et al., 2011). Even though these results suggest peer influence can be considered a risk factor in adolescence, it may also promote cautious behavior (Brown, Bakken, Ameringer, & Mahon, 2008). The process underlying these peer effects on risk-taking behavior is not yet fully understood. The present study employed a social norms perspective to examine the positive and negative effects of peer advice on gambling behavior. Social norms can be defined as expectations about appropriate behavior endorsed by a group (reviewed in McDonald & Crandall, 2015). Through social norms peers can potentially encourage risky as well as risk-averse behavior. Using this novel approach in an experimental task, we set out to investigate how social norms conveyed through different types of peer advice relate to risk-taking behavior during adolescence.

Peer effects: The underlying process

One hypothesis about the process underlying peer effects is that peer presence negatively influences adolescents' cognitive control functions by increasing impulsivity during decision-making (O'Brien, Albert, Chein, & Steinberg, 2011; Weigard, Chein, Albert, Smith, & Steinberg, 2014). Delay discounting is one form of impulsivity and can be described as the tendency to exhibit impatience when given a choice between an immediate small reward versus a larger but delayed reward (Romer, 2010). Recent experimental studies investigating delay discounting showed that the presence of peers increased young adults' (age 18-22 years) preference for immediate rewards over larger delayed rewards (O'Brien et al., 2011; Weigard et al., 2014). Another study showed that after viewing impulsive decisions of age-matched peers, young adults (age 18-25 years) had a preference for smaller, earlier payments as well (Gilman, Curran, Calderon, Stoeckel, & Evins, 2014).

A second hypothesis states that peer presence either 'primes' the social-emotional system for reward opportunities or influences both the reward and control systems (Albert et al., 2013; Chein et al., 2011; Smith, Steinberg, Strang, & Chein, 2015). In line with this second hypothesis, the presence of peers may increase the subjective value of rewards, for example by making rewards more arousing, and thereby also increase the preference for a risky choice over a safe alternative (Albert et al., 2013). These aspects of adolescent risk-taking have been well captured in developmental dual-process and imbalance models (Galván, 2010; Somerville, Jones, & Casey, 2010; Steinberg et al., 2008), which propose that adolescents show heightened social-emotional sensitivity in early adolescence and protracted development of cognitive control in late adolescence. Peer effects could then be a factor that tips the balance to less control and more reward sensitivity, leading to risk-taking behavior.

Studies that employed a video driving game have shown that both passive (friends observing performance; Chein et al., 2011) and active (friends calling out advice; Gardner & Steinberg, 2005) peer influence resulted in riskier driving in adolescents (age 13-18 years) but not in adults. The impact of active feedback is generally larger than passive observation (Munoz Centifanti et al., 2014), but this seems to be dependent on task-specifics (e.g. Haddad et al., 2014). Taken together, there is evidence from experimental studies showing that adolescents are sensitive to both passive peer presence and active peer influence when taking risks.

A social norms perspective on peer effects

Another useful framework for understanding peer influence on risk-taking behavior is the *social norms perspective* (Bandura, 1986; Cialdini & Trost, 1998; Van Hoorn, Van Dijk, Meuwese, Rieffe, & Crone, 2016). Social norms specify which social behaviors are accepted in the peer context and whether such behaviors will elicit approval from peers (Berger, 2008; McDonald & Crandall, 2015). These norms may not always encourage an increase in risk-taking, but may instead also promote a decrease in risk-taking behavior (Brown et al., 2008). In general, adults are more likely to act according to social norms when a situation is novel, ambiguous, or uncertain (Cialdini & Trost, 1998). Given that social acceptance is important during adolescence (Sebastian, Viding, Williams, & Blakemore, 2010), individuals may be especially susceptible to social norms during this time – and even more so in situations of uncertainty. One previous study showed increased risk-taking in 15-17 year-olds as a result of peer *presence* in a probabilistic gambling task (PGT), but only for gambles with a lower gain-loss probability (Smith et al., 2014).

Naturalistic studies that employed the social norms perspective have shown that there is variability in adolescent risky driving outcomes with peer passengers that may be dependent on how these peers behave (Simons-Morton et al., 2011; Simons-Morton et al., 2014). The effect of peer presence on teenage males' (age 16-18 years) simulated driving behavior was investigated by comparing driving alone to driving in the presence of a risk-accepting peer and a risk-averse peer (Simons-Morton et al., 2014). Evidence for a general effect of peer presence was found, which is consistent with prior studies showing that driving with a peer leads to more risky driving (e.g., Allen & Brown, 2008; Pradhan et al., 2014). However, driving with a risk-accepting peer increased risky driving more than driving in the presence of a risk-averse peer. These findings show that social norms influence risk-taking behavior, and sensitivity to these norms may explain variability in risk-taking behavior. However, to date it is unknown how social norms conveyed by peer advice and uncertainty interact in risky decision-making during adolescence.

The present study

In this study we tested the effects of peer advice on risk-taking behavior under varying uncertainty conditions. This novel approach combining social norms with experimental methods allowed us to manipulate different advice types that either enhanced or reduced risk-taking while we varied the uncertainty associated with the outcomes of the risk. We tested the hypothesis that adolescents are specifically sensitive to peer advice when outcomes are uncertain. For this purpose we designed a card-guessing task to investigate risk-taking behavior, referred to as Guess Gambling Game (GGG) (similar to Critchley, Mathias, & Dolan, 2001; Delgado, Miller, Inati, & Phelps, 2005; Smith et al., 2015). On each trial the participant was shown a playing card and was asked to guess whether a subsequently drawn card would have a higher or lower value than the current card. Then, participants bet a variable number of poker chips on whether they guessed correctly. Risk-taking behavior was operationalized in this task as the number of chips bet. The GGG was played alone and in the presence of anonymous online peers. Participants were told that the online peer watched their decision and would give them advice on how many chips to bet. This peer advice was experimentally controlled to be *low bet* advice (bet 1 or 2 chips), *medium bet* advice (bet 4 or 6 chips) or *high bet* advice (bet 8 or 9 chips). Because the task consisted of a guess and a gamble, we were able to disentangle the effects of peers on guessing behavior (the ability to make a rational choice in line with the card probability) and gambling behavior (risk-taking behavior).

Our first analysis tested the hypothesis that guessing behavior would show a dichotomous pattern in both the alone and peer advice conditions, in which participants would select ‘higher’ for cards 1-4, ‘lower’ for cards 6-9, and would have no preference for card 5. In this card condition we expected a 50% probability of ‘higher’ (Critchley et al., 2001). This pattern is in accordance with previous work that illustrates that adolescents, like children and adults, can make accurate decisions about probabilities (Reyna & Farley, 2006; Van Duijvenvoorde & Crone, 2013; Van Leijenhorst et al., 2010).

Second, we examined the influence of the type of peer advice on gambling behavior. Although we expected to find a general increase in betting behavior with peers present (Munoz Centifanti et al., 2014; O’Brien et al., 2011; Smith et al., 2014; Weigard et al., 2014), based on the social norms conveyed in peer advice we predicted to find a differentiated pattern (Simons-Morton et al., 2014). In line with social norms theory, we hypothesized that participants would place their bets in accordance with the advice expressed by the online peer (i.e., low bet, medium bet or high bet) and that these effects would be largest in the most uncertain situation (Cialdini & Trost, 1998; Smith et al., 2014).

In the current study, we collected data from adolescents age 15-17 years for several reasons. First, we wanted a comparable sample to previous studies of interest. Smith et al. (2014) studied 15-17 year olds and studies from the social norms perspective used 16-18 year olds because of the US legal driving age (Simons-Morton et al., 2011; 2014). Across the literature there is some inconsistency with regard to the definitions of adolescence.

Especially those aged 18+ are alternately called (late) adolescents, youths, or young adults. To avoid confusion, our sample did not include 18-year olds. Fifteen-year olds were included in this study for practical reasons as well, given that we included participants from two consecutive school years, which included 15-16 year olds and 16-17 year olds. Second, this age group is specifically interesting because neuroimaging work has shown that adolescent risk-taking behavior peaks around the age of 15-17, when the brain is particularly sensitive to rewards (e.g. Braams et al., 2015). The specific age-range allowed us to test hypotheses about this age group and explore individual differences in terms of gender. A meta-analysis suggests higher rates of gambling behavior in males relative to females over the age range of 10-21 years old (Byrnes, Miller, & Schafer, 1999). Moreover, some literature points to enhanced sensitivity to peer influence in males relative to females either across all of the adolescent period (Steinberg & Monahan, 2007) or most pronounced in 13-15 year olds (Sumter, Bokhorst, Steinberg, & Westenberg, 2009). Therefore, we expected males to be more influenced by the online peers than females.

2. Methods

Participants

The sample consisted of 76 adolescents between the ages of 15 and 17 years (M = 15:9, SD = 6 months, range 15:0-17:1), including 44 males (58%) and 32 females (42%). Six additional participants from the original sample (N = 82) had to be excluded due to incomplete data. Both parental consent and participant's consent for minors was obtained from all participants. All adolescents for whom we obtained informed consent participated in the study. Participants were recruited from several consecutive years in a school that teaches secondary vocational education (Dutch school system: VMBO). We did not collect information regarding parental income or parental education level. However, participants were mostly Caucasian and the school was located in a middle-class neighborhood in the Netherlands (Knol, 2012).

To obtain an estimate of general intellectual ability, participants completed Raven's Standard Progressive Matrices (SPM) (Raven, Raven, & Court, 1998). Raven's SPM consists of 60 items, classified in five sets (A through E) of 12 items each. Each item consists of a 2 x 3 or 3 x 3 matrix figure including one empty cell. Below the figure, six (for sets A and B) or eight (for sets C through E) pieces are displayed. From these pieces, the participant has to select the one piece that completes the figure. The different sets and items within a set increase in difficulty. Based on the number of correct items, estimated IQ scores were obtained using international norms (Raven, Raven, & Court, 1998). Due to missing data ($N = 3$), we included the IQ scores from $N = 73$ participants in the final sample. All IQ scores from the final sample fell within the average to above average range, $M(SD) = 108.78$ (9.92); 85-125. There was no significant difference in IQ for the two genders (M_{female} $(SD) = 107.17$ (9.12) and M_{male} $(SD) = 109.84$ (10.37), $t(71) = 1.13$, $p = .264$).

Measures

Guess Gambling Game. We designed a computerized task with playing cards, the Guess Gambling Game, that incorporated two types of decision-making: guessing behavior and gambling behavior. Trials started with one playing card that was presented face up, from a deck of cards ranging between hearts 1 (Ace) to hearts 9. Subsequently, the second card was presented with the reverse side up, such that the value of this card was unknown. Participants were asked to guess whether the second card would be higher or lower than the first card. After this guess, participants placed a bet ranging from 1 to 9 chips and they found out whether they guessed correctly. If the gamble was correct, the number of chips bet was doubled and added up to the number of remaining chips to provide a final score for that trial [e.g. a bet of 8 chips following a correct guess resulted in a score of 17 (8 chips x 2 added to 1 remaining chip)]. However, when the guess was incorrect, the participant lost the chips that were placed in the bet, but kept the chips that were not bet in the trial [e.g. a bet of 8 chips following an incorrect guess resulted in a score of 1 (the chip that was not bet)].

Each trial was played with a new deck of playing cards and a new stack of 9 poker chips, such that each trial was unrelated to previous trials. The experiment consisted of 160 trials: card 5 was shown 32 times and all other cards were shown 16 times each. Participants were not informed of how many times each card would be shown. Participants first played Guess Gambling Game alone in a block of 40 trials. The next three blocks of 40 trials (120 in total) were played with an online peer, indicated by a messenger symbol in the corner of the screen. These peers were 50% female (60 trials), indicated by a pink messenger symbol, and 50% male (60 trials), indicated by a blue messenger symbol. We chose not to counterbalance the order of alone and peer advice because prior studies have shown that there can be carry-over effects (Van Hoorn et al., 2016), and we aimed to create a pure baseline before introducing peer influence. Note that we did not examine possible effects of the gender of the peer, because there were too few trials to draw valid conclusions, instead we controlled for possible peer gender effects by counterbalancing male and female peers.

The fictitious online peer watched the performance on the entire trial and gave participants advice on how many chips to bet, indicated by a number next to the messenger symbol (Figure 1). We manipulated three types of betting advice: low bet (bet 1 or 2 chips), medium bet (bet 4 or 6 chips) or high bet (bet 8 or 9 chips). To maintain credibility of the advice given by peers, the advice for card 1 and 9 was always to bet 9 chips. Low, medium, and high advice were each randomly provided 32 times during the trials in which card 2 to 8 were presented (1/3 of 96 trials).

Figure 1. Example of a trial with peer advice in the Guess Gambling Game. Card 2 of hearts is shown while a male peer is watching, as indicated by a blue messenger symbol in the upper corner. The participant guesses that the second card will be higher than the first card. Following the guess, the online peer gives advice to place a bet of 9 chips, indicated with a number below the messenger symbol. The participant decides to follow the advice of the peer and places a bet of 9 chips. This is a correct guess, and therefore the score for this trial is 9 x 2 = 18 points.

To control for possible button press effects, half of the participants used their left index finger to guess ‘higher’ and their right index finger to guess ‘lower’, while the buttons were reversed for the other half of the participants.

Procedure

The study was conducted in a quiet classroom in which the task was individually administered to participants using a laptop computer. The experimenter provided standardized verbal instructions about the procedures and was present at all times to provide help with the instructions. In addition, the task was preceded by an extensive written instruction and practice trials. Participants completed three different elements during the study: first the Guess Gambling Game, then Raven's SPM, and finally the RPI questionnaire. Participants were told that their final score on the GGG was calculated by resolving the outcomes of 4 randomly selected trials at the end of the gambling task. All trials had the same probability to be included in the final score and therefore, each trial was equally important. Participants could choose between two possible rewards: a small amount of money related to their final score (unbeknownst to the participants, the final score always corresponded to a 3 Euro reward) or a lottery ticket for a bigger reward (an iPod or 2 cinema tickets). No differences in gambling behavior or peer effects were found between participants that chose the immediate or delayed reward. Participants were debriefed about the peer manipulation and goals of the study after all data had been collected.

3. Results

Guessing behavior

First, we examined if participants' guessing behavior was related to the actual probability of a higher card being drawn and whether this was influenced by peer presence (i.e., whether they were playing alone or with peer advice). We expected to find a dichotomous pattern in which participants select 'higher' for cards 1 to 4 and 'lower' for cards 6 to 9, whereas 50% probability was expected for card 5. We submitted the percentages of 'higher' guesses to a 2 (Condition: Alone, peer advice) x 9 (Card: 1 to 9) x 2 (Gender: Male, female) repeated measures ANOVA. Figure 2 shows the mean (*SE*) percentage of 'higher' guesses per card.

This analysis resulted in a main effect of Card ($F(8, 592) = 1160.92$, $p < .001$, $\eta_p^2 = .940$), which shows that participants' guesses were influenced by the probabilities associated with the different cards. Post-hoc analyses (Bonferroni-corrected; for all comparisons see Supplementary Table 1) revealed that the percentage of 'higher' guesses was highest for cards 1-2 and slightly lower for cards 3-4, but guesses for these cards were still in the high range (above 90%). As expected, card 5 was associated with approximately 50% 'higher' guesses, which was significantly less than for cards 1-4 and significantly higher than for cards 6-9. Finally, card 9 was associated with the lowest percentage of 'higher' guesses, and though cards 6-8 were associated with slightly more 'higher' guesses, percentages were in the low range (below 10%). Taken together, guesses followed the expected dichotomous pattern.

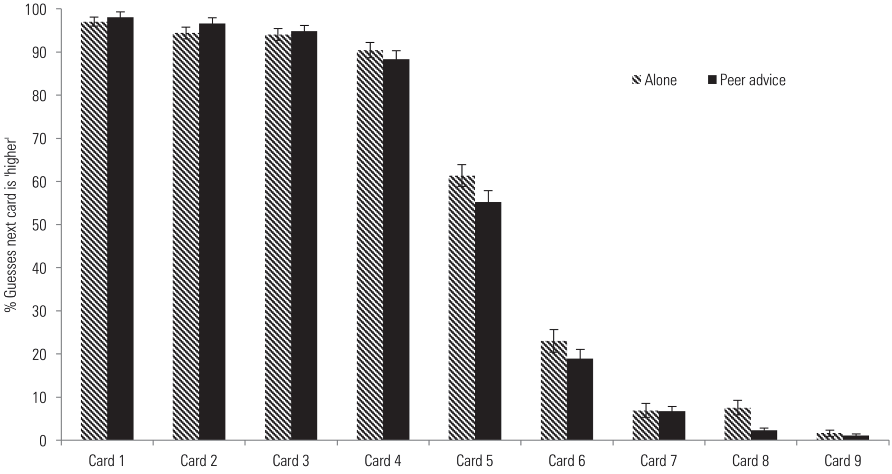


Figure 2. Means (*SE*) for the percentage of guesses that the next card drawn will be higher for each card condition and peer condition. Alone trials are displayed in patterned bars and peer advice trials are displayed in black bars.

The ANOVA also revealed a main effect of Peer presence, $F(1, 74) = 4.55$, $p = .036$, $\eta_p^2 = .058$, qualified by a Card x Peer presence interaction, $F(8, 592) = 2.40$, $p = .015$, $\eta_p^2 = .031$, showing that the effect of the presence of an online peer varied as a function of card condition. Post-hoc analyses (Bonferroni-corrected) revealed that for card 5 ($p = .044$), and card 8 ($p = .002$) participants guessed that the next card would be higher more often in the alone compared to the peer advice condition. The interaction between Gender and Peer presence was not significant, indicating that the effect of peers on guesses was similar for males and females. Lastly, there was an interaction between Card and Gender, $F(8,592) = 3.81$, $p < .001$, $\eta_p^2 = .049$. The differences between the genders were specific to card 2 (males > females, $p = .044$), card 6 (females > males, $p = .017$) and card 8 (females > males, $p = .043$). In these three conditions, males tended to follow the probabilities associated with the cards more than females, respectively a higher % of 'higher' guesses for card 2 and a lower % of 'higher' guess for cards 6 and 8.

Peer advice and gambling behavior

Next, we tested whether the type of advice given by the online peer influenced the number of chips bet by participants. In these analyses we included only *rational* trials (i.e., trials in which participants guessed 'higher' for cards 1 to 4 and 'lower' for cards 6 to 9) because this is a more conservative test that reduces noise in the data. This selection led to the removal of 4.42% of the data (see the supplement for the results from analyses including all trials). Cards with equal probabilities were combined into five card conditions (card conditions 1&9, 2&8, 3&7, 4&6 and 5). For this analysis card condition 1&9 was left out because for those cards the peer advice was always to bet 9 chips. Therefore, in the analyses presented below we included four card conditions.

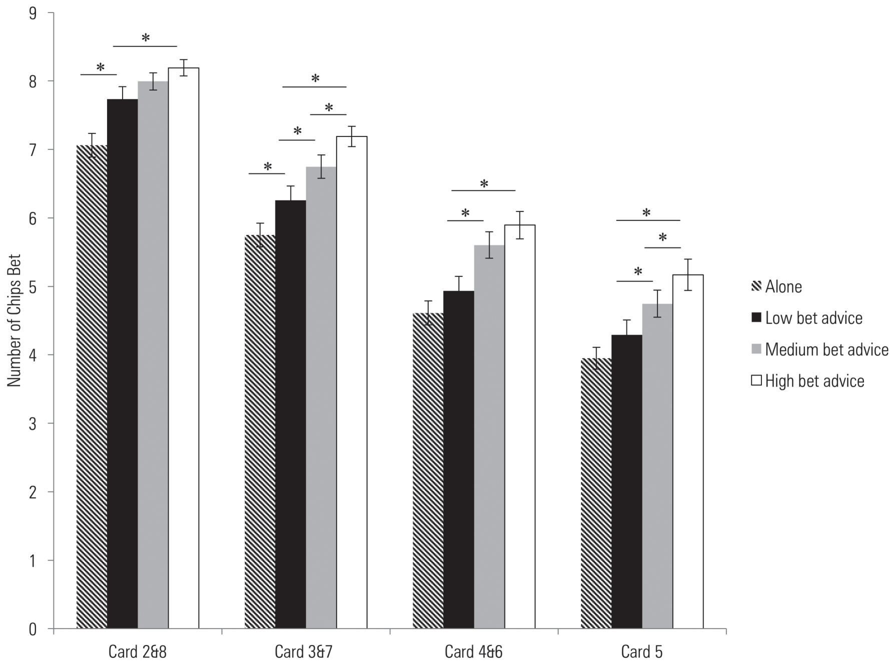


Figure 3. Mean number (SE) of chips bet for alone trials in patterned bar, low bet advice in black bar, medium bet advice in gray bar, and high bet advice in white bar for each card condition separately. *Indicates significant difference at $p < .05$ level (Bonferroni-corrected).

A repeated measures ANOVA was performed with Advice (4; Alone, low, medium, high advice) and Card condition (4; Cards 2&8, 3&7, 4&6, and 5) as within-subject factors and Gender (2; Male, female) as between subjects factor. This analysis yielded two main effects for Advice ($F(3, 222) = 45.76$, $p < .001$, $\eta_p^2 = .380$) and Card condition ($F(3, 222) = 245.70$, $p < .001$, $\eta_p^2 = .769$). These effects were qualified by an Advice x Card condition interaction, $F(9, 666) = 2.32$, $p = .014$, $\eta_p^2 = .030$). Means *(SE)* for number of chips bet per card condition are displayed in Figure 3.

Post-hoc analyses (Bonferroni-corrected) were performed to examine how advice influenced bets for card conditions (for all post-hoc comparisons see Supplementary Table 2). In card condition 2&8 and 3&7 there were significant differences between playing alone and low advice ($p = .001$ and $p = .016$, respectively), such that participants placed higher bets for the low advice condition than for the alone condition. However, in conditions 4&6 and 5, there were no significant differences between alone and low advice (both p's $>$ .05). Furthermore, participants bet more chips for card conditions 3&7 ($p = .001$), 4&6 ($p < .001$), and 5 ($p < .001$), but not 2&8 ($p > .05$) when medium advice was given compared to low advice. The contrast of medium versus high advice revealed that, only for card condition 3&7 and 5, participants placed more chips following high advice compared to medium advice (p's $= .002$). In these categories, participants bet more chips when they received high advice from peers than when they received medium advice.

Taken together, in all card conditions the number of chips bet increased when high advice was given compared to when low advice was given (card condition 2&8, $p = .038$; other p's $< .001$). This increase in bets was larger when higher uncertainty was associated with the outcome, from a 16% increase in the most certain 2&8 condition, to a 20% increase in card condition 3&7 and 4&6, and a 30% increase in card 5. The difference in increase between card condition 5 and the other card conditions was significant (p's $< .05$), whereas the other comparisons between card conditions showed no significant differences (p's $> .05$). Finally, there was an interaction effect of Gender and Card condition, $F(3, 222) = 2.89$, $p = .036$, $\eta_p^2 = .038$. Further analyses indicated that this effect was specific to card condition 2&8 ($p = .009$). Males bet more chips than females in this condition, $M_{males}(SE) = 8.09$ (.17), $M_{females}(SE) = 7.40$(.19). There were no gender differences in the other card conditions (all p's $> .05$). There was no Gender x Advice interaction ($p > .05$).

Reaction times and gambling behavior

Lastly, we tested whether the type of advice given by the online peer influenced reaction times (RTs). We submitted average RTs to a repeated measures ANOVA, with Advice (4; Alone, low, medium, high) and Card condition (4; Cards 2&8, 3&7, 4&6, and 5) as within-subject factors and Gender (2; Male, female) as between subjects factor. This analysis yielded main effects for Advice ($F(3, 222) = 29.51$, $p < .001$, $\eta_p^2 = .285$) and Card condition ($F(3, 222) = 11.27$, $p < .001$, $\eta_p^2 = .132$). These main effects were further qualified by an interaction-effect of Advice and Card condition ($F(9, 666) = 9.20$ ($p < .001$), $\eta_p^2 = .111$). In addition, we found a main effect for Gender ($F(1, 74) = 8.31$, $p = .005$, $\eta_p^2 = .101$). Overall, males ($M_{males}(SE) = 921.08$ ms (50.41)) responded faster than females

($M_{females}$ *(SE)* = 1144.98 ms (59.11)). Mean RTs *(SE)* for each card condition separately are shown in Figure 4.

Post-hoc analyses (Bonferroni-corrected) for the Advice x Card condition interaction showed that RTs did not differ for card condition 2&8, 4&6, and 5 when playing alone compared to when low advice was given (all p's > .05). Only in card condition 3&7 was the RT for low advice shorter than for alone (p = .024). When we compared low advice versus medium advice, for card condition 2&8, 3&7, and 4&6 RTs were shorter for low than for medium advice (p's < .001), but there was no difference in card condition 5 (p > .05). For card conditions 3&7 and 4&6, but not card condition 2&8 and 5 (p's > .05), RTs during high advice were longer than for the medium advice (card condition 3&7, p = .044; card condition 4&6, p = .002). For all reaction time comparisons, see Supplementary Table 2.

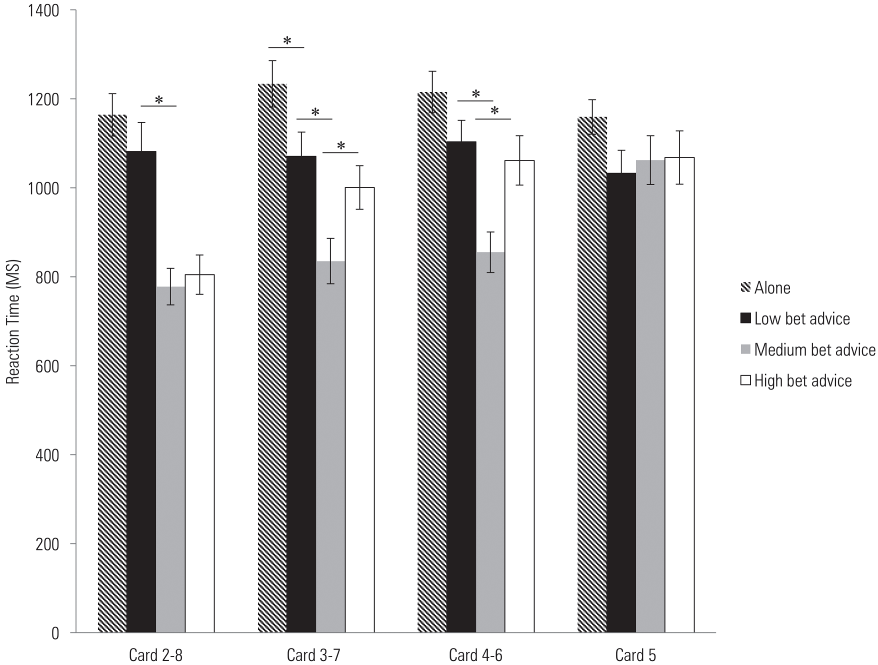


Figure 4. Average reaction times in MS (*SE*) for alone trials in patterned bar, low bet advice in black bar, medium bet advice in gray bar, and high bet advice in white bar for each card condition separately. *Indicates significant difference at p < .05 level (Bonferroni-corrected).

4. Discussion

The aim of the present study was to examine the effects of peer advice on risk-taking behavior from a social norms perspective. This was investigated with a card-guessing task, the Guess Gambling Game (GGG), in which participants received advice from online peers about their decisions. Before playing with peer advice, participants played some trials alone, without peer advice. The GGG included two types of decisions: a guess (is the next card higher or lower) and a gamble (betting chips). Our key finding is that the effects of peer influence on gambling behavior were dependent on the uncertainty associated with the cards, as well as on the social norms conveyed by online peer advice.

The results of this study revealed that guesses showed a dichotomous pattern, which followed the outcome probabilities associated with the cards in both the alone and peer advice conditions. Consistent with prior studies, participants most often selected 'higher' for cards 1 to 4 and 'lower' for cards 6 to 9, while choices for card 5 showed a 50% probability (Critchley et al., 2001; Smith et al., 2014). The similarity between the guessing patterns when playing alone and with peer advice supports the notion that the presence of peers does not alter adolescents' ability to reason about card probabilities or expected value (Reyna & Farley, 2006; Van Duijvenvoorde & Crone, 2013; Van Leijenhorst et al., 2010). As expected, gambling behavior was influenced by general peer presence. Participants placed higher bets when they played in the presence of online peers than when they played alone. These findings corroborate previous work showing effects of peer influence in information-limited contexts such as driving (Chein et al., 2011 age 13-16; Gardner & Steinberg, 2005 age 14-18; Munoz Centifanti, 2014 age 16-20) and information-rich contexts such as Wheel of Fortune tasks (Haddad et al., 2014 age 11-18; Smith et al., 2014 age 15-17). The current study extends this previous work, by showing that different types of advice yield a nuanced pattern of risk-taking behavior in interaction with varying uncertainty in 15-17 year olds.

Peer influence on risk-taking behavior: uncertainty and social norms

In the GGG we used several card conditions, ranging from decisions with a highly uncertain outcome (card 5) to decisions with highly certain outcomes (e.g. card condition 2&8). In all card conditions, participants placed higher bets when they played with peer advice compared to when they played alone, and on average the number of chips bet decreased as uncertainty about the outcomes increased. Importantly, participants' decisions were influenced by the advice given by online peers. Participants placed higher bets when they were given high advice compared to low advice. Risk-taking with a high bet advice compared to a low bet advice increased with uncertainty of the gambles, from a small rise (16%) in the relatively certain condition to a substantial rise (30%) in the most uncertain condition. These findings suggest that, for decisions with a relatively certain outcome, the presence of peers rather than the type of advice is the most important factor influencing decision-making, whereas for decisions with a relatively uncertain outcome, the type of peer advice is the most important factor.

