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# Adolescent brain in a social world: Unravelling the positive power of peers from a neurobehavioral perspective

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**ABSTRACT**

Adolescence is a period of growing focus on social interactions and relationships. The peer context is one of the most significant developmental contexts in this transitional period and positive peer experiences contribute positively to adolescent well-being. Although negative peer influence on antisocial behaviour has received much attention, we know less about the positive power of peers such as on prosocial behaviour. Functioning in a social context involves affective and regulatory processes, as well as understanding others and mentalizing. In this article, I highlight neuroscientific studies examining prosocial decision-making in the peer context. Based on studies combining economic exchange paradigms with sociometric assessments of peer relations, I show that prosocial behaviour for friends involves activation of the ventral striatum and the temporoparietal junction, brain regions associated with affective-motivational processes and other-oriented thinking. Differential developmental trajectories of these brain regions across adolescence can be critical in understanding the developmental significance of peer relationships and its links with developmental outcomes.

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*Would you jump off a bridge if your friends did?* Most people have heard this question – maybe even from their own parents – which summarizes in a nutshell the power that friends can have. Adolescent behaviour and attitudes are hot topics for many adolescents and their parents, especially when it comes to behaviours considered to be dangerous or risky. Research demonstrates that peer influence plays a crucial role in the prevalence of various antisocial and health-risk behaviours, such as smoking, alcohol use, risk-taking behavior, or traffic accidents (Borsari & Carey,

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2001; Boyer, 2006; De Vries et al. 2003; Dishion et al., 1997; Kobus, 2003; Maxwell, 2002; Prinstein et al. 2001; Scholte et al., 2008; Van Hoorn et al. 2017), and even internalizing problems have been reported to be susceptible to influence by friends (Prinstein, 2007; Zalk et al., 2010). Prior research has focused on understanding the age-related increase in resistance to peer influence (Albert et al., 2013; Sumter et al., 2009) and the factors that might contribute to this resistance (Gardner et al., 2008; Grosbas et al., 2007; Mrug et al., 2011; Pfeifer et al., 2011).

However, peers are not always negative sources of influence. Friendships potentially buffer against maladaptive outcomes such as depressive symptoms (Bollmer et al. 2005; Bukowski et al., 2010; Hodges et al., 1999; Masten et al., 2010), and they can have a positive influence on, for example, academic motivation and achievement (Ryan, 2001), and prosocial behaviour (Barry & Wentzel, 2006; Van Hoorn et al., 2016; Wentzel et al., 2004). Current efforts that focus on making adolescents more resilient to peer influence might actually be counter effective when it comes to such *positive* peer influences. Moreover, although we know of the power of peers in terms of their effects on developmental outcomes and mental health, mechanisms through which peers influence these outcomes remain a fundamental question in the field of developmental psychology (Brechwald & Prinstein, 2011; Prinstein & Giletta, 2020). In this article, I focus on cognitive neuroscience research examining the neural processes involved in peer interactions. I highlight studies examining the neural systems involved in social interactions with friends and focus particularly on how the peer context modulates neural activation patterns underlying prosocial behaviours. As such, this overview provides opportunities for an understanding of the mechanisms through which peers might support positive developmental trajectories and well-being.

## Adolescent social development

Adolescence is a critical transitional phase between childhood and adulthood that is mainly characterized by change (Crone & Dahl, 2012). Hormonal changes occurring around age 8–10 for girls and approximately two years later for boys are considered to be the fundamental basis and the onset of this transitional phase (Goddings et al., 2019; Peper & Dahl, 2013). Besides the physical changes, adolescents go through major cognitive and social changes. One of the most significant characteristics of this transitional phase is the increasing autonomy from parents and adults, also referred to as social reorientation, a process that eventually helps adolescents to develop into adults with social goals and commitments. Along with the transition from elementary to secondary school, adolescents become embedded in a much larger and complex social school context. Compared to children, adolescents spend most of their time in the company of peers and the majority of this time is spent without adult supervision (Lam et al., 2014). With fewer adults around, adolescents turn more often to their peers for information and advice. Thus, peers' opinions become very important, if not the most important, and friendships rate very high on the priority list of young people. Understanding the power of peers is even more important for the current generation, where according to a survey from the United States, 99% of young people have a mobile phone, more than 58% of them have at least one type of social media profile, and 46% report that they use online rather than face-to-face communication, most of the time being in contact with their friends (Ahmed, 2019). Being accepted by the peer group becomes more important, where particularly friends' opinions are vital for adolescents' identity development (Dahl et al. 2018). Anecdotally, one 16-year-old study participant has once summarized her sentiment about her friends 'My friends, they are my everything', which might come quite close to how many adolescents experience the role of friendships in this phase of life.

