



Universiteit  
Leiden  
The Netherlands

## Neural underpinnings of peer experiences and interactions: a review of social neuroscience research

Güroğlu, B.; Veenstra, R.

### Citation

Güroğlu, B., & Veenstra, R. (2021). Neural underpinnings of peer experiences and interactions: a review of social neuroscience research. *Merrill-Palmer Quarterly: Journal Of Developmental Psychology*, 67(4), 416-456. doi:10.1353/mpq.2021.0021

Version: Publisher's Version

License: [Licensed under Article 25fa Copyright Act/Law \(Amendment Taverne\)](#)

Downloaded from: <https://hdl.handle.net/1887/3562660>

**Note:** To cite this publication please use the final published version (if applicable).



PROJECT MUSE®

---

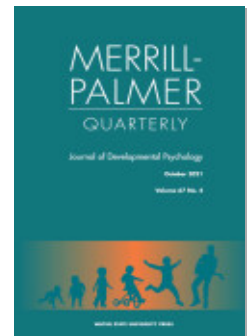
## Neural Underpinnings of Peer Experiences and Interactions: A Review of Social Neuroscience Research

Berna Güroğlu, René Veenstra

Merrill-Palmer Quarterly, Volume 67, Number 4, October 2021, pp. 416-456 (Article)

Published by Wayne State University Press

DOI: <https://doi.org/10.1353/mpq.2021.0021>



➔ *For additional information about this article*

<https://muse.jhu.edu/article/856076>

## Neural Underpinnings of Peer Experiences and Interactions: A Review of Social Neuroscience Research

Berna Güroğlu *Leiden University*

René Veenstra *University of Groningen*

In peer relations research, interest is increasing in studying the neural underpinnings of peer experiences in order to understand how peer interactions relate to adjustment and well-being. This review provides an overview of 27 studies examining how positive and negative peer experiences with *personally familiar* peers relate to neural processes. The review illustrates the ways that researchers have creatively designed controlled functional magnetic resonance imaging (fMRI) experiments employing real-life relationships. The review highlights evidence supporting the role of reward and affect sensitivity, as well as neural sensitivity to social exclusion in relation to peer experiences. Further, the review highlights research about how peer experiences modulate neural underpinnings of risk-taking and prosocial behavior. The review concludes with the challenges that studies aiming to combine peer and brain research face and provides avenues for future research.

Adolescence is a period of positive and negative opportunities, for which the development of both peer relations and the brain is important. When children grow into adolescence, the prominence of peers becomes salient. Adolescents shift their attention from parents to peers, yielding peer relationships as a domain that becomes increasingly important for support, companionship, belongingness, and their social, emotional, and mental development (Bagwell & Bukowski, 2018). The extent to which

---

Berna Güroğlu, Institute of Psychology; and René Veenstra, Department of Sociology.

This review was supported by the Netherlands Organisation for Scientific Research (NWO) (Dutch National Research Agenda [NWA] Start Impulse 400.17.602). René Veenstra received further support through an NWO VICI grant (project number 453-14-016).

Address correspondence to Berna Güroğlu, Department of Developmental and Educational Psychology, Leiden University, Pieter de la Court Building, Wassenaarseweg 52, 2333 AK Leiden, The Netherlands. Phone: +31 71 5271825. E-mail: bguroglu@fsw.leidenuniv.nl.

*Merrill-Palmer Quarterly*, October 2021, Vol. 67, No. 4, pp. 416–456. Copyright © 2022 by Wayne State University Press, Detroit, MI 48201.

adolescents spend time with peers also reflects the increased salience of peers. In general, adolescents spend much more time with friends than with parents or other adults, weigh peer opinions more heavily, and often focus on fitting in the peer network and being compatible to their friends (Laursen & Veenstra, 2021).

This increasing importance of peers in adolescence is also joined by some changes in the adolescent brain, such as the protracted development of the prefrontal and temporal cortex and the increased maturation of the limbic system in concert with pubertal hormonal changes. These changes are related to enhances in abstract thinking and mentalizing abilities. In its basic form, *mentalizing* is about understanding that others may have different beliefs, also referred to as the *theory of mind* (ToM). Although this skill develops already in early childhood (Frith & Frith, 2003), adolescents improve in their ToM skills (Gabriel et al., 2021) and taking others' perspectives (Dumontheil et al., 2010). This growth enhances abstract thinking, metacognitive thinking, and role-taking, which are crucial for adolescents to establish, maintain, and reflect upon significant peer relationships. As such, these cognitive changes influence adolescents' concept of friendship (where they value interpersonal aspects such as trust, reciprocity, fairness, intimacy, and support), as well as the *ability* to establish and maintain positive peer relationships such as friendships.

Compared with children, adolescents become increasingly better at *self-regulation*, referring to their ability to set goals, plan accordingly, and execute them. The increasing capacity to regulate affect and behavior does not mean that adolescents always make smart decisions. For instance, even though adolescence is (physically) the healthiest life period, overall mortality rates increase dramatically from childhood to adolescence, also referred to as the *adolescent health paradox* (Dahl, 2004). The primary source of this increase in mortality rates is the lack of boundaries and the difficulty in controlling emotions and behavior, which results in accidents, violence, depression, and various risky behaviors, including substance abuse.

The variation in the pace and manner in which different brain regions develop is an explanation for this adolescent health paradox (Casey et al., 2008). Specifically, there is an elevated development of subcortical brain structures such as the ventral striatum—important for coordinating motivation and reward-driven behavior, including reward anticipation and social acceptance—that underlie the socio-affective sensitivities in early adolescence to mid-adolescence (Dumontheil, 2016; Van Duijvenvoorde et al., 2016; Wierenga et al., 2018). This elevated development of subcortical brain regions goes along with a protracted development of the prefrontal brain regions that are crucial for various cognitive–regulatory functions

such as planning, reasoning, and self-control. The *dual systems model*, also known as the *maturational imbalance model*, suggests that understanding this discrepancy in the development of the subcortical and prefrontal brain regions is important to understand adolescent behavior (Casey, 2015; Casey et al., 2008; Steinberg, 2008).

The responses to rewards peak in adolescence (Braams et al., 2014b; Schreuders et al., 2018a). This reward sensitivity results in an increased tendency to seek out novel experiences and excitement while the prefrontal brain regions has not matured yet. This maturational imbalance lends adolescents to be more sensitive to rewards, particular *social* rewards such as being accepted or rejected by others. Although the heightened reward sensitivity might be a vulnerability in some contexts, it might also promote well-being and positive outcomes in other contexts (Crone & Dahl, 2012; Crone & Fuligni, 2020; Telzer, 2016). Whether the heightened reward sensitivity is maladaptive or adaptive depends on the social context (Do et al., 2020).

This article will review studies that combine peer and brain research. The heightened significance of actual peer experiences in adolescence might be best represented by studies that focus on experiences and interactions with *personally familiar* peers, such as friends, rather than unfamiliar or anonymous peers. Compared with interactions with unfamiliar peers, interactions with personally familiar peers evoke stronger activation in subcortical brain regions of affect and motivation, the *social brain network* of medial prefrontal and temporal regions involved in mentalizing and self- and other-oriented thinking, as well as in regulatory lateral prefrontal brain regions (Güroğlu et al., 2008). This enhanced activation across the brain during interactions with familiar others further attests to the salience of real-life relationships. Therefore, in this review, we focus on studies that combine functional magnetic resonance imaging (fMRI) with real-life peer interactions and experiences. The selection criteria for studies included in our review were (a) the live presence of a peer involved in the task design; (b) the use of an explicit measure of a personal relationship, such as the name of a best friend, in the task design; (c) the use of self-reported peer relationships, such as peer relationship quality or peer victimization; or (d) the assessment of social preference or popularity in the peer group by using peer nominations.