These findings are in agreement with social learning theory (Bandura, 1986). Similar to behavior in the domain of risky driving (Simons-Morton et al., 2011; 2014), gambling behavior varied according to different social norms. Moreover, in line with our hypothesis, peer norms were most influential in the highly uncertain situation (Smith et al., 2014; Cialdini & Trost, 1998). Learning from social norms in peer influence seems to play an important role in the variability seen in risk-taking behavior during adolescence. In general, adolescents tend to overestimate the degree to which their peers take risks and consequently adapt their behavior to that flawed perception (Prinstein & Wang, 2005). In the current study, however, social norms were made explicit by the advice of the online peers. Adolescents may have been inclined to conform to these norms, because they wanted to be accepted by their peers.

Overall, analyses of the reaction times showed that peer presence did not simply facilitate the decision-making process. Under high uncertainty (card 5), participants made their decisions equally quickly when online peers provided them with advice and when they played alone. Interestingly, medium and high advice in card condition 2&8 facilitated the decision-making process (i.e., shorter reaction times), but low advice in the 2&8 condition resulted in longer reaction times, suggesting additional decision-making conflict. One alternative interpretation of these results may be that longer reaction times in these conditions are the result of confusion or disbelief in the task. However, we suggest that this seemingly contradictory effect of peer advice on reaction times is due to the nature of the advice. The advice to bet 1 or 2 chips is not rational in the relatively certain card condition, given that the probability of a favorable card is relatively high. We interpret this contradiction in reaction times as participants taking more time to think about their response upon encountering 'irrational' advice.

Our results suggest that impulsivity alone cannot explain the effects of peer presence on reaction times (also see Krajbich, Bartling, Hare, & Fehr, 2015). Moreover, these findings are different from the findings from studies that focused on delay discounting (Gilman et al., 2014; O'Brien et al., 2011; Weigard et al., 2014) which did find an increase in impulsivity in the presence of peers. Therefore future studies should examine the role of impulsivity and the facilitating versus hindering effects of peers on reaction times in more detail (for a recent discussion on impulsivity, see Steinberg & Chein, 2015).

Gender differences in risk-taking behavior

A secondary goal of this study was to explore whether there were gender differences in susceptibility to peer influence on risk-taking behavior. Although subtle, the gender effect in guessing behavior seems to imply that males tended to guess more in line with expected value than females. In terms of gambling behavior, males showed more risk-taking behavior than females but only in relatively certain decisions. These risks in the relatively certain condition can be considered as an adaptive form of risk-taking behavior because the benefits (double chips) associated with this decision are far more likely to occur than the potential costs (Byrnes et al., 1999). These results fit with previous work on gender differences, showing that males are generally less risk-averse and more sensitive to peer influence than females (Byrnes et al., 1999; Steinberg & Monahan, 2007; Sumter et al., 2009). The "gender gap" in risk-taking behavior seems to vary with the type of risk-taking, age (i.e., decrease over development) and task context but is commonly found in gambling tasks (Byrnes et al., 1999).

Limitations

The age range of participants included in the present study was relatively narrow (15- to 17-year-olds). Although this sample is very comparable to the age range that was previously studied, is of specific interest in terms of brain development, and gave us the opportunity to explore individual differences in gender, it limits our ability to directly compare adolescents to children and/or adults. Given that the broader adolescent peer influence literature has included a larger age-range (11-to-22 year-olds) and shows consistent effects of peer influence, we speculate that our findings may generalize to younger and older adolescent populations. Based on the literature we expect that peer effects would be augmented in adolescents compared to adults (Gardner & Steinberg, 2005). Developmental comparisons would be a relevant extension of the present study and should be addressed in future research, such that we can test whether adolescents are more sensitive to social norms than children or adults.

Another possible limitation of this study is that the task order may have influenced the bets placed and reaction times between alone and peer advice trials, as all participants first played alone and then with peer advice. This order may have resulted in practice or learning effects, and therefore the results should be replicated with a counterbalanced design. Moreover, even though none of the participants reported disbelief in the online peer manipulation, this belief was not directly assessed.

Finally, the social situation provided in this experiment is less complex than social relationships in real-life. A different anonymous online peer gave advice on every trial, such that there was no relationship involved between the participant and the peer and each decision was equally important. We used anonymous peers in this task to control for possibly confounding assumptions about behaviors or beliefs of friends. However, to increase ecological validity, future research could address the effects of the opinions of real friends or include peer characteristics such as social status or likeability in a school environment (see e.g. Burnett Heyes et al., 2015; Welborn et al., 2016). Another interesting direction for future research would be to vary aspects of this task, for example to investigate real-world situations with larger rewards, or to examine social versus monetary reward.

Conclusions

This is the first experimental study that examined peer influence on risk-taking behavior from a social norms perspective. We showed that peers do not alter adolescents' ability to make a rational guess in line with probabilities. Rather, our findings implicate that peer effects on gambling behavior were more nuanced, depending on both social norms conveyed in peer advice and uncertainty associated with the outcome. Together, these results contribute to the understanding of the process underlying peer influence on risk-taking behavior. To gain a deeper understanding of this complex process, future studies should move beyond peer presence effects, to investigating what it is exactly about these peers that results in changes in behavior. In uncertain circumstances, it does seem to make a difference what crowd an adolescent hangs out with. This has important implications for interventions, for example by informing the design of a peer intervention in which we can use peer advice to promote more cautious behavior, that in turn may lead to reduced health-risk behaviors in adolescence.

5. Supplementary material

Peer advice and gambling behavior

We removed 4.42 % of the data for being *irrational* trials. These were trials on which 'lower' was guessed for cards 1 to 4 and 'higher' for cards 6 to 9, which is not in line with the associated probabilities. Results from analyses including all trials were comparable but did result in additional significant differences. In card condition 2&8, the difference between low and medium advice was significant ($p < .05$), and in card condition 4&6, the difference between medium and high advice was significant ($p < .05$).

Peer advice and gambling behavior: Cards 1 and 9

Bets for cards 1 and 9 were analyzed separately to examine whether we would find a similar pattern to the other card conditions. In a repeated measures ANOVA with Condition (2; Alone, high bet advice) and Card (2; 1, 9) as within-subjects factors and Gender (2; Male, female) as a between subjects factor, we found main effects for Peer advice and Card, qualified by an interaction effect of Peer advice x Card, $F(1,74) = 20.72$, $\eta_p^2 = .219$. For card 9 but not card 1, there was a significant increase in number of chips bet when participants played with peer advice compared to alone, M_{alone} (SE) = 8.00 (.16), $M_{peeradvice}$(SE) = 8.76(.08).

Reaction times and gambling behavior: Cards 1 and 9

We also analyzed Cards 1 and 9 separately to examine whether we would find a similar RT pattern. In a repeated measures ANOVA with Condition (2; Alone, high bet advice) and Card (2; Card 1, 9) as within-subject factors and Gender (2; Male, female) as a between subjects factor, we found main effects for Peer advice and Card, qualified by an interaction, $F(1,74) = 5.35$, $p = .024$, $\eta_p^2 = .075$. This interaction indicates that the effect of advice varied as a function of card type. For both cards, there was a significant decrease of reaction time when participants played with peer advice compared to alone (Card 1: M_{alone} (SE) = 954.98(44.30), $M_{peeradvice}$ (SE) = 641.43(36.04); Card 9: M_{alone} (SE) = 1109.19(21.17), $M_{peeradvice}$ (SE) = 687.00 (37.16)). In addition, this analysis yielded a main effect for Gender ($F(1,74) = 6.80$, $p = .011$, $\eta_p^2 = .084$), indicating that overall, males (M (SE) = 766.19 (40.80) responded faster than females (M (SE) = 930.11(47.84) for both cards.

Self-reported resistance to peer influence (RPI)

In addition, we explored individual differences in self-reported resistance to peer influence. Due to missing data ($N = 3$), we included the RPI scores from 73 participants in the final sample. The total scores on the RPI questionnaire in our sample were between 1.50 and 3.80, with M (SD) = 2.98 (.48), and there were no differences between males and females, $t(71) = -.271$, $p > .05$. The scores in our sample were comparable to previously published reports (Dutch sample: Sumter et al., 2009; US sample: Steinberg & Monahan, 2007). To examine whether the change from alone to playing with peers was related to individual differences in resistance to peer influence, we calculated difference scores between the number of chips bet in alone versus peer advice trials, averaged over all cards and for each card condition separately (1&9, 2&8, 3&7, 4&6, 5).

Contrary to our expectations, there were no significant correlations between any of these difference scores for the number of chips bet and the total scores on the RPI questionnaire. This may be due to the fact that the RPI intends to capture sensitivity to peers more generally, whereas our experiment measures one specific domain: gambling behavior (also see Sim & Koh, 2003). Alternatively, our methods may not have allowed us to capture all individual variability in gambling behavior. An exciting novel direction to test individual differences in gambling behavior is to use linear mixed models, which are more applicable to take into account individual differences. Future studies could use a peer influence task in combination with these models to further test the relation with individual differences measures.

2

Table S1. *Mean differences in % guesses that the second card will be 'higher' for all card comparisons.*

	Card 1	Card 2	Card 3	Card 4	Card 5	Card 6	Card 7	Card 8
Card 2	2,18							
Card 3	3,12	0,94						
Card 4	8,25**	6,08*	5,14					
Card 5	38,55**	36,37**	35,43**	30,30**				
Card 6	75,65**	73,47**	72,53**	67,39**	37,09**			
Card 7	90,19**	88,01**	87,07**	81,94**	51,64**	14,55**		
Card 8	92,14**	89,96**	89,03**	83,89**	53,59**	16,50**	1,95	
Card 9	96,08**	93,92**	92,96**	87,83**	57,53**	20,44**	5,89*	3,94*

* $p < .05$ and ** $p < .001$ indicate (Bonferroni-corrected) significant differences between cards.

Table S2. *Mean differences in chips bet and reaction times for all combinations of advice types.*

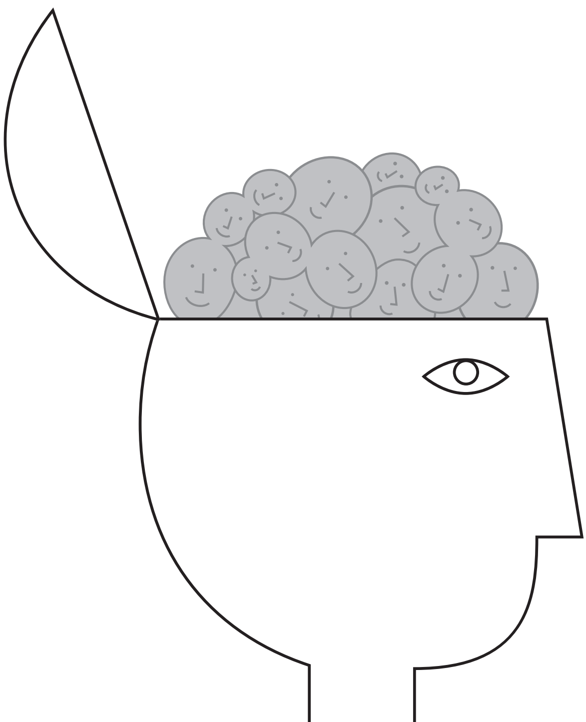
			Chips bet			RT bet	
Card condition	Advice	Alone	Low	Medium	Alone	Low	Medium
2&8	Low	-0,67*			82,19		
	Medium	-0,93**	-0,26		386,14**	303,95**	
	High	-1,13**	-0,46*	-0,20	359,39**	277,20**	26,75
3&7	Low	-0,51*			163,39*		
	Medium	-0,10**	-0,49*		398,58**	235,20**	
	High	-1,44**	-0,93**	-0,44*	232,96**	69,57	-165,63**
4&6	Low	-0,32			112,32		
	Medium	-0,99**	-0,67**		360,19**	247,87**	
	High	-1,28**	-0,96**	-0,29	153,93*	41,61	-206,26**
5	Low	-0,34			126,69		
	Medium	-0,79**	-0,45**		97,17	-29,51	
	High	-1,22**	-0,88**	-0,43*	91,57	-35,12	-5,60

* $p < .05$ and ** $p < .001$ indicate (Bonferroni-corrected) significant differences between peer advice conditions.

Chapter 3:

Peer influence on prosocial behavior

This chapter is published as: Van Hoorn, J., Van Dijk, E., Meuwese, R., Rieffe, C., & Crone, E. A. (2016). Peer influence on prosocial behavior in adolescence. *Journal of Research on Adolescence, 26*(1), 90-100.



Abstract

Adolescence is a time of increased sensitivity to peer influence, which creates vulnerabilities but also opportunities. In this study we examined the influence of peers on prosocial behavior in 12-16 year old adolescents ($N = 197$). We utilized a public goods game in which participants made decisions about the allocation of coins between themselves and the group. Participants received manipulated peer feedback on a subset of decisions. Results indicate a significant interaction between feedback condition (prosocial, antisocial, or no feedback) and allocation choices: prosocial behavior increased after prosocial feedback and decreased after antisocial feedback. These findings support the idea that peer influence creates not only vulnerabilities, but also opportunities for healthy prosocial development and social adjustment learning.

1. Introduction

Why would a teenager who is usually well behaved agree to vandalize a bus stop with his friends? Although one could think of several reasons, there is most likely some form of peer influence behind such behavior. Puzzled parents try to understand why their teenagers act the way they do, and self-help books for teenagers feature intriguing subjects such as *The complete idiot's guide to surviving peer pressure for teens* (Chemiss & Sluke, 2002). In general, peer influence has negative connotations in society. Yet a compelling question is whether peer influence may also serve a positive function. Many have argued that adolescence is a sensitive period for adaptive socio-cultural development (for a review, see Blakemore & Mills, 2014). This study aims to explore the effect of peer influence by examining feedback on adolescents' prosocial decisions.

Social relationships in adolescence

Adolescence is characterized by an increased complexity in social behavior (Lerner & Steinberg, 2004). During this period of socio-cultural development, changes take place concerning healthy identity formation, autonomy in decision-making, intimacy, and sexuality (Dahl, 2004; Pfeifer & Peake, 2012; Steinberg & Morris, 2001). These changes in the social self also bring about changes in relationships with peers and family (Steinberg, 2011). Frequency of face-to-face contact and digital communication with peers increases, whereas time spent with family decreases (Brown, 2004; Rideout, 2012). In addition, friendships become more intimate and supportive, and peers become more important in decision-making (Berndt, 1992; Larson, Richards, Moneta, Holmbeck, & Duckett, 1996).

Within this changing social context, it is important to distinguish between different types of peer relationships (Brechwald & Prinstein, 2011). Besides dyadic bonds with a friend or multiple close friends, adolescents also form relationships with the broader peer group (Klima & Repetti, 2008). That is to say, from middle childhood most interactions with peers occur in groups (Rubin, Bukowski, & Parker, 2006). Previous research has examined a wide variety of peer group types such as cliques, known members of the larger peer group, or an undefined reference group of peers (Prinstein & Dodge, 2008). In the present study, we focus on peer influence from the perspective of an unknown peer group. The reason for focusing on peer influence of unknown peers is to make the context comparable to situations in which adolescents do not know everyone in the peer group, such as in larger public settings, or Internet websites (Weigard, Chein, Albert, Smith, & Steinberg, 2014).

Through peer influence, peers can encourage both harmful and healthy behaviors (Brown, Bakken, Ameringer, & Mahon, 2008). According to social learning theory, adolescents learn social behaviors from valued peers and their peers' reinforcement of displayed behavior (Bandura, 1986). Behavioral display and reinforcement, common forms of peer influence, are processes through which adolescents acquire social norms from the peer group (Brown et al., 2008). In turn, these social norms guide approved and accepted behaviors, informing adolescents of what they ought to do in the peer context (Brechwald & Prinstein, 2011; Cialdini & Trost, 1998). Not only are social norms powerful regulators of behavior and attitudes, but the individual's perception of those norms has an impact as well (Berger, 2008; Prinstein & Wang, 2005). Additionally, the group norms that are acquired may be incorporated in subsequent individual decision-making (Berger, 2008).

In line with this theory of social learning, empirical evidence has consistently shown that peers are a powerful source of influence in adolescence (see for reviews: Brechwald & Prinstein, 2011; Veenstra, Dijkstra, Steglich, & Van Zalk, 2013*)*. Ongoing concern about the health risks associated with negative influence of peers has led to research that focuses mainly on risk-taking and antisocial behaviors (Albert, Chein & Steinberg, 2013; Padilla-Walker & Bean, 2009; Sim & Koh, 2003). Although peer influence and social learning have mostly been linked to these behaviors, they may also be instrumental in prompting adolescents to adopt other types of behavior, such as prosocial behavior (Allen & Antonishak, 2008; Telzer, Fuligni, Lieberman, & Galvan, 2013; Wentzel, 2014).

Prosocial behavior and peer influence

Prosocial behavior can be defined as "voluntary behavior intended to benefit others" and entails a broad multidimensional domain of behaviors, such as altruistic helping, sharing and cooperation (Eisenberg, Fabes, & Spinrad, 2006, p. 646; Padilla-Walker & Carlo, 2014). It includes interpersonal helping behavior, but also cooperation that benefits one's group (Batson & Powell, 2003; Penner, Dovidio, Piliavin, & Schroeder, 2005). These different aspects of prosocial behavior all tap into slightly different processes (Wentzel, 2014). In the current study, we specifically focused on cooperation and operationalized prosocial behavior as cooperation choices that result in a benefit for the group, but in a loss for the individual. With regard to developmental patterns of prosocial behavior, studies have found that adolescents typically exhibit more prosocial behavior than younger children (7-12 year olds) in the domain of sharing and donating (Eisenberg et al, 2006).

Previous work that examined peer influence on prosocial behavior has employed various techniques, including self-report or hypothetical situations, and more recently the use of sophisticated quantitative tools such as social network analysis (Brechwald & Prinstein, 2011; Veenstra et al., 2013). Studies that employed self-report or hypothetical situations suggested that friends or acquaintances can influence prosocial behavior either directly (e.g., the urge to perform a prosocial act) or indirectly (e.g., through expectations or closeness with a friend) (Barry & Wentzel, 2006; Berndt, 1979; Padilla-Walker, Frazer, Black, & Bean, 2014; Wentzel, Filisetti, & Looney, 2007). Recent work that applied social network analyses to study socialization within friendships in children (10-year-olds) also provided some evidence that friends influence prosociality (Logis, Rodkin, Gest, & Ahn, 2013). Other studies focused on the influence of the peer group on prosocial behaviors and showed that the larger peer group exerts influence on prosocial behavior in early adolescents as well (Berger & Rodkin, 2012; Ellis & Zabartany, 2007). Taken together, these studies led to the hypothesis that peers in dyads and peer groups can influence prosocial behavior in adolescence.

The present study

The research aim of this study was to investigate peer influence on prosocial behavior and the process of social learning with an experimental design. We focused on adolescents aged 12-16-years, because prior studies showed that peer influence effects are particularly large in this developmental phase (e.g., Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005; Steinberg & Monahan, 2007). A well-known and validated experimental approach for studying the process of social decision-making is the use of social dilemmas (for a review, see Van Lange, Joireman, Parks, & Van Dijk, 2013). In the context of developmental psychology, these games are particularly informative in studying the development of core features of social decision-making, such as acting upon social norms and fairness considerations (Crone, Will, Overgaauw, & Güroğlu, 2014).

The public goods game (PGG) is a social dilemma that incorporates self-interest and concern for the group as two key motivational aspects of prosocial behavior when asked to divide tokens in a group (Ledyard, 1995). We adapted the typical PGG so that participants repeatedly made real and anonymous social decisions in a group, while no information was provided about the decisions of the other group members. To test the hypothesis that peers influence prosocial choices, we introduced peer influence on the decisions in the game. Participants played several rounds of the PGG on the computer in a group of four classmates, while a spectator group of ten same-age peers from another school was supposedly online during half of the rounds. Depending on the between subject condition, these supposed spectators could provide antisocial feedback, prosocial feedback, or no feedback. In the *antisocial feedback* condition, keeping tokens to the self (i.e., maximizing one's own outcome) received many thumbs up from the peer group, whereas in the *prosocial feedback* condition, donations to the group received many thumbs up. In the *no feedback* control condition the spectator group was online, but participants did not receive feedback on their decisions. After the rounds in which the spectator group provided feedback on decisions, the spectator group went offline and participants played several rounds without peer feedback; these anonymous rounds were similar to the first rounds of the PGG.

First, we hypothesized that prosocial behavior would decrease after antisocial feedback from peers (Chein et al., 2011; Gardner & Steinberg, 2005). Prosocial behavior in this task was defined as the number of tokens donated to the group. In accordance with social learning theory, we expected that the social learning process would entail learning about the social norm of the peer group, and consequently, that participants would incorporate this social norm in their decision-making (Bandura, 1986; Berger, 2008). Because the spectator group in the antisocial feedback condition provided many thumbs up when the participant kept tokens to the self, we expected to see a gradual *decrease* in prosocial behavior over trials in which antisocial feedback was provided.

Second, previous studies suggested that peers have a positive influence on prosocial behavior (Barry & Wentzel, 2006; Berger & Rodkin, 2012; Berndt, 1979; Logis et al., 2013). We hypothesized that prosocial behavior would gradually *increase* after prosocial feedback from peers, as large donations to the group were evaluated with many thumbs up and a similar social learning process could be anticipated for this type of feedback. Third, we hypothesized that prosocial behavior in the no feedback condition would remain in between the levels of prosocial behavior displayed in the feedback conditions over the course of the task. In the absence of feedback, no extrinsic motivation such as a social norm was provided to induce a behavior change.

Fourth, we hypothesized a *carry-over effect* of peer feedback in the prosocial and antisocial feedback conditions. In line with social learning theory, social behaviors may be learned through several sources of information, such as social evaluations (Bandura, 1986). Playing several trials with norms of the spectator group in the peers public goods game may provide information about different behavioral alternatives, thereby socializing adolescents through expectations and social reinforcement for their actions (Eisenberg et al., 2006). Thus, we expected that the effects of feedback would be apparent in subsequent individual decisions even if the peer group would no longer be present and watching, because we expected participants to maintain the social norm (Bandura, 1986; Berger, 2008). In the antisocial feedback condition, we predicted that the donations to the group would be smaller in the anonymous rounds after peer feedback relative to baseline trials. In the prosocial feedback condition, we expected to find a higher level of donations to the group in the anonymous rounds after peer feedback relative to baseline trials.

2. Method

Sample and Participant Selection

The sample consisted of 197 adolescents between the age of 12 and 16 years (M = 14.14, SD = 1.09, range 12.38-16.48), including 110 girls (56%) and 87 boys (44%). The ethnic composition of the sample was 94% Dutch, 5% Moroccan, and 1% classified as "Other". No measure for socio-economic status (SES) was obtained for this sample. Besides the age-range, no other exclusion criteria were applied in this study. We recruited participants from three high schools teaching various academic levels in and around Leiden, the Netherlands. Both parental consent and participant's consent for minors was obtained for all participants. The participation rate was high (94%). Thirteen participants from the original sample (N = 210) were excluded due to incomplete data. For a subset of the participants (N = 120), a short version of Raven's progressive matrices was obtained as an index for estimated intelligence. Raven data from the remaining participants were unavailable due to technical difficulties. All raw estimated IQ scores were in the normal range (M = 39.29, SD = 4.28; see Table 1).

Participants were divided amongst the three conditions in a semi-random manner, $N = 49$ (25%) in the antisocial feedback condition, $N = 50$ (25%) in the no feedback condition and $N = 98$ (50%; oversampling) in the prosocial feedback condition. The prosocial feedback condition was oversampled to conduct further analyses on positive peer influence in relation to, for example, self-presentational tactics and resistance to peer influence. Supplementary materials are available upon request from the first author.

Measures

Peers public goods game. A linear public goods game (Harbaugh & Krause, 2000; Ledyard, 1995) was adapted to meet the goals of this study. Participants were divided into groups of four anonymous classmates to play the PGG online. They were told that the topic of the study was decision-making in groups and that their group would get the opportunity to earn a monetary bonus. At the beginning of each round, participants were given ten tokens with an exchange value of 50 Eurocents per token. No further rationale was provided for the number or value of the tokens. Subsequently, they made a decision whether they wanted to keep the tokens to themselves or contribute to the group by giving any portion of the tokens to the public goods pot. They were informed that after each round, donated tokens were multiplied by two and then divided equally amongst the four group members, independent of the individual contributions.

Thus, the individual optimal strategy in this game is to donate nothing, whereas the optimal strategy for the whole group is for all members to donate all tokens (Harbaugh & Krause, 2000). Given that individual contributions are multiplied by two, in this four-person group the net return of contributing for example one token is that one loses 0.50 token (i.e., the net return is negative; the token is multiplied by 2, but then divided equally among all 4 group members). Donating the token thus constitutes a loss to the individual. However, on the collective level, if all group members would contribute one token, the group would profit (4 tokens multiplied by 2, then divided by 4 group members equals 2 tokens) and all group members would earn more than if they each kept the tokens to themselves.

To prevent learning from the decisions of the fellow group members, participants did not receive feedback about the payoff after each round. All choices were made individually and anonymously, and participants were told that their fellow group members could not see their respective donations. The peers public goods game consisted of twenty trials, divided in three phases. First, participants played five self-paced baseline trials (trials 1-5), in which they made their decisions individually and anonymously. Second, participants learned that a spectator group of ten same age peers would be online during the consequent rounds (trials 6-15) and that the spectator group could see their decisions on the task (Figure 1A). Additionally, they were told that the peers from the spectator group would evaluate each decision. During this second phase they played 10 trials with peer feedback, which was displayed within a randomized interval of 3 – 7 s after the participant made a decision (Figure 1B). Third, after these 10 online trials, the spectator group went offline and could not see the participant's decision anymore. Participants played 5 more trials (trials 16-20), similar to the baseline trials in which they made their decisions individually and anonymously.

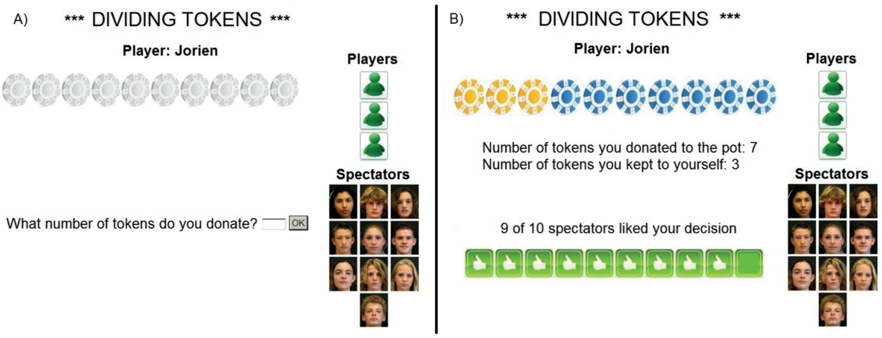


Figure 1. Peers public goods game.

(A) Online Decision Screen. The three players (green) are anonymous classmates, who are not able to see the decisions of the participant. The fictitious spectator group is online, indicated by pictures of same-age peers (5 males/5 females). These peers can see the decisions of the participant. (B) Online Prosocial Feedback Screen. The participant donated seven tokens to the group of anonymous classmates (blue) and kept three tokens (yellow). The fictitious spectator group provided prosocial feedback on the decision. Nine thumbs up indicate that nine out of ten peers liked the allocation of tokens.

We utilized a between-subjects design in which we compared two types of feedback: antisocial feedback, prosocial feedback, and no feedback as a control condition. In the antisocial feedback condition, keeping tokens to the self (i.e., maximizing one's own outcome) received many thumbs up, whereas in the prosocial feedback condition, donations to the group received many thumbs up. The no feedback control condition was similar to the feedback conditions in the sense that participants were informed that a spectator group would evaluate their decisions, so participants anticipated the possibility of feedback. The only difference in the *no feedback* control condition was that after making their decisions, participants were not shown any feedback.

The feedback participants received was dependent on the condition and contingent on the decision that was made. An example of the feedback is presented in Figure 1B. More specifically, participants were told that the peers from the spectator group would judge their decision with a *like* if they liked the decision and would leave the box empty if the decision was not liked. If a participant in the prosocial feedback condition donated zero, one, two or three tokens to the group, they received one or two thumbs up from the spectator group (randomly varied). When participants donated four, five or six tokens to the group, they received four, five or six thumbs up, and finally, they received nine or ten thumbs up if they donated seven, eight, nine or ten tokens to the group. The exact reverse feedback pattern was used in the antisocial feedback condition, such that high donations to the group received only one or two thumbs up, and low donations to the group resulted in nine or ten thumbs up. A written statement indicating the number of peers that liked the participant's choice accompanied the likes. For example, in Figure 1B nine likes indicate feedback that nine out of ten peers liked the decision of the participant.

Pictures of the 10 peers from the spectator group (previously validated in Gunther Moor, Van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010) were presented on the screen when participants made their decision in these online trials. The spectator group pictures were semi-randomly drawn from a database (age-matched; 5 males/5 females), and the same peer group was present during all trials.