The social changes during adolescence are not independent of the cognitive development that adolescents go through. Adolescents become increasingly better at self-regulation, in their ability to set goals, plan accordingly, and execute them; they become better at learning, as well as at complex forms of reasoning and thinking. These cognitive changes are also reflected in their mentalizing abilities, which refer to understanding others' minds and perspectives. In its basic form mentalizing is about understanding that others may have different beliefs than the self. Although this skill develops already in early childhood (Frith & Frith, 2003), adolescents become increasingly better at taking others' perspectives (Dumontheil et al., 2010). These cognitive changes also influence adolescents' concepts of friendship, where they, compared to children, value interpersonal aspects such as trust, reciprocity, fairness, intimacy, and support more in their friendships.

## Neurobiological models of adolescent development

Our knowledge on the social and cognitive changes across adolescence is not necessarily based on research on brain development. However, research on brain development has made at least two concrete contributions to our knowledge on adolescent development. First, in the 1970s, the general belief was that brain development is essentially complete by childhood. But based on accumulating evidence since 1990s we now know that the brain goes through significant changes across adolescence, which lasts much longer than previously thought, stretching even towards the mid-twenties (Giedd et al., 1999; Mills et al., 2016). Second, we now know that not all parts of the brain develop in the same pace and manner, which has been crucial for our understanding of adolescent behaviour and development (Casey et al., 2008). Early to mid-adolescence is a period of substantial change in subcortical brain structures such as the amygdala, thalamus, hippocampus, and the striatum (Dennison et al., 2013). Ventral striatum is part of the reward circuitry of the brain and has been recognized as an important core for coordinating motivation, reinforcement, and thus playing a crucial role in reward-driven behaviour and learning (Galván, 2014). By now, there is compelling evidence that adolescent striatum responses to rewarding events are stronger than in children or adults. For example, striatum responses to winning money increases in early adolescence and peaks in mid-adolescence, around the age of 16 (Braams et al., 2014; Schreuders, Braams et al., 2018), and this elevated response is rather due to hormonal changes than to age (Wierenga et al., 2018). In contrast to the developmental patterns observed in these subcortical structures, the cortical brain regions, such as the prefrontal cortex, that is crucial for various executive functions such as planning, reasoning, behavioural control, and the temporoparietal junction (TPJ), that underlies other-oriented thinking such as perspective-taking and mentalizing, show protracted developmental patterns into late adolescence (Tamnes et al., 2017). The developmental trajectories of these prefrontal and cortical brain regions are proposed to be independent of the pubertal hormonal changes and to reflect age-related development across adolescence (Nelson et al., 2005).

Current neuroscience models of adolescent development, such as those referred to as the *Imbalance model* (Casey, 2015; Casey et al., 2008) or the *Dual Systems Model* (Steinberg et al., 2008), suggest that this discrepancy in the developmental patterns of the subcortical versus prefrontal and temporal cortical brain regions is crucial in our understanding of adolescent behaviour. The common underlying idea in these models is that the differential developmental patterns of the subcortical and cortical regions and the relatively weak connectivity between these regions result in an imbalance where adolescent behaviour is substantially driven by the functionally more mature subcortical regions. The reward sensitivity results in an increased tendency to seek out novel experiences and excitement, while the prefrontal cortex, that is crucial for various executive functions such as planning, reasoning, behavioural control, has not fully matured yet. This is actually why a teenager's brain has often been compared to a *car without brakes*. The idea behind the analogy is that it is as if the powerful accelerator of the car is in place but there is no skilful driver to hit on the brakes when necessary (Steinberg, 2005). As such, the prevailing view on adolescent brain development has been that the elevated responses in the striatum lend adolescents liable to engaging in risky and health-compromising behaviours (Steinberg, 2008).

