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Chapter 1:

General introduction

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) (Bronfenbrenner & 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”).

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

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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). Studies that employed self-report

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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
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. 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.

![Brain regions](image)

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.

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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.