By reviewing peer research conducted from a neuroscientific perspective, this study has two aims. First, we aim to provide an overview of the bidirectional relations that have been identified between neural processes and peer experiences. Second, we aim to illustrate how researchers have designed creative studies, including the operationalization of peer

relationships. In the next sections, we discuss the findings of social neuroscientific studies by examining neural activation patterns based on positive and negative experiences with personally familiar peers. In the appendix, we have listed the brain areas that are related to peer experiences, including their abbreviations and general function descriptions, as well as the evidence for their relation with peer experiences and interactions.

### *How Positive Peer Experiences Are Related to Neural Activity*

Positive peer experiences, such as being accepted by peers and having friends, are related to positive self-evaluations, positive affect, well-being, and fewer internalizing problems (Bagwell & Bukowski, 2018). Benefits of friendships extend to protection against maladjustment caused by negative peer experiences (Hodges et al., 1999; Marion et al., 2013), decreased cortisol levels during stressful events (Heinrichs et al., 2003), and having a greater chance of a longer and healthier life (Holt-Lunstad et al., 2010). However, we still know little about the mechanisms and the neurobiological basis by which peer relations are related to (mal)adjustment.

Table 1 summarizes the design of the neuroscientific studies on positive experiences with familiar peers. Across these studies, positive peer relationships are operationalized as friendships based on, for instance, nominations of friends, reported time spent with friends, assessments of friendship networks, or friends accompanying participants during data collection. The first fMRI study among familiar peers was set up to examine whether the type of relationship (familiar versus unfamiliar) and emotional valence (positive versus negative or neutral) is related to activity in brain areas known to be involved in reward and social information processing (Güroğlu et al., 2008). In this study, a group of young adults (age 22–23) rated the extent to which they liked their fellow orchestra members, as well as a selection of celebrities. Once in the scanner, participants were shown a personalized set of stimuli with pictures and could respond (using a joystick) by approaching or avoiding this stimulus or by remaining neutral. The more positive a relationship was, the more participants responded with approach. Several social brain regions, including the precuneus, the temporal parietal junction (TPJ), and the medial prefrontal cortex (mPFC), were more active during interactions with personally familiar peers (i.e., orchestra members) than with personally unfamiliar peers (i.e., celebrities). Particularly, several brain regions, including the ventral striatum, amygdala, and the ventromedial prefrontal cortex (vmPFC), showed greater activity when participants saw pictures of their friends rather than other peers or celebrities. These brain regions have been shown to be involved in

reward processing and positive affect. Based on the significance of reward processing for mood regulation and altered reward responsiveness in mood disorders, these findings suggest that interactions with friends as *social rewards* might contribute to mental health through their role in supporting reward-related neural activation (Güroğlu et al., 2008). As such, friendships might result in sustained activation of neural systems involved in reward processing and thereby support mental health. At the same time, individuals with healthy functioning of these neural systems might be more likely to act in ways that support formation or maintenance of friendships. Thus, although these findings do not allow conclusions about causal pathways, they inform us about the neural mechanisms that may be involved in how positive peer experiences are related to mental health, as well as on the need of longitudinal studies in examining causal relations.

**Table 1.** Social neuroscientific studies on positive experiences with familiar peers

First author (year)*	N	Age (mean or range)	Peer measure	fMRI paradigm
Güroğlu (2008)	22 F 6 M	22.6	Peer-liking ratings (1–5) within an orchestra for liked, neutral, and disliked peers combined with nominations for friends and disliked peers	Social interaction simulation task with opportunity to approach or avoid personalized stimuli of familiar peers and unfamiliar others
Chein <sup>a</sup> (2011)	21 F 19 M	14–29	Participants brought two same-age, same-sex friends to the scanning session	Risk-taking behavior (Stoplight task) in alone and friend-present conditions
Masten (2012)	13 F 8 M	19.8	Self-reported amount of time spent with friends outside of school by using a daily diary	Social exclusion (Cyberball) by unfamiliar peers
Meyer (2013)	12 F 4 M	21.7	Participants brought same-sex best friend to the scanning session	Observed social exclusion (Cyberball) of friend versus stranger

*Continued*

**Table 1.** Social neuroscientific studies on positive experiences with familiar peers (*Continued*)

First author (year) <sup>a</sup>	N	Age (mean or range)	Peer measure	fMRI paradigm
Braams <sup>b</sup> (2014a)	18 F 13 M	20.9	Nomination of a same-sex best friend	False-choice gambling task to examine reward-based feedback processing; participant can win money for self, best friend, or unfamiliar disliked peer
Braams <sup>b</sup> (2014b)	132 F 117 M	8–25	Nomination of a same-sex best friend	False-choice gambling task to examine reward-based feedback processing; participant can win money for self, best friend, or unfamiliar disliked peer
Braams <sup>b</sup> (2017a)	117 F 116 M	9–26	Nomination of a same-sex best friend	False-choice gambling task to examine reward-based feedback processing; participant can win money for self and best friend
Braams <sup>b</sup> (2017b)	151 F 135 M	8–27	Nomination of a same-sex best friend	False-choice gambling task to examine reward-based feedback processing; participant can win money for best friend and mother
Smith <sup>a</sup> (2015)	20 F 20 M	14–19 and 25–35	Participants brought two same-age, same-sex friends to the scanning session	Card-guessing task conditions with or without friend present
De Water (2017)	17 F 14 M	14.5	Peer nominations received for popularity (most minus least popular) and social preference (liked most minus liked least)	Social exclusion (Cyberball)
Ambrosia (2018)	24 F 26 M	16.2	Adolescents (targets) and a close friend were video recorded during conversations	Observation of personalized videos with positive and neutral affect of best friend and unfamiliar peer
Meuwese <sup>b</sup> (2018)	15 F 16 M	14.4	Peer nominations in classrooms for social preference (liked-most minus liked-least nominations)	False-choice gambling task to examine reward-based feedback processing; participant can win for self or best friend

*Continued*



**Table 1.** Social neuroscientific studies on positive experiences with familiar peers (*Continued*)

First author (year)*	N	Age (mean or range)	Peer measure	fMRI paradigm
Schreuders (2018b)	12 F 15 M	21.3	Peer-liking ratings (1–5) of classmates and nominations of friends used for determining liked (friends), neutral, and disliked peers	Allocation task (Dictator game) of maximizing self-gain (selfish choices) or other's gain (prosocial choices) with decisions for personalized stimuli of liked, neutral, disliked, and unfamiliar peers
Morelli (2018)	23 F 23 M	19.3	Participants brought a same-sex close friend to the scanning session	Card-guessing game to examine reward-based feedback processing; participant can win money for self or <i>watch</i> best friend or unfamiliar player win money
Schreuders (2019)	21 F 29 M	14.6	Peer liking ratings (1–5) of classmates used for determining liked (friends), neutral, and disliked peers	Allocation task (Dictator game) of maximizing self-gain (selfish choices) or other's gain (prosocial choices) with decisions for personalized stimuli of liked, neutral, disliked, and unfamiliar peers
Schreuders <sup>b</sup> (2021)	68 F 55 M	8–25	Longitudinal best-friend nominations used to determine participants with stable and unstable best friendships across 4 years (3 time points)	False-choice gambling task to examine reward-based feedback processing; participant can win money for self or best friend
Van de Groep (2020)	17 F 15 M	22.6	Nomination of a same-sex best friend	Allocation task (Dictator game) of maximizing self-gain (selfish choices) or other's gain (prosocial choices) with decisions (made alone or with an audience) for the best friend or an unfamiliar peer

*Note.* Age range is indicated (instead of mean age) for studies with a broad age range. F = Female; M = Male; fMRI = functional magnetic resonance imaging.

\*Referenced by the first author and year. Please see individual author entries in the References for more information.

<sup>a,b</sup> Superscripts indicate studies with data originating from overlapping samples.