It is important to realize that such models of adolescent brain do not imply that *all* teenagers act like 'cars without breaks', but that they rather shape current views of adolescence as a highly important phase of life. Along with the increased vulnerabilities, this important phase is also characterized by increased opportunities (Crone & Dahl, 2012). There are certain contexts and situations that might be, for example, more likely to trigger the subcortical activation, weaken the activation of the prefrontal cortex or influence the communication between these two regions. There is increasing evidence to suggest that, while the heightened reward sensitivity might be a vulnerability in some contexts, it might also have adaptive functions that serve to promote well-being (see Telzer, 2016 for an overview). These social and motivational contexts are crucial in determining the direction (maladaptive versus positive) in which reward seeking can orient adolescents. Importantly, the contexts that are highly salient for adolescents are the social contexts that involve peers and friends (Davey et al., 2008; Nelson et al., 2005). Although developmental changes in peer relations and friendships across adolescence have been documented (Poulin & Chan, 2010), we still have limited understanding of how these social behavioural changes relate to adolescent brain development. Considering the motivational salience of the peer context for adolescent behaviour, it is imperative to incorporate the social contexts involving peers into neuroscientific studies on adolescent development.

A cognitive neuroscience approach to studying peer relations offers a unique avenue by examining whether the same neural response underlies different behaviours, such as prosocial and selfish behaviours, depending on the peer context.

## The neurobiological bases of social interactions with real-life peers

There is vast research showing that peer experiences shape behaviour and developmental outcomes (Rubin et al. 2006). On the one hand, negative peer experiences, such as rejection by the peer group, have been associated with negative developmental outcomes, such as higher levels of internalizing and externalizing problems (Platt et al. 2013; Prinstein & Greca, 2004). On the other hand, positive peer experiences such as being liked and accepted by the peer group have been associated with positive evaluations about the self, positive affect, well-being and less internalizing problems (Kim & Cicchett, 2009; Oberle et al. 2009; Srivastava & Beer, 2005).

In order to better understand the neural mechanisms that underlie these links between peer experiences and developmental outcomes, in recent years, an increasing number of studies have been examining neural activation patterns in relation to the peer context. One frequently employed approach in doing this has been to examine brain activation patterns in relation to *unfamiliar* peers, such as during social decision-making with peers (e.g., Gunther Moor et al., 2012; Güroğlu, Van den Bos, Van Dijk et al. 2011; Güroğlu, Will et al. 2014; Van Hoorn et al., 2016; Will et al., 2015) or during peer evaluation (e.g., Gunther Moor et al., 2010; Guyer et al., 2012, 2014; Jarcho et al., 2015; Silk et al., 2014; Somerville et al., 2013). Importantly, the heightened significance of peer experiences might be best represented by studies that examine interactions with *personally familiar* peers, such as friends or classmates, rather than unfamiliar or anonymous peers. The salience of personally familiar peer contexts is supported by enhanced brain activation during social interactions with personally familiar peers compared to interactions with unfamiliar peers across a wide array of brain regions (Güroğlu , Haselager et al., 2008). However, incorporating personally familiar (i.e., real-life) peers into experimental designs of neuroscientific studies involves specific challenges. These experimental designs require personalized sets of stimuli for each participant, which mean that researchers need to have access to peer relationship information of the participants, such as by having access to a complete peer group where sociometric assessments can be conducted (e.g., Güroğlu , Haselager et al., 2008), or to information on current or prior peer experiences of the study participants (e.g., Meuwese, Braams et al. 2018; Will et al., 2016). Another approach might be to ask participants to bring along a friend to the scanning session (e.g., Chein et al., 2011), which, however, is not feasible when studying negative peer experiences (such as relationships with disliked peers or bullies).