Procedure

The study was conducted in a regular computer room or media library at school, with adolescents who were enrolled together in class. If possible, participants were separated by an empty seat. The experimenter explained the procedure to the class. The study was composed of three different online elements: a task in which they were asked to divide coins (PGG), a computer game with puzzle pieces (Raven), and finally several questionnaires. These questionnaires were used to provide additional information for future studies. After the procedure was explained to the class, all participants agreed to the procedure and started at the same time during the PGG to ensure the credibility that they were playing with their classmates. Three research assistants were present at all times to provide help. After the online individual instruction we included three quiz questions to ensure that all participants understood the PGG; they could not start with the game unless the right answer to these questions was provided. During the subsequent debriefing, participants were informed about the exact setup of our study; after all participating classes on a school were tested. Afterwards, the participants were given a small present for their participation in the study.

Data analysis

To control for possible confounding effects of estimated intelligence and gender, we conducted two separate analyses on prosocial behavior in the PGG in which we included these variables. Neither gender nor estimated intelligence appeared significant and these variables were excluded from further analyses. Additionally, participants were asked whether they fully understood the instructions of the PGG and, indirectly, whether they believed the spectator group was real. We performed additional analyses in which we excluded participants of whom we suspected did not fully understand or believe the task ($N = 9$) and found no changes in the results. Hence, we included all participants ($N = 197$) in the final analyses.

3. Results

Demographic variables

Table 1 shows the demographic variables of the sample for each feedback condition separately. Analyses indicated no significant differences between feedback conditions in terms of sex, age and estimated intelligence.

Table 1. *Demographic variables*

	Antisocial feedback $N = 49$	Prosocial feedback $N = 98$	No feedback $N = 50$
Sex (M; %)	23 (47%)	41 (42%)	23 (46 %)
Age in years (*SD*)	13.91 (1.07)	14.20 (1.13)	14.25 (1.01)
Short Raven IQ (*SD*)	39.29 (3.95)	39.38 (4.03)	39.11 (5.19)

Peers Public Goods Game

To analyze the temporal pattern of donations in the PGG, the trials were split into four blocks of five trials: (1) offline trials 1-5, (2) online trials 6-10, (3) online trials 11-15, (4) offline trials 16-20. The donations to the group were assessed by a 3 (Feedback: antisocial feedback, prosocial feedback, no feedback) x 4 (Block: 1, 2, 3, 4) ANOVA with repeated measures of the last factor. Means for the number of tokens donated to the group in block and feedback condition are displayed in Figure 2.

The analysis showed a main effect of feedback, $F(2, 193) = 3.68$, $p = .027$, *partial* $\eta^2 = .047$. Donations to the group in the antisocial feedback condition, *M (SD)* = 3.64 (0.26), were lower than in the prosocial feedback condition, *M (SD)* = 4.44 (0.18), $p = .039$. Donations to the group in the no feedback condition, *M (SD)* = 3.87 (0.18), were in between the prosocial and antisocial feedback condition and did not differ from either, both p's = *ns*. This main effect of feedback was qualified by a feedback x block interaction, $F(6{,}579) = 30.23$, $p < .001$ (Greenhouse-Geiser corrected), *partial* $\eta^2 = .239$. Further analyses were done to examine the pattern of donations over trials for each feedback type separately. In the antisocial feedback condition, we found that adolescents donated significantly fewer tokens to the group over trials after feedback from their peers; donations were lower in block 2 after antisocial feedback from peers than in block 1, $p < .001$. A further decrease was found in block 3 compared to block 2, $p = .008$. During the offline trials in block 4, the donations to the group were significantly higher than in block 3, $p = .011$.

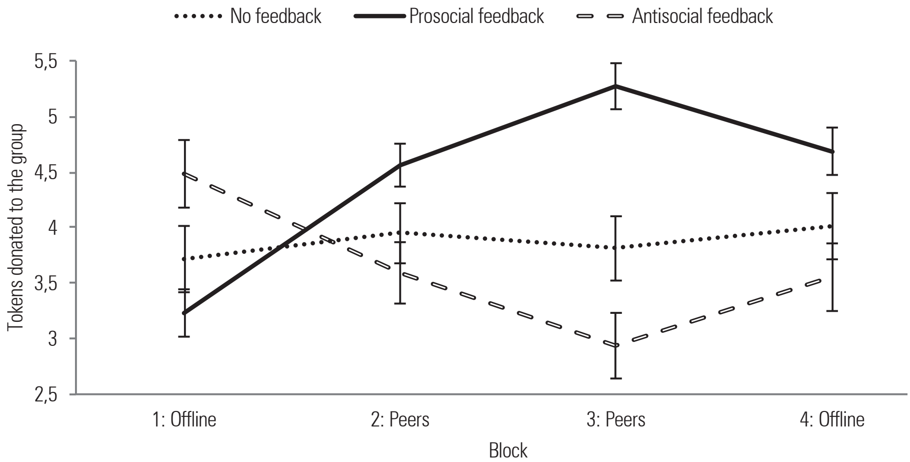


Figure 2. Mean number of tokens (*SE*) donated to the group over the course of the PGG task.

In line with our predictions, the findings of the prosocial feedback condition revealed a positive effect of peer influence. Adolescents in the prosocial feedback condition donated significantly more to the group after feedback from their peers; more tokens were donated to the group in block 2, in which participants received prosocial feedback from peers, than in block 1, $p < .001$. We found a further increase in donations in block 3 compared to block 2, $p < .001$. In block 4, the donations to the group were lower than in block 3, $p < .001$. However, adolescents who received prosocial feedback showed significantly higher donations in block 4 than block 1, $p < .001$.

The donations to the group in the no feedback condition did not change during the online trial blocks by the presence of peers (without feedback), all p's = *ns*. Levene's test indicated equal variances ($F(1{,}98) = .10$, $p = ns$) in the online trial blocks (block 2 and

3) compared to block 1. Finally, we examined the hypothesized carry-over effect in the antisocial feedback and prosocial feedback conditions. We expected that the feedback provided in online block 2 and 3 would still influence decisions during the offline trials in block 4, where feedback was no longer provided. This effect, indicated by a significant difference between donations to the group in block 4 and baseline block 1, was found in both antisocial and prosocial feedback conditions. Thus, even though the peer effects diminished from block 3 to 4 in both the antisocial and prosocial conditions, adolescents in the antisocial feedback condition showed significantly lower donations in block 4 relative to block 1, $p = .004$. Similarly, adolescents who received prosocial feedback showed significantly higher donations in block 4 than in block 1, $p < .001$.

4. Discussion

The goal of the present study was to examine peer influence on prosocial behavior and the process of social learning. The key finding in our study was that changes in prosocial behavior depended on the behavior that was liked by the peer group. Prosocial behavior decreased when peers liked the decision to keep tokens to the self, and similarly prosocial behavior increased when peers liked decisions to donate the tokens. When no feedback was provided, prosocial behavior remained stable and did not change over multiple consecutive decisions. As expected, the level of prosocial behavior in the no feedback condition remained in between the levels of prosocial behavior displayed in the feedback conditions over the course of the task.

Peer influence on prosocial behavior

Our findings build on a large body of research indicating that peers are a major influence in adolescent decision-making (Albert et al., 2013; Brechwald & Prinstein, 2011). We showed that peers can have a direct *negative* influence on prosocial behavior. Moreover, we demonstrated that peers may also have a direct *positive* influence on prosocial behavior in adolescence. These findings provide support for the theoretical viewpoint of adolescence being a period that creates not only vulnerabilities, but also opportunities for healthy prosocial development and social adjustment learning (Blakemore & Mills, 2014; Crone & Dahl, 2012).

The change in level of prosocial behavior over the course of the task suggests that the process of social learning is a key mechanism for adapting to the social norms of the peer group (Bandura, 1986). In both feedback conditions, the patterns of prosocial behavior imply that adolescents first learned the social norms from the spectator group of peers and consequently incorporated those norms in their decision-making (Berger, 2008; Harbaugh & Krause, 2000). Thus, peer influence appears crucial in the transmission of group norms (Clasen & Brown, 1985). As one of our participants nicely put it:

"I thought it was useful to be able to see what peers thought about my decisions. That way you know whether you don't make really crazy decisions. Even though the decisions are for yourself, it is nice to see what others think of them [decisions]."

Because social acceptance and approval are highly salient in adolescence, a time period of social reorientation in which peers' opinions become more important, social reward is likely an important guide for social behavior (Berger, 2008; Somerville, 2013; Steinberg & Morris, 2001; Wentzel, 2014). An intriguing follow-up question that we tested was whether the peer effects of prosocial and antisocial feedback would be apparent in consequent individual decisions, with peers no longer present. As expected, this carry-over effect was present after both prosocial and antisocial peer feedback. A higher level of prosocial behavior was displayed in consequent individual decisions after prosocial feedback compared to baseline, and a lower level of prosocial behavior was found in consequent decisions when antisocial feedback was provided. It may be noted that there was an initial difference in the level of prosocial behavior between the prosocial and antisocial feedback conditions on the baseline trials. We believe that this difference can be attributed to chance, because the participants were randomly assigned to conditions and there were no significant differences between groups on measures of age, sex ratio and estimated IQ. Interestingly, both prosocial and antisocial peer feedback seem to override these initial differences in the level of prosocial behavior.

These findings may imply that social norms provided by the group are to some extent maintained in subsequent individual decision-making. Even though there was a small trend towards the baseline from block 3 (peer presence) to block 4 (alone), prosocial behavior in the prosocial and antisocial feedback conditions was clearly different between the first and last alone blocks. Note, however that this design only allows us to draw conclusions about short-term effects. The observed change in the trajectory of prosocial behavior in both conditions may indicate that participants eventually return to the initial level of prosocial behavior. Previous work suggests that the extent to which social norms truly guide social decision-making and behavior depends on whether those norms are internalized, rather than just learned by the individual (Staub, 1972). For future research it would be interesting to add additional rounds of the public goods game, to further examine to what extent the social norms provided by peer feedback are internalized and continue to guide individual decisions over time. Ideally, a longitudinal design could be implemented to study the sustainability of a causal relation between peer effects and prosocial behavior.

Peer presence effects on prosocial behavior

Prosocial behavior did not change over the course of the task by the mere presence of peers when no feedback was provided. These findings suggest that feedback provided by peers is crucial in actuating change in prosocial behavior. In contrast, in other domains of behavior the presence of friends and acquaintances has previously been linked to change in behavior. For example, an increase has been observed in risk-taking behavior by the mere presence of peers (Chein et al., 2011; Gardner & Steinberg, 2005). Although social influence theories suggest that the relationship between the adolescent and source of the influence (e.g., friendship quality) may relate to consequent behavior change, the question remains whether friends exert more influence on behavior than unfamiliar peers from the larger peer group (Berndt, 2002; Hartup, 2005).

A recent study illustrated that the belief that an anonymous peer is watching an adolescent participant in the MRI-scanner induces self-conscious emotions and autonomic arousal, even when there is no decision-making process involved (Somerville et al., 2013). Thus, it seems that the mere presence of unknown peers already elicits strong neurophysiological responses. In addition, this feeling of being observed by an anonymous peer has also been linked to a change in reward-related behavior: adolescents who believe unknown peers are observing them show a preference for immediate rewards as opposed to long-term rewards (Weigard et al., 2014). Interestingly, those findings illustrate effects of peer presence on behavioral and neurophysiological measures (Somerville et al., 2013; Weigard et al., 2014), however in the present study we did not find an effect of peer presence on prosocial behavior. This disparity suggests that the effects of peer presence may depend on the domain of behavior (i.e., risk-taking behavior or prosocial behavior) (Sim & Koh, 2003).

One possible interpretation is that the differential effect of peer presence for risk-taking behavior and prosocial behavior is related to the social norms associated with behaviors in each domain. In experimental risk-taking paradigms, such as the Stoplight game (Chein et al., 2011), the injunctive norm for risk-taking behavior in the presence of peers originates from the individual's perception of risk-taking behaviors of those peers (Cialdini & Trost, 1998). In general, adolescents tend to overestimate the degree to which their peers engage in risk-taking behavior (Prinstein & Wang, 2005). Subsequently, an individual may engage in risk-taking behavior as frequently as perceived in the peer group. These overestimated risk-taking behaviors are then expected to elicit approval and positive social reward from the peer group. Peer presence may thus reinforce the perceived social norm and thereby lead to increased risk-taking behaviors (Prinstein & Wang, 2005).

The present study adopted the social dilemma approach to study prosocial behavior. It may be less evident which of the two dilemmatic options (i.e., further the self-interest or the collective interest of the group) peers will accept in the public goods game. We suggest that peer presence did not lead to a change in prosocial behavior, because the norms related to prosocial behavior are more ambiguous than in the risk-taking paradigm and are not reinforced by the mere presence of peers.

Limitations and conclusions

This study had several limitations. First, we used an age group of adolescents ranging from 12-to-16-year-olds. This narrow age-range limits our ability to make developmental comparisons with other age groups such as children or adults. The *direction* of this peer effect could be similar in other age groups such as adults and children. An expectation derived from this study is that the *strength* of the effect might differ between age groups based on the hypothesis of increased social sensitivity in adolescence (Blakemore & Mills, 2014; Wentzel, 2014). One could argue that this increased social sensitivity might result in stronger effects of peer influence on prosocial behavior in adolescence. Developmental comparisons would be an informative extension of the present study that should be addressed in future research. Additionally, this paradigm included only peers to provide feedback on the decisions. An interesting direction for future research is to introduce different actors, such as adults or family members, in the paradigm, as it creates a possibility to examine whose feedback is most influential. Second, our paradigm was designed to measure peer influence and the social learning process during the task and consequently only conclusions about short-term effects can be drawn. At present, it is unclear to what extent the social norms provided by peer feedback are internalized and continue to guide individual decisions over time.

Third, a person's expectation about the behavior of others is another major factor that has been shown to affect prosocial behavior in the public goods game (Dijkstra, 2012; Fishbacher, Gächter, & Fehr, 2001; Gächter & Fehr, 2000). That is, participants may expect other group members to adapt their behavior in line with the social norms of the peer group. Consequently it is possible that participants adjusted their own behavior because they thought that other group members would adapt to the peer norms. Our design does not allow us to disentangle the direct effects of peer feedback and possibly indirect effects of peer feedback on the other group members, because feedback was consistent across trials. In future research, it will be interesting to apply the paradigm to real social interactions to examine the complex interplay between prosocial choices and expectations about prosocial choices.

Despite these limitations, this was the first study that utilized an experimental design in which real, on-the-spot, prosocial behavior was measured. The current study focused on one aspect of prosocial behavior: cooperation. The findings from our new paradigm are consistent with previous work in which other developmental measures were utilized, suggesting that the experimental paradigm is a valid measure that taps into a similar process (Barry & Wentzel, 2006; Berger & Rodkin, 2012; Berndt, 1979; Ellis & Zabartany, 2007; Padilla-Walker et al., 2014; Logis et al., 2013; Wentzel et al., 2007). In future studies it will be important to study peer effects on other aspects of prosocial behavior as well, for example sharing and altruistic helping. In addition, it will be valuable to relate these effects to real-life behavior, such as donating behavior.

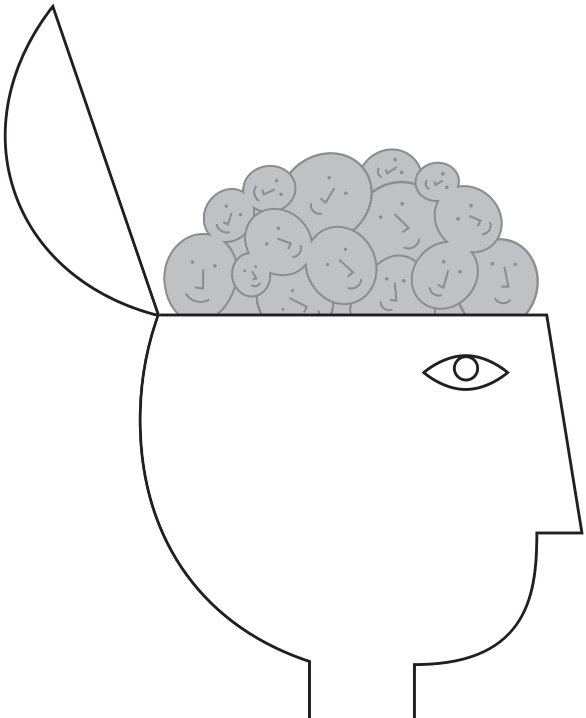
Moreover, we attempted to address a gap in current knowledge by providing insights about the process of social learning in peer influence. For these purposes, we aimed to show that useful results about the process of prosocial behavior in adolescence can be obtained with the novel peers public goods paradigm. Thus, in the present study, we provided a social context that admittedly may be less complex than social situations in everyday life. Future studies using the basics of this experimental paradigm may include several variations in social context to provide an even better match of day-to-day social situations. For example, an interesting suggestion for future research would be to examine the effects of peer influence and peer presence of a spectator group that includes actual friends.

In conclusion, our study provides support for the view of adolescence as a period of vulnerabilities, but also a period of opportunities for social learning and adaptation. Teenagers who vandalize a bus stop with their friends, could instead be encouraged by their peers to be prosocial.

Chapter 4:

Neural correlates of peer influence on prosocial behavior

This chapter is published as: Van Hoorn, J., Van Dijk, E., Güroğlu, B., & Crone, E. A. (2016). Neural correlates of prosocial peer influence on public goods game donations during adolescence. *Social Cognitive and Affective Neuroscience.* doi:10.1093/scan/nsw013



Abstract

A unique feature of adolescent social re-orientation is heightened sensitivity to peer influence when taking risks. However, positive peer influence effects are not yet well understood. The present fMRI-study tested a novel hypothesis, by examining neural correlates of prosocial peer influence on donation decisions in adolescence. Participants (age 12-16 years; $N = 61$) made decisions in anonymous groups about the allocation of tokens between themselves and the group in a public goods game. Two spectator groups of same-age peers – in fact youth actors – were allegedly online during some of the decisions. The task had a within-subjects design with three conditions: (1) *Evaluation:* spectators evaluated decisions with likes for large donations to the group, (2) *Spectator:* spectators were present but no evaluative feedback was displayed, and (3) *Alone:* no spectators nor feedback. Results showed that prosocial behavior increased in the presence of peers, and even more when participants received evaluative feedback from peers. Peer presence resulted in enhanced activity in several social brain regions including mPFC, TPJ, precuneus, and STS. TPJ activity correlated with donations, which suggests similar networks for prosocial behavior and sensitivity to peers. These findings highlight the importance of peers in fostering prosocial development throughout adolescence.

1. Introduction

Adolescence is a transition period between childhood and adulthood with major changes in cognitive and social-affective reasoning (Steinberg & Morris, 2001). Social evaluation is highly salient during this time and adolescents become more sensitive to peer influence (Albert, Chein, & Steinberg, 2013; Blakemore & Mills, 2014; Gardner & Steinberg, 2005). Neuroimaging studies have shown that changes in social cognition during adolescence are paralleled by changes in the social brain network (Blakemore, 2008; Blakemore & Mills, 2014; Crone & Dahl, 2012; Van Overwalle, 2009). In this network that supports thinking about self and others, brain regions such as medial prefrontal cortex (mPFC), temporal parietal junction (TPJ) and superior temporal sulcus (STS) show developmental changes in structure and function throughout adolescence (Blakemore, 2008; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014).

Peer influence has been most extensively studied in the context of adolescent risk-taking and reward-related processing in the brain. Several studies have shown that adolescents engage in more risk-taking behavior when they are being observed or accompanied by peers (Albert et al., 2013; Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005; Smith, Steinberg, Strang, & Chein, 2015). Brain regions associated with the affective processing of risks and rewards, like the ventral striatum, are more activated when peers observe risky choices and this effect is larger in adolescents than in adults (Chein et al., 2011). Very few studies, however, have assessed whether peers can also influence behavior in a *prosocial* manner. Recent behavioral findings indicate that peers influence donations in a public goods game such that adolescents show higher levels of prosocial behavior when peers provide positive feedback to prosocial behavior (Van Hoorn, Van Dijk, Meuwese, Rieffe, & Crone, 2016). The current study seeks to expand this research and sets out to test how peer influence is associated with the activation of brain regions involved in (pro)social behavior during adolescence.

Previous research in adults has suggested an important role of the mPFC and the ventral striatum in the context of peer evaluation. When adults were asked to report their behavioral tendencies with regards to social norms in the presence of observers, increased activation in mPFC and ventral striatum was found compared to the absence of observers (Izuma, Saito, & Sadato, 2010a). Moreover, one prior study examining prosocial donation rates in adults has shown that the presence of observers during donations was associated with increased activity in ventral striatum (Izuma, Saito, & Sadato, 2010b). There is also consistent evidence across imaging studies that mPFC is active when individuals are "mentalizing," or thinking about thoughts or attributes of the self and others (Frith & Frith, 2006). Finally, mPFC is implicated in social influence and relates to persuasion-induced behavior change after social influence (Falk, Berkman, Mann, Harrison, & Lieberman, 2010; Falk et al., 2014; Welborn et al., 2016).

From a developmental perspective, several studies have additionally reported that mPFC is more active in adolescence than in adulthood when performing mentalizing tasks (Blakemore, 2008; Burnett, Bird, Moll, Frith, & Blakemore, 2008; Gunther Moor et al., 2012). These effects are largest during early adolescence (Gunther Moor et al., 2012; Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2011). Possibly, (early) adolescence is a time window when peers have a heightened influence on mPFC activity (Braams, Peters, Peper, Güroğlu, & Crone, 2014; Pfeifer et al., 2009; Somerville et al., 2013).

Present study

The goal of this study was to investigate the effects of peers on prosocial behavior and neural activity in adolescence. We examined developmental patterns in adolescents of two age groups: 12-13 year-olds and 15-16 year-olds. Peer influence in fMRI studies has previously been examined in a relatively wide age-range of adolescents, ranging from 14-19 year-olds (Chein et al., 2011; Smith et al., 2015; Welborn et al., 2016). However, behavioral work shows strongest peer influence effects in 13-16 year-olds (Gardner & Steinberg, 2005) and increased self-reported peer resistance between ages 14 and 18 years (Steinberg & Monahan, 2007). Moreover, previous fMRI studies that investigated mentalizing and reciprocity in social interactions showed a heightened mPFC response in early adolescents (12-14 years) and a decrease to adult levels in 15-17 year-olds (Gunter Moor et al., 2012; Van den Bos et al., 2011). Therefore, we tested if peer influence effects were different in early (12-13 years) versus mid adolescence (15-16 years).

The present study used a novel paradigm to test effects of peer influence on prosocial behavior, in which we aimed to disentangle peer effects on neural activity during the decision-making and feedback phase. For that purpose we adapted the public goods game (PGG), a well-established method to investigate prosocial behavior, specifically cooperation that benefits one's group rather than own outcome (Batson & Powell, 2003; Ledyard, 1995; Penner, Dovidio, Piliavin, & Schroeder, 2005). Behavior in the PGG is not necessarily altruistic, but represents an important dimension of prosocial behavior, which is giving to the group for the benefit of others.

In this social dilemma, participants make decisions in anonymous groups about the allocation of tokens between themselves and the group. Prosocial behavior is measured as the number of tokens donated to the group. Peer influence is examined by asking participants to perform the task with spectators who provided prosocial feedback by giving thumbs up to larger donations (Evaluation condition), with spectators present but no feedback (Spectator condition), and without spectators (Alone condition). The spectator groups were composed of age-matched youth actors who were present at the start of each session. Participants met these peers beforehand, thereby increasing the ecological validity of the design because a 'real' social context was created.

We predicted that being observed by spectators would lead to increased activity in mPFC when making PGG donations (Izuma et al., 2010b). In addition, we expected that the impact of peer influence on mPFC activity would be larger for 12-13 year-olds than for 15-16 year-olds, as prior findings have shown that mPFC activity is most malleable in this age range (Gunther Moor et al., 2012; Van den Bos et al., 2011).

2. Methods

Participants

This study included participants of two age groups: 12-13 year-old adolescents (M_{age} = 12.93; N = 31; 15 males) and 15-16 year-old adolescents (M_{age} = 16.08; N = 30; 14 males). An additional 4 participants from the original sample (total N = 65) were excluded either due to excessive movement (N = 3; > 3 mm in any direction) or technical problems (N = 1). Further background information about the final sample can be found in Supplementary Table 1. Participants were recruited via local secondary schools and through our participant recruitment database. The majority of the participants was born in the Netherlands (93%) and a minority was born elsewhere (England (3%) and USA (1%)), or missing (2%). All participants were fluent in both spoken and written Dutch. We screened participants in a private telephone conversation to ensure that they were free of neurological disorders, psychiatric disorders or any MRI contra indications. When at the lab, all participants and their parents signed an informed consent form prior to the start of the study. The institutional review board of Leiden University Medical Centre approved all procedures.

To obtain an estimate of IQ, we used the subscales Similarities and Block Patterns from the Wechsler Intelligence Scale for Children (WISC-III) for participants under 16 years and the same subscales from the Wechsler Intelligence Scale for Adults (WAIS-III) for participants 16 years and older (Wechsler, 1991; Wechsler, 1997). The estimated IQ scores fell within the normal range for all participants (M = 109.67; SD = 10.72) and did not differ between age groups ($t(59) = 1.58$, $p > .05$).

4

Experimental design

Peers public goods game. Participants played an adapted version of the public goods game (Harbaugh & Krause, 2000; Ledyard, 1995; Van Hoorn et al., 2016). Participants were explained that they played the PGG online within a group of four anonymous players. These other players allegedly were anonymous same-age peers who were also participating in the study and participants would not meet these players before or after the study. Participants received the instruction that the experiment was about decision-making in groups, and their group would get the opportunity to obtain a monetary bonus. Each round, participants received five tokens with an exchange value of either €1, €1,50 or €2 per token. These different exchange values were included to keep the participants engaged in the task, but were not of main interest in this study.

Participants had to make a decision about the allocation of the tokens between themselves and their fellow group members. If they contributed to the group by giving any portion of the tokens to the public goods pot, then the donated tokens were multiplied by two and divided equally amongst the group. Therefore, the optimal strategy for the individual group members in this game is to donate nothing to the public goods pot, whereas on the collective level the group would earn most if all members would donate all of their tokens (Harbaugh & Krause, 2000). That is, with individual contributions being multiplied by two and then divided equally over four players, the individual's net return of contributing one token is negative (one loses 0.50 token). Hedonistic, or egoistic motivations thus cannot explain contributions; this is why contributions to the public good are viewed as prosocial behavior (Penner et al., 2005). Participants could not see the decisions of the other players in the group, nor the payoff after each round. This was done to ensure that participants made each choice independently. In addition to the standard endowment, they were informed that one round of the PGG task would be selected by the computer for actual payout.

The task consisted of two runs with 36 trials (i.e., 72 trials in total), presented in three feedback conditions. Each run consisted of three blocks with 12 trials in an 'Alone-Spectator-Evaluation' fixed order of conditions. We used a fixed order of conditions so that we could avoid social norm induction through feedback before baseline (i.e., playing alone). Subsequent analyses demonstrated that analyses for the two runs separately resulted in very comparable effects as the collapsed analyses presented in the Results section. For completeness, these additional analyses are presented in the Supplementary Material. At the start of each 12-trial block, a condition start screen was presented for 2 seconds displaying the text "No spectators", "Spectators", or "Spectators with evaluation". Within this set of 12 trials, the sequence of the events was as follows: Each trial started with the stimulus screen which was presented for 5 seconds, followed by a 3-second waiting screen. Next, the feedback screen was presented for 2 seconds (see Figure 1 for screens and presentation time).

In the *Evaluation* condition, the feedback screen displayed images of five spectators and feedback through 'likes' (thumbs up), reinforcing prosocial behavior. Peer feedback was dependent on the decision that the participant made. When participants donated zero or one token to the group, they received zero thumbs up in the feedback condition. Donating two tokens resulted in two thumbs up, and donating three tokens resulted in four thumbs up. Finally, for a donation of four or five tokens, participants received five thumbs up (cf. Van Hoorn et al., 2016).

In the *Spectator* condition, the feedback screen displayed pictures of five different peers, and participants were informed that these peers would also evaluate their decisions but these evaluations would not be displayed. Feedback was displayed as a blurred signal and was therefore not informative. In the *Alone* condition, participants played with their anonymous group members but without spectators, thus both spectators and feedback were blurred. The reason to include the blurred images was to keep the amount of visual stimulation as similar as possible between the conditions. Trials were separated with a 500 milliseconds-13.2 seconds jitter during which a fixation cross was presented. If participants did not respond within the time frame of 5 seconds, the text "Too late!" was displayed, after which a new trial started. These trials on which the participant did not respond in time were modeled separately and were not included in the analyses.

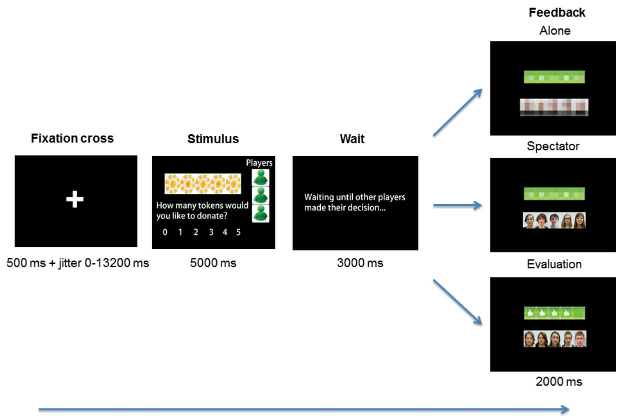


Figure 1. Illustration of the peers public goods game. Each round, participants made decisions in a group about the allocation of five tokens between self and fellow group members. The group consisted of three anonymous age-matched peers, displayed in green. These group members were unable to see the decisions of the participant. Participants played three types of rounds: (1) alone, with group only (2) with spectators present who would evaluate their decisions, but feedback was blurred, and (3) with spectators present who would provide prosocial feedback with 'likes'. In this example 4 out of 5 spectators liked the decision of the participant.