*Positive Peer Experiences and Social Exclusion*

A set of three studies have examined the role of positive peer experiences in social exclusion. One study (Masten et al., 2012) examined whether positive peer experiences protect against subsequent negative experiences such as social exclusion. In this study, older adolescents (age 18) reported about the amount of time spent with friends outside of school by using a daily diary. Two years later, participants underwent a simulated experience of social exclusion during an fMRI scan. Social exclusion was manipulated through the *Cyberball* task (Williams et al., 2000), a virtual ball-tossing game that has been effectively shown to simulate exclusion. Prior neuroimaging studies using *Cyberball* have shown that social exclusion involves heightened activation of two brain regions—the dorsal anterior cingulate cortex (dACC) and the anterior insula—which are further implicated in a variety of cognitive and emotional processes, including physical pain (Eisenberger, 2012), negative affect (Shackman et al., 2011), and expectancy violation and unfairness (Güroğlu et al., 2010; Sanfey et al., 2003). Particularly, the overlap in the neural responses to physical and social pain may point to a common neural alarm system crucial for survival (Eisenberger & Lieberman, 2004). Masten and colleagues (2012) showed that these regions known to be involved in affective responses to negative social treatment were less active during social exclusion when participants had a history of positive peer experiences (assessed as more time spent with friends). This finding contributes to a better understanding of how friendships might contribute to well-being by suggesting that maintaining positive relationships may attenuate neural hypersensitivity to negative peer interactions later in life. As peer rejection is associated with increased depressive symptoms, these findings point to mechanisms through which positive peer experiences might support mental health and even contribute to survival from an evolutionary perspective. The neural mechanisms of how friendships might support mental health differs from those highlighted by Güroğlu and colleagues (2008), suggesting that there might be multiple pathways of how positive peer experiences relate to mental outcomes. It could be that individuals who spend a lot of time with their friends might perceive social stressors (such as exclusion) as less threatening, possibly because they know they have good, reliable friends and have internalized their acceptance and have higher self-esteem. Those adolescents also may have other characteristics that make them less sensitive to rejection. However, causal pathways cannot be established based on these correlational findings, and longitudinal studies are crucial for resolving these issues.

A second study (De Water et al., 2017) has examined the links between high peer status (popularity and acceptance) and neural responses to social exclusion in mid-adolescence (age 14–15). Findings show that dACC activation during social exclusion is positively related to peer acceptance scores, which might seem contradictory to the findings of Masten and colleagues (2012), where positive peer experiences over time were related to lower dACC activation during social exclusion. Although peer acceptance and spending a lot of time with friends might be related to each other positively, low peer acceptance in the classroom does not necessarily indicate spending less time with friends out of school. These seemingly contradictory findings highlight the importance of which aspect of peer relationships we focus on, and that it is important to examine peer experiences both in and outside the school setting. The increased dACC activation shown by De Water and colleagues (2017) might be related to the unexpectedness of social exclusion, as accepted peers are less likely to experience social exclusion. Further, participants' popularity was related positively to greater activity in the ventral striatum (involved in emotional salience processing) and the medial prefrontal cortex (mPFC, involved in understanding others' emotions and self-referential processing) during social exclusion, but only when excluders were popular virtual players (which was manipulated by the investigators using vignettes). These findings were interpreted as that being excluded by popular players might be more threatening for popular individuals and thus be perceived as more salient and self-relevant (De Water et al., 2017). However, these brain regions, particularly the mPFC, are involved in a variety of processes. De Water and colleagues used *Neurosynth* (a database that can be used to link brain regions to psychological processes based on prior findings from fMRI studies) to support their interpretations. Nevertheless, the interpretations remain speculative. The strength of their study is, however, that the findings highlight the importance of status of peers involved in social exclusion when examining links between peer experiences and social exclusion.

Such contextual factors were also examined in a third study with young adults (Meyer et al., 2013), where participants (age 22) were asked to come to the scanning session together with their gender-matched best friend. During the scanning session, participants watched as their best friend and a stranger (unfamiliar peer) were excluded in a round of Cyberball. Compared with observing a stranger being excluded, exclusion of the best friend resulted in stronger activation of the affective brain regions (dACC and insula), as well as the mPFC, a brain region involved in self-referential thinking and mentalizing for close peers. Moreover, mPFC activation was more strongly associated with activation of the affective pain

regions while observing the exclusion of a friend rather than a stranger. Stronger activation of these brain regions (mPFC, dACC, and insula) while observing exclusion has been shown to be related to both higher empathic traits and higher prosocial behaviors toward the victim (i.e., excluded person) as assessed by prosocial e-mails to the victims after observing their exclusion. Furthermore, the link between empathic traits and prosocial behavior toward victims was mediated by an activation of the mPFC during the observation of exclusion (Masten et al., 2011b). Although the sample size was small ( $N = 16$ ), these findings cautiously suggest an empathic response to a close other's emotional experiences, which also might support attachment-related processing and mediate the relation between empathy and prosocial behaviors. These findings might be relevant for our understanding of how empathy for close others contributes to prosocial behaviors. For example, across the ages of 9–23, individuals respond in increasingly prosocial ways (by allocating more money) to unfamiliar victims of social exclusion (Will et al., 2013). A study examining the development of brain structure in relation to such other-regarding behaviors has shown that this age-related increase in prosocial behavior is mediated by gray-matter development in the mPFC (Sul et al., 2017). As such, the development of brain regions, such as the mPFC, might play an important role in how individuals respond to social exclusion. The development of the mPFC might thus contribute to the development of peer relationships by supporting prosocial behaviors (e.g., by helping victims) toward others who are treated negatively by peers. As such, the findings by Meyer et al. (2013) are relevant for understanding the neural mechanisms that might support friendship maintenance.

### *Positive Peer Experiences and Reward and Affect Sensitivity*

Reward processing is important for motivation and reinforcement learning, and well-functioning of the brain reward circuitry is central to mental health (Chau et al., 2004; Ng et al., 2019). Behavior is highly intertwined with social rewards in social interactions, where contextual information is crucial for decisions and behavior (Bhanji & Delgado, 2014). Considering the relevance of basic social reward processing for relationships and the finding that friendships are involved in stronger activation of the ventral striatum (Güroğlu et al., 2008), several studies based on a large longitudinal study (Braams et al., 2014a, 2014b; Braams & Crone, 2017b) directly addressed the question of whether receiving rewards for best friends relates to ventral striatum activity in a simple feedback-processing task. In this fMRI task, participants could win or lose money for themselves, their same-sex best friend, an unfamiliar disliked peer, or their mother. The findings

revealed that winning for the self as well as winning for a best friend or the mother (but not for a unfamiliar disliked peer) were related to stronger neural activation in the ventral striatum (Braams et al., 2014a, 2014b; Braams & Crone, 2017b). Moreover, vicarious gaining for a best friend was related positively to friendship quality for girls (Braams et al., 2014b), and in girls there were age-related increases in ventral striatum activity when winning for friends compared with winning for the self or the mother (Braams & Crone, 2017b). These gender-specific effects suggest developmental changes in motivations related to friends in girls: vicarious rewards for friends grow more important in late adolescence and early adulthood.

In a follow-up study (Meuwese et al., 2018) with a subsample of the longitudinal sample, it was examined whether ventral striatum activity when winning for oneself or for a best friend is related to social preference. In school classes, social preference was assessed based on the difference between peer nominations received for like and dislike. Being socially preferred was related to less ventral striatum activity *when winning for the self*, which might indicate that a lower focus on self-benefits is related to a higher level of social preference. Another follow-up study (Schreuders et al., 2021) examined striatal activity to winning for a best friend in relation to best friendship stability across an interval of 4 years (three assessments with 2-year intervals). Participants with a stable best friendship (having the same best friend across 4 years) were distinguished from participants with unstable best friendships (who had a different best friend at each measurement). Winning for the self was associated with a mid-adolescence peak (around age 16) in striatal activity. The same peak was found for winning money for best friends, but only for participants with stable best friendships. A similar study on vicarious reward processing for friends showed that individuals who displayed more vicarious reward activity in the ventral striatum when observing a close friend win rewards were more likely to act prosocially in daily life (as assessed by self-reports of prosocial spending behavior; e.g., how much they spent monthly on gifts for others or donations to charities; Morelli et al., 2018). Together, these findings suggest that individual differences in friendship formation and maintenance, as well as in prosocial behavior, might be supported by motivational systems at the neural level. As such, they corroborate the findings of the Güroğlu et al. (2008) study and highlight the relevance of the reward system for engagement in positive peer relationships. The next step is to design studies that relate these individual differences in peer relationships and the underlying neural patterns to various outcome measures (e.g., mental health, social networks, and goal attainment) to better understand the relation between development of peer relationships and long-term outcomes.