## The neurobiological bases of friendships

Friendships, defined as voluntary mutual dyadic relationships based on companionship and strong affective ties, have been particularly related to positive developmental outcomes (Güroğlu, Van Lieshout et al. 2017; Hartup, 1996; Newcomb & Bagwell, 1995). There is strong evidence supporting the particular developmental significance of friendships across the life-span (Hartup & Stevens, 1997). Benefits of friendships seem to extend to all kinds of health indices, including having higher chances of a longer and healthier life (Holt-Lunstad et al., 2010), and decreased cortisol levels during stressful events (Heinrichs et al., 2003). Children with friends feel better and happier (Hartup, 1996), partly due to the feeling of uniqueness that best friendships provide (Demir et al., 2013). Having friends also protect against the effects of negative peer experiences: children who are bullied, avoided, or excluded by their peers are more likely to develop depressive symptoms over time, but this is not the case for children with a protective friendship (Bukowski et al., 2010; Hodges et al., 1999). Similarly, *not being liked* by classmates at age 15 is related to lower life satisfaction 30 years later, but only for those who do not have a friend as a teenager (Marion et al., 2013).

Despite this evidence on the significance of friendships for well-being, the mechanisms by which friendships are related to mental health and the neurobiological basis of this critical developmental factor are largely unknown. In a pioneering study (Güroğlu , Haselager et al., 2008), we have sought out to answer this question by examining the neu ral correlates of social interactions with real-life peers. To this end, a student orchestra was recruited where first all orchestra members filled out sociometric questionnaires and subsequently a subgroup of eligible members participated in an imaging study. Once in the scanner, the participants saw pictures of orchestra members and were asked to imagine a social interaction with the person they see. Each participant was shown a personalized set of stimuli with pictures of their fellow orchestra members who they like (i.e., friends), dislike or feel neutral towards. One of the most striking findings of this study was that seeing pictures of friends was specifically related to strongest ventral striatum responses. Ventral striatum is implicated in motivation and reward processing and it has been shown to be crucial for mood regulation, as well as in linking early life adversities to adolescent depression (Davey et al., 2008; Goff & Tottenham, 2015). Ventral striatum responses to social rewards have further been supported by subsequent research that shows elevated striatum responses to winning money for friends compared to disliked others (Braams et al., 2014), as well as to acceptance by unfamiliar peers (Gunther Moor et al., 2010). Although this correlational finding does not allow conclusions regarding directionality of effects, friendships might speculatively support mental health and well-being by inducing increased levels of striatal activity and providing support against depressed mood. This view is in line with other findings that support the protective role of friendships against social exclusion (Masten et al., 2010) or childhood adversities (Van Harmelen et al., 2020).

In a recent study with Schreuders, Braams, and colleagues (2019), we further examined striatum responses to winning for best friends across a wide age range of 8 to 25 years. Participants took part in a functional magnetic resonance imaging study three times with two-year interval, where they played a simple coin-tossing game where they could win or lose money for their best friend. In order to examine individual differences in friendship, we differentiated between participants who had the same best friend across they five year (i.e., stable friendship group) and individuals who had a different best friend at each of the three measurements (i.e., unstable friendship group). First, we found the same striatum response to winning for best friends as to winning for the self. We also found that striatum responses to winning money for a best friend also increase with age and peak around the age of 16, but only for those who have stable best friendships. This intriguing finding suggests that ventral striatum is involved in tracking social motivations and that individual differences in friendship formation and maintenance (i.e., stability) might be supported by motivational systems at the neural level. Importantly, the experimental designs of these studies examining the role of friendship contexts on brain activation do not involve behavioural responses. Findings on differential neural activation patterns dependent on the context thus crucially inform us on how contexts (in this case, friendships) modulate neural processes, independent of behaviour or social desirability effects as in behavioural studies. Together, these findings open pathways to further investigate the mechanisms through which friendships as developmental contexts might be related to well-being.