Adolescent actors as peers. Adolescent actors (N = 44) were recruited through local theater schools and received an endowment of €5 per session. They signed up for at least one or more sessions, so there were different spectator groups for each participant depending on which actors could attend the session. We aimed for each participant to get introduced to 6 out of 10 spectators (3 males and 3 females) before the start of the experiment. Introduction to 6 rather than all 10 spectators was for pragmatic reasons, to balance between ecological validity of the design and having enough actors present for each participant. Effort was made to have a sufficient number of actors in each session. In 75% of the sessions there were 6 actors present, in 20% of the sessions 5 actors, and in 5% of the sessions less than 5 actors were present.

Pictures of all actors were taken beforehand and we asked the actors to show a neutral facial expression. These pictures were rated by 30 independent adolescent raters (ages 14-16) on neutrality and estimated age. The actors were rated as relatively neutral ($M = 4.42$, $SD = 0.72$) on a scale ranging from 1 (not at all neutral) to 7 (very much neutral). The estimated age of the actors fell within the age-range of our participants, ($M = 15.17$, $SD = 0.89$), indicating that the pictures of the actors were valid for use within our paradigm. Finally, participants rated the pictures on the dimension of likeability after the scanning session on a scale of 1 (do not like at all) to 10 (like very much). Participants rated the online peers with an overall likeability of $M(SD) = 6.37(1.34)$.

Procedure

Participants arrived with their best friend at the scanning session, as part of a larger study on peer relationships. The best friend participated in a different part of the study, which will be reported elsewhere. They were explained that the experimenters were waiting for more participants, and a couple minutes later the actors walked into the room accompanied by an experimenter. The participant got introduced to the actors and shook hands (similar to Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). The group was told that the goal of the study was to examine what happens in the brain when you play games with others, and that they would all be playing online games with each other on the Internet, with the participant playing the game in the MRI scanner. It was explained that not all of the peers had arrived yet (i.e., the other 4 from the spectator group that consisted of 10 peers in total), but that we would already take the participant to the mock-scanner while we waited for the remaining peers to arrive. This procedure was used to balance between feasibility and credibility.

After being introduced, the actors left the facility through a side door and the participant was taken to the mock-scanner to get familiar with the scanning procedure. The participant listened to pre-recorded scanner sounds, received instructions for the task and played 5 practice trials. It was explicitly addressed that participants would not play with their best friend during the PGG task. In addition, it was explained that the participants would play the game with three other players in another room that they had not met yet and that everyone in the group would be anonymous. The scan session lasted approximately one hour. After the scan session participants filled out questionnaires and the two subtests from the WISC-III/WAIS-III were administered. Finally, participants received an endowment (€30) for their participation as part of a larger study and €2 additional earnings for the task. They were debriefed about the setup of the larger study and learned that all participants in fact received an amount of €2 for the PGG. None of the participants expressed doubts about the cover story during debriefing.

MRI data acquisition

Data were obtained with a 3 Tesla Philips scanner at the Leiden University Medical Center, using a standard head coil. The subjects saw the visual stimuli projected on a screen through a mirror attached to the head coil. The task consisted of two runs that lasted 7 minutes each. We collected the functional data using a T2*-weighted echo-planar pulse sequence (38 contiguous 2.75 mm oblique axial slices, using sequential acquisition, FOV = 220 mm, 80 × 80 matrix, TR = 2.2 sec, TE = 30 ms, 2.75 × 2.75 mm in-plane resolution). The first two volumes of each run (215 volumes each) were discarded to allow for T1-equilibration effects. To provide anatomical reference, a high-resolution 3D T1-FFE scan was acquired (TR = 9.76 ms; TE = 4.59 ms, flip angle = 8 degrees, 140 slices, 0.875 × 0.875 × 1.2 mm^3 voxels, FOV = 224 × 168 × 177 mm^3). In addition, a high-resolution 3D T1-weighted anatomical image was collected after the functional scans (TR = 9.751 ms, TE = 4.59 ms, flip angle = 8°, 140 slices, 0.875 mm × 0.875 mm × 1.2 mm, and FOV = 224.000 × 168.000 × 177.333). To prevent head motion, participants were restricted with foam inserts that surrounded the head. The translational movement parameters did not surpass the threshold of 1 voxel (<3 mm) for all directions, participants and scans. Average head movement was 1.2 mm (SD = .92 mm) and did not differ between age groups, $t(59) = 1.60$, $p = .114$.

4

fMRI preprocessing and statistical analysis

Data preprocessing and analysis was performed with SPM8 (Wellcome Department of Cognitive Neurology, London). We corrected for rigid body motion and the structural and functional volumes were spatially normalized to T1 templates. The normalization algorithm used a 12-parameter affine transform together with a nonlinear transformation involving cosine basis functions and resampled the volumes to 3 mm cubic voxels. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997). Functional volumes were spatially smoothed with a 6-mm FWHM isotropic Gaussian kernel.

We conducted statistical analyses on individual subjects' data using the GLM in SPM8. The fMRI time series were modeled as a series of zero duration events convolved with the hemodynamic response function (HRF). Stimulus onset, i.e., the moment of decision-making, and feedback onset were modeled as separate events of interest. The 6 start screens showing whether participants were in the alone, spectator or evaluation condition (presented in both runs) were modeled separately. In pair-wise contrasts, the least-squares parameter estimates of height of the best-fitting canonical HRF for each condition were used. We submitted the resulting contrast images, computed on a subject-by-subject basis, to group analyses.

At the group level, we computed two ANOVAs to investigate responses on stimulus onset and feedback onset. We used a 3 (Condition: Alone, Spectator, Evaluation) x 3 (Token value: €1, €1,50 and €2) ANOVA for stimulus onset and feedback onset separately. Task-related responses were considered significant if they exceeded a voxel-wise threshold of $p < .05$ FWE-corrected. This threshold was chosen to minimize Type-I errors. To test for individual differences on a whole brain level, we lowered the threshold to uncorrected $p < .001$ to balance between Type-I and Type-2 errors, because individual differences may not survive stringent corrections across all voxels in the brain (Lieberman & Cunningham, 2009). Using this threshold of uncorrected $p < .001$ with a minimum cluster of contiguous voxels of 10, we examined age group differences in whole brain interaction analyses with the between-subjects factor Age group.

In addition, we performed whole brain regression analyses on stimulus onset with the mean number of tokens donated, to test across the whole brain whether stimulus-related activation correlated with the average number of tokens that were donated per individual. These analyses were also performed at an uncorrected threshold of $p < .001$ with a minimum cluster of 10 contiguous voxels to balance between Type-I and Type-2 errors.

Region of interest analysis

The whole brain results across all participants were further examined in Region Of Interest (ROI) analyses to test for age group differences. The reason for using ROI analyses is because the age group differences are typically subtle and may not survive correction across all voxels of the brain. The MarsBar toolbox for SPM8 (Brett et al., 2002; http://marsbar.sourceforge.net/) was used to conduct ROI analyses for examination of activation patterns found in the clusters from the whole-brain analyses. Activation patterns that spanned across several regions of the brain were masked with the anatomical regions of the Marsbar Anatomical Toolbox. ROIs were averaged across the activated voxels in these regions and the coordinates of the center of mass are reported in the text.

3. Results

Behavioral results

To test peer effects on prosocial behavior, we examined the number of tokens donated to the group in the three conditions. The mean number of tokens donated per condition was submitted to a repeated measures ANOVA with Condition (3), Run (2), and Token value (3) as within-subject factors and Age group (2) as between-subject factor. This analysis yielded significant main effects for all three within-subject factors, Condition ($F(2, 118) = 50.08$, $p < .001$, *partial* $\eta^2 = .459$), Run ($F(1, 59) = 7.03$, $p = .01$, *partial* $\eta^2 = .107$), and Token value $F(2, 118) = 28.73$, $p < .001$, *partial* $\eta^2 = .327$). The main effect of Condition showed that participants donated more tokens to the group when there were spectators present and even more when spectators were present who provided feedback (p's $< .001$). This main effect was qualified by a Run x Condition interaction ($F(2, 118) = 7.45$, $p = .001$, *partial* $\eta^2 = .112$).

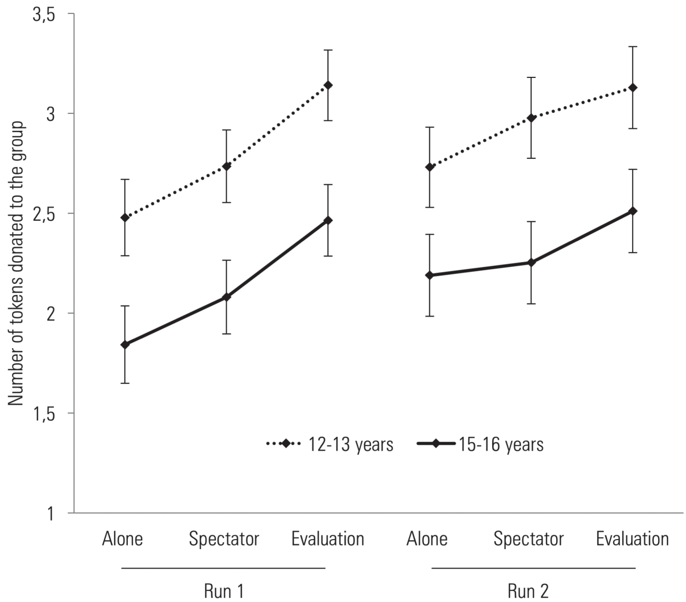


Figure 2. Mean *(SE)* number of tokens donated to the group in the PGG displayed for the two age groups separately. Dotted line indicates 12-13 year olds and full line indicates 15-16 year-olds.

Post-hoc comparisons showed that the same condition pattern was present in run 1 ($F(2,118) = 54.37$, $p < .001$, *partial* $\eta^2 = .48$) and run 2 ($F(2,118) = 16.29$, $p < .001$, *partial* $\eta^2 = .216$), but this pattern was more differentiated in run 1 than in run 2. Based on the observation that the pattern was similar, in the fMRI analyses we collapsed across runs to increase power. Separate fMRI analyses per run are presented in the Supplementary Material.

The main effect of Token value showed highest donations for the €1 tokens, lower donations for the €1,50 tokens ($p = .001$) and least for the €2 tokens ($p < .001$). The between-subject comparisons resulted in a main effect of Age group showing that the younger age group donated more tokens in all conditions, $F(1, 59) = 6.21$, $p = .016$, *partial* $\eta^2 = .095$. There were no Age group x Condition interactions, no Token value x Age group or Token value x Condition interactions, nor a three way interaction between Token value x Age group x Condition (see Figure 2).

fMRI analyses at stimulus onset

Stimulus onset: Whole brain analysis. The first set of fMRI analyses examined neural responses at stimulus onset, when the participants made their decision about the allocation of tokens between themselves and the group. A repeated measures ANOVA with factors Condition (3 levels: Alone, Spectator, Evaluation) and Token value (3 levels: €1, €1,50 and €2) yielded a significant main effect of Condition in a widespread network of brain areas, including dorsomedial PFC, precuneus, superior temporal sulcus and temporo-parietal junction (see Figure 3). There was no effect for Token value, nor a Condition x Token value interaction suggesting that the activation patterns were similar for all 3 types of tokens.

Next, we tested each of the contrasts separately using repeated measures ANOVAs. Spectator > Alone resulted in activation in precuneus, bilateral TPJ and bilateral STS; these regions were more active when participants made a decision with spectators present than when playing alone (Figure 3A). Evaluation > Alone resulted in overlapping patterns of activation and additional activation in the dmPFC (Figure 3B; Table S2 for the complete list of activated regions). The contrasts Evaluation > Spectator and Spectator > Evaluation yielded no significant results.

We performed separate whole brain interaction analyses including the between-subjects factor Age group, to test for differences in neural activity between the two adolescent groups. None of these analyses resulted in significant interactions with Age group (also not when the threshold was lowered to $p < .001$ uncorrected for multiple comparisons, at least 10 contiguous voxels). However, the differences between groups may not survive corrections across all the voxels in the brain. Given that we had *a priori* hypotheses regarding age group differences in social brain regions, we followed up the analyses reported above with ROI analyses, in which we tested for each region specifically for interaction between Condition and Age group.

Stimulus onset: Post-hoc ROI analyses for age group differences. To investigate interactions between Age group and Condition at stimulus onset, we extracted ROIs based on the *F*-test showing a main effect of Condition, collapsed across all participants. This analysis was not biased for age differences or direction of contrast differences. The selected ROIs were dorsomedial PFC (masked with the anatomical superior medial frontal cortex, collapsed across left and right), left and right TPJ, and left and right STS. For each ROI, an Age group (2) x Condition (3) ANOVA was conducted. We collapsed across Token value because there were no effects of Token value in the whole brain analyses.

First, in the dmPFC the Alone, Spectator, and Evaluation conditions all differed significantly from each other (Alone > Spectator, $p < .001$; Spectator > Evaluation, $p = .02$). Moreover, the ANOVA yielded an Age group x Condition interaction, $F(2,118) = 3.31$, $p = .04$. Post-hoc comparisons revealed that the difference between the Alone and Evaluation condition was larger for early adolescents (age 12-13) than for late adolescents (age 15-16) (Figure 3C). Second, in left STS, the Alone condition was significantly different from the Spectator condition ($p < .001$), but Spectator was not significantly different from the Evaluation condition ($p = .121$). There was also a significant Age group x Condition interaction, $F(2,118) = 5.69$, $p = .004$. The difference between the Alone and Evaluation condition was again larger for the younger than the older age group, but this difference was only significant in the interaction term and not within conditions (Figure 3D).

For right STS and right TPJ, the Alone condition was significantly different from the Spectator condition ($p's < .001$), but Spectator was not significantly different from the Evaluation condition ($p_{rSTS} = .124$ and $p_{rTPJ} = .273$). Finally, for left TPJ the Alone, Spectator and Evaluation conditions were all significantly different from each other (Alone > Spectator, $p < .001$; Spectator > Evaluation, $p = .031$). The right STS, left TPJ and right TPJ ROIs did not result in Age group x Condition interactions.

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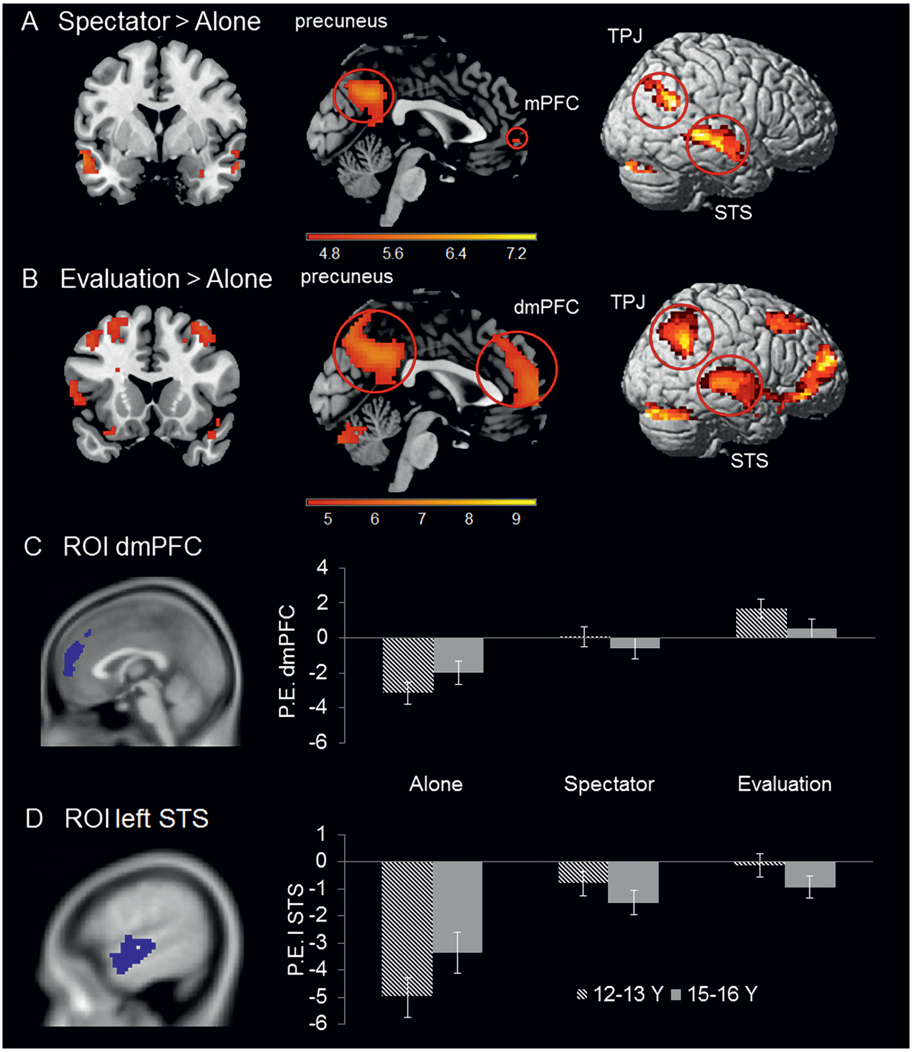

Figure 3. (A) Areas identified in the contrast Spectator > Alone at stimulus onset. (B) Areas identified in the contrast Evaluation > Alone at stimulus onset. Evaluation > Spectator yielded no significant findings at stimulus onset. All contrasts are FWE-corrected, $p < .05$. (C & D) Graphs illustrate two follow-up ROI analyses performed on dmPFC (MNI: 0 52 19) and left STS (MNI: -60 -12 3) extracted from the main effect of Condition. Both regions show a Condition x Age group interaction, see text for explanation. Striped bars indicate means *(SE)* for 12-13 year olds and grey bars indicate means *(SE)* for 15-16 year olds.

Stimulus onset: Relations with task behavior. For each contrast, we then tested the relation between brain activation and average task donations per individual with whole-brain regressions analyses. In the Evaluation > Alone contrast, a positive relation with donating behavior on the task was found in left TPJ and left STS. Interestingly, there was an overlap between the brain regions activated in the regression contrast Evaluation > Alone (displayed in green) and the main contrast Evaluation > Alone (displayed in red) (see Figure 4). This might indicate that adolescents who act more prosocial are also more sensitive to being evaluated. For Evaluation > Spectator, we also found a positive relation between mean number of tokens donated and right TPJ and right STS (see Table S3 for a full list of activated regions). The network of brain activation from this regression did not show an overlap with the main contrast Evaluation > Spectator. Spectator > Alone regression analyses yielded no results in relevant brain areas.

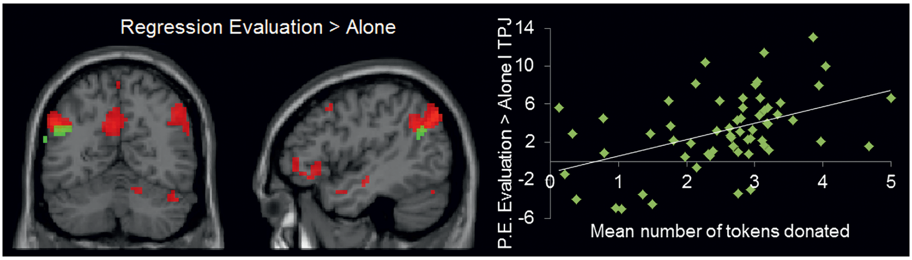

Figure 4. An overlap between the brain regions (including left TPJ: -48 -60 24) that become active in the regression with mean tokens donated for Evaluation > Alone displayed in green (uncorrected, >10 voxels, $p < .001$) and contrast Evaluation > Alone displayed in red from the main ANOVA (FWE-corrected, $p < .05$).

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fMRI analyses at feedback onset

Feedback onset: Whole brain analyses. With the second set of fMRI analyses we examined neural responses at feedback onset, i.e., when the feedback screen was presented. Whereas participants received feedback from the spectator group about their decision in the Evaluation condition, they received blurred feedback in the Spectator condition and no feedback nor spectators (blurred images) in the Alone condition. A repeated measures ANOVA with factors Condition (3 levels: Alone, Spectator, Evaluation) and Token Value (3 levels: €1, €1,50 and €2) yielded a significant main effect of Condition in a widespread network of brain areas, including bilateral insula, right amygdala, right IFG, right TPJ and dmPFC. There was no effect for Token Value, nor a Condition x Token value interaction suggesting that the activation patterns were similar for all 3 types of tokens.

The contrasts Evaluation > Alone and Spectator > Alone showed, as expected, activation in a wider brain network involving fusiform face area, amygdala and insula, which are core brain regions for face processing (Figure 5A and 5B). The contrast Evaluation > Spectator revealed increased activity in dmPFC, right amygdala, and bilateral insula, as well as right IFG and right superior parietal cortex (SPC) (Figure 5C; see Table S4 for the complete list of

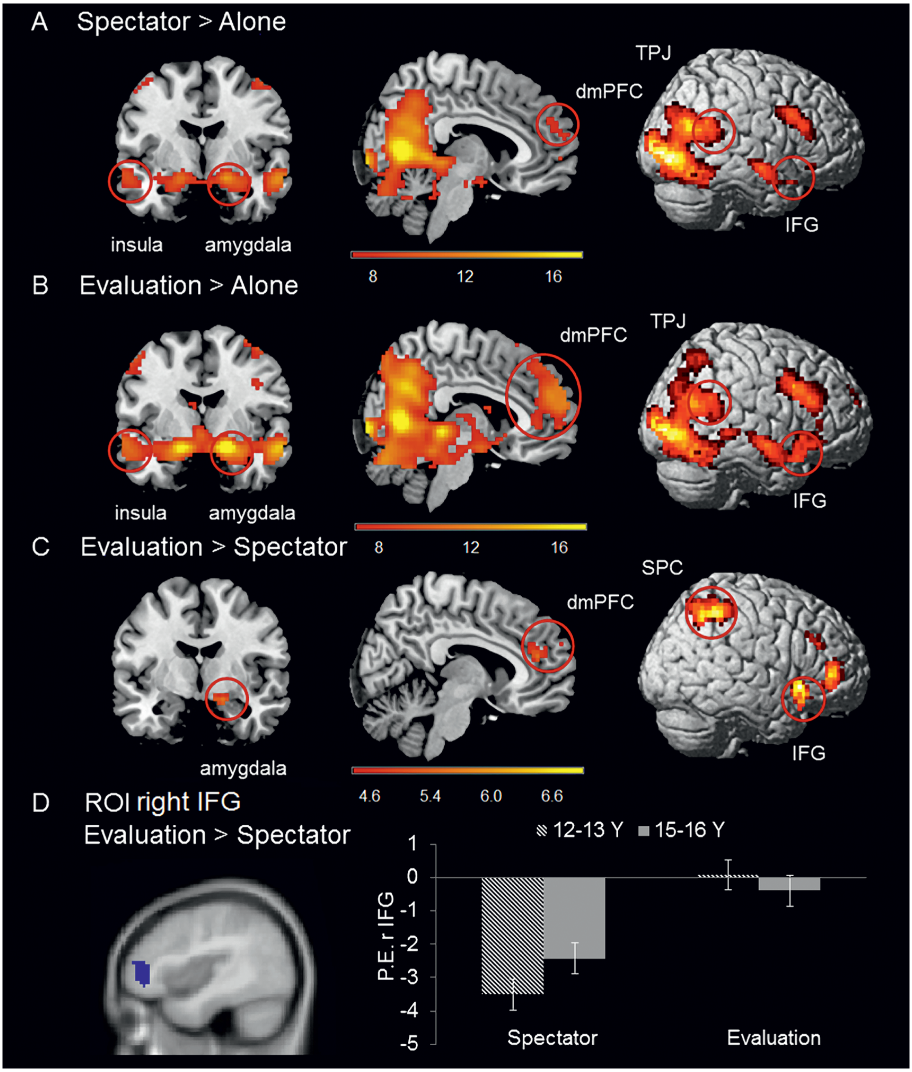

Figure 5. (A) Areas identified in contrast Spectator > Alone at feedback onset. (B) Areas identified in contrast Evaluation > Alone at feedback onset. (C) Areas identified in contrast Evaluation > Spectator at feedback onset. All contrasts are FWE-corrected, $p < .05$. (D) Graph illustrates follow-up ROI analysis performed on right IFG (MNI: 42 45 3) extracted from contrast Evaluation > Spectator. The STS region showed a Condition x Age Group interaction, see text for explanation. Striped bars indicate means *(SE)* for 12-13 year olds and grey bars indicate means *(SE)* for 15-16 year olds.

activated regions). To investigate the age-effects in the Evaluation > Spectator condition, we performed a 2-sample *t*-test across the whole brain, but this contrast did not result in Age group x Condition interactions (also not when the threshold was lowered to $p < .001$ uncorrected for multiple comparisons, at least 10 contiguous voxels).

Feedback onset: Post-hoc ROI analyses for age group differences.
Given that we were specifically interested in the effects of peer feedback (thumbs) versus peer presence (scrambled thumbs), we extracted ROIs from the Evaluation > Spectator contrast across all participants (Figure 5C). We explored whether there were age differences in activity patterns of each of these ROIs. For each ROI, an Age group (2) x Condition (2) ANOVA was performed. Only the right IFG showed an interaction effect between Age group and Condition ($F(1,59) = 4.16$, $p = .046$), revealing that the younger age group showed a larger differentiation between the Spectator and Evaluation conditions than the older age group (Figure 5D).

4. Discussion

The present study examined the neural correlates of peer influence on prosocial behavior with an adapted public goods game (PGG) in 12-16 year-old adolescents. Neural correlates were investigated during donation choices and peer feedback. During donation choices, peer presence resulted in higher donations and enhanced activity in several social brain regions including the dmPFC, TPJ, precuneus and STS. This social brain network is involved in mentalizing and social cognitive processes (Blakemore, 2008; Blakemore & Mills, 2014). Interestingly, individual differences analyses resulted in two important findings. First, TPJ activity correlated positively with the donation amounts, suggesting similar networks for prosocial behavior and sensitivity to peers. Second, during donation decisions peer presence effects were larger in dmPFC and STS for the younger adolescents (12-13 year-olds).

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Adolescence is a time of major social re-orientation, with changes in social behavior paralleled by changes in the social brain network (Blakemore, 2008; Blakemore & Mills, 2014; Nelson et al., 2005). A unique feature of adolescent social behavior is heightened sensitivity to peer evaluation, as peer feedback becomes an increasingly important tool to navigate the complex social world (Albert et al., 2013; Somerville, 2013). The current findings revealed that peer presence increases prosocial behavior, even more when peers provide prosocial feedback (see also Van Hoorn et al., 2016). These results are consistent with previous work in adults, in which the mere presence of observers increased donations to charity (Izuma et al., 2010a).

In terms of neural activity, the social brain network (dmPFC, TPJ, STS) becomes active when making donating choices in the presence of peers. These findings resonate with past work on prosocial behavior in a family context and public goods contributions in adults (Telzer, Masten, Berkman, Lieberman & Fuligni, 2011; Bault, Pelloux, Fahrenfort, Ridderinkhof, & Van Winden, 2015). Within the social brain network, the mPFC is thought to incorporate salient contextual cues such as social evaluation with emotional valuation processes (Blakemore, 2008; Frith & Frith, 2012; Somerville et al., 2013). It was previously found that even the most basic form of social evaluation - being looked at without performing any task - elicited increased mPFC activation in adolescents (Somerville et al., 2013). In addition, mPFC is implicated in social influence (Falk et al., 2010; 2014; Welborn et al., 2016). The current findings concur with these prior studies by showing that dmPFC is more active when making donating choices when peers are observing these choices (Izuma et al., 2010b; Somerville et al., 2013; Somerville, 2013). Interestingly, there were no neural differences between the Evaluation and Spectator conditions, which may imply that anticipation of active and passive peer influence rely on the same neural mechanisms of social cognition. Participants in both conditions were instructed that the spectators would judge their decisions, but the evaluation was only visible in the Evaluation condition. Speculatively, this may suggest that neural activity during stimulus onset represents the feeling of being judged, independent of receiving feedback.

Earlier work in the domain of peer influence also implicates the involvement of the ventral striatum, such that ventral striatum activity is enhanced during the peer presence condition (Chein et al., 2011; Izuma et al., 2010a; Smith et al., 2015). One commonly used interpretation is that peer presence makes behavior (i.e., risk-taking or donating) more rewarding. Contrary to this literature, the current study did not reveal enhanced striatum activity. Our findings suggest that the presence of peers may not be specifically related to activation of the ventral striatum, but instead heightens activity in brain areas that are already involved in that particular behavior. In our task, this implies more activity in mentalizing areas such as dmPFC, TPJ and STS.

An important additional goal of this study was to examine how neural activity to peer presence overlaps with individual differences in donation choices. Here we found that TPJ activity in the Evaluation > Alone contrast was positively correlated with donation amounts. These findings indicate that adolescents who act more prosocial show higher activation in this brain region when being evaluated by others. These results fit with prior findings from Van den Bos et al. (2011), who showed that increased involvement of the TPJ was associated with more advanced forms of social perspective-taking behavior. Moreover, TPJ activity has been related to self-reported altruism and charitable giving (Hare, Camerer, Koepfle, O'Doherty, & Rangel, 2010; Tankersly, Stowe, & Huettel, 2007). A tentative hypothesis is that heightened perspective taking when peers are present during decision-making may result in more prosocial behavior. This question should be addressed in more detail in future studies.