*Positive Peer Experiences and Decision-Making*

Social interactions often involve decision-making processes, where peers are part of socialization processes that can support health-compromising (e.g., risky) or positive (e.g., prosocial) behaviors, which will be separately discussed in this section.

*Risk-taking behavior*

In one study (Chein et al., 2011), researchers examined the influence of friends' presence in a risk-taking context. Participants were asked to bring two same-age, same-sex friends to the scanning session. In the *alone* condition, participants completed the *Stoptlight* driving game without observers. The *Stoptlight* task is a simple driving task in which participants, from a driver's perspective, control the progression of a vehicle along a straight track. In the *peer* condition, participants were informed that their friends were going to observe their actions from a monitor in the neighboring scanner control room. Adolescents made more risky decisions in the peer condition, as indicated by the number of car crashes when crossing the intersections at yellow or red light. In the peer condition, adolescents demonstrated greater activity in the affective node, including the ventral striatum and parts of the vmPFC, which predicted subsequent risk-taking, which was an effect that was not found for adults. This study also found that the more participants were susceptible to peer influence (based on self-reports of resistance to peer influence), the greater was the striatal activity when playing the game with peers watching compared with the alone condition (Chein et al., 2011). The age by context interaction in reward-related ventral striatum activation was also reported in another study based on the same sample, but using a card-guessing task with less risk involvement (Smith et al., 2015). This card-guessing task is comparable with the feedback-processing task used by Schreuders et al. (2021), where participants in both tasks made a guess upon which they were presented with a reward or not. As such, the findings by Smith and colleagues (2015) also support the peer context effect on adolescent striatal sensitivity outside the context of risk-taking.

Findings from the *Stoptlight* driving task also showed that adolescents had lower lateral prefrontal cortex (lPFC) activation compared with adults, signaling lower levels of regulatory control (Chein et al., 2011). Together, the adolescent neural reward sensitivity to the peer context and lower regulatory brain activation are suggested to explain increased risky decisions in the presence of peers. The combined pattern of striatal and lPFC activity in relation to risky behavior in the peer context has been pivotal for our understanding of how neural activation patterns might explain social behaviors shaped by peers, specifically in adolescence. However, this age

effect in the IPFC was not replicated in the study by Smith and colleagues (2015), suggesting that involvement of the IPFC might be more related to the decision-making context, whereas peer presence seems to alter the experience of reward processing.

Another study on risk-taking behavior (Ambrosia et al., 2018) examined the role of behavioral and neural sensitivity to peer positive affect in risky behaviors in an even more ecologically valid experimental design. In this study, adolescents (targets) and their best friend were video recorded as they engaged in a conversation, with 5 minutes devoted to the most fun they have ever had together and 5 minutes devoted to a fun or exciting event they would like to plan together. These videos were used in the fMRI study to assess neural responses to positive affect by friends and were also coded for behavioral assessments of reciprocal positive affect between the friends. The findings revealed that adolescents who engaged in more real-life risk-taking exhibited either a combination of high reciprocal positive affect behavior and greater activity in the left ventrolateral prefrontal cortex (vlPFC, involved in self-regulation and affect, such as impulsive sensation seeking) or the opposite combination—that is, low reciprocal positive affect behavior and less vlPFC activity. This U-shaped relationship between neural-behavioral responses to friend's positive affect and risk-taking behavior suggests that there might be multiple pathways to how peer experiences might relate to high levels of risky behavior. As such, the findings by Ambrosia et al. (2018) highlight individual differences in the general patterns that were exposed by the study by Chein and colleagues (2011).

### *Prosocial behavior*

A set of other studies examined how specific relationships modulate neural patterns underlying prosocial and selfish behavior among young adults (Schreuders et al., 2018b) and adolescents (Schreuders et al., 2019). These studies included, prior to scanning, nominations and ratings provided by participants about their classmates. In the scanner, participants were asked to make coin allocation decisions for their friends, neutral classmates, disliked classmates, and unfamiliar peers. Participants could make selfish choices that maximized their own gain or prosocial choices that maximized the other's gain. In both adolescents and adults, prosociality toward friends was related to greater activity in the putamen, a specific part of the dorsal striatum, which is possibly involved in the reward anticipation (Schreuders et al., 2018b, 2019). Moreover, adolescents who had more conflicts and negative interactions with their friends had less putamen activity when they were prosocial to those friends, suggesting that individual differences in friendship quality might link to reward-related neural activity associated with social behavior (Schreuders et al., 2019). Again, in both age

groups, comparable parts of the posterior parietal cortex—the superior parietal lobule (SPL) in adolescents and the inferior parietal lobule (IPL)/TPJ in adults—were more strongly activated during prosocial decisions for friends. These regions have been shown to be involved in mentalizing skills, including attention, understanding, and integration of perspectives and intentionality, supporting the relevance of these skills for prosocial behaviors for close friends. Stronger activation of the IPL/TPJ when making coin allocations for friends (versus unfamiliar peers) was also shown in a similar study of prosocial and selfish decision-making with young adults (Van de Groep et al., 2020). These findings are in line with findings by Braams et al. (2014a) showing that social brain regions, including the precuneus, TPJ, and the dorsal MPFC, are in general more strongly activated during processing of outcomes for peers compared with outcomes for the self. Moreover, the TPJ and the precuneus are more strongly activated during processing of outcomes for friends than for the self in early adolescence (Braams & Crone, 2017a). The findings from these studies suggest that neural processes related to reward, motivation, and other-oriented thinking might underlie in-group approach and prosocial behaviors and drive formation and maintenance of friendships.

Taken together, these studies highlight the involvement of the motivational circuitry and the social brain regions in how peers might influence social decision-making processes at the neural level. These findings also point out that whereas peers might heighten reward sensitivity in contexts of risky decisions, they might modulate neural processes in social brain areas in contexts involving prosocial decision-making (Van Hoorn et al., 2016). Future studies need to examine how these neural circuitries might interact with one another in rather complex real-life situations where multiple sources of positive and negative peer influences might be present simultaneously. The findings from a meta-analysis examining social context effects on neural processes of adolescent decision-making (Van Hoorn et al., 2019) support this notion that understanding development of neural processes in social context requires targeting processes of affect, regulation, and social information processing simultaneously in momentary contexts.

#### *How Negative Peer Experiences Are Related to Neural Activity*

Considering the heightened peer sensitivity in adolescence, it does not come as a surprise that negative peer experiences, such as being rejected or victimized by peers, are related to negative self-evaluations, negative affect, ill-being, and externalizing and internalizing problems (Platt et al., 2013; Prinstein & La Greca, 2004). These associations are not only concurrent; peer victimization is shown to be related to increased externalizing and internalizing problems through their effects on hostile and self-blaming



attributions, respectively (Perren et al., 2013). Moreover, peer victimization predicts heightened inflammatory responses to social stress (Giletta et al., 2018). Considering that neural responses to peer rejection might be a marker of adolescents' risk for depression (Masten et al., 2011a), neurobiological research may inform us about the pathways in which adverse peer experiences influence adolescent mental health. Neuroscientific studies with a focus on negative peer experiences have operationalized negative experiences either in terms of peer rejection, based on peer nominations received for being liked least rather than liked most, or self-reported peer victimization. Table 2 summarizes the design of the social neuroscientific studies on negative experiences with familiar peers. These studies examine the impact of peer experiences usually as antecedents that contribute to the neural responses to social experiences and behaviors.