## The neurobiological bases of prosocial behaviour in the peer context

Social behaviour is inevitably influenced by the context in which decision-making takes place (Rilling & Sanfey, 2011). In recent years, an increasing number of studies have been using various forms of economic exchange games borrowed from experimental economics are being used to study decision-making in laboratory settings. These games have also proven to be highly efficient in studying developmental patterns of various forms of prosocial behaviour, such as trust, reciprocity, or fairness related decision-making as in the form of giving or sharing (Will & Güroğlu, 2016). Moreover, these allocation games are highly suitable for examining peer context effects on prosocial behaviour. In one study, we examined the role of mere peer presence on social decision-making (Van Hoorn et al., 2016). In this study, we asked adolescents to play a Public Goods Game with two anonymous peers, where they could donate money for the public good, maximizing outcomes all players, or keep money for themselves, which would maximize their own outcomes. The participants made their decisions in different conditions: in some conditions, they were alone and made their decisions privately, whereas in others they were watched by a panel of unfamiliar peers, who were, in reality, a group of youth actors recruited to act as confederates of the study. Furthermore, on some trials of the game, the peer panel could also give feedback on the donations made by the participants, by giving a 'thumbs-up' suggesting approval. The results showed that all adolescents made more donations when they believed that they were being watched by a peer panel. Further, when the peer panel actively encouraged prosocial behaviour by giving more 'thumbs-up' for higher number of donations, adolescents ended up donating even more than when they were simply observed by the peers. These behavioural findings are pivotal in demonstrating *positive* peer influence (at the mere level of peer presence) in an experimental setting. At the neural level, when the participants were watched by their peers and received feedback, they had higher activation in a set of brain regions that have been associated with mentalizing, including the dorsal medial prefrontal cortex (mPFC), precuneus, the TPJ and the superior temporal sulcus (STS). Findings of a recent study (Van de Groep et al., 2020) examining audience effects on prosocial decision-making (in the form of donations) also show increased activation of a temporal region comprising the TPJ and the inferior parietal lobule (IPL). Together, these neural findings are important in showing that peer presence can also strengthen brain activity related to mentalizing and other-oriented thinking (e.g., Somerville et al., 2013; see Crone & Fuligni, 2020 for a review).

Such allocation games that involve asking participants to distribute a stake of valuable coins between themselves and another peer have been shown to effectively assess different forms of prosocial behaviour and their neural correlates (see for reviews Burke et al., in press; Will & Güroğlu, 2016). Using different allocation games, it has been shown that prosocial behaviour increases across early childhood (Benenson et al., 2007; Fehr et al., 2008). In a study conducted with more than 1200 children and adolescents aged between 9 and 18, we have shown that children and adolescents have a strong preference for distributions of equity (Meuwese et al., 2015). However, we also showed that although choosing equity remains a strong norm across these ages, with increasing age adolescents become more flexible and deviate from the strict norm of equity when equity is costly or inefficient.

Experimental studies based on allocation games are also useful in examining how different interaction partners influence social behaviour, which might be more difficult to assess in real-life settings. Imagine that you are given a valuable coin to keep. You can now choose to give one other coin to a stranger, someone you have not met before and will never meet. Giving this coin to the other person does not cost you anything and will only result in equity, that is, one coin for each. If you do not want to give this coin to the other person, you still walk away with one coin you already received and the other person gets nothing. You might be surprised to hear that only 40% to 50% of young adults are likely to prefer equity where both parties walk away with one coin (Güroğlu, Van den Bos, & Crone, 2014). Now imagine that the options are slightly different: you either get two coins for yourself and give nothing to the other person, or you can share the two coins equally and give one of your coins to the other. This time equity is costly for you. This time only about 30% of young adults are likely to do so (Güroğlu, Van den Bos, & Crone, 2014). But what if the person at the receiving end is your best friend? Actually, more than 80% of young adults are likely to choose to give a coin or share your coins with your best friend. Whereas only about 60% of 9- and 10-year-olds give or share with their friends, adolescents become increasingly more prosocial as they get older (Güroğlu, Van den Bos, & Crone 2014). Furthermore, we have shown that increasing perspective-taking skills partially explains age-related increases in giving behaviour to friends, which further supports the role of development in other-oriented thinking in social behaviour towards peers (Güroğlu, Van den Bos, & Crone 2014; Van de Groep et al., 2019). With increasing age adolescents' decisions become more differentiated where friends get more special treatment. Actually, friends get special treatment, even when they act in ways that they should not. In one study (Spaans et al., 2018), we used similar coin division games to examine children and adolescents' treatment of bullies and victims. We found that children and adolescents punish bullies by giving them fewer coins, even to the extent that they are willing to pay extra money to punish them. But not when the bully was their friend (Spaans et al., 2018). In other words, when it comes to the power of friends, not only are we willing to give and share, we are also willing to turn a blind eye to their misbehaviour.