Secondly, we addressed the question if younger adolescents are more susceptible to peer influence in terms of behavior and neural activity. Behaviorally, younger adolescents (age 12-13 years) gave larger donations to the group in all task conditions – alone, with spectators present and evaluation. These findings fit with recent studies showing that younger adolescents are more prosocial towards unknown others (Burnett Heyes et al., 2015; Güroğlu, van den Bos & Crone, 2014; Meuwese, Crone, de Rooij & Güroğlu, 2015). Nevertheless, other studies have suggested that in general prosocial behavior does not necessarily increase across adolescence, but that there is an increase in sensitivity to the perspective of others in prosocial decision-making (Van den Bos et al., 2011). The exact developmental trajectory of prosocial behavior is possibly sensitive to task demands and social context.

The social influence effects are consistent with results from prior research. In an earlier study, participants were asked to rate the riskiness of scenarios, subsequently shown either peers' or adult' opinions about these scenarios, and then asked to rate the scenarios again (Knoll, Magis-Weinberg, Speekenbrink, & Blakemore, 2015). The 12-14 year-olds showed more sensitivity to social influence from peers than adults, whereas older adolescents (age 15-18 years) showed similar sensitivity for peers and adults. Another behavioral study illustrated that younger adolescents (12-13 year-olds) were more sensitive to social exclusion during the experimental paradigm Cyberball than older adolescents (14-16-years) (Sebastian, Viding, Williams, & Blakemore, 2010). Thus, younger adolescents may be more susceptible to contextual cues.

Consistent with this hypothesis, on a neural level we found larger effects in younger adolescents in dmPFC and left STS when being evaluated by peers relative to being alone. Even though there were Age group x Condition interactions in the core brain regions of interest, there were only main effects of age with respect to donating behavior. Future studies should examine the brain behavior relations in more detail across adolescent development. Heightened dmPFC activity in the current task shows an interesting overlap with past work in young adolescents during social emotions and prosocial decision-making tasks (Burnett et al. 2008; Gunther Moor et al., 2012; Van den Bos et al., 2011). Specifically, one prior study focused on prosocial changes by examining the neural correlates of reciprocity in 12-14 year-olds, 15-17 year-olds and young adults. In the 12-14 year-olds, mPFC activity was elevated when participants showed reciprocal behavior, whereas the other age groups showed similar levels of mPFC activity also when defecting others (Van den Bos et al., 2011). Thus, together with the prior behavioral studies these results indicate that younger adolescents may be more sensitive to social context (Wolf, Bazargani, Kilford, Dumontheil, & Blakemore, 2015).

Finally, we explored neural responses to peer evaluation at feedback onset. This analysis resulted in increased activity in lateral PFC and SPC, a network typically related to learning and cognitive control, as well as dorsal mPFC, IFG, insula and amygdala, related to mentalizing and emotional processing (Blakemore, 2008; Nelson & Guyer, 2011; Nelson, Lau, & Jarcho, 2014; Peters, Braams, Raijmakers, Koolschijn, & Crone, 2014). Within the process of peer feedback, learning and cognitive control areas may be involved to regulate own actions and adapt to the opinions or behaviors of others, which is typically associated with increased activity in lateral PFC and SPC (Peters et al., 2014). Although past work has related the IFG to a wide range of functions, one interpretation of IFG activity may be that it plays a role in (re)appraisal of social stimuli and updating expectancies that result from social feedback (Nelson & Guyer, 2011; Guyer, Choate, Pine, & Nelson, 2012). Likewise, insula activity has been related to prediction error fluctuations in the social learning context, specifically in adolescents (Jones et al., 2014). These exploratory analyses need to be replicated but provide interesting starting points for future research. It should be noted that in the current paradigm it is difficult to entirely disentangle the neural correlates of feedback from donation choice, because there was no jitter between donation choice and feedback. We addressed this issue by having a relatively long stimulus display (5 s) and waiting period (3 s) for each trial. Nonetheless, this affects the interpretation of a direct comparison between these moments in the task.

In conclusion, we show that peer presence when making donations consistently evoked activity in the social brain network, and that monitoring of peer feedback is associated with activity in a network of regions associated with learning and control, mentalizing and emotional processing. Developmental differences during decision-making suggest that 12-13 year-olds are more sensitive to peer influence on prosocial behavior than 15-16 year-olds, and that dmPFC may play an important role in the social evaluation process. These findings shed light on how peers may positively impact outcomes in adolescence. Stimulating prosocial development in adolescents might set the stage for adaptive development extending into adulthood (Jones et al., 2014). These findings have implications for society, as they may indicate that introducing community services to early adolescents - when prosocial behavior is especially malleable - can possibly foster prosocial development over time.

5. Supplementary Material

Table S1. *Descriptives of final sample*

	12-13 year olds *N* = 31	15-16 year olds *N* = 30	Total sample *N* = 61
M_{age} (*SD*)	12.93 (.60)	16.08 (.53)	14.48 (1.68)
M:F ratio (%M)	15 M/16 F (48%)	14 M/16 F (47%)	29 M/32 F (48%)
Estimated IQ (*SD*)	111.77 (9.6)	107.50 (11.5)	109.67 (10.72)
Parental income*			
Lower class	17%	13%	15%
Middle class	23%	37%	30%
Upper class	60%	50%	55%
Parental education**			
Primary education	0%	0%	0%
High school	2%	4%	3%
Vocational training	14%	6%	10%
Professional training	36%	16%	27%
University – college	0%	10%	5%
University – master	44%	64%	53%
Other	2%	0%	2%

Note. * Average middle class yearly income in the Netherlands is between €30.000 and €40.000 (CBS, 2014). In this table, income below €30.000 is classified as lower class, and income higher than €40.000 is classified as upper class. For two-parent families the parent with the highest income is reported.

** In the Dutch school system, MBO education is oriented towards practical vocational training, whereas HBO education (university of applied sciences) is oriented towards higher learning and professional training. For two-parent families the parent with the highest educational degree is reported.

fMRI analyses at stimulus onset for runs separately

Stimulus onset: Post-hoc ROI analyses. To investigate possible effects of Run, we used the original ROIs (i.e., over runs collapsed) based on the *F*-test showing a main effect of Condition. The selected ROIs were dmPFC (masked with the anatomical superior medial frontal cortex, collapsed across left and right), left and right TPJ, and left and right STS. For each ROI, an Age group (2) x Condition (3) x Run (2) ANOVA was conducted. We collapsed across Token value because there were no effects of Token value in the whole brain analyses. First, for left STS and right STS there were main effects of Condition (left STS: $F(2,118) = 49,195$, $p < .001$; right STS: $F(2,118) = 49,195$, $p < .001$), but no main effects nor interactions with Run (see Figure S1).

Table S2. *Summary of whole-brain analysis at stimulus onset for each condition separately (FWE-corrected, p <.05).*

Contrast	Region	MNI (x, y, z)			Z-value	Volume[1]
Spectator > Alone						
	L middle temporal gyrus	-63	-9	-12	7.69	342
	R middle temporal gyrus	63	-9	-9	7.04	263
	Precuneus	0	-54	36	6.62	450
	R supramarginal gyrus	48	-51	27	6.19	157
	L supramarginal gyrus	-48	-51	30	5.14	48
	L inferior frontal gyrus	-48	30	-6	5.66	26
	Parahippocampal gyrus	-33	-15	-18	5.48	23
	Putamen	-27	-9	0	5.45	11
	Globus pallidus	24	-15	-6	5.44	31
Evaluation > Alone						
	R superior temporal gyrus / BA22	66	-27	-3	Inf	1932
	L superior temporal gyrus	-63	-24	6	7.57	873
	L superior temporal gyrus	-36	-39	15	5.37	12
	Precuneus / BA33	-12	-48	33	7.41	659
	Angular gyrus	-51	-63	33	7.13	320
	Inferior parietal lobule	48	-63	42	6.58	314
	Medial frontal gyrus	36	24	45	5.95	155
Evaluation > Spectator						
	No clusters of activation					

Note. [1] Volume of activation in mm^3 (k^E). BA refers to Brodmann's area.

Table S3. *Summary of whole-brain regression analyses showing a positive relationship with total tokens donated at stimulus onset (uncorrected, p <.001, at least 10 contiguous voxels).*

Contrast	Region	MNI (x, y, z)			Z-value	Volume[1]
Spectator > Alone						
	L cerebellum	-27	-39	-27	4.03	11
	R cerebellum	9	-36	-27	3.43	24
Evaluation > Alone						
	Middle temporal gyrus (TPJ)	-48	-60	24	3.63	29
	L supramarginal gyrus	-60	-57	21	3.61	15
	Postcentral gyrus	27	-36	66	3.59	17
Evaluation > Spectator						
	Precentral gyrus	48	-15	27	4.04	19
	R superior temporal gyrus	57	-63	27	3.92	11
	Middle frontal gyrus	-39	9	36	3.78	20
	R superior temporal gyrus	57	-33	15	3.58	14

Note. [1] Volume of activation in mm^3 (k^E). Positive relationships are displayed for each contrast separately. Analyses for negative relationships showed no significant clusters of activation.

Table S4. Summary of whole-brain analysis at feedback onset for each condition separately (FWE-corrected, p $<$ *.05).*

Contrast	Region	MNI (x, y, z)			Z-value	Volume[1]
Spectator > Alone						
	Fusiform gyrus	39	-48	-18	Inf	5197
	R amygdala / Parahippocampal gyrus	21	-6	-15	Inf	141
	Middle temporal gyrus / BA21	57	-6	-15	Inf	141
	Middle frontal gyrus / BA9	48	12	30	7.52	225
	L amygdala / Parahippocampal gyrus	-18	-9	-15	7.08	25
	R Inferior frontal gyrus	33	33	-9	6.52	21
	L Superior temporal gyrus / BA22	-54	-9	-9	5.68	59
	L Superior temporal gyrus	-48	-48	15	5.60	25
	Middle frontal gyrus	-39	12	30	5.50	13
Evaluation > Alone						
	Fusiform gyrus	39	-48	-18	Inf	5019
	R amygdala / parahippocampal gyrus	21	-6	-15	Inf	1015
	L amygdala / parahippocampal gyrus	-18	-9	-15	Inf	435
	Middle frontal gyrus	54	18	33	Inf	402
	Sub-gyral / BA20	39	-12	-27	6.91	13
	Medial frontal gyrus / BA9	6	48	27	6.21	90
	L thalamus	-21	-30	-3	6.07	36
	L superior parietal lobule / BA7	-27	-57	48	5.36	21
	Middle frontal gyrus	-39	15	30	5.35	11
	L superior temporal gyrus	-54	-45	9	5.34	11
	R inferior frontal gyrus	45	33	3	5.31	12
Evaluation > Spectator						
	R inferior frontal gyrus / BA47	33	18	-9	6.87	177
	R inferior frontal gyrus / BA10	42	45	3	6.53	108
	L inferior frontal gyrus / BA 47	-30	18	-12	5.86	70
	Amygdala / parahippocampal gyrus	18	-6	-15	5.54	16
	Medial frontal gyrus / BA9	6	42	18	5.48	31
	Middle frontal gyrus	48	33	27	5.32	19

Note. [1] Volume of activation in mm^3 (k^E). BA refers to Brodmann's area.

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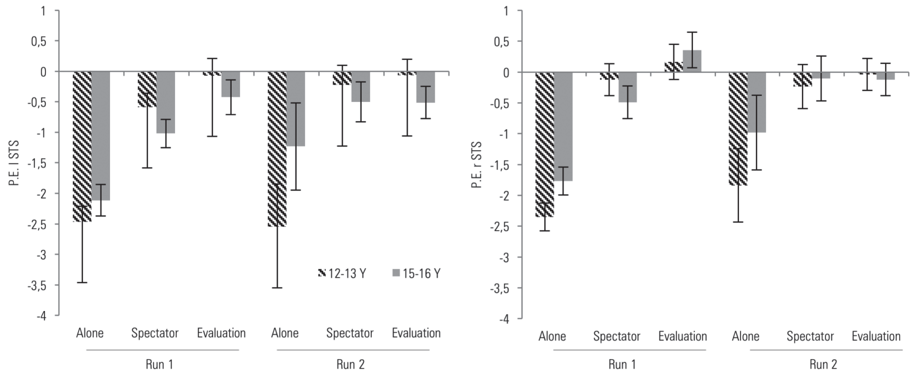

Figure S1. Graphs illustrate follow-up ROI analyses performed on left STS (left) and right STS (right) extracted from the main effect of Condition for runs separately. Striped bars indicate means *(SE)* for 12-13 year olds and grey bars indicate means *(SE)* for 15-16 year olds.

Second, the analysis for mPFC yielded main effects of Condition and Run. These effects were qualified by a Condition x Run interaction, $F(2,118) = 9.178$, $p < .001$. Moreover, there was a Condition x Age interaction, $F(2,118) = 3.306$, $p = .040$, but no interaction between Run and Age group. When we examined the runs separately, the main effect of Condition was present in both runs, but stronger in run 1, $F(2,118) = 34.867$, $p < .001$, than in run 2, $F(2,118) = 3.985$, $p = .021$, see Figure S2.

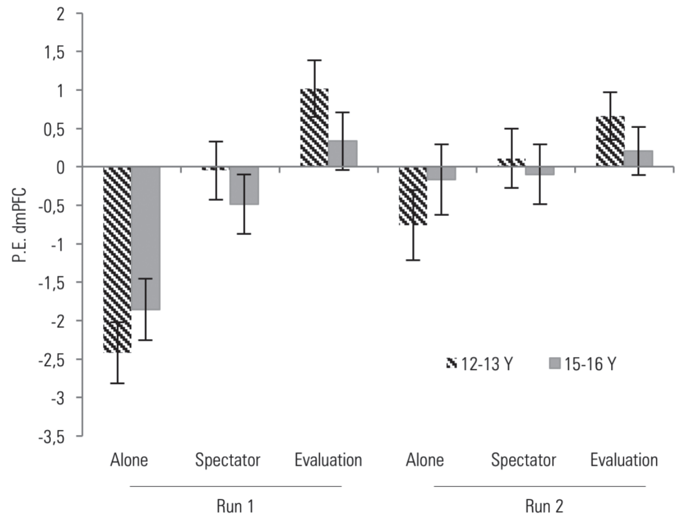

Figure S2. Graph illustrates follow-up ROI analysis performed on dmPFC extracted from the main effect of Condition for runs separately. Striped bars indicate means *(SE)* for 12-13 year olds and grey bars indicate means *(SE)* for 15-16 year olds.

The analyses for left and right TPJ yielded very similar results. For the left TPJ, we observed main effects of Condition and Run. These effects were qualified by a Run x Condition interaction, $F(2,118) = 15.666$, $p < .001$. When we examined the runs separately, the main effect of Condition was present in both runs, but significant in run 1, $F(2,118) = 51.702$, $p < .001$, and at trend level in run 2, $F(2,118) = 2.892$, $p = .059$. There was no interaction with age. In the right TPJ, analyses also yielded a main effect of Condition, $F(2,118) = 31.488$, $p < .001$, and Run, $F(1,59) = 27.027$, $p < .001$. These effects were qualified by a Run x Condition interaction, $F(2,118) = 15.550$, $p < .001$. When we examined the runs separately, the main effect of Condition was present in both runs, but significant in run 1, $F(2,118) = 46.985$, $p < .001$ and at trend level in run 2, $F(2,118) = 3.058$, $p = .051$. There was no interaction with age (see Figure S3).

Taken together, these analyses showed that there are no interactions between Run and Age in any of the ROIs. Further, dmPFC, and left and right TPJ showed interactions between Run and Condition. For these regions, the condition effects were stronger in run 1 but also present in run 2. These findings indicate that, although there is some effect of time on task, the within subject manipulation of Condition was present in both runs.

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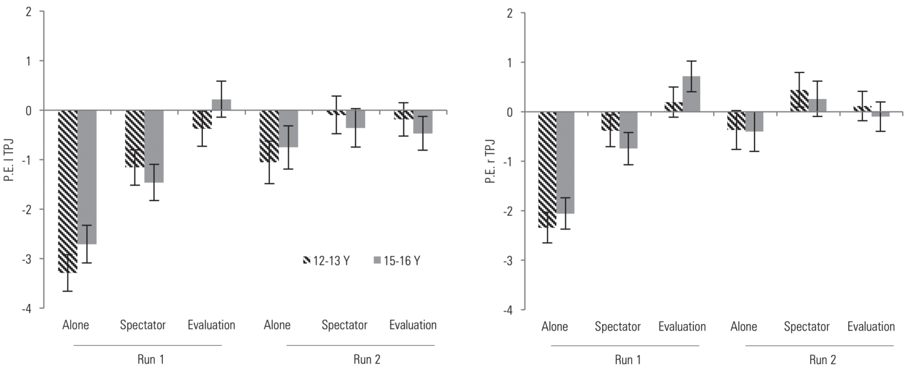
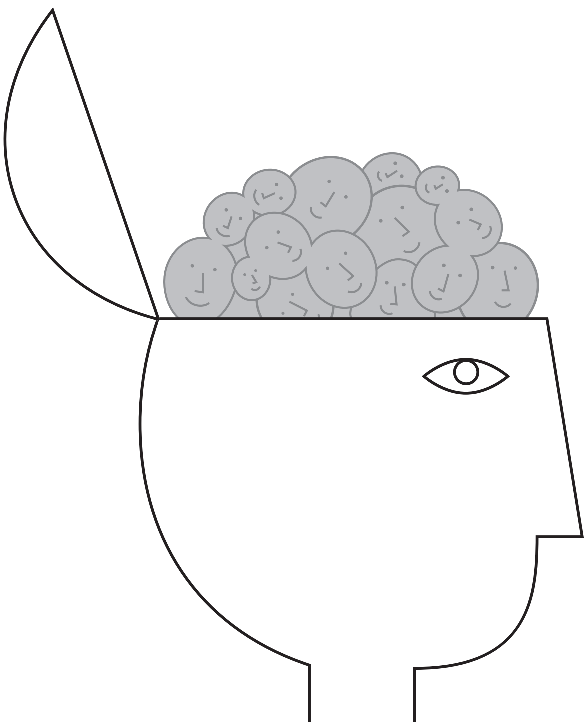


Figure S3. Graphs illustrate follow-up ROI analyses performed on left TPJ (left) and right TPJ (right) extracted from the main effect of Condition for runs separately. Dark grey bars indicate means *(SE)* for 12-13 year olds and light grey bars indicate means *(SE)* for 15-16 year olds.

Chapter 5:

Peer influence on prosocial behavior in autism

This chapter is under revision as: Van Hoorn, J., Van Dijk, E., Crone, E. A., Stockmann, L. & Rieffe, C. Peers influence prosocial behavior in adolescent boys with autism spectrum disorders.



Abstract

Peer influence has a profound impact on decision-making in typically developing (TD) adolescents. In this study, we examined to what extent adolescents (age eleven-seventeen years; $N = 144$) with and without autism (ASD) were influenced by peer feedback on prosocial behavior, and which factors were related to individual differences in peer feedback sensitivity. In a public goods game, participants made decisions about the allocation of tokens between themselves and their group – in the absence or presence of peer feedback. ASD and TD adolescents were sensitive to peer feedback on prosocial behavior. More autism traits and social interest were associated with less sensitivity to antisocial feedback. These results suggest that peer feedback creates opportunities for social adjustment in ASD and TD adolescents.

1. Introduction

For most high-functioning individuals with autism spectrum disorders (ASD), challenges in the social domain are the most disabling aspect of the disorder (Lai, Lombardo, & Baron-Cohen, 2014; Travis & Sigman, 1998). These social difficulties grow more pronounced when children transition into adolescence, as the social world becomes increasingly focused on the peer group (Carter et al., 2014; Nelson, Jarcho, & Guyer, 2016). A large body of literature acknowledges peers as a powerful source of socialization in typically developing (TD) adolescents (Albert, Chein, & Steinberg, 2013; Brechwald & Prinstein, 2011). Despite the negative connotations of peer influence, emerging evidence points to relations with positive psychosocial outcomes, such as increased prosocial behavior (Van Hoorn, Fuligni, Crone, & Galván, 2016). However, it is currently unclear to what extent adolescents with ASD are influenced by their peers – for better or for worse. The current study aims to examine the effects of peer influence on prosocial decisions of adolescents with and without ASD.

Peer influence in adolescence

Peer influence is often associated with direct pressure to adjust behaviors or attitudes to the group (Brown, Bakken, Ameringer, & Mahon, 2008). However, common modes of influence also include behavioral display and reinforcement of displayed behavior by valued peers (Bandura, 1986). Through peer influence adolescents acquire social norms that specify unwritten rules for approved social behaviors in the peer context (McDonald & Crandall, 2015). Social norms as well as their perception can drive behaviors and attitudes, especially when situations are novel or uncertain (Berger, 2008; Cialdini & Trost, 1998). For example, the *mere presence* of peers increases risky driving in adolescence (Albert et al., 2013) and such an increase may be guided by the individual's perception of the social norms in the peer group. Additionally, risk-stimulating *peer feedback* leads to more risky driving behavior in adolescents than peer feedback that is risk-averse (Simons-Morton et al., 2014). Prosocial behaviors such as cooperation and intentions to volunteer are similarly influenced by peer feedback (Choukas-Bradley, Giletta, Cohen & Prinstein, 2015; Van Hoorn, Van Dijk, Rieffe, Meuwese, & Crone, 2016). Changes in cooperation depend on which type of behavior is endorsed by a peer group (Van Hoorn et al., 2016b). When peers value decisions to donate tokens to the group (i.e., prosocial feedback), cooperative choices increase. On the other hand, when peers value decisions to keep tokens to the self (i.e., antisocial feedback), adolescents show a decrease in cooperative choices. These results implicate that peer feedback provides an opportunity for social adjustment learning in typical development (Van Hoorn et al., 2016b).

Like TD adolescents, those with ASD develop increased orientation to peers (McGovern & Sigman, 2004). However, adolescents with ASD often struggle with navigating social situations in the peer context (Tantam, 2003). Given the nature of social difficulties in ASD, it may be that ASD adolescents show an attenuated sensitivity to peer influence as compared to TD. One study investigated conformity using a child-friendly version of the classic Asch paradigm in children (age seven to eleven) with and without ASD (Yafai, Verrier, & Reidy, 2014). In this task children were asked to indicate which one of three sample objects was the same size as the stimulus object - and were presented with incorrect information by the experimenter ("most people think…"). Children with ASD conformed less to the opinion of others than TD children, and more autism traits were negatively related with the likelihood to conform in the TD sample.

In the domain of prosocial behavior, TD adults have been found to donate more money to charity when observed by peers, whereas adults with ASD donated the same amount regardless of the presence of an observer (Izuma, Matsumoto, Camerer, & Adolphs, 2011). Collectively this work suggests that children with ASD conform less to social pressure from adults, and adults with ASD are less sensitive to the presence of other people than their TD counterparts. Yet, it is unknown whether adolescents with ASD are sensitive to feedback from *peers*, during a developmental period in which the peer context is crucial for development (Nelson et al., 2016).

Moreover, individual differences exist in the extent to which both TD and ASD adolescents interact with their social environment (McGovern & Sigman, 2004; Steinberg & Monahan, 2007). A key factor in differential sensitivity to peers may be social interest - the motivation to engage with one's social world (Chevallier et al., 2012). In TD adolescents, individual differences are reported in the desire for friendship (Richard & Schneider, 2005). As a result, those with a high desire for relationships with peers may be more influenced by their peers than those with low social interest. While individuals with ASD show less social interest, individual differences within the spectrum are acknowledged with regards to social impairments, and potentially also social interest (Chevallier et al., 2012; Jones & Klin, 2009; Sedgewick, Hill, Yates, Pickering, & Pellicano, 2016). For example, in adolescents with ASD the extent to which individuals are socially engaged predicts adaptive social behavior (McGovern & Sigman, 2004). These individual differences across groups imply that it is essential to complement a between-groups approach (ASD-TD) with a continuous approach (investigating autism symptoms in the total sample) to investigate sensitivity to peer feedback and the role of social interest in this process.

Present study

The main goal of this study was to investigate to what extent boys (aged eleven to seventeen years) with and without ASD are influenced by peer feedback on prosocial behavior, and whether social interest may play a role in individual differences in peer feedback sensitivity. We focused on this specific age range because peer influence is highly salient during adolescence (Albert et al., 2013). Only boys were included because they represent the largest part of the ASD population with a ratio of 4.5:1 to girls (CDC, 2014). To achieve this goal we used a previously validated paradigm called the peers public goods game (PGG), in which participants had to make decisions about the allocation of tokens between themselves and their group (see Van Hoorn et al., 2016b). The number of tokens donated to the group in the PGG is a measure for prosocial behavior (Penner, Dovidio, Piliavin, & Schroeder, 2005). Although giving to the group for the benefit of others is not necessarily altruistic behavior, it represents an important aspect of prosocial behavior (Batson & Powell, 2003).

We examined peer influence by having the participants complete the task under different conditions. Participants made prosocial decisions in a group while online age-matched spectators were present who provided feedback (Feedback condition), with spectators present but no feedback (Spectators condition) and without spectators (Alone condition). We used a between-subjects design to compare two types of feedback on prosocial behavior, similar to Van Hoorn et al (2016b). In the Prosocial Feedback condition, the spectators valued prosocial decisions (i.e., donations to the group), but not selfish decisions (i.e., keeping tokens to the self). In the Antisocial Feedback condition, this was the exact opposite, as peers valued selfish decisions, but not prosocial decisions.

More specifically, the first aim of the current study was to compare the sensitivity to peer feedback and its effect on prosocial behavior in adolescent boys with and without ASD. We hypothesized that boys with ASD would be less sensitive to peer influence on prosocial behavior than TD boys (Izuma et al., 2011; Yafai et al., 2014). Our second aim was to examine whether in the *total sample* the severity of autism symptoms and social interest (indices: social reward sensitivity, resistance to peer influence) were related to peer feedback sensitivity. We expected that boys with fewer autism symptoms and higher social interest would be more sensitive to peer feedback (Richard & Schneider, 2005; McGovern & Sigman, 2004).

2. Method

Participants

The total sample consisted of 144 adolescents between the age of eleven and seventeen years (M = 14.83, SD = 1.40, range 11.50 – 17.58), including 75 boys with ASD (52%) and 69 typically developing boys (48%). Before the start of the study, the institutional review board approved all procedures and consent was obtained from participants and their parents. The majority of the ASD group was recruited from a specialized school for adolescents with autism and a normal intelligence (N = 71), whereas another 4 ASD participants were recruited together with TD participants from a regular high school. School admission criteria included a normal intelligence (IQ > 80) and a clinical ASD diagnosis according to the *Diagnostic and Statistical Manual of Mental Disorders – Fourth Edition* (DSM-4, American Psychiatric Association, 2000). The diagnoses were established before the start of the study by independent child psychiatrists and psychologists and retrieved from school files. Given the spectrum approach in the DSM-5, we did not make a distinction between autism subtypes in the current study (DSM-5; American Psychiatric Association, 2013). Parent-reported scores on the Social Responsiveness Scale (SRS) (N = 125; N = 19 missing) confirmed symptoms for the last 6 months with scores in the clinical range (SRS > 60) for the ASD group but not for the TD group, $t(123) = -15.87$, $p < .001$ (Roeyers, Thys, Druart, De Schryver & Schittekatte, 2012). Comorbid psychiatric disorders were reported for 24% of the ASD group including 17% AD(H)D, 4% DCD, 1% OCD, 1% Gilles de la Tourette; and another 4% was unknown.

The TD group was recruited from three regular high schools teaching several academic levels in the Netherlands and matched the ASD group on education level. Psychiatric disorders were reported in 3%, specifically ADD and ADHD; 82% reported no disorders and information was missing for an additional 15% because parent questionnaires were missing. Further background information about the sample can be found in Table 1.

Table 1. *Participant characteristics ASD group and TD group*

	ASD (N = 75)	TD (N = 69)
Age (*SD*)	14.75 (1.46)	14.91 (1.33)
Range	11.50 – 17.42	12.58 – 17.58
Total IQ (*SD*)	116.53 (10.20)	105.48 (9.48)**
Range	90 - 137	83 – 130
Autism symptoms SRS (*SD*)	83.82 (24.87)	26.86 (12.15)**
Range	38 - 141	6 – 55
Verbal understanding CELF (*SD*)	10.51 (2.31)	10.48 (2.58)
Range	6 - 15	5 - 15
Interpersonal competence (*SD*)	4.51 (0.61)	5.33 (0.58)**
Range	2.97 – 6.07	3.37 – 6.47
Country of birth: Netherlands	94%	93%
Other	6%	7%
Treatment	77%	0%
Medication	39%	1%
Parental income[1]	ASD (N = 54)	TD (N = 49)
Lower income	46%	29%
Middle income	19%	20%
Upper income	35%	51%
Parental education[2]	ASD (N = 69)	TD (N = 60)
Primary education	0%	2%
High school	6%	0%
Vocational training	22%	15%
Professional training	38%	38%
University – college	12%	5%
University – master	17%	37%
Other	6%	3%

** $p < .001$, * $p < .05$ *Note.* CELF = Clinical Evaluation of Language Fundamentals®–Fourth Edition (CELF®-4), subtest Understanding Spoken Paragraphs. Treatment = social skills training, psycho education or more specific training such as anger regulation. Medication = methylphenidate (restlessness) or risperidone (behavioral problems). Parent-rated interpersonal competence scores (ICS; Cairns, Leung, Gest, & Cairns, 1995) were collected from N = 67 parents in ASD group and N = 58 parents in TD group.