**Table 2.** Social neuroscientific studies on negative experiences with familiar peers

First author (year)*	N	Mean age	Peer measure	fMRI paradigm
Casement (2014)	120 F	16	Self-reported peer victimization (at age 11–12)	Card-guessing task (reward anticipation)
Telzer (2015)	26 F 20 M	14.8	Self-reported peer conflict (cutoff: on >25% of the days) with a close friend or boy/girlfriend by using a daily diary (during 14 days across 2 years: 3 waves)	Risk-taking behavior (Balloon Analogue Risk Task (BART))
Rudolph <sup>a</sup> (2016)	47 F	15.5	Self-reported chronic victimization (during 7 years)	Social exclusion (Cyberball)
Will <sup>b</sup> (2016b)	18 F 26 M	14.0	Longitudinal peer status (accepted versus rejected) assessed by peer nominations for social preference during 6 years (like-most minus like-least nominations)	Social exclusion (Cyberball)
Will <sup>b</sup> (2016a)	17 F 26 M	14.0	Longitudinal peer status (accepted versus rejected) assessed by peer nominations for social preference during 6 years (like-most minus like-least nominations)	Allocation task (Dictator game) of maximizing self-gain (selfish choices) or other's gain (prosocial choices) with decisions for unfamiliar peers and excluders and includers from prior social exclusion (Cyberball) task

*Continued*

**Table 2.** Social neuroscientific studies on positive experiences with familiar peers (*Continued*)

First author (year)*	N	Mean age	Peer measure	fMRI paradigm
Will <sup>b</sup> (2018)	18 F 28 M	14.0	Longitudinal peer status (accepted versus rejected) assessed by peer nominations for social preference during 6 years (like-most minus like-least nominations)	Allocation task (Dictator game) of maximizing self-gain (selfish choices) or other's gain (prosocial choices) with decisions for unfamiliar peers
McIver (2018)	36 F 9 M	17.7	Self-reported peer victimization	Social exclusion (Cyberball)
Telzer <sup>a</sup> (2018)	46 F	15.5	Self-reported chronic victimization (during 7 years)	Risk-taking behavior (Stoplight task)
Swartz (2020)	24 F 24 M 1 NB	13.4	Self-reported bullying and peer victimization	Emotional expression processing of angry and fearful faces
Asscheman (2019)	55 M	10.4	Longitudinal peer status (accepted versus rejected) assessed by peer nominations for social preference during 3 years (like-most minus like-least nominations)	Social exclusion (Cyberball)

*Note.* F = Female; M = Male; NB = nonbinary; fMRI = functional magnetic resonance imaging.

\*Referenced by the first author and year. Please see individual author entries in the References for more information.

<sup>a,b</sup> Superscripts indicate studies with data originating from same or overlapping samples.

### *Negative Peer Experiences and Social Exclusion*

Several studies have used the Cyberball paradigm to examine how negative peer experiences are related to neural responses to social exclusion. One study with the Cyberball paradigm examined whether early adolescents (age 14) with a history of chronic peer rejection display enhanced neural responses to social exclusion compared with stably accepted adolescents (Will et al., 2016b). The history of peer experiences was based on peer nominations received during 6 years in elementary school, where a social preference score (peer nominations received for “liked most” minus “liked least”) was computed across the 6 years. Stably accepted adolescents

scored in the upper 10th percentile and chronically rejected adolescents scored in the lower 10th percentile for social preference. In contrast to prior studies using the Cyberball task in a block design (i.e., based on average neural activation in inclusion and exclusion blocks), this study used an event design. By defining events based on whether participants receive a ball in both exclusion and inclusion blocks, this design also enabled examination of incidental exclusion, referring to simply not receiving the ball. The findings revealed that chronic rejection was related to greater activity in the dACC during social exclusion, as well as during incidental exclusion in an overall social context of inclusion.

Another study (Asscheman et al., 2019) with a similar longitudinal design has examined these processes in primary-school children (age 10; all boys) and assessed peer nominations in the 3 years prior to the fMRI assessment. The upper 35% and lower 35% cutoff on average social preference scores were used to determine the stably accepted and chronically rejected children. Using an event-related Cyberball design as in the Will et al. (2016b) study, the findings with this younger sample did not replicate prior findings from adolescent samples regarding differences in neural activation patterns during social exclusion between rejected and accepted children. Instead, findings showed that boys with chronic peer rejection showed greater activity in lateral PFC during early phases of social exclusion compared with boys with stable peer acceptance status in the past. Considering the role of this region in emotion regulation and attention allocation, it might nevertheless be that children with adverse peer experiences are more sensitive to early signs of exclusion by peers and exert higher levels of emotion control during exclusion, which is an interpretation still in line with prior findings.

Two studies have focused on the neural correlates of social exclusion by using a block design with the Cyberball task (i.e., comparing neural signals from blocks of inclusion and exclusion) in relation to self-reported peer victimization. One study (Rudolph et al., 2016) compared girls with a history of chronic peer victimization (age 8–15) with girls with minimal exposure to peer victimization in their neural responses to social exclusion, as well as how these neural responses are related to internalizing symptoms. Chronically victimized girls had victimization scores 0.75 *SD* above the mean, whereas non-victimized girls scored 0.75 *SD* below the mean for at least 3 years. The findings revealed that heightened activity in the dACC and the anterior insula during social exclusion was associated with more internalizing symptoms in victimized girls, but not in non-victimized girls. Furthermore, this link between heightened neural responses to social exclusion in victimized girls was mediated by avoidance motivation, suggesting

that adverse peer experiences might result in internalizing problems through a tendency to avoid potential social threats. The second study (McIver et al., 2018) compared victimized adolescents with defenders of cyberbullying and non-victimized adolescents (age 17) in neural responses to social exclusion. Although the findings of the previous study (Rudolph et al., 2016), relating peer victimization to neural sensitivity to social exclusion, were not replicated, peer-victimized individuals were found to have heightened neural activation compared with both defenders and non-victimized adolescents in multiple frontal, parietal, and limbic regions, which have been shown to be involved in emotion processing and other higher-order executive processes. The lack of replication across these two studies can be due to the rather small sample size of 15 participants in each condition in the McIver et al. study, but it can also be due to the way peer victimization has been operationalized: The Rudolph et al. study examined longitudinal victimization patterns across 3 years, whereas identification of victimization groups in the McIver et al. study was based on a single assessment of peer victimization administered prior to the fMRI assessment.

Taken together, these findings suggest that chronically rejected children and adolescents with heightened neural sensitivity to exclusion may not only experience more adverse reactions to actual peer rejection but also show hypervigilance to potential social threats and a tendency to avoid the possibility of future rejection. Such neural sensitivity to social threats might result in avoidant or aggressive behaviors that evoke further rejection by peers. Accumulating negative experiences in the peer context, such as chronic rejection or victimization, might also further strengthen heightened neural responses to these adverse interactions. Future studies should aim to investigate the additive effect of long-term adverse peer experiences by, for example, recruiting participants with chronic and temporary peer victimization experiences and comparing them with those who have not been victimized by peers.

### *Negative Peer Experiences and Reward and Affect Sensitivity*

Another study (Casement et al., 2014) examined the role of the reward circuitry in the link between exposure to social stressors such as peer victimization and depression in adolescent girls. Self-reported peer victimization at age 11–12 was found to be related to a decreased response to potential monetary rewards by the mPFC, which was associated positively with depressive symptoms at age 16. Given the relevance of mPFC in reward evaluation and self-relevant motivational processing, findings point in the direction of the relevance of adverse peer experiences in the functioning of

the reward circuitry and further risk for depressive symptoms. This interpretation is in line with prior findings (Güroğlu et al., 2008) suggesting that positive peer interactions might contribute to a well-functioning reward system, as well as to mental health. The relation between peer experiences and the functioning of affect-related subcortical brain regions, such as the amygdala, has also been shown by a study (Swartz et al., 2020) examining the link between self-reported bullying and victimization and neural processing of emotional expression such as anger and fear. Specifically, higher amygdala activity for angry faces and lower amygdala activity for fearful faces predicted more bullying behavior, whereas higher amygdala activity for both angry and fearful faces predicted higher peer victimization. Speculatively, amygdala activation patterns in relation to bullying might be caused by hostile attribution biases, whereas amygdala activity in relation to victimization might be caused by increased social avoidance. These findings suggest pathways for how peer experiences might be related to patterns of social information processing.