What are the neural underpinnings of prosocial behaviour towards friends compared to others? In two fMRI studies, we examined how specific relationships modulate neural patterns underlying prosocial behaviour in separate samples of young adults (Schreuders et al., 2018) and adolescents (Schreuders et al., 2019). To this end, we first collected information on participants' relationships with all their classmates in classrooms. Next, during the scanning session, we asked them to make coin allocation decisions for their friends and for classmates they dislike. First, in both age groups, we found that making prosocial choices for friends was related to higher levels of activation in the putamen, a specific part of the striatum. Moreover, adolescents who had more conflicts and negative interactions with their friends had lower levels of activation in this region when they were being nice to those friends (Schreuders et al., 2019). But in adults making *selfish* decisions for disliked peers was *also* related to higher striatum activation (Schreuders et al., 2018). In short, we observed that striatum responses underlying the same behaviour are different for different interaction partners. Differential activation of the striatum depending on whom you are interacting with might be related to reinforcement of certain behavioural patterns in that relationship context and influence formation or maintenance of relationships over time (Güroğlu, Haselager et al., 2009). These findings showing striatal involvement in prosocial behaviour are crucial for our understanding of the motivational role that striatum might play in social context. For example, ventral striatum responses to vicarious rewards for friends have also been found to relate to real-life prosocial behaviours, supporting the role of sensitivity to vicarious rewards in motivating prosocial behaviour (Morelli et al., 2018). Moreover, these findings are further in line with other studies that show that ventral striatum responses for prosocial rewards (directed towards one's family) are associated with less risky behaviours over time (Telzer et al., 2013) and that heightened striatum activity might specifically promote adaptive and prosocial behaviours (Do, Prinstein, & Telzer, in press).

Second, prosocial decisions for friends involved stronger activation of parietal temporal regions (TPJ-IPL in adults and a similar region, superior parietal lobe (SPL) in adolescents) involved in mentalizing and other-oriented thinking (Schreuders et al., 2018, 2019). Other studies also show involvement of similar brain regions in relation to adjusting prosocial behaviour to social distance of others (Strombach et al., 2015). These findings extend prior suggestions on the role of other-oriented thinking in social decision-making (Crone, 2013) by further showing that interaction partners further modulate brain activation in these regions. A role for the temporoparietal brain regions in social decision-making is further in line with findings of a recent meta-analysis that suggests that the temporal brain regions are specifically involved in social decisions that are to a larger extent influenced by others (Van Hoorn et al., 2019).

## Concluding remarks, a working model, and future directions

In this article, I have highlighted the role of peers in adolescent social behaviour and development and the invaluable insights that a neurobehavioral perspective offers to a better understanding of the power of peers. In peer influence literature, negative peer influence that leads to increased health-risk behaviours has received far more attention than positive peer influence. Thus, here I particularly focus on studies that examine the neural underpinnings of prosocial behaviour and how the peer context modulates behaviour and its neural components. Although studies demonstrating peer influence on developmental outcomes are abundant, I emphasize here that a social cognitive neuroscience perspective can make critical contributions to our understanding of the relation between peer relationships and positive developmental outcomes (Uchino et al., 2007).

Here I focus particularly on *positive* peer influences. However, it is crucial to examine individual differences in susceptibility to positive *and* negative peer influences using controlled experimental designs that expose adolescents to peer influence in *both* directions. Such designs will enable us to understand individual differences in susceptibility to peer influence and, for example, whether the same adolescents who are more susceptible to negative influences are *also* susceptible to positive peer influence. The answer to this question would be positive according to theoretical models of differential susceptibility to context. Environmental influence on developmental outcomes has been examined within theoretical frameworks of differential susceptibility to context, with a particular focus on populations who might be more vulnerable to environmental factors than others (Belsky et al., 2007; Ellis et al., 2011). These models posit that adolescents who are highly susceptible are influenced of better or worse, depending on their social experiences, whereas adolescents with low susceptibility are less influenced by the social context. However, whereas these models acknowledge that some adolescents may be particularly sensitive to negative experiences (cf. diathesis-stress view, Ellis et al., 2011), others who may be particularly sensitive to positive experiences have been largely ignored (Crone & Dahl, 2012). So far, studies based on models of differential susceptibility in relation to the peer contexts have been based on measures of genotype or temperament (Brendgen, 2012; Falk et al., 2012). For example, affiliation with aggressive friends was found to be a risk factor leading to increased aggression, but only for children with a genetic vulnerability to aggression (Van Lier et al., 2007), whereas close reciprocal friendships were found to protect genetically vulnerable children from depression (Brendgen et al., 2013). Although the possible role of neural susceptibility to social contexts in shaping adolescent behaviour and developmental outcomes has been acknowledged (Schriber & Guyer, 2016), investigations testing this model of *neural* susceptibility to social contexts is largely lacking (Do et al. in press). Figure 1 displays a model of neurobiological susceptibility to the peer context which suggests that neurobiological sensitivity to peers may moderate the extent to which peer contexts shape developmental outcomes. In this article, I highlight the neural processes of motivation (as implied by striatum involvement) and other-oriented thinking (as implied by TPJ involvement) in playing a crucial role in prosocial behaviour in the context of peer relations. Increasing evidence points to the significant role of adolescent brain development in