[1] Income below €30,000 is classified as lower income, middle income between €30,000 and €40,000 and income higher than €40,000 is classified as upper income. For two-parent families the parent with the highest income is reported. [2] For two-parent families the parent with the highest educational degree is reported.

To test for possible confounding group differences, we obtained IQ scores for intelligence and used the subtest "Understanding Spoken Paragraphs" of the Clinical Evaluation of Language Fundamentals (CELF) as an indication of verbal language comprehension (Semel, Wiig, & Secord, 2003). Full IQ scores for N = 70 were collected from school files for the ASD group (N = 5 missing). We administered the subscales Similarities and Block Patterns from the Wechsler Intelligence Scale for Children (WISC-III; participants $<$ 16 years) and Wechsler Intelligence Scale for Adults (WAIS-III; participants 16 years and older) to obtain an estimate of IQ in the TD group. Estimated IQ scores were obtained for $N = 64$ ($N = 5$ missing). The estimated IQ scores fell within the normal range for all participants and were higher in the ASD group than TD group ($t(132) = -6.48$, $p < .001$). This discrepancy between education level and IQ has been documented before and may be due to the ASD symptomatology (Estes, Rivera, Bryan, Cali, & Dawson, 2011).

Participants were assigned to the two feedback conditions in a semi-random manner, with $N = 37$ (26%) in the ASD prosocial feedback condition, $N = 35$ (24%) in the TD prosocial feedback condition, $N = 38$ (26%) in the ASD antisocial feedback condition, and $N = 34$ (24%) in the TD antisocial feedback condition.

Experimental task

Peers public goods game. Participants played the peers public goods game (PGG), an adapted version of the economic game in which prosocial behavior is operationalized as cooperation to benefit one's group (see Van Hoorn et al., 2016b). Participants were led to believe that they would connect online to a group consisting of three other anonymous age-matched group members. In fact, participants played the task individually and there were no other players. They were told that they had to make anonymous and independent decisions in this group of four peers and that their group would get the opportunity to earn a monetary bonus. Each round, participants received five tokens with an exchange value of 50 Eurocents per token. Then, they made a decision whether they wanted to keep any amount of the tokens to themselves or contribute to their group by giving tokens to the public goods pot. Giving to the public goods pot was beneficial to the group, because all donated tokens were multiplied by two and divided equally amongst the 4-person group, independent of the respective contributions. Importantly, anonymity of decisions was guaranteed as participants could not see the decisions of fellow group members, nor could these other group members see the participants' decision. This was done to ensure that participants made their choices individually, rather than learning from the decisions of the group members. For a more extensive background of the PGG, we refer to Van Hoorn et al. (2016b).

The PGG consisted of thirty trials divided over four conditions (see Figure 1A). First, participants played five *Alone* trials (trials 1 – 5), during which decisions were made individually within the group. Each trial started with a fixation screen presented for 500 ms, followed by the stimulus screen (5000 ms) during which participants had to make their decision. Subsequently a waiting screen was displayed with a random presentation time between 2000 and 4000 ms, which displayed the text “Waiting until other players made their decision” (see Figure 1B for all screens and display times).

Second, participants were told that a spectator group of five same age peers would be online during the next ten *Spectators* rounds (trials 6 - 15). The presence of these peers was simulated in the task. These spectators would evaluate their decisions, but this evaluation was blurred and therefore not informative. The trial screens in this condition were similar to those in the alone block, with the addition of a feedback screen. The feedback screen contained photos of the five peers as well as their blurred evaluation and was displayed for 3000 ms (see Figure 1C: Spectator).

In the third *Feedback* condition (trials 16 – 25) participants played ten trials with a different spectator group of five peers. They learned that these spectators would evaluate their decisions with ‘likes’, or thumbs up for a valued decision, and that the green box would be empty if they disliked the decision. In this condition, the feedback screen was composed of photos of the spectator group and the evaluation of the participant’s decision (see Figure 1C: Feedback). Lastly, the spectators went offline again, and participants played another five trials in the *Alone after feedback* condition (26 – 30) that were similar to the first five trials.

We used a mixed design with between-subjects conditions to compare two types of feedback on decisions: prosocial feedback and antisocial feedback. The TD group and the ASD group were randomly assigned to either the prosocial or antisocial feedback condition. In the prosocial feedback condition, we programmed the feedback such that spectators rewarded donations to the public goods pot with many likes, while in the antisocial feedback condition spectators gave many likes for keeping tokens to the self. As such, evaluations were dependent on the between-subjects condition as well as the participant’s decision made on each respective trial. An overview of donations and associated likes in each condition is presented in Table 2.

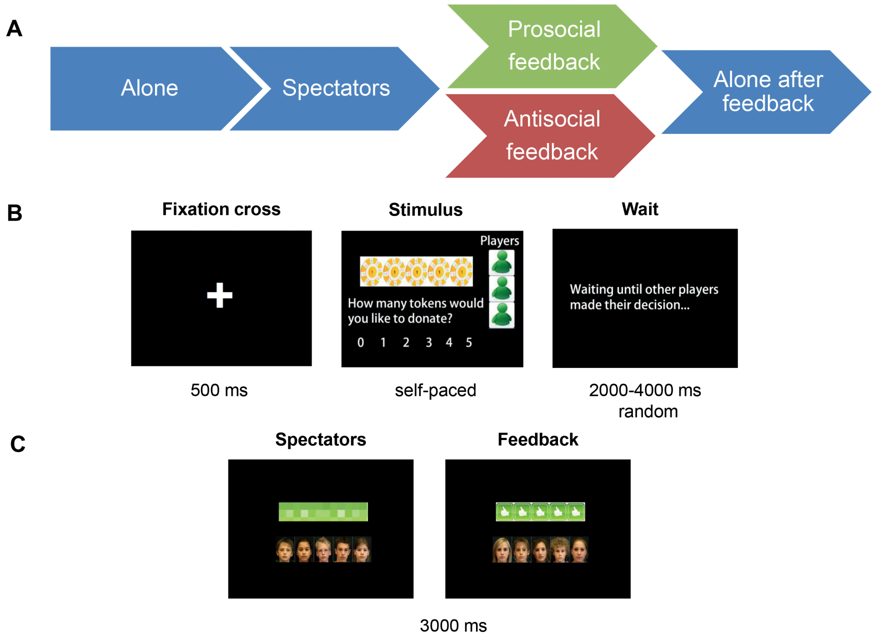


Figure 1. Illustration of the Peers Public Goods Game.

(A) Participants played four types of rounds in the PGG: *Alone*, only with group; *Spectators,* with spectators present who would evaluate their decisions, but blurred feedback; *Feedback* with spectators present who would provide either prosocial or antisocial feedback with 'likes', depending on the between-subjects condition; and *Alone after feedback*, again with group only.

(B) Illustration of screens in the alone condition. Each round, the participant makes an independent decision within their group about the allocation of five tokens between themselves and the group. The group consisted of three online age-matched peers, displayed in green to guarantee anonymity. These group members were unable to see the decisions of the participant.

(C) In the *Spectators* condition, a spectator screen followed alone trial screens. Five online spectators were able to see the decisions of the group and would evaluate these decisions, but their feedback was displayed as a blur. This condition was not of interest in the current study, but disentangles peer presence from peer feedback. In the *Feedback* condition, a feedback screen followed alone trial screens. Five different online spectators were present and provided feedback with 'likes' or thumbs up. In this case, five out of five spectators liked the participant's decision.

Table 2. *Feedback given by spectator group in the prosocial and antisocial feedback conditions.*

Number of tokens donated to the group	Prosocial feedback	Antisocial feedback
0 tokens		
1 token		
2 tokens		
3 tokens		
4 tokens		
5 tokens		

The photos of the peers in the two spectator groups were selected from a database of morphed adolescent faces. The photos in this database were non-existent identities created through overlaying pictures of two individuals (i.e., by morphing). Independent raters had previously rated these photos on several dimensions and the ten most neutral (5 males and 5 females) were selected for the current task. These photos were rated as $M(SD) = 5.02$ (0.37) on a scale of 1 (not at all neutral) – 7 (very neutral). Photos were matched on age group, which led to two different spectator groups for 11-14 year olds and 15-17 year olds.

Social interest questionnaires

Social Reward Questionnaire (SRQ-A). The Social Reward Questionnaire measures individual differences in the value of several types of social rewards (Foulkes, Viding, McCrory, & Neumann, 2014). The English version of the SRQ for adolescents includes the scales Admiration (being flattered, liked and gaining positive attention), Negative Social Potency (being cruel, callous and using others for personal gains), Passivity (giving others control over decisions), Prosocial Interactions (having kind, reciprocal relationships) and Sociability (engaging in group interactions) with a total of 20 items; no total score can be computed. The internal consistency is adequate for both groups. A bilingual Dutch-English speaker translated the items into Dutch using the forward-backwards method and we consulted the first author to make sure that the content of the translated items reflected the original SRQ items.

Resistance to Peer Influence (RPI). The Resistance to Peer Influence questionnaire assesses general resistance to peer influence, with the goal of disentangling susceptibility to peer pressure from antisocial behavior and risk-taking behavior (Steinberg & Monahan, 2007; Sumter, Bokhorst, Steinberg, & Westenberg, 2009). The scale has 10 pairs of statements and participants first have to choose which statement applies most to them, and then indicate to what extent. An example statement is "Some children think it is more important to be an individual than to adjust to the group" BUT "Other children think it is more important to adjust to the group than to be an individual". The responses are coded on a 4-point scale ranging from "Really True" or "Sort of True" as potential answers for each statement and the total RPI score is calculated as a mean of the 10 items. A high score on this questionnaire points to a high resistance to peer influence, whereas a low score implies a low resistance (Steinberg & Monahan, 2007).

Procedure

The study was conducted in an empty (class)room at school with an experimenter. All participants were tested one-on-one such that the experimenter could provide help when necessary. Experimenters were trained with video-feedback on the instructions and administration of the tasks and care was taken to take into account the needs of the ASD group, providing a structured research environment. The study was composed of three elements: (1) a task in which participants were asked to divide tokens (PGG), (2) filling out several online questionnaires, and (3) tasks with the experimenter. These tasks included the subtest Understanding Spoken Paragraphs (CELF) for all participants and the subtests of the WISC-III/WAIS-III for the TD group only, since full IQ scores were available in the ASD group.

Following the PGG instructions, including three practice trials, we administered some quiz questions to ensure that participants understood the task. Participants were informed that the computer would randomly pick one round from all PGG rounds that would be their payout for participation. In fact all participants randomly received 1, 2 or 3 euros (mean 2 euros) as compensation, as well as a small present. The payout was varied to increase credibility, because several boys from the same school class took part in the study. After all participants on a school were tested, participants were debriefed about the exact setup and goals of the study. Parents filled out a set of online questionnaires to provide background information about the sample.

Data analyses

The first aim of this study was to compare feedback sensitivity on prosocial behavior in boys with and without ASD. Effects of peer feedback in the PGG were analyzed with a Repeated Measures (RM) ANOVA, with the four PGG conditions Alone, Spectators, Feedback, and Alone after feedback as within-subjects factors. Between subjects-factors were Diagnosis (ASD and TD) and Feedback type (Prosocial feedback and Antisocial feedback). To control for possible confounding effects of estimated intelligence, we first conducted a RM ANOVA in which TIQ was included as a covariate. There were no significant effects for TIQ and therefore we excluded this variable. Second, we reran the analyses excluding ASD participants with comorbidity ($N = 18$) and TD participants with a diagnosis ($N = 2$), as well as participants who expressed doubts about belief of the task ($N = 2$) and found no changes in the results. Third, we conducted the RM ANOVA excluding ASD participants with a SRS score lower than 60 (i.e., below clinical range; $N = 12$) and found no changes in the results. Hence, we report about all participants in the Results section ($N = 144$).

Our second aim was to investigate how the severity of autism symptoms (SRS) and social interest (SRQ and RPI) relate to peer feedback sensitivity in the total sample. Peer feedback sensitivity was defined as the difference score "Feedback-Alone", i.e., the difference between donations in the feedback condition and baseline alone condition. Note that in the antisocial feedback condition, a negative difference score indicates sensitivity to peer feedback, because donations in the Feedback condition are smaller than the Alone condition. Data were analyzed with separate multiple regression models for the Prosocial feedback condition and the Antisocial feedback condition. Because of missing data in SRS and TIQ, a total of $N = 56$ participants were included in the prosocial feedback analysis and $N = 60$ participants in the antisocial feedback analysis. Predictor variables were SRS, all SRQ subscales, and RPI score, as well as TIQ to assess potential effects of intelligence.

3. Results

Descriptives ASD and TD group

Table 3 shows the mean scores on the questionnaires for the ASD and TD group separately. Mean inter-item correlations showed that the subscales were suitable for both ASD and control group, although only the RPI was below the recommended .20 for the ASD group. A *t*-test revealed that the ASD group and TD reported similar levels of Resistance to Peer Influence ($t(142) = -0.24$, $p = .810$). Separate *t*-tests revealed that differences between the groups emerged on the SRQ scales Passivity ($t(142) = -4.38$, $p < .001$) and Sociality

($t(142) = 2.19$, $p = .030$). Findings indicated that the ASD group had a higher preference for other people to make decisions for them, while they tend to engage less in group interactions relative to the TD group.

Table 3. *Mean scores on social interest questionnaires for ASD group and TD group*

Mean (*SD*)	No. items	Answer range	ASD ($N = 75$)	TD ($N = 69$)	*M* IIC ASD/TD
RPI	10	1 – 4	2.99 (0.45)	2.97 (0.52)	.14/.24
SRQ Admiration	4	1 – 7	5.00 (1.23)	5.01 (0.89)	.40/.24
Negative social potency	5	1 – 7	2.23 (0.88)	2.32 (0.77)	.32/.24
Passivity	3	1 – 7	3.24 (1.11)	2.49 (0.93)**	.40/.32
Prosocial Interactions	5	1 – 7	5.88 (0.65)	5.78 (0.73)	.29/.39
Sociality	3	1 – 7	5.10 (1.26)	5.52 (1.04)*	.42/.46

** $p < .001$, * $p < .05$

Abbreviations. RPI = Resistance to Peer Influence. SRQ = Social Reward Questionnaire. IIC = inter-item correlation. *Note.* Within the ASD sample, the Antisocial feedback group scored slightly higher ($p = .051$) on the RPI, $Mean_{PROS}(SD) = 2.89(0.48)$, $Mean_{ANTI}(SD) = 3.09(0.39)$. Within the TD sample, the Prosocial feedback group scored higher on SRQ Sociality ($p = .043$), $Mean_{PROS}(SD) = 5.77(0.78)$, $Mean_{ANTI}(SD) = 5.26(1.22)$.

Task: Peers Public Goods Game

To analyze the donations to the group in the ASD and TD group, we conducted a 2 (Diagnosis: ASD and TD) x 2 (Feedback type: prosocial feedback, antisocial feedback) x 4 (Condition: Alone, Spectator, Feedback, Alone 2) ANOVA with repeated measures of the last factor. Means for the number of tokens donated to the group in each condition for the groups are displayed in Figure 2.

Results indicated a main effect of Condition, qualified by a Feedback type x Condition interaction ($F_{GG}(3,420) = 19.39$, $p < .001$, $\eta_p^2 = .122$). There was no between-subjects effect nor interaction effect of Diagnosis, indicating that there was no behavioral difference between the ASD group and TD group. In a post-hoc comparison across Feedback types, there was no significant difference between the Alone condition and Spectators condition ($p = 1.000$). We further assessed the donation patterns for the two feedback types separately. In the Prosocial feedback condition, significantly more tokens were donated to the group when prosocial feedback was provided compared to playing Alone or with Spectators (both *p's* $< .001$). In the following Alone after feedback trials, adolescents returned to the initial Alone donation rate ($p = 1.000$).

the Antisocial feedback condition, findings revealed that fewer tokens were donated to the group when spectators provided antisocial feedback relative to playing Alone or with

5

Spectators (Feedback-Alone $p = .002$; Feedback-Spectator $p < .001$). Again, the donations in Alone after feedback and Alone were similar ($p = .115$).

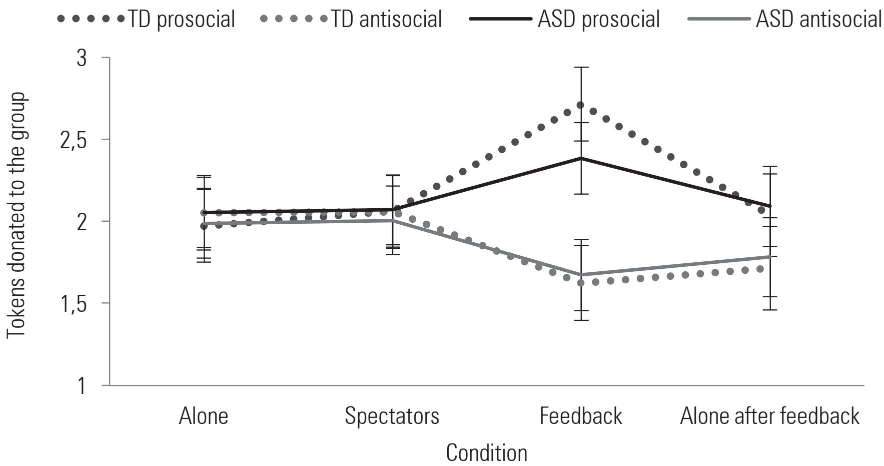


Figure 2. Mean number of tokens (out of 5 tokens) donated to the group under each PGG condition, displayed for ASD group and TD group separately for illustrative purposes. Error bars represent 1 standard error of the mean. There were neither main effects nor interaction effects of Diagnosis, indicating that adolescents with and without ASD showed no behavioral differences in the PGG. The interaction effect of Feedback type x Condition showed that participants donated more tokens in the prosocial feedback condition, and less tokens in the antisocial feedback condition.

Individual differences: Severity of autism symptoms and social interest

Regression analyses were conducted to examine how individual differences in autism symptoms and social interest play a role in sensitivity to peer feedback in the total sample. We conducted separate analyses for the Prosocial feedback condition and the Antisocial feedback condition. In each analysis we included autism symptom severity (SRS score), social reward (SRQ subscales), sensitivity to peers (RPI) and total IQ in model 1, and the interactions between SRS and these variables in model 2 to predict the difference score Feedback-Alone. In the Prosocial feedback condition, sensitivity to peer influence was not predicted by individual differences in our variables ($p = .767$). In the Antisocial feedback condition both models were significant. However, the R^2_{change} of model 2 was not significant ($p = .413$), indicating that model 1 was the best fit to the data ($F(8,51) = 2.95$; $R^2_{adj} = .212$, $p = .009$). The results of the antisocial feedback analysis are summarized in Table 4.

Table 4. *Multiple regression analysis: Sensitivity to antisocial peer feedback*

Model 1: Antisocial feedback	Correlations $N = 60$	β	*t*
SRS score	.241~	.288*	2.10
TIQ	N/A	-.421*	-3.22
RPI	.289*	.282*	2.23
SRQ: Admiration	.264*	.355*	2.78
Negative Social Potency	-.030	-.054	-0.40
Passivity	-.046	-.004	-0.03
Sociality	-.163	-.131	-1.00
Prosocial interactions	.043	.029	0.22

** $p < .001$, * $p < .05$ ~ p = .066.

Note. Correlations reported are partial correlations between the difference score Feedback-Alone and other variables, controlled for TIQ.

The strongest positive predictor in the model was SRQ Admiration, (β = .355, $t = 2.78$, $p = .008$), followed by SRS score (β = .288, $t = 2.10$, $p = .041$) and RPI (β = .282, $t = 2.23$, $p = .030$). This demonstrates that in the total sample, boys with more ASD symptoms, higher self-reported resistance to peers and more enjoyment of being admired for doing good were less sensitive to antisocial peer influence. On the other hand, TIQ was a negative predictor of the sensitivity to peer influence, (β = -.421, $t = -3.22$, $p = .002$) revealing that boys with a lower IQ were more sensitive to antisocial peer influence.[4]

4. Discussion

The goal of the present study was to examine peer influence on prosocial behavior in eleven-to-seventeen year-old boys with and without ASD. This was investigated with the peers public goods game (PGG) during which participants were asked to make decisions within their group in the presence or absence of peer feedback. Our key finding is that boys with and without ASD were sensitive to peer feedback on prosocial behavior. Participants donated more tokens to the group when peers endorsed prosocial behavior. Yet, prosocial behavior decreased when peers liked selfish behavior. Individual differences analyses showed that within the total sample, those with more autism symptoms and social interest were less sensitive to antisocial peer influence. Lower intelligence was associated with more sensitivity to antisocial peer influence. These outcomes will be further discussed below.

4 *Note.* If we do not include TIQ, autism symptoms are no longer a significant predictor in the regression model. This suggests that intelligence compensates for autism symptoms.

Peer feedback on prosocial behavior in TD and ASD adolescents

The current findings provide novel insights about feedback sensitivity in TD and ASD adolescents. In line with previous work, TD adolescents adjusted their prosocial behavior to social norms conveyed by peer feedback (Choukas-Bradley et al., 2015; Van Hoorn et al., 2016b). We replicated earlier results indicating that peers can provide a negative influence as well as a positive influence on prosocial behavior (Van Hoorn et al., 2016b). Although peer influence is often portrayed as vulnerability associated with an increase in health-risk behaviors, it is equally important to recognize the opportunity that lies in learning from peers during adolescence (Albert et al., 2013; Brechwald & Prinstein, 2011; Van Hoorn et al., 2016a).

Unexpectedly, we found that adolescents with ASD were also sensitive to feedback from peers, at least in the prosocial domain. Despite the social impairments that characterize ASD, the peer context seems an important environment for learning about social norms concerning prosocial behavior. These social norms entailed what the peer group considered an appropriate response in the peer context (i.e., what you are "ought" to do) (McDonald & Crandall, 2015). The disparity with previous research, which suggested diminished conformity in ASD, may result from different behavioral domains studied. Most likely, children with ASD did not conform in the context of incorrect factual information, because they tend to have a strong sense for what is factually right and have great attention to detail (Lai et al., 2014; Yafai et al., 2014). In the domain of prosocial behavior, the present findings suggest that adolescents with ASD are attuned to the peer environment, which could foster socially adaptive behavior.

In the above analysis we made a strict distinction between ASD and TD adolescents based on ASD diagnosis. More recently, autism traits have also been studied on a continuum; with individual variability in those with an ASD diagnosis and with the potential that typically developing people can also possess autism traits to a certain extent (DSM-5, APA, 2013; Yafai et al., 2014). Corroborating this perspective, the range of SRS scores indicating autism traits in the present sample shows an overlap in the ASD and TD group, although they differ significantly on a group level. Therefore, we also took a continuous approach across the total sample of adolescents, in which we examined the level of autism symptoms and the potential role of social interest in explaining individual differences in feedback sensitivity.

Individual differences in peer feedback sensitivity

In the individual differences analyses, we found that higher levels of autism symptoms and more social interest predicted less sensitivity to *antisocial* peer feedback. This specificity may be attributed to the nature of advice in the antisocial feedback condition: peer endorsement of selfish behavior. Socialization of prosocial behavior starts already early in development, when adults teach children appropriate prosocial behaviors so that they will fit in the norms of society (Padilla-Walker & Carlo, 2014). However, when children grow older, they interact with a wider range of agents including peers and social media (Rendell et al., 2011). Perhaps, those with higher levels of autism traits are less sensitive to antisocial peer feedback because being selfish is not in line with a previously learned prosocial norm from adults. Alternatively, those with more autism traits may be less sensitive to peer feedback endorsing selfish behavior because they take a more instrumental approach to prosocial behavior (Schmitz, Banerjee, Pouw, Stockmann, & Rieffe, 2015). That is, all group members including participants themselves earn more money if the group donates their tokens to the public goods pot, rather than when group members make selfish decisions. Those with higher levels of autism traits may be more focused on the overall outcome than being accepted by the online peer group.

Social interest was operationalized in the present study by the indices sensitivity/resistance to peers (RPI, Steinberg & Monahan, 2007) and social reward (SRQ, Foulkes et al., 2014). More self-reported resistance to peer influence and enjoyment of being admired for doing good were related to less sensitivity to antisocial feedback. This implicates that autism symptoms and social interest may constitute a protective factor for sensitivity to antisocial peer feedback in prosocial decision-making. On the other hand, low intelligence may represent a risk factor, as those with lower intelligence were more sensitive to antisocial feedback. This corroborates previous work reporting a positive relationship between intelligence and self-reported *resistance* to peer influence (RPI) within a large sample (Steinberg & Monahan, 2007). Potentially, adolescents with a lower IQ have more difficulties deciding what the 'right' option is in the current social dilemma, and are therefore more easily swayed in a selfish direction by peer feedback.

Taken together, these individual differences analyses revealed unique insights into the question how autism traits and social interest are related to peer feedback sensitivity. In future research, these findings need to be replicated. Social interest is a broad concept, including social attention, social reward and social maintaining (Chevallier et al., 2012). In the current study, we have focused on two specific indices relevant to adolescence and it would be important to examine how the current results map onto other aspects of social interest.

Limitations

One limitation which should be noted is that we included only high-functioning adolescent boys with ASD. As a consequence, we cannot generalize the findings to the entire ASD population, which encompasses a broad range of social, intellectual as well as language capacities in boys and girls (Jones & Klin, 2009). Nonetheless, to our knowledge this is the first study that investigated sensitivity to peer feedback in such large samples of ASD and TD adolescents. Future research needs to extend these findings with developmental comparisons and in different domains such as risk-taking behaviors. The specificity of the source of feedback should be determined, as the current study investigated peer feedback from an unknown peer group and did not compare feedback from different sources.

In addition, the current task environment is a relatively structured social situation, and as such did not allow us to manipulate all factors that play a role in more complex social situations. At present we can only draw conclusions about a *short-term* effect of peer feedback (Van Hoorn et al., 2016b). A longitudinal design could be employed to investigate whether peer feedback continues to guide prosocial decisions in adolescents with and without ASD. Moreover, we have used the social reward questionnaire for the first time in a Dutch ASD and TD adolescent sample and this requires more thorough validation (Foulkes et al., 2014). Nonetheless, the current study can be considered a stepping-stone, which examined whether in principle this process is present in adolescents with ASD.

Conclusions and future directions

The key finding of this study was that adolescents with ASD showed sensitivity to peer feedback on prosocial behavior. More insight into the peer influence process in this population advances our knowledge of the vulnerabilities and the opportunities that may arise in the interactions with peers. Crucially, ASD adolescents seem attuned to the peer environment, which may create opportunities for social adjustment. Given the relation of autism symptoms to sensitivity to antisocial feedback, but not prosocial feedback, it may be that they operate through separate pathways. To gain more understanding of the motivations and processes underlying peer influence in ASD, future research could examine its underlying neural correlates in the developing brain.

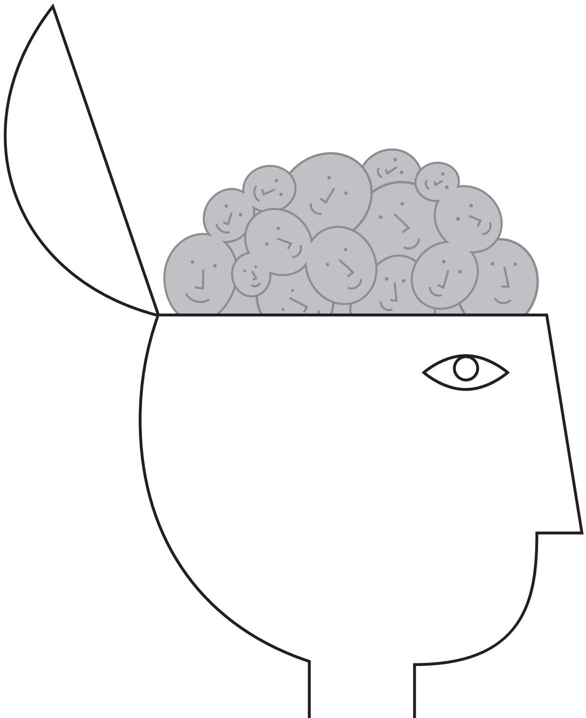
For instance, some high-functioning individuals with ASD have been found to learn and apply social rules as a compensatory strategy to mask mentalizing problems in social situations (Hill & Frith, 2003; Jameel, Vyas, Bellesi, Cassell, & Channon, 2015). The current study did not allow us to disentangle potential compensatory strategies from actual recruitment of mentalizing abilities in the peer context. A previous neuroimaging study in TD adolescents showed involvement of the social brain network (i.e., brain regions that underlie mentalizing) during decision-making with peer feedback compared to alone (Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). A tentative hypothesis would be that ASD adolescents recruit social brain areas less if they use compensatory strategies rather than mentalizing skills during decision-making with peers present (Koster-Hale, Saxe, Dungan, & Young, 2013).

This study also has more practical implications, as it may provide a building block for interventions. To date interventions designed to increase prosocial interactions in ASD seem promising, but what works for whom is still unclear (Ledford, King, Harbin, & Zimmerman, 2016). The current findings suggest a peer component in treatment may be effective to increase prosocial behaviors in ASD. Future research should determine other individual and environmental factors that may facilitate or hinder sensitivity to peer feedback in complex real-life social situations, such that our findings can be translated into practice.