### *Negative Peer Experiences and Decision-Making*

#### *Risk-taking behavior*

A few studies have examined the relation between negative peer experiences and the neural processes underlying risky behaviors. One study (Telzer et al., 2018) examined whether girls with a history of chronic self-reported peer victimization (age 8–14) would show greater risk-taking behavior (measured with the Stoplight driving game) after being exposed to social exclusion (using the Cyberball paradigm), and whether neural responses during risk-taking differed between victimized and non-victimized girls (age 15). A particular strength of this study is the use of an ecologically valid experimental design where participants' risk-taking behavior was examined in face of a negative social experience (based on a Cyberball manipulation) that can be viewed as a threat to social needs and thus a social trigger. Chronically victimized girls showed greater activity in the ventral striatum, amygdala, and vmPFC when making risky choices. Because these brain regions are involved in reward anticipation, emotional arousal, and social influence, these findings suggest that the expected value of high-risk rewards might be heightened in youth who have a history of peer victimization. Neural responses to successful outcomes (without a crash in the Stoplight task) following a risky decision were higher in the ventral striatum in chronically victimized youth, which might further indicate increased sensitivity to risk-taking in these adolescents because of the potentially rewarding aspects of these outcomes. Finally, safe decisions

during the task were related to heightened dorsolateral prefrontal cortex (dlPFC) and vlPFC activation in chronically victimized girls compared with non-victimized youth. Combined with the behavioral findings that victimized girls showed more risk-taking behavior in the task (following social exclusion), risky choices might be prepotent in victimized youth, who might need to exert greater cognitive control to make safe choices.

Another study (Telzer et al., 2015) on risk-taking behavior examined whether more chronic peer conflict and low peer support would be associated with a heightened affective neural response during risk-taking behavior. Assessments of peer conflict and support were based on daily diaries across a period of 14 days at two waves with a 1-year interval (age 14); shortly after the second daily-diary assessment, participants took part in an fMRI study. In the fMRI assessment, risk taking was assessed with the Balloon Analogue Risk Task (BART), where participants are shown a virtual balloon and are given the option to pump and thus inflate the balloon, which can either grow larger (resulting in larger monetary gain) or explode at one point (resulting in losing all accumulated monetary gain). The findings revealed that peer conflict was associated with greater risk-taking behavior, especially for adolescents with low self-reported peer support. At the neural level, peer conflict was associated with greater activity in the ventral striatum and the anterior insula during risk taking, again especially for adolescents with low self-reported peer support. This heightened neural activity may reflect the rewarding and saliency aspects of risk taking—aspects that may be enhanced by negative peer relationships and the anticipation of peer approval by engaging in risky behavior. This is consistent with the stress-buffering model of social relationships (Coan & Sbarra, 2015; Cohen et al., 2001) and underscores the importance of the quality of adolescents' peer relationships for risk-taking behavior. Taken together, these findings suggest that conforming to peers is instrumental for gaining social acceptance and establishing stronger peer connections, an effect that is exacerbated in youth who experienced chronic peer victimization or chronic peer conflict.

### *Prosocial behavior*

Two studies (Will et al., 2016a, 2018) have examined the relation between prior peer experiences and neural components of social decision-making. In one study (Will et al., 2016a), participants were first exposed to social exclusion by using the Cyberball paradigm (Will et al., 2016b) and subsequently asked to make coin allocations for Cyberball players who had included or excluded them. This design enabled the examination of the neural circuitry involved in forgiveness and punishment of peers involved

in social exclusion and the extent to which these are modulated with prior long-term peer experiences. Compared with stably highly accepted adolescents, chronically rejected adolescents exhibited greater activity in the dorsal striatum and the lateral PFC when they refrained from punishment and forgave the Cyberball excluders. This heightened activity in the dorsal fronto-striatal network suggests that chronically rejected adolescents might have to exert greater levels of executive control to act prosocial toward peers who have not treated them well. Considering evidence showing higher levels of behavior-regulation difficulties in children and adolescents with chronic peer rejection, these findings have implications for processes through which negative peer experiences are held in place.

A second study (Will et al., 2018) examined the neural correlates of fairness decisions in the same sample of stably accepted and chronically rejected adolescents. Findings showed that stably accepted adolescents were more likely to share their money with unfamiliar peers than chronically rejected adolescents when sharing was not costly. Stably accepted adolescents, compared with chronically rejected adolescents, exhibited greater activity during costly sharing decisions in brain regions involved in perspective taking, such as the TPJ, posterior superior temporal sulcus (pSTS), and temporal pole, and the detection of social norm violations, such as the anterior cingulate cortex and anterior insula. Taken together, these two studies provide insight into processes underlying the widely established link between peer experiences and prosocial behavior.

Finally, two studies (Schreuders et al., 2018b, 2019) have operationalized negative peer experiences at the dyadic level—that is, in the form of an antipathy relationship based on dislike. These studies have examined the extent to which the social context of interpersonal relations modulate prosocial decisions and their underlying neural basis. Assessments of dislike relationships were based on participants' nominations of least liked rather than most liked given to classmates. Behavioral results show that interaction partners matter: Both adolescents and adults were more prosocial toward liked than toward disliked peers, with neutral and unfamiliar peers being in between. Interestingly, prosocial decisions for disliked peers were not associated with any significant heightened neural activation compared with other types of peers in adolescence (Schreuders et al., 2019). In adults (Schreuders et al., 2018b), however, making selfish decisions for disliked peers was associated with increased activity in the putamen and in the STS, which is a region within the social brain network and related to mentalizing processes. Putamen activation is particularly interesting as it is in line with other findings showing higher striatum activity for mistakes made by competitors than by collaborators (De Bruijn et al., 2009) and when envied

peers experience misfortune (Takahashi et al., 2009). However, antipathy relationships are rather difficult to study because they are more diverse than friendships, and there might be a variety of reasons and processes involved in dislike between individuals (Abecassis, 2003), making it difficult to detect neural activation patterns that underlie behavior in these interactions. Future studies may further investigate the role of affect and mentalizing processes in the development of antipathies. A better understanding of peer relationships based on antipathy (or hatred as the extreme end of negative affect) is relevant. Also links between long-term adverse peer experiences, such as chronic rejection or victimization, and negative dyadic peer relations and their underlying neural basis have been uninvestigated, so many research questions remain to be answered.

### *Conclusion*

In this article, we provided an overview of studies that have examined the neural processes related to positive and negative experiences with familiar peers. So far, 27 studies have employed study designs that combine fMRI and peer research. There is large variety in the main research questions of these studies, which impedes conducting a meta-analysis and reaching strong overarching conclusions. However, we would like to highlight several lines of overlapping findings that emerge from the studies reviewed.

First, positive peer experiences such as close friendships or high social preference are related to activation of neural systems of motivation and affect, in particular the ventral striatum, a central brain region for reward processing, approach, and learning (Braams et al., 2014b; Chein et al., 2011; Gurođlu et al., 2008; Meuwese et al., 2018; Morelli et al., 2018; Van de Groep et al., 2020). Evidence showing that these neural activation patterns are also related to prosocial behaviors and friendship characteristics further points to the relevance of these neural systems in establishing and maintaining positive relationships. Healthy functioning of the reward system has been shown to be crucial for mental well-being (Davey et al., 2008; Nelson et al., 2005; Telzer, 2016; Tremblay et al., 2005). As such, the findings of the reviewed studies contribute to our understanding of the mechanisms through which positive peer relationships are related to well-being.