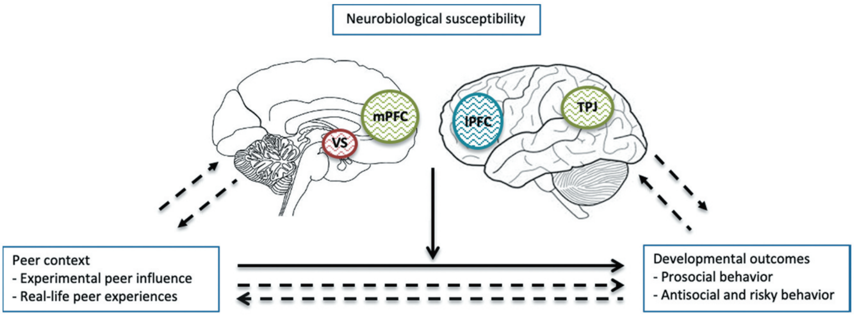


**Figure 1.** The model of neurobiological susceptibility to the peer context suggests that brain regions involved in affect and motivation (in red; VS), self- and other-oriented thinking (in green; respectively mPFC and TPJ), and regulatory control (in blue; lPFC) moderate moderates the extent to which peer contexts shape developmental outcomes (indicated by solid arrows). Here, peer context refers to experimental effects of peer influence, such as peer presence effects, or social decision-making with different types of real-life peers; developmental outcomes refer to various forms of prosocial and antisocial behaviours. [Based on proposed model by Schriber & Guyer, 2016]. Brain on left depicts a medial view, brain on right depicts a lateral view; abbreviations: VS: ventral striatum; mPFC/lPFC: medial/lateral prefrontal cortex; TPJ: temporoparietal junction.

triggering socio-affective sensitivities (Blakemore, 2010), as well as in changes in self- and other-oriented thinking (Crone & Fuligni, 2020). Whereas the elevated development of subcortical brain structures such as the ventral striatum underlies the socio-affective sensitivity in early and mid-adolescence, the protracted development of frontal and temporal cortical structures, such as the prefrontal cortex (PFC) and the TPJ, underlie the development of self- and other-oriented thinking and (pro)social behaviour. In future studies, these processes of motivation and other-oriented thinking should be further examined in relation to the prefrontal cortex involved in regulatory processes (e.g., lateral PFC) and self-oriented thinking (e.g., medial PFC) in order to further illuminate how processes of motivation, behavioural regulation, and self- and other-oriented thinking interact to influence social behaviour in peer contexts. Considering the recent advances in our understanding of the maturing adolescent brain, an integrative approach that brings together the social context of peer interactions with the study of neural mechanisms of behaviour is essential in understanding the mechanisms of peer influence.

Finally, the combination real-life peer relationships with fMRI research is highly challenging as it requires multiple data collection sessions in peer contexts (such as the classroom) to chart out relationship networks *and* extensive lab visits of each participant to collect brain imaging data.

However, the combination of brain and social networks will yield unique information relating brain function to individual differences in both experimentally induced peer influence paradigms and real-life experiences in the peer group and, for example, in the context of best friendships. Such future efforts are promising in opening pathways for our understanding of peer influence and the role of adolescents' flexibility in differentiating between positive and negative sources of peer influence. I propose that it is this flexibility, rather than pure resistance to peer influence, that is likely to lead to the most desirable outcomes where adolescents can resist negative influences but be open to positive sources of influences.

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