Chapter 6:

Summary and general discussion

This chapter is partly based on: Van Hoorn, J., Fuligni, A. J., Crone, E. A., & Galván, A. (2016). Peer influence effects on risk-taking and prosocial decision-making in adolescence: Insights from neuroimaging studies. *Current Opinion in Behavioral Sciences, 10,* 59-64. doi: 10.1016/j.cobeha.2016.05.007



1. Summary

So, were my parents right when they warned me about negative peer influence as a teenager? The answer that many parents, including mine, have often heard is *"Yes, but…"*

The main goal of this thesis was to investigate peer influence on decision-making in adolescence. Taken together, the studies in this thesis provide a scientific basis to refine the negative connotations of peer influence. The effects of peers on risk-taking behavior are present, but are dependent on context. Adolescents take into account both social norms from peer feedback and the uncertainty associated with outcomes in risky decisions (**Chapter 2**). Moreover, I delved into the adaptive side of peer influence, which to date has received little attention in research. Peers can both increase and decrease prosocial behavior in typically developing (TD) adolescents and those with autism spectrum disorders (ASD), illustrating that peer influence can also lead to positive psychosocial outcomes (**Chapter 3** and **Chapter 5**). Finally, I examined the underlying neural processes and showed that prosocial peer influence is underlined by a network of social brain regions in the adolescent brain that is involved in thinking about the self and others (**Chapter 4**). A summary of each of these chapters will be described below, followed by an overall discussion, future directions, implications and conclusions.

Peer influence on risk-taking behavior

The first empirical chapter (**Chapter 2**) describes the effects of peer feedback on risk-taking behavior and the validation of a novel experimental paradigm, the guess gambling game (GGG). Peer influence plays a central role in the increase of risk-taking behavior during adolescence (Albert et al., 2013; Brechwald & Prinstein, 2011). However, at present the processes underlying peer influence on risk-taking are not fully understood. In this study I examined how peer advice influenced risk-taking behavior in adolescents between fifteen and seventeen years of age. I implemented the GGG to measure risk-taking behavior in the peer context. In this card-guessing game, participants were presented with two playing cards from a deck of hearts ranging between one (Ace) and nine. After the first card was presented face up participants were asked to guess whether the next card would be higher or lower (*guess*). In addition, participants could place a variable bet with poker chips on whether they guessed correctly (*gamble*). This task provided the possibility to disentangle peer effects on rational guesses and gambling (i.e., risk-taking behavior); and to vary the uncertainty of the outcome, with card 5 being most uncertain, whereas card 1 and 9 had entirely certain outcomes.

The GGG was played alone in one condition and with manipulated advice from online peers on how many chips to bet (*low* bet, *medium* bet or *high* bet advice) in the other. As such, the different advice types signaled social norms about how many tokens to bet. Findings indicated that guessing patterns were similar with and without peers present. This result suggests that the presence of peers does not change the ability to reason about card probabilities (Reyna & Farley, 2006; Van Duijvenvoorde & Crone, 2013; Van Leijenhorst et al., 2010). However, in line with previous work gambling behavior increased in the presence of peers (e.g. Gardner & Steinberg, 2005; Smith et al., 2014). Importantly, effects of peer advice on gambling behavior were differentiated depending on the uncertainty associated with gambles as well as the social norms signaled by peer advice. Peer feedback was most influential in such uncertain situations. In conclusion, during gambling decisions adolescents seem to make active meaning of the context, integrating information from peer feedback and outcome (un)certainty. These findings resonate with the economic decision-making literature that suggests that adolescents have the cognitive capacity to make prudent decisions, but tend to pursue more risky courses of action in a 'hot' context (for example with peers) (Figner et al., 2009; Shulman et al., 2016). This differentiated effect of peer feedback demonstrates the value of a social norms approach in examining the process underlying peer effects. Subsequently, I applied this approach to a new paradigm that measures prosocial decision-making during adolescence.

Peer influence on prosocial behavior and its neural correlates

In **Chapter 3** I examine the adaptive side of peer influence as a process that may create opportunities for prosocial development during adolescence (Allen & Antonishak, 2008; Crone & Dahl, 2012). Some evidence from non-experimental studies suggested links between peer influence and prosocial outcomes in dyads and larger peer groups (e.g. Barry & Wentzel, 2006; Berger & Rodkin, 2011), but such outcomes have not been studied before with an experimental task. In this study I validated a novel experimental paradigm called the peers public goods game (PGG) in a large sample of adolescents twelve to sixteen years of age. In this social dilemma, participants made decisions in an anonymous four-person group about the allocation of tokens between themselves and the group (Harbaugh & Krause, 2000; Ledyard, 1995). Participants were informed that all tokens donated to the group would be doubled and split over the four group members. They were also told that they could keep the tokens that they did not donate. As such, participants had to balance self-interest and concern for the group in making their prosocial decisions (Ledyard, 1995). In this task on-the-spot prosocial behavior was quantified as the number of tokens donated to the group.

To test the hypothesis that peers influence prosocial decision-making, adolescents played the PGG alone and with manipulated peer feedback from a group of spectators for a number of decisions. Results indicated that changes in prosocial behavior were dependent on the social norms of the peer group. Prosocial behavior increased after prosocial peer feedback (i.e., likes for large donations to the group) and decreased after antisocial peer feedback (i.e., likes for not donating). There were no changes in prosocial behavior when participants played with peers only present (i.e., peers observing behavior). These findings highlight the view that peer influence creates not only vulnerabilities, but also opportunities for prosocial development and social adjustment learning. Next, I examined what happens in the adolescent brain during prosocial decision-making with peers present.

Chapter 4 describes the results of an fMRI study in which I used a modified version of the PGG task (Chapter 3) to examine the neural correlates of prosocial peer influence on prosocial behavior during adolescence (ages 12-16 years). Previous neuroimaging work has shown that *risk-taking* in the presence of peer results in enhanced ventral striatum (VS) activity in adolescents, but not in (young) adults (Chein et al., 2011). Yet, the neural processes underlying prosocial peer influence effects are not well understood. Previous research in adults suggests a role for medial prefrontal cortex (mPFC) and VS in the context of peer evaluation. The mPFC is implicated in mentalizing (thinking about self and others), social cognitive processes and social influence (Izuma, Saito, & Sadato, 2010b; Falk et al., 2014; Welborn et al., 2016).

In the MRI scanner, participants played the PGG alone, with spectators observing decisions, and with prosocial feedback. This time, the online spectator groups of same age peers were in fact youth actors who participants had met before the start of the study. Behavioral results showed that prosocial behavior increased in the presence of peers, and even more when participants received prosocial feedback from peers. On the neural level, peer presence during donation choices resulted in enhanced activity in several social brain regions including dorsal mPFC, TPJ, precuneus, and STS. These findings highlight the role of mentalizing regions in peer influence and are consistent with research relating to the effect of prosocial behavior towards the family (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011) and public goods donations in adulthood (Bault, Pelloux, Fahrenfort, Ridderinkhof, & Van Winden, 2015). Peer presence effects were larger in dmPFC and STS for early adolescents (12-13 years olds) than for mid-adolescents (15-16 years olds), suggesting that younger adolescents may be more susceptible to their social context. These findings shed light on the role of peers in fostering prosocial development throughout adolescence. With this background in typical development, I turn to Chapter 5 that examines peer influence effects in adolescents with autism.

Peer influence on prosocial behavior in autism

Like typically developing adolescents, those with autism spectrum disorders (ASD) show a social reorientation towards peers when they transition from childhood to adolescence (McGovern & Sigman, 2004; Carter et al., 2014). However, adolescents with ASD often struggle to understand social situations (Tantam, 2003). Given the difficulties in social interaction and interaction as well as theorized diminished motivation, I hypothesized that adolescents with ASD would show attenuated sensitivity to the peer context (Yafai, Verrier, & Reidy, 2014). In the study described in **Chapter 5**, I examined whether adolescents with and without autism were influenced by peer feedback on prosocial behavior. In addition, I investigated whether autism symptoms and social interest were related to individual differences in feedback sensitivity. Hence, the PGG included a prosocial and antisocial feedback condition (slightly adapted from Chapter 3 and Chapter 4) and was applied in a large sample of adolescent boys with and without ASD in the ages of eleven to seventeen years.

Findings showed that ASD and TD adolescents were sensitive to peer feedback concerning prosocial behavior. Replicating the earlier behavioral findings, participants donated more tokens when peers endorsed prosocial behavior. There was a decrease in prosocial behavior when peers liked selfish behavior. Interestingly, I discovered that adolescents with ASD were also sensitive to peer feedback on prosocial decisions. Despite atypical social development, peer feedback may create an opportunity for social adjustment learning in ASD adolescents. Within the total sample those with more autism symptoms and more social interest were less sensitive to *antisocial* peer influence. Taken together, autism symptoms and social interest may constitute a protective factor for sensitivity to antisocial peer feedback. These findings provide a building block for interventions and suggest that a peer component may affect change in prosocial behaviors in adolescents with ASD.

2. General discussion

Taken together, the studies presented in this thesis show that peer influence in adolescence can be characterized as a socialization process that leads to health-compromising risky behaviors (i.e., increased gambling), but also to positive psychosocial outcomes (i.e., increased prosocial behavior). In this section, I highlight several discussion points that result from the work in this thesis. First, we need to verify whether the current findings converge within the broader domain of prosocial behavior. Next, it is important in peer influence research to consider the differences between peer presence and peer feedback, as well as the salience of the source of influence because these factors influence peer effects.

Then I discuss the neural correlates of prosocial peer influence and the implications for neurodevelopmental models. Finally, I propose that we need to investigate how unique the findings in the final chapter are to autism spectrum disorders.

The studies in this thesis show that peers influence prosocial decisions of adolescents – for better and for worse. This is consistent with views of adolescence as a period of flexibility and adaptation, and being specifically attuned to the social context (Blakemore & Mills, 2014; Casey, 2015; Crone & Dahl, 2012). Yet prosocial behavior is a multidimensional construct that encompasses various types of behaviors, of which one specific type was assessed in this thesis: cooperation to benefit one's group (Padilla-Walker & Carlo, 2014; Wentzel, 2014). It is important to examine how the current findings map on other types of prosocial behaviors. A recent experimental study found that peers also positively affected intentions to volunteer in adolescence (Choukas-Bradley, Giletta, Cohen, & Prinstein, 2015), providing initial evidence for convergence of experimental peer effects within the domain of prosocial behavior.

Across the current studies, peer observation without feedback (*peer presence*) increased prosocial behavior when participants met adolescent actors as peers before the start of the study (Chapter 4), but showed no effect when these peers were anonymous online others (Chapter 3 and Chapter 5). This disparity suggests that the effects of peer observation may be dependent on the salience of the peers who evaluate these decisions. Peer influence and friendship theories suggest that peer effects are stronger for friends (see Berndt, 2002; Hartup, 2005), although such comparisons have not been directly tested to date. Comparing friends or known peers to unknown peers in an experimental design raises multiple issues concerning background knowledge, including whether social norms and their perception in daily life match with manipulated social norms. That is, would friends approve or encourage prosocial behavior in daily life (i.e., injunctive norms) or does the class engage in such behaviors (i.e., descriptive norms) (McDonald & Crandall, 2015)? Adding a questionnaire that taps into positive and negative perceived peer norms, such as the recently developed Peer Group Norm questionnaire, would be an important step towards addressing this issue (Marshall-Denton, Véronneau, & Dishion, 2016). Taken together, to gain a deeper understanding of the complex peer influence process, it is important to consider *what it is* about those peers and which *processes* lead to subsequent changes in behavior. One way of examining these processes is to investigate what happens in the brain during decision-making.

During prosocial decision-making peers evoked activation in the social brain network, including cortical social brain areas (dorsomedial PFC and TPJ) (Chapter 4). This suggests that making prosocial decisions with peers present activates social-cognitive processes (e.g. Welborn et al., 2016; Somerville et al., 2013). However, there was no evidence for reward-related activity during prosocial decision-making with peers present. Previous work reported that peer influence during risk-taking behavior elicits heightened activation in subcortical reward-processing areas, mainly ventral striatum (VS) (Chein et al., 2011, Smith et al., 2015). That finding has been interpreted as evidence that peer presence increases the motivational salience of rewards, or in other words, that peers make risky behavior more rewarding. The PGG task was optimized to examine peer effects on prosocial behavior and did not have an outcome phase, because participants did not learn about the contributions of the other players. As such, the anticipation of reward was also dependent on decisions of the other group members and may not have provided a steady learning signal for the VS (see meta-analysis Silverman, Jedd, & Luciana, 2015).

In trying to explain these neural findings, I propose that perhaps peer influence heightens activity in task-relevant brain areas, contingent on the type of behavior. Heightened activity may be reflected as enhanced reward-related processing in VS during risk-taking behavior, and in social brain areas such as mPFC and TPJ in the context of prosocial behavior. Currently, it is unclear how the motivational circuit and social brain network interact to shape peer influence processes. The recent refinement of the dual systems model (Shulman et al., 2016) acknowledges that social context moderates developmental effects in decision-making, but does not consider how this expands the neural circuitry involved (Pfeifer & Allen, 2016). The current findings speak to this debate and highlight that it is crucial to study the affective and social brain networks and their interactions with cognitive control networks collectively rather than separately. Doing so may be possible with a task that draws upon both affective and social processes to begin with (e.g., gambling for a friend; Braams, Peters, Peper, Güroğlu, & Crone, 2014), and adding a peer influence condition. Using different analyses, such as functional connectivity, may also shed light on how the social brain network interacts with affective and control neural networks during decision-making with peers present (see e.g. Somerville et al., 2013).

Finally, both typically developing (TD) adolescents and those with autism spectrum disorders (ASD) are influenced by peer feedback. Hence, it seems that the basic process of learning from peers is present in ASD adolescents despite atypical social development. It is crucial to investigate whether these findings are specific to ASD and how they relate to other clinical groups characterized by atypical social development. For example, adolescents with conduct disorder may be less influenced by peer feedback, whereas those with social anxiety disorder may be especially attuned to peer feedback (Haller, Cohen Kadosh, Scerif, & Lau, 2015; Klapwijk et al., 2016). With an increased understanding of the interactions in the peer context in typical and atypical social development, we may be able to help adolescents navigate this time of their lives as an opportunity rather than vulnerability for development.

3. Future directions

There are many other outstanding questions for future research. For instance, to what extent do peers affect cognitive control during adolescence? Initial evidence shows that adolescent – but not adult – performance on a cognitive relational reasoning task is affected by an audience (Wolf, Bazargani, Kilford, Dumontheil, & Blakemore, 2015). A recent follow-up neuroimaging study used a similar relational reasoning paradigm with somewhat different audiences and showed that relational reasoning performance decreased in both adolescents and adults, while activity in the fronto-parietal network increased in the presence of a peer for adolescents only (Dumontheil, Wolf, & Blakemore, 2016). Taking a slightly different approach, one recent study related brain activation in control systems (inferior frontal gyrus and basal ganglia) during a go-no-go task to simulated driving behavior with a peer one week later (Cascio et al., 2015). Activation in control systems was predictive for safer driving when a cautious peer confederate was present; but not with a risk-encouraging peer confederate. This context-dependent activation implicates that neural resources are used differently depending on characteristics of the source of influence (Cascio, Scholz & Falk, 2015).

Moreover, most studies, including those in this thesis, have not compared peer influence to other sources of influence, such as parents. In the neutral domain, peer and parental influence seem to rely on the same neural basis (Welborn et al., 2016). These brain areas include mentalizing areas (mPFC, TPJ), reward-related areas (vmPFC) and areas associated with self-control (vlPFC). The neural findings align with developmental comparisons in the domain of social influence on risk-taking, which suggest that peers are more influential than adults only in early adolescence (12-14 year-olds) (Knoll et al., 2015). Indeed, in the prosocial influence task early adolescents relative to mid-adolescents showed more differentiation in dmPFC activation during decision-making with peer feedback than alone. These neural findings suggest that early adolescents are more sensitive to the peer context in the domain of prosocial behavior. More research is needed to replicate these findings, further clarify neural and behavioral developmental patterns and compare sources of influence in various contexts (risk-taking, prosocial, neutral) in order to draw conclusions about the specificity of the current findings.

Besides the features of the *source* of influence on which this thesis was mostly focused, characteristics of the *target* of influence may also magnify or mitigate effects of peer influence (Brechwald & Prinstein, 2011). Several factors have been of interest in research, including age and gender, but also personality traits such as responsivity to (social) reward (Gardner & Steinberg, 2005; Reniers, Beavan, Keogan, Furneaux, Mayhew, & Wood, 2016; Stautz & Cooper, 2014; Steinberg & Monahan, 2007). Developmental patterns in sensitivity to peer influence seem to differ depending on the methods employed and domain of behavior studied (see e.g. Berndt, 1979). We are only beginning to understand how the interaction between individual traits and characteristics of the social environment embedded in various domains of behavior shape the complex process of peer influence. Future studies investigating individual differences in sensitivity to peer influence would benefit from comprehensive samples covering childhood to far in adulthood, cross-sectional designs using more specific definitions of adolescence, and longitudinal designs to examine change within individuals over time (also see Van Duijvenvoorde, Peters, Braams, & Crone, in press).

4. Practical implications

This research provides a scientific basis to reshape predominantly negative connotations associated with peer influence in society. Peer influence effects on risk-taking behavior represent one side of this phenomenon. Understanding the processes underlying peer influence on risk-taking may provide targets for intervention. Doing so is crucial in order to help adolescents navigate this developmental period successfully and bring down the 300% rise in morbidity and mortality due to preventable risk-taking behaviors (CDC, 2013). A review of previous interventions reports that the use of the social norms approach to decrease drinking behavior in college students yielded mixed results (Prentice, 2008). These campaigns have mainly focused on descriptive norms (for example, introducing a true norm about how many drinks are "normal") and have barely touched upon injunctive norms (e.g., peers endorsing restraint in drinking behavior). The findings in this thesis suggest that injunctive norms may be a good target to induce a positive change in drinking behavior.

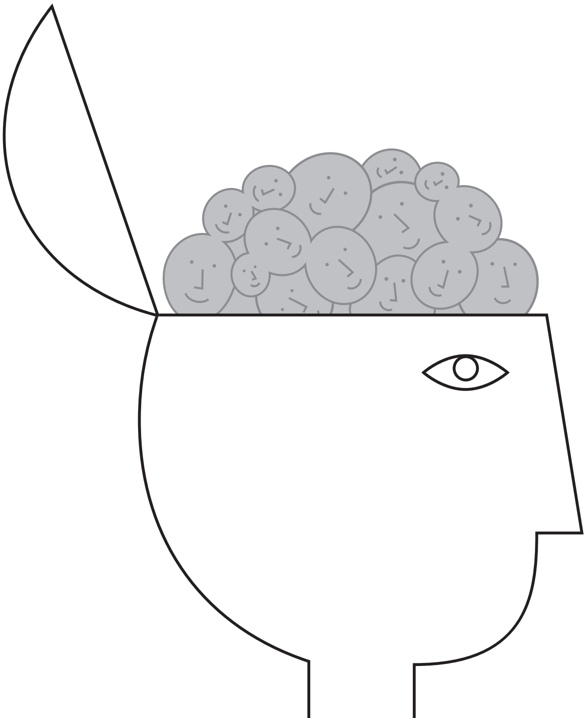
The other side of peer influence can be described as an opportunity for prosocial development and social adjustment learning. The findings are also a promising basis for interventions to promote prosocial behaviors. One example is the Good Behavior Game designed for primary schools in which disruptive and non-disruptive students work together in small teams (Van Lier, Huizink, & Vuijk, 2011). Peer influence and social norms may contribute to the effects of this intervention, because the entire team gets a reward for endorsing positive and prosocial classroom behavior. So far, programs for adolescents have received less attention (but see CEPIDEA; Caprara, Luengo Kanacri, Zuffianò, Gerbino, & Pastorelli, 2015). A recent meta-analysis about school-based interventions does suggest that early adolescents are more sensitive than children to interventions focused on positive peer relations, because of the increased salience of fitting in and having good relationships with peers (January, Casey, & Paulson, 2011). This meta-analysis is in line with the findings in this thesis and suggests that adolescence is a period during which an intervention to promote prosocial behaviors with a peer component may be effective.

Finally, this research also has clinical implications. Chapter 5 showed that boys with and without autism spectrum disorders (ASD) are influenced by feedback from peers. This attunement to the peer environment opens doors for training social skills and prosocial behavior. Given the tremendous heterogeneity in ASD, it is yet unclear which interventions work for whom (Ledford et al., 2016). The findings suggest that peer feedback may be an effective mechanism to alter prosocial behaviors in high-functioning boys with ASD. Naturally, findings from a controlled experimental environment do not directly map on complex real-life social situations and we need to identify individual and environmental factors that magnify or mitigate sensitivity to peer feedback. Collaborations between experimental and intervention research could be fruitful in determining which active ingredients are necessary for interventions in TD and ASD adolescents.

5. Conclusions

In conclusion, this thesis provides a comprehensive overview of peer influence effects on decision-making. Peer influence can be characterized as a socialization process that leads to health-risk behaviors on the one hand, and positive psychosocial outcomes on the other hand. The neural findings further inform the debate about including social context in neurodevelopmental models of decision-making in adolescence, and show that affective and control networks should be studied collectively with social brain networks. By further researching the effects of peer influence, we may be able to assist adolescents in navigating a complex social phase of their lives. Eventually, these results can contribute to interventions aimed at decreasing risk-taking and promoting prosocial behavior in adolescence, with possibly long lasting effects into adulthood.

Nederlandse samenvatting



1. Introductie

"Als je vrienden in de sloot springen, doe jij het dan ook?"

Als adolescent hebben mijn ouders me regelmatig geprobeerd duidelijk te maken dat de invloed van vrienden negatief kan zijn. Hadden ze gelijk? Wetenschappelijk onderzoek laat inderdaad zien dat er een toename is in risicogedrag wanneer adolescenten samen met hun vrienden zijn (Albert, Chein, & Steinberg, 2013; Brechwald & Prinstein, 2011). Voorbeelden van risicogedrag zijn onder andere het drinken van grote hoeveelheden alcohol, te hard rijden met de auto en roken (Boyer, 2006). De toename van risicogedrag wordt geassocieerd met een toename van 300% in sterftecijfers, terwijl adolescenten fysiek gezien juist in de meest gezonde fase van hun leven zijn (CDC, 2013). Daarom is het cruciaal meer inzicht te krijgen in hoe vrienden en leeftijdsgenoten de beslissingen van adolescenten beïnvloeden.

Recent onderzoek laat zien, dat adolescenten niet alleen negatief worden beïnvloed door leeftijdgenoten. De adolescentie wordt tevens gedefinieerd als een periode van adaptatie en kansen in plaats van enkel een periode van kwetsbaarheid (Crone & Dahl, 2012). Zo zou de invloed van leeftijdgenoten ook beschermend kunnen zijn tegen de toename van risicogedrag of zelfs leiden tot positieve uitkomsten, zoals bijvoorbeeld meer prosociaal gedrag (Allen & Antonishak, 2008). Onder prosociaal gedrag wordt gedrag verstaan zoals helpen, samenwerken en delen (Padilla-Walker & Carlo, 2014). Tot nu toe is er nog weinig onderzoek gedaan naar de effecten van leeftijdgenoten op prosociaal gedrag. Sommige studies suggereren dat leeftijdgenoten prosociaal gedrag kunnen beïnvloeden in een 1-op-1 situatie of in grotere groepen (Barry & Wentzel, 2006; Berger & Rodkin 2012). Meer onderzoek naar de beïnvloeding van prosociaal gedrag door leeftijdgenoten kan de positieve kant van dit proces voor de ontwikkeling van adolescenten in beeld brengen.

Dit proefschrift draagt bij aan de huidige kennis over de invloed van leeftijdgenoten op het maken van beslissingen in de adolescentie. Het doel is om de invloed van leeftijdgenoten op risicogedrag en prosociaal gedrag te onderzoeken en de onderliggende mechanismen in de hersenen in kaart te brengen. Naast adolescenten zonder psychopathologie worden ook adolescenten met een autisme spectrum stoornis (ASS) onderzocht, een klinische groep gekenmerkt door atypische sociale ontwikkeling (DSM-5, APA, 2013). Het is belangrijk om beter te begrijpen hoe leeftijdgenoten prosociaal gedrag kunnen beïnvloeden, omdat prosociaal gedrag gerelateerd wordt aan vele positieve uitkomsten, zoals vriendschappen, mentale gezondheid en goede resultaten op school (Lam, 2012).

2. Adolescentie, peer pressure en sociale normen

De adolescentie is de ontwikkelingsperiode tussen de kindertijd en volwassenheid. De start wordt gemarkeerd door de puberteit, terwijl het eindpunt vaak meer cultureel bepaald wordt door het bereiken van volwassen sociale doelen. Traditioneel wordt de periode van de adolescentie ingedeeld in drie ontwikkelingsfases: vroege adolescentie (10-13 jaar), mid-adolescentie (14-17 jaar) en late adolescentie (18-vroege twintiger jaren) (Steinberg, 2008). De adolescentie wordt gekenmerkt door enorme veranderingen, zoals ontwikkeling van de identiteit, exploratie van de omgeving en meer onafhankelijk worden van ouders (Crone & Dahl, 2012). Naast deze fysieke, sociale en cognitieve veranderingen wordt de sociale wereld ook heel anders. De sociale focus gaat van spelen met leeftijdgenoten naar de integratie binnen een groep van leeftijdgenoten (Nelson, Jarcho, & Guyer, 2016). Zo wordt het erg belangrijk om geaccepteerd te worden in de groep en op een positieve manier geëvalueerd te worden door leeftijdgenoten (Blakemore & Mills, 2014; Somerville, 2013). Gedurende de adolescentie wordt er meer tijd doorgebracht met leeftijdgenoten dan in de kindertijd, zowel face-to-face als online door verschillende vormen van sociale media (Lam, McHale, & Crouter, 2014; Lenhart, 2015). Toch is het zo dat relaties met leeftijdgenoten de bestaande relaties met ouders aanvullen en niet zozeer vervangen (Smetana et al., 2006).

Peer pressure wordt gedefinieerd als de directe druk om je aan te passen aan de mening van leeftijdgenoten (Brown et al., 2008). Echter, de invloed van leeftijdgenoten is vaak ook meer subtiel en indirect. Indirecte vormen van invloed zijn bijvoorbeeld het kopiëren van gedrag en het aanmoedigen van gedrag door anderen. In dit proefschrift maak ik een onderscheid tussen *feedback* van leeftijdgenoten ("actieve" invloed van leeftijdgenoten of aanmoediging) en *aanwezigheid* van leeftijdgenoten ("passieve" invloed van leeftijdgenoten). De sociale normen theorie stelt dat adolescenten door de invloed van leeftijdgenoten sociale normen leren over gepast gedrag in de context van leeftijdgenoten (Bandura, 1986; Cialdini & Trost, 1998). Dit kan bijvoorbeeld zijn "Ik moet bier drinken" of "Ik moet mijn best doen op school". Niet alleen sociale normen zelf liggen ten grondslag aan gedrag en attitudes, maar ook de perceptie van deze normen (Berger, 2008). In de context van risicogedrag wordt er gedacht dat adolescenten vaak overschatten hoeveel risico hun leeftijdgenoten nemen (Prinstein & Wang, 2005). Als adolescenten zich dan vervolgens conformeren aan deze perceptie, zou dit kunnen resulteren in een interactieve toename van risicogedrag.

Epidemiologische studies laten zien dat leeftijdgenoten een cruciale factor zijn in de toename van verschillende vormen van risicogedrag in de adolescentie, zoals auto ongelukken, roken en het drinken van grote hoeveelheden alcohol (Wang, Cai & Duncan, 2015). Ook de meerderheid van het experimentele onderzoek in het laboratorium laat deze toename in risicogedrag zien. In het laboratorium is door verschillende onderzoeksgroepen gekeken naar risicogedrag met computertaken zoals autorijden (Stoplicht spel), de ballontaak (BART) en goktaken (o.a. Rad van Fortuin, Kaartspel, Schatkisten). Andere onderzoekers hebben gekeken naar de invloed van sociale normen in een rijsimulator om meer ecologisch valide rijcondities te creëren (Simons-Morton et al., 2014). Adolescenten namen meer risico's wanneer er een leeftijdgenoot bij hen in de simulator zat die risico's nam, dan als deze leeftijdgenoot risico's vermeed. Deze bevindingen laten zien, dat sociale normen een belangrijke rol spelen in het onderzoeken van risicogedrag in het bijzijn van vrienden en leeftijdgenoten.

Anderzijds laat recent onderzoek zien dat de invloed van leeftijdgenoten ook adaptief gedrag zoals leren en prosociaal gedrag kan beïnvloeden. Zo lieten deelnemers bij een leertaak meer exploratief gedrag en een hoger leer-rendement zien in het bijzijn van leeftijdgenoten, dan wanneer zij de taak alleen deden (Silva, Shulman, Chein, & Steinberg, 2015). "Prosociaal gedrag" is een complex construct, dat verwijst naar vrijwillig gedrag waar een ander voordeel van heeft (Eisenberg, Fabes, & Spinrad, 2006). Er vallen verschillende soorten gedrag onder, zoals delen, helpen en samenwerking binnen een groep waar iedereen van profiteert (Padilla-Walker & Carlo, 2014). Enkele studies die met vragenlijsten prosociaal gedrag onderzocht hebben, leveren bewijs voor een link tussen de invloed van leeftijdgenoten en verschillende prosociale uitkomsten gedurende de ontwikkeling. Ook binnen sociale netwerken van kinderen is bekend, dat vrienden prosociaal gedrag beïnvloeden in een 1-op-1 situatie en binnen een grotere groep.

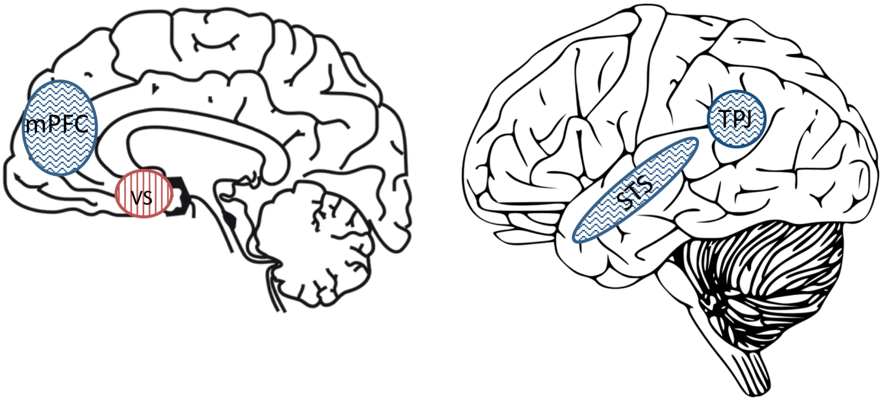
In dit proefschrift heb ik één type prosociaal gedrag onderzocht: samenwerking waar je groep voordeel van heeft. Kijken naar samenwerking binnen een groep is bij uitstek interessant in de adolescentie, omdat vanaf de kindertijd de meeste interacties met leeftijdgenoten plaatsvinden binnen een groep (Rubin et al., 2006). Deze vorm van samenwerking is gemeten met een munten verdeel taak, de "Public Goods Game" (Harbaugh & Krause, 2000; Ledyard, 1995). Deelnemers aan het onderzoek werden gevraagd om binnen een groep van vier anonieme leeftijdgenoten munten te verdelen en kregen de kans om als groep een geldbonus te verdienen. Ze konden besluiten om munten aan de gezamenlijke pot te geven (samenwerking – en daarmee de geldbonus te verdienen als groep), of om een deel van de munten voor zichzelf te houden (geen samenwerking). Het voordeel van het gebruiken van een experimentele taak zoals de Public Goods Game is, dat het de kans biedt om prosociaal gedrag op dat moment in de tijd te kwantificeren en dat je kunt kijken naar oorzaak-gevolg.

Samengevat laat de literatuur over de invloed van leeftijdgenoten zien dat de adolescentie een periode is van specifieke sensitiviteit voor de sociale omgeving, wat zowel kansen als kwetsbaarheden kan creëren voor de ontwikkeling. Met deze achtergrond focus ik nu op de verdere ontwikkeling van het brein, dat parallel loopt aan de veranderingen in het gedrag gedurende de adolescentie.

3. De ontwikkeling van het brein in de adolescentie

In de afgelopen decennia is er veel vooruitgang geweest in technieken om het brein te bestuderen. Met een techniek als kernspintomografie (Magnetic Resonance Imaging; MRI) kunnen we een kijkje nemen in het brein van de adolescent. Door het gebruik van MRI kunnen we onder andere de ontwikkeling van hersenstructuur (sMRI) en hersenfunctie (fMRI) onderzoeken; oftewel welke hersengebieden worden gebruikt bij het uitvoeren van een taak. *Structurele* MRI studies hebben consistent bewijs geleverd dat de hersenen zich blijven ontwikkelen tot ongeveer het 25ᵉ levensjaar. De veranderingen in gedrag tijdens de adolescentie worden gerelateerd aan veranderingen in de hersen*functie*. Een belangrijk neuropsychologisch model om risicogedrag te verklaren is het imbalans model (Somerville, Jones, & Casey, 2010; Steinberg, 2008). Dit model veronderstelt, dat de controlesystemen in het brein zich langzaam ontwikkelen, terwijl het beloningssysteem hyperactief is in de adolescentie. Het controlesysteem omvat de prefrontale cortex en is betrokken bij redeneren en de regulatie van gedrag. Het beloningssysteem bestaat uit het ventraal striatum (VS), betrokken bij leren en het voorspellen van beloningen en de amygdala, betrokken bij associatief leren en emotie (Casey, 2015).

De meeste onderzoeken naar risicogedrag in de adolescentie hebben zich gefocust op het ventraal striatum (zie Figuur 1). De literatuur laat zien dat activiteit in het ventraal striatum na het ontvangen van een beloning piekt bij adolescenten – in vergelijking met kinderen en volwassenen (Silverman, Jedd, & Luciana, 2015). Deze piek in activatie lijkt uitvergroot te worden wanneer adolescenten risico's nemen in de aanwezigheid van leeftijdgenoten. Chein en collega's (2011) vroegen adolescenten, jongvolwassenen en volwassenen om de Stoplicht taak (een computertaak die risicogedrag tijdens het autorijden meet) alleen te spelen of met een vriend erbij. Met een vriend erbij nam het risicogedrag van adolescenten toe – maar niet van (jong)volwassenen – en dit was gerelateerd aan een verhoogde activatie in het ventraal striatum. Samengevat suggereren deze bevindingen dat de aanwezigheid van leeftijdgenoten risicogedrag meer belonend maakt, wat er voor lijkt te zorgen dat adolescenten meer gemotiveerd zijn om risico's te nemen.



Figuur 1. Het ventraal striatum (VS) is betrokken bij risicogedrag en verwerken van beloning. De medial prefontal cortex (mPFC), STS (superior temporal sulcus) en TPJ (temporo-parietal junction) zijn betrokken bij het verwerken van sociale informatie.

Een tweede lijn van onderzoek heeft de beoordeling van leeftijdgenoten onderzocht buiten de context van risicogedrag. Dit onderzoek laat zien dat beoordeling door leeftijdgenoten gelinkt is aan verhoogde activatie in een netwerk van hersengebieden dat soms het "sociale brein" wordt genoemd. Dit netwerk is betrokken bij het nadenken over jezelf en anderen en bestaat uit de medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ) en superior temporal sulcus (STS) (Blakemore & Mills, 2014; Frith & Frith, 2012; zie Figuur 1). Deze sociale brein gebieden worden niet beschreven in het imbalans model, dat zich enkel richt op de beloningsgebieden en controlesysteem. Daarom weten we tot op heden nog niet precies hoe het beloningssysteem en het sociale brein samenwerken in het proces van beïnvloeding door leeftijdgenoten.

Het idee hebben dat je bekeken wordt door leeftijdgenoten zorgt zelfs zonder het doen van een taak al voor verhoogde activatie in het sociale brein (mPFC) bij adolescenten, in vergelijking met kinderen of volwassenen (Somerville et al., 2013). Eén studie heeft vergeleken wat er in de hersenen gebeurt bij invloed van ouders en leeftijdgenoten op de beoordeling van kunstwerken door adolescenten (Welborn et al., 2016). Invloed van leeftijdgenoten en ouders liet activiteit zien in dezelfde hersengebieden, inclusief sociale brein gebieden, een beloningsgebied en controlegebieden. Ook het maken van prosociale beslissingen gedurende de adolescentie zorgt voor hersenactiviteit in het sociale brein netwerk en beloningsgebieden (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010; Van den Bos et al., 2011). Daarnaast hebben het sociale brein en de beloningsgebieden connecties met het controlesysteem, om egoïstische of zelf-georiënteerde beslissingen te controleren.

Leeftijdgenoten zouden dus mogelijk prosociale beslissingen kunnen beïnvloeden door het triggeren van het sociale brein netwerk, waarvan eerder bewezen is dat het betrokken is bij prosociaal gedrag. Om het onderliggende proces van de invloed van leeftijdgenoten volledig te kunnen begrijpen is het belangrijk om met fMRI naast risicogedrag ook prosociaal gedrag te onderzoeken.

4. De invloed van leeftijdgenoten bij adolescenten met autisme

Voor adolescenten met autisme spectrum stoornissen (ASS) is het begrijpen van de sociale wereld niet eenvoudig (Lai, Lombardo, & Baron-Cohen, 2014). Deze neuropsychologische ontwikkelingsstoornis wordt gekenmerkt door problemen met sociale communicatie en interactie (DSM-5, APA, 2013) en gaat vaak hand in hand met weinig wederkerige vriendschappen en moeite in de omgang met leeftijdgenoten (Orsmond, Kraus, & Seltzer, 2004; Muller, Schuler & Yates, 2008). Echter, van adolescenten zonder ASS weten we dat de context van leeftijdgenoten juist van belang is om sociaal gedrag te leren. Vooralsnog is het onduidelijk of en hoe adolescenten met ASS beïnvloed worden door hun leeftijdgenoten. Adolescenten met ASS zouden minder gevoelig kunnen zijn voor de invloed van leeftijdgenoten, gegeven de atypische sociale ontwikkeling en mogelijk verminderde sociale motivatie (Chevallier et al., 2012).

Eerder onderzoek heeft onder andere conformiteit en sociale reputatie onderzocht bij mensen met ASS. Eén studie heeft het klassieke paradigma van Asch aangepast. Hierbij wordt aan deelnemers binnen een groep gevraagd welke van drie lijnen hetzelfde is als een voorbeeldlijn, waarbij het merendeel van de andere groepsleden het verkeerde antwoord geeft (Asch, 1956). In de aangepaste versie voor kinderen van 9 tot 11 jaar werden deze lijnen veranderd naar meer concrete objecten zoals slangen en wortels (Yafai, Verrier, & Reidy, 2014). De bevindingen lieten zien dat kinderen met ASS zich minder aanpasten aan de mening van anderen dan kinderen zonder ASS. Op een zelfde manier lijken volwassenen met ASS minder gevoelig voor hun sociale reputatie. Zo laten volwassenen met ASS geen toename zien in donaties aan een goed doel wanneer zij geobserveerd worden door anderen, terwijl volwassenen zonder ASS meer doneren, wanneer zij geobserveerd worden.

5. Doelen van dit proefschrift

Het doel van dit proefschrift is om de invloed van leeftijdgenoten op het maken van beslissingen in de adolescentie te onderzoeken – in adolescenten met en zonder ASS. Dit proefschrift omvat de resultaten van vier studies, uitgevoerd met experimentele gedragstaken en functionele MRI. In **Hoofdstuk 2** beschrijf ik een nieuwe experimentele goktaak om feedback van leeftijdgenoten op risicogedrag te bestuderen. Het doel van deze studie was om te onderzoeken of de feedback van leeftijdgenoten meer effect had als adolescenten een gok waagden met een onzekere uitkomst dan een gok met een meer zekere uitkomst. In **Hoofdstuk 3** beschrijf ik een nieuwe experimentele munten verdeel taak om de feedback van leeftijdgenoten op prosociaal gedrag te onderzoeken. Deze studie had als doel om effecten van de aanwezigheid van leeftijdgenoten, prosociale en antisociale feedback op prosociaal gedrag te onderzoeken. **Hoofdstuk 4** gaat over een functionele MRI studie waar ik de munten verdeel taak heb gebruikt in de MRI scanner. Het doel van deze studie was het onderzoeken van de neurale processen in de hersenen, die ten grondslag liggen aan effecten van prosociale feedback en aanwezigheid van leeftijdgenoten op prosociaal gedrag. In **Hoofdstuk 5** heb ik de munten verdeel taak gebruikt in een groep van adolescenten met en zonder autisme – om prosociale en antisociale feedback van leeftijdgenoten op prosociaal gedrag te kunnen vergelijken bij deze twee groepen.

6. Samenvatting van de resultaten

Dus, hadden mijn ouders gelijk toen ze me waarschuwden voor de negatieve invloeden van vrienden? Het antwoord dat veel ouders, inclusief die van mij, ongetwijfeld vaker hebben gehoord is *"Ja, maar…"*

De studies in dit proefschrift vormen gezamenlijk een wetenschappelijke basis om de negatieve connotaties van de invloed van leeftijdgenoten te kunnen nuanceren. De effecten van leeftijdgenoten op risicogedrag zijn aanwezig, maar zijn afhankelijk van de context. Bij risicogedrag nemen adolescenten zowel de sociale normen van leeftijdgenoten als de onzekerheid van de uitkomst in overweging (**Hoofdstuk 2**). Daarnaast heb ik gekeken naar de positieve kant van de invloed van leeftijdgenoten, waar tot op heden nog weinig onderzoek naar is gedaan. Leeftijdgenoten kunnen prosociaal gedrag zowel stimuleren als doen afnemen in adolescenten met en zonder autisme (**Hoofdstuk 3** en **Hoofdstuk 5**). Tot slot heb ik de neurale processen in de hersenen onderzocht en laten de bevindingen zien dat prosociale invloed van leeftijdgenoten samenhangt met activiteit in sociale brein gebieden – een netwerk van gebieden dat betrokken is bij het nadenken over jezelf en anderen (**Hoofdstuk 4**). Hieronder volgt een samenvatting van elk hoofdstuk.

6.1 Invloed van leeftijdgenoten op risicogedrag

De eerste studie (**Hoofdstuk 2**) beschrijft de effecten van feedback van leeftijdgenoten op risicogedrag en de validatie van een nieuwe goktaak, de "Guess Gambling Game". De invloed van leeftijdgenoten speelt een belangrijke rol in de toename van risicogedrag gedurende de adolescentie. Echter, tot op heden is het proces wat daaraan ten grondslag ligt nog niet geheel duidelijk. In deze studie heb ik onderzocht hoe het advies van leeftijdgenoten risicogedrag beïnvloedt bij een groep adolescenten tussen 15 en 17 jaar. Bij het spelen van de goktaak kregen de deelnemers twee speelkaarten te zien uit een stapel Harten tussen Aas (1) en 9. De eerste kaart was zichtbaar voor de deelnemer, maar de tweede kaart lag met de rug naar boven en de deelnemer werd gevraagd te gokken of de tweede kaart hoger of lager zou zijn. Dit noemden we *rationeel raden*, omdat je rekening kunt houden met de kansen van de kaarten. Vervolgens kregen deelnemers de kans om pokerchips in te zetten op hoe zeker ze waren van hun antwoord (*gokken*). Met deze taak konden we dus bestuderen wat de invloed is van leeftijdgenoten op rationeel raden en gokken, onze maat van risicogedrag. Daarnaast konden we de onzekerheid van de uitkomst manipuleren, met kaart 5 als meest onzeker, terwijl kaart 1 en 9 helemaal zeker waren.

De goktaak werd eerst alleen gespeeld en vervolgens met advies van leeftijdgenoten, die zogenaamd online waren. In werkelijkheid was dit advies echter in de computer geprogrammeerd. De online leeftijdgenoten gaven advies aan de deelnemers over hoeveel pokerchips ze in moesten zetten (lage, medium of hoge inzet). De verschillende typen advies gaven dus sociale normen aan over hoeveel pokerchips ingezet moesten worden. De bevindingen lieten zien dat het patroon voor rationeel raden hetzelfde was met en zonder leeftijdgenoten. Dit suggereert dat de aanwezigheid van leeftijdgenoten er niet voor zorgt, dat adolescenten worden belemmerd in het redeneren over de kansen geassocieerd met verschillende kaarten. Echter, adolescenten gingen wel meer gokken met pokerchips in het bijzijn van leeftijdgenoten. Het effect van het advies hing af van de onzekerheid van de uitkomst en de sociale normen in het advies. Het advies van leeftijdgenoten had het meeste invloed wanneer adolescenten een onzekere gok waagden. Deze bevindingen laten zien dat adolescenten op een actieve manier betekenis geven aan hun omgeving en de informatie uit het advies van hun leeftijdgenoten integreren met informatie over kansen bij het maken van hun keuze. Dit is in overeenstemming met studies uit de economische literatuur, die laten zien dat adolescenten de cognitieve capaciteiten hebben om goede keuzes te maken, maar dat ze in een "affectieve" context (bijvoorbeeld in de aanwezigheid van vrienden) vaak toch meer risicovolle keuzes maken. Het gedifferentieerde effect van peer feedback demonstreert dat het belangrijk is om naar sociale normen te kijken in onderzoek naar de invloed van leeftijdgenoten. In het volgende hoofdstuk heb ik deze sociale normen aanpak toegepast op de munten verdeel taak, die prosociale beslissingen meet in de adolescentie.

6.2 Invloed van leeftijdgenoten op prosociaal gedrag en neurale processen

In **Hoofdstuk 3** heb ik de positieve kant van de invloed van leeftijdgenoten onderzocht, als een proces dat kansen creëert voor prosociale ontwikkeling gedurende de adolescentie. Er lijkt een link te zijn tussen invloed van leeftijdgenoten en prosociale uitkomsten in 1-op-1 relaties en grotere groepen, maar zulke uitkomsten zijn tot op heden nog niet onderzocht met een experimentele taak. In deze studie werd een nieuw experimenteel paradigma, de "Peers Public Goods Game", gevalideerd bij een grote groep adolescenten tussen de 12 en 16 jaar. In deze munten verdeel taak maken deelnemers beslissingen in een anonieme groep van vier personen over het verdelen van munten tussen zichzelf en de groep. Deelnemers kregen te horen dat alle munten die aan de groep werden gegeven, zouden worden verdubbeld en verdeeld over alle groepsleden. Daarnaast mochten ze de munten houden, die ze niet aan de groep gaven. Deelnemers moesten dus kiezen tussen het belang van zichzelf en het belang van de groep – immers, de hele groep zou meer krijgen als iedereen munten zou weggeven, omdat de munten verdubbeld werden. In deze taak werd prosociaal gedrag gemeten als het aantal munten dat deelnemers aan de groep gaven.

Om de hypothese te testen dat leeftijdgenoten prosociale beslissingen beïnvloeden, speelden de adolescenten het munten verdeel spel enkele rondes alleen en enkele rondes met gemanipuleerde feedback van online leeftijdgenoten. Ook deze feedback was voorgeprogrammeerd. De resultaten laten zien dat veranderingen in prosociaal gedrag afhankelijk waren van de sociale normen van de leeftijdgenoten. Prosociaal gedrag nam toe na prosociale feedback (duimen omhoog voor donaties aan de groep) en nam af na antisociale feedback (duimen omhoog voor munten voor jezelf houden). Er was geen verandering in prosociaal gedrag wanneer deelnemers de taak speelden met leeftijdgenoten, die enkel aanwezig waren (observatie). Deze bevindingen benadrukken dat de invloed van leeftijdgenoten niet alleen negatieve effecten heeft, maar ook een kans is voor prosociale ontwikkeling. De volgende stap was onderzoeken wat er gebeurt in het brein van de adolescent bij het maken van prosociale beslissingen in het bijzijn van leeftijdgenoten.

Hoofdstuk 4 beschrijft de resultaten van een fMRI studie waar een gemodificeerde versie van de munten verdeel taak werd gebruikt om de neurale processen te onderzoeken, die ten grondslag liggen aan prosociale invloed van leeftijdgenoten op prosociaal gedrag gedurende de adolescentie. De adolescenten in dit onderzoek waren ingedeeld in twee leeftijdsgroepen: 12-13 jaar en 15-16 jaar. Eerder fMRI onderzoek wees uit dat *risicogedrag* met vrienden erbij resulteert in verhoogde activatie in het beloningsgebied (ventraal striatum; VS) bij adolescenten, maar niet bij (jong)volwassenen. Echter, de neurale processen die ten grondslag liggen aan prosociale invloed van leeftijdgenoten zijn nog niet duidelijk. Op basis van eerdere studies zijn er aanwijzingen dat de medial prefrontal cortex (mPFC; onderdeel van het sociale brein) en het ventraal striatum betrokken zijn bij beoordeling door leeftijdgenoten. De medial prefrontal cortex is betrokken bij het nadenken over jezelf en anderen, het verwerken van sociale informatie en sociale beïnvloeding.

In de MRI scanner speelden deelnemers het munten verdeel spel alleen, met toeschouwers die beslissingen observeerden en met prosociale feedback van toeschouwers. Deze keer waren de online toeschouwers acteurs van dezelfde leeftijd, die deelnemers voor het onderzoek ontmoet hadden. De feedback was ook deze keer in de computer geprogrammeerd. Gedragsresultaten lieten zien dat prosociaal gedrag toenam in de aanwezigheid van leeftijdgenoten en nog meer toenam wanneer deelnemers prosociale feedback kregen. In het brein zorgde de aanwezigheid van leeftijdgenoten bij het maken van prosociale beslissingen in verhoogde activiteit in verschillende sociale brein hersengebieden, inclusief dorsomedial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), precuneus en superior temporal sulcus (STS). Deze bevindingen benadrukken de rol van sociale brein gebieden in de invloed van leeftijdgenoten en dit is in overeenstemming met onderzoek naar het effect van prosociaal gedrag naar de familie en studies die het munten verdeel spel (zonder leeftijdgenoten) gebruikt hebben bij volwassenen. De effecten van leeftijdgenoten waren groter voor vroege adolescenten (12-13 jaar) dan mid-adolescenten (15-16 jaar). Dit zou kunnen betekenen dat vroege adolescenten meer beïnvloed worden door de sociale context. Deze bevindingen benadrukken de rol van leeftijdgenoten in het stimuleren van prosociaal gedrag gedurende de adolescentie. Met deze achtergrond in adolescenten zonder psychopathologie, gaan we nu kijken naar adolescenten met autisme spectrum stoornissen.

6.3 Invloed van leeftijdgenoten op prosociaal gedrag bij adolescenten met ASS

Ook adolescenten met een autisme spectrum stoornis (ASS) laten een "sociale heroriëntatie" richting leeftijdgenoten zien in de transitie van kindertijd naar adolescentie.

Echter, adolescenten met ASS hebben vaak moeite met het begrijpen van sociale situaties. Gegeven de problemen in sociale interactie en theorie over verminderde sociale motivatie in autisme, was de hypothese dat adolescenten met ASS minder gevoelig zouden zijn voor de context van leeftijdgenoten. In de studie beschreven in **Hoofdstuk 5** heb ik onderzocht of adolescenten met en zonder autisme beïnvloed werden door invloed van leeftijdgenoten op prosociaal gedrag. Daarnaast heb ik gekeken of de mate van autisme symptomen en sociale interesse gerelateerd waren aan individuele verschillen in gevoeligheid voor feedback van leeftijdgenoten. De munten verdeel taak had een prosociale feedback en antisociale feedback conditie en werd toegepast in een grote groep van enkel jongens met en zonder ASS in de leeftijd van 11 tot 17 jaar.

De bevindingen lieten zien dat adolescenten met en zonder ASS gevoelig zijn voor feedback van leeftijdgenoten op prosociaal gedrag. In overeenstemming met resultaten uit de vorige hoofdstukken, nam prosociaal gedrag toe als leeftijdgenoten dit positief beoordeelden. Adolescenten met ASS waren dus ook gevoelig voor feedback van leeftijdgenoten op prosociale beslissingen. Ondanks atypische sociale ontwikkeling, kan de feedback van leeftijdgenoten dus een kans creëren voor het leren van sociaal aangepast gedrag bij adolescenten met ASS. Binnen de gehele groep, dus onafhankelijk van diagnose, waren degenen met meer autisme symptomen en sociale interesse minder gevoelig voor *antisociale* feedback van leeftijdgenoten. Autisme symptomen en sociale interesse zouden dus een protectieve factor kunnen zijn in de gevoeligheid voor antisociale feedback van leeftijdgenoten. Deze resultaten bieden een bouwsteen voor interventies, en suggereren dat het toevoegen van een feedback component kan helpen om prosociaal gedrag te stimuleren bij adolescenten met ASS.

7. Praktische implicaties van het onderzoek

Dit onderzoek vormt een wetenschappelijke basis om de overwegend negatieve connotaties over de invloed van leeftijdgenoten te veranderen. De invloed van leeftijdgenoten op risicogedrag is één kant van dit fenomeen. Het begrijpen van de processen, die ten grondslag liggen aan de invloed van leeftijdgenoten op risicogedrag kan helpen om interventies te verbeteren. Het is cruciaal om adolescenten succesvol door deze leeftijdsfase heen te helpen en de 300% toename in sterftecijfers aan te pakken. Bestaande interventies die een sociale normen aanpak hebben toegepast laten tot nu toe wisselende resultaten zien. Deze campagnes hebben met name gefocust op "descriptieve" normen, zoals het introduceren van een ware norm over hoeveel drankjes op een avond normaal is. Weinig interventies hebben zich gericht op “injunctieve” normen, zoals bijvoorbeeld de aanmoediging van leeftijdgenoten om meer of juist minder te drinken. De bevindingen in dit proefschrift wekken de suggestie dat deze laatstgenoemde sociale normen een goed doel kunnen zijn om een positieve verandering teweeg te brengen in drinkgedrag.

De andere kant van dit fenomeen, de invloed van leeftijdgenoten op prosociaal gedrag, kan gezien worden als een kans voor prosociale ontwikkeling. De bevindingen zijn een veelbelovende basis voor interventies gericht op het bevorderen van prosociaal gedrag. Een voorbeeld hiervan is de “Good Behavior Game”, een interventie voor basisscholen waar kinderen die de klas verstoren, samenwerken in kleine teams met kinderen die zich goed gedragen. De invloed van leeftijdgenoten en sociale normen zouden kunnen bijdragen aan het succes van deze interventie, omdat het gehele team een beloning krijgt voor het aanmoedigen van positief en prosociaal gedrag in de klas. Tot nu toe hebben interventies voor adolescenten minder aandacht gekregen (zie voor een uitzondering het CEPIDEA programma in Italië). Een recente meta-analyse wekt de suggestie dat vroege adolescenten meer gevoelig zijn voor interventies voor de verbetering van relaties met leeftijdgenoten, omdat het juist belangrijk is in deze periode om bij de groep te horen. Deze meta-analyse is in overeenstemming met de bevindingen in dit proefschrift en laat zien dat de (vroege) adolescentie een goede periode is voor interventies om prosociaal gedrag te stimuleren en dat feedback van leeftijdgenoten een effectieve component kan zijn.

Tenslotte heeft dit onderzoek ook klinische implicaties. Hoofdstuk 5 liet zien dat adolescenten met en zonder autisme spectrum stoornissen worden beïnvloed door feedback van leeftijdgenoten. Deze aandacht voor de feedback van leeftijdgenoten opent deuren om sociale vaardigheden en prosociaal gedrag te trainen. Het is tot op heden onduidelijk welke interventies werken en voor wie, omdat autisme spectrum stoornis een zeer heterogeen beeld is. De bevindingen in dit proefschrift laten zien dat feedback van leeftijdgenoten een effectief mechanisme zou kunnen zijn om prosociaal gedrag te veranderen bij hoog-functionerende jongens met ASS. Natuurlijk is het zo dat resultaten uit de gecontroleerde omgeving van een experiment niet direct toepasbaar zijn op complexe situaties in het echte leven. Het is belangrijk om te identificeren welke individuele en omgevingsfactoren de gevoeligheid voor feedback van leeftijdgenoten vergroten of verkleinen. Samenwerking tussen experimentele onderzoekers en interventie onderzoekers zou vruchtbaar kunnen zijn in het vaststellen welke actieve ingrediënten noodzakelijk zijn voor interventies in adolescenten met en zonder ASS.

8. Conclusies

Dit proefschrift beschrijft de effecten van leeftijdgenoten op het maken van beslissingen. De invloed van leeftijdgenoten kan gekarakteriseerd worden als een socialisatie proces dat aan de ene kant kan leiden tot een toename in risicogedrag en aan de andere kant tot positieve psychosociale uitkomsten. De bevindingen in het adolescenten brein informeren het debat binnen de wetenschap over het toevoegen van sociale context in neuropsychologische ontwikkelingsmodellen van risicogedrag in de adolescentie; en laat zien dat beloningssystemen en controle netwerken bestudeerd moeten worden in samenhang met sociale brein gebieden. Als we de invloed van leeftijdgenoten verder onderzoeken, kunnen we adolescenten helpen in het navigeren door een complexe sociale fase van het leven. Uiteindelijk kunnen deze resultaten bijdragen aan interventies gericht op een afname in risicogedrag en een toename in prosociaal gedrag gedurende de adolescentie, met mogelijk langdurige effecten tot in de volwassenheid.

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Van Hoorn, J., Van Dijk, E., Meuwese, R., Rieffe, C., & Crone, E. A. (2016). Peer influence on prosocial behavior in adolescence. *Journal of Research on Adolescence, 26*(1), 90-100.

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Van Hoorn, J., Van Dijk, E., Crone, E. A., & Rieffe, C. (under revision). Peers promote prosocial behavior in high-functioning adolescent males with autism spectrum disorders.

Curriculum Vitae

Jorien van Hoorn was born on March 21st 1988 in Vlaardingen, the Netherlands. She graduated high school from Stedelijk Gymnasium Schiedam in 2006. After graduation she obtained a BSc in Psychology at Leiden University (propaedeutic exam cum laude). In 2010 she started the Research MSc Developmental Psychology at Leiden University, combined with courses from the professional MSc Child & Adolescent Psychology. She obtained her Research MSc cum laude. In 2012 she received a 3-year NWO Research Talent Grant to fund her PhD in the Brain & Development Lab, under the supervision of Prof. Dr. Eveline Crone, Prof. Dr. Eric van Dijk and Prof Dr. Carolien Rieffe. During the start of her PhD Jorien also completed a clinical internship at the department of Neurodevelopmental Disorders of Curium-LUMC in Oegstgeest, where she obtained her diagnostics registration (Basis Aantekening voor Psycho Diagnostiek; BAPD). After completing her PhD research, Jorien started working as a postdoctoral research associate in September 2016, at UNC Chapel Hill in the Developmental Social Neuroscience Lab under supervision of Dr. Eva Telzer.