Second, studies point to a stronger activation of regions in the social brain network, including the mPFC, the precuneus, and the TPJ, in relation to positive peer experiences, at the dyadic level, with friends (Braams et al., 2014a, 2017a; Schreuders et al., 2018b, 2019; Van de Groep et al., 2020) and at the group level, in terms of social preference (Will et al., 2018). In some studies, these activation patterns were related to specific forms



of behavior, such as making prosocial decisions for friends (Schreuders et al., 2018b, 2019), suggesting that processes such as perspective taking might support prosocial behavior toward close others, which might in turn contribute to the maintenance of these positive relationships. In other studies, activation of the social brain regions was independent of behavior, but dependent on the specific relationship, referring to friends versus unfamiliar peers (Meyer et al., 2013; Van de Groep et al., 2020), suggesting that the social context of a specific relationship might relate to spontaneous activation of networks that support other-oriented thinking, which is eventually likely to support prosocial behaviors toward close others. Future research may want to examine the importance of balancing between multiple goals in adolescence, including self-oriented goals and other-oriented goals (Crone & Fuligni, 2020; Sijtsema et al., 2020). This balancing between the self and others, however, may vary based on whether friends, a romantic partner, antipathies, or unfamiliar peers are present and maybe also on the interaction context (e.g., home, community, school, or sports activity). The ability to successfully vary based on who is present in which context may hinge on the capacity to flexibly engage different neural circuits (Guyer & Jarcho, 2018). Our review focused on familiar peers. However, taking the perspectives of strangers (unfamiliar peers) is also an important way to connect to new individuals or outgroups in the larger network (Müller-Pinzler et al., 2016).

Finally, a popular research question addressed in different studies on negative peer experiences (in the form of peer rejection or victimization) has been the examination of neural responses to social exclusion. The findings point to a neural sensitivity to negative peer interactions, such as (possible) social exclusion, as indicated by heightened neural responses in regions of affect and affect regulation, including the dACC, insula, and IPFC (Asscheman et al., 2019; McIver et al., 2018; Rudolph et al., 2016; Will et al., 2016a). Other studies have employed a wide range of tasks (e.g., decision-making tasks, face processing, or reward processing), but the conclusion points to heightened affective sensitivity (Casement et al., 2014; Swartz et al., 2020; Telzer et al., 2015; Will et al., 2016a) along with difficulties in emotion regulation (as evidenced by enhanced PFC activation in safe or prosocial choices) in youth with negative peer experiences (Telzer et al., 2015, 2018; Will et al., 2016a). These findings contribute to our understanding of stability in negative peer experiences, such as rejected peer-status stability over time, for example through hostile attribution biases (Perren et al., 2013; Reijntjes et al., 2011) that might be related to a neural basis of social information processing (Kellij et al., 2022; Mayeux et al., 2007). Considering the link between positive and negative peer

experiences, in childhood and adolescence, and adult adjustment and well-being (Bagwell et al., 1998), social neuroscientific studies have the potential to contribute to our understanding of the mechanisms of these links.

### *Challenges and Directions for Future Research*

Research aiming to bring our social world with its interactions, relationships, and social networks into the scanner face particular practical challenges. Social neuroscientific studies aiming to examine neural responses that are relevant to actual peer interactions need to have carefully designed experiments in order to accurately sample neural activation, and create experimental conditions to probe responses from specific brain regions to specific social cues and behaviors (Guyer & Jarcho, 2018). The research questions that can be investigated are restrained by the physical environment of a single individual lying alone in an fMRI scanner.

Considering this challenge, the reviewed studies addressed the research questions creatively. Some studies related neural regions to self-reports of friendship quality, peer conflict and support, time spent with peers, or self-reports of peer victimization. Other studies focused on the relation of neural regions with dyadic relationships, which is typically more complicated and effortful, because it usually involves personalized sets of stimuli for each participant or even asking participants to bring along a friend to the scanning session. This may increase the credibility of the research design (particularly when deception is involved), as well as make the perceived interaction much more significant for the participant.

In this regard, studies on negative peer experiences face extra challenges as such designs cannot bring a peer along. Some studies on negative peer experiences have employed peer nominations in classrooms. Such sociometric assessments are valuable in assessing the relationship context efficiently. However, these designs typically require researchers to have access to a complete peer network, such as a classroom or an extracurricular activity group. An ideal brain and social network data collection would include data from complete peer networks with information on individuals (e.g., peer acceptance, peer rejection, and perceived popularity), dyads (e.g., friendship quality and stability), and the network (e.g., social norms).

Several researchers have achieved this goal by adding fMRI assessments to existing longitudinal studies of peer experiences (e.g., Asscheman et al., 2019; Rudolph et al., 2016; Will et al., 2016b). Findings from these studies are valuable for our understanding of how past experiences are related to current neural processing. However, the ideal data collection would have prospective data on the development of the brain and the social

network. Such a study can easily become complicated, intense, and expensive because of fMRI eligibility, parental consent, and missing data from the group members. A possibility to overcome these problems would be to reach out to potential participants before entering secondary education, obtain fMRI consent, and ask the school to place the participating students in one class. Another possibility would be to use a youth panel to design and inform a study that fits with their online media use and organize, for instance, a gaming event. Furthermore, it is wise to look for naturalistic opportunities to examine peer groups. A perfect example is a recent study where participants completed an isolated 3-week hiking expedition in the Arctic Circle during which they only interacted among themselves (Block et al., 2018).

If we combine brain and social network research, it would be possible to examine whether greater synchrony in parts of the affective node and cognitive–regulatory node are related to more successful communication between peers or to stronger peer influence (Falk & Bassett, 2017). A study that combined brain and social network research (O’Donnell et al., 2017) showed that adolescents who had social network positions with greater potential for information brokerage (i.e., they connected more friends who did not otherwise know each other) also had enhanced activity in mentalizing brain regions. The question is whether the social network position affects the brain structure or vice versa (Lamblin et al., 2017). A valuable endeavor in this direction recruited an entire cohort of 279 students in a graduate program (Parkinson et al., 2018). All students provided relationship information by indicating who their friends were in the social network. Next a subset of 42 participants were invited to take part in an fMRI study where each participant watched the same collection of video clips, which evoked a variety of responses. Findings showed that neural responses to these video clips were more similar among friends and that similarity decreased with increasing distance in their real-life social network, suggesting that friends might be similar to one another in how they perceive the world around them. This combination of social network assessments with brain research is promising for our understanding of interpersonal and intragroup compatibility (Laursen & Veenstra, 2021).

The literature we reviewed largely focused on adolescents. This focus reflects methodological constraints: Young children are sometimes unable to understand and perform complex experiments as they lie still in the scanner (Guyer & Jarcho, 2018). However, two studies among younger children were able to use a false-choice task (Braams et al., 2014b) or the Cyberball task (Asscheman et al., 2019). Further social neuroscientific research in

childhood is needed to track how the young brain reacts to positive and negative peer experiences, which is fundamental to understanding how neural pathways critical to the affective and cognitive–regulatory nodes are established. Moreover, studies with a developmental perspective are necessary in order to examine the role of adolescent brain development in the development of peer relations. Among the studies reviewed, only six spanned a wide age range (i.e., Braams et al., 2014b, Braams & Crone, 2017a, 2017b, and Schreuders et al., 2021, based on the largely overlapping sample of 8- to 25-year-olds; and Chein et al., 2011, and Smith et al., 2015, based on the largely overlapping sample of 14- to 35-year-olds) and examined developmental changes. There is a strong need for research with developmental designs in order to examine how age-related changes in peer relations relate to brain development. The lack of such research probably indicates the difficulty of setting up large-scale studies combining social network information with fMRI assessments, as such studies are intense (requiring real-life social network information and laboratory assessments of neuroimaging) and costly due to the large number of participants required in order to examine developmental change. Moreover, ideally such studies should aim to disentangle age-related changes from pubertal changes, which further complicates such studies (Van Duijvenvoorde et al., 2019; Wierenga et al., 2018).

Findings from studies on adolescent specific behavior in the peer context have been crucial in our understanding of adolescence. However, not all adolescents act in ways that are in line with the maturational imbalance model of adolescent brain development. There are large individual differences in adolescent susceptibility to social contexts (Schriber & Guyer, 2016). Individual differences in neurobiological susceptibility to the peer context might moderate the extent to which peer contexts shape developmental outcomes of risk-taking or prosocial behavior (Güroğlu, 2020). Future research on individual differences in developmental pathways is imperative in furthering our understanding of the interaction between the adolescent brain and peer development (Becht & Mills, 2020). By informing us on the neural underpinnings of risky or prosocial behaviors in different social contexts, neuroimaging studies contribute to our understanding of how peer relationships might contribute to not only mental health but also survival.

Finally, we regret to point out that all 27 studies we reviewed were conducted in Western cultures. Understanding how the brain responds to peers in other cultures will be an important future direction. For instance, implementing research on positive and negative peer experiences in

collectivistic societies may reveal a different neural signature of social exclusion (Meyer et al., 2013). A meta-analysis of 35 studies examining socio-cognitive processes in individuals from Western and East Asian cultures showed that East Asian participants had greater neural activity in the brain regions related to inference of others' mind and emotion regulation, whereas individuals from Western cultures had enhanced neural activity in the brain areas related to self-relevance encoding and emotional responses (Han & Ma, 2014). Even within Western cultures, participants who take part in fMRI research are from families with relatively higher socioeconomic status. It is challenging to engage families from diverse backgrounds (in terms of education, ethnicity, and wealth) in neuroscientific studies. However, future research will benefit from extra efforts to investigate the research questions charted out here in more diverse samples.

To conclude, adolescents are primed to monitor experiences and interactions with agemates and are responsive to peer feedback. There is an increasing interest in studies that examine the neural underpinnings of peer experiences in order to understand how peer interactions relate to adjustment and well-being. So far, 27 studies examined how positive and negative peer experiences with personally familiar peers relate to neural processes. A challenge will be to assess neurological data in complete social networks and link neural profiles to social network processes, such as similarity selection and peer influence. Research that examines the development of both peer relations and the brain has high potential, full of avenues for further research.

## References

- Abecassis, M. (2003). I hate you just the way you are: Exploring the formation, maintenance, and need for enemies. *New Directions for Child and Adolescent Development, 102*, 5–22. <https://doi.org/10.1002/cd.86>
- Ambrosia, M., Eckstrand, K. L., Morgan, J. K., Allen, N. B., Jones, N. P., Sheeber, L., Silk, J. S., & Forbes, E. E. (2018). Temptations of friends: Adolescents' neural and behavioral responses to best friends predict risky behavior. *Social Cognitive and Affective Neuroscience, 13*, 483–491. <https://doi.org/10.1093/scan/nsy028>
- Asscheman, J. S., Koot, S., Ma, I., Buil, J. M., Krabbendam, L., Cillessen, A. H. N., & Van Lier, P. A. C. (2019). Heightened neural sensitivity to social exclusion in boys with a history of low peer preference during primary school. *Developmental Cognitive Neuroscience, 38*, 100673. <https://doi.org/10.1016/j.dcn.2019.100673>

- Bagwell, C. L., & Bukowski, W. M. (2018). Friendship in childhood and adolescence: Features, effects, and processes. In W. M. Bukowski, B. Laursen, & K. H. Rubin (Eds.), *Handbook of peer interactions, relationships, and groups* (2nd ed., pp. 371–390). Guilford Press.
- Bagwell, C. L., Newcomb, A. F., & Bukowski, W. M. (1998). Preadolescent friendship and peer rejection as predictors of adult adjustment. *Child Development, 69*, 140–153. <https://doi.org/10.1111/j.1467-8624.1998.tb06139.x>
- Becht, A. I., & Mills, K. L. (2020). Modeling individual differences in brain development. *Biological Psychiatry, 88*, 63–69. <https://doi.org/10.1016/j.biopsych.2020.01.027>
- Bhanji, J. P., & Delgado, M. R. (2014). The social brain and reward: Social information processing in the human striatum. *WIREs Cognitive Science, 5*, 61–73. <https://doi.org/10.1002/wcs.1266>
- Block, P., Heathcote, L. C., & Burnett Heyes, S. (2018). Social interaction and pain: An arctic expedition. *Social Science & Medicine, 196*, 47–55. <https://doi.org/10.1016/j.socscimed.2017.10.028>
- Braams, B. R., & Crone, E. A. (2017a). Longitudinal changes in social brain development: Processing outcomes for friend and self. *Child Development, 88*, 1952–1965. <https://doi.org/10.1111/cdev.12665>
- Braams, B. R., & Crone, E. A. (2017b). Peers and parents: A comparison between neural activation when winning for friends and mothers in adolescence. *Social Cognitive and Affective Neuroscience, 12*, 417–426. <https://doi.org/10.1093/scan/nsw136>
- Braams, B. R., Güroğlu, B., De Water, E., Meuwese, R., Koolschijn, P. C., Peper, J. S., & Crone, E. A. (2014a). Reward-related neural responses are dependent on the beneficiary. *Social Cognitive and Affective Neuroscience, 9*, 1030–1037. <https://doi.org/10.1093/scan/nst077>
- Braams, B. R., Peters, S., Peper, J. S., Güroğlu, B., & Crone, E. A. (2014b). Gambling for self, friends, and antagonists: Differential contributions of affective and social brain regions on adolescent reward processing. *NeuroImage, 100*, 281–289. <https://doi.org/10.1016/j.neuroimage.2014.06.020>
- Casement, M. D., Guyer, A. E., Hipwell, A. E., McAloon, R. L., Hoffmann, A. M., Keenan, K. E., & Forbes, E. E. (2014). Girls' challenging social experiences in early adolescence predict neural response to rewards and depressive symptoms. *Developmental Cognitive Neuroscience, 8*, 18–27. <https://doi.org/10.1016/j.dcn.2013.12.003>
- Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology, 66*, 295–319. <https://doi.org/10.1146/annurev-psych-010814-015156>
- Casey, B. J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review, 28*, 62–77. <https://doi.org/10.1016/j.dr.2007.08.003>

- Chau, D. T., Roth, R. M., & Green, A. I. (2004). The neural circuitry of reward and its relevance to psychiatric disorders. *Current Psychiatry Reports*, *6*, 391–399. <https://doi.org/10.1007/s11920-004-0026-8>
- Chein, J. M., Albert, D., O'Brien, L., Uckert, K., & Steinberg, L. (2011). Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Developmental Science*, *14*, F1–F10. <https://doi.org/10.1111/j.1467-7687.2010.01035.x>
- Coan, J. A., & Sbarra, D. A. (2015). Social Baseline Theory: The social regulation of risk and effort. *Current Opinion in Psychology*, *1*, 87–91. <https://doi.org/10.1016/j.copsyc.2014.12.021>
- Cohen, S., Gottlieb, B. H., & Underwood, L. G. (2001). Social relationships and health: Challenges for measurement and intervention. *Advances in Mind-Body Medicine*, *17*, 129–141.
- Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews Neuroscience*, *13*, 636–650. <https://doi.org/10.1038/nrn3313>
- Crone, E. A., & Fuligni, A. J. (2020). Self and others in adolescence. *Annual Review of Psychology*, *71*, 447–469. <https://doi.org/10.1146/annurev-psych-010419-050937>
- Dahl, R. E. (2004). Adolescent brain development: A period of vulnerabilities and opportunities [Keynote address]. *Annals of the New York Academy of Sciences*, *1021*, 1–22. <https://doi.org/10.1196/annals.1308.001>
- Davey, C. G., Yücel, M., & Allen, N. B. (2008). The emergence of depression in adolescence: Development of the prefrontal cortex and the representation of reward. *Neuroscience & Biobehavioral Reviews*, *32*, 1–19. <https://doi.org/10.1016/j.neubiorev.2007.04.016>
- De Brujin, E. R. A., De Lange, F. P., Von Cramon, D. Y., & Ullsperger, M. (2009). When errors are rewarding. *Journal of Neuroscience*, *29*, 12183–12186. <https://doi.org/10.1523/JNEUROSCI.1751-09.2009>
- De Water, E., Mies, G. W., Ma, I., Mennes, M., Cilllessen, A. H. N., & Scheres, A. (2017). Neural responses to social exclusion in adolescents: Effects of peer status. *Cortex*, *92*, 32–43. <https://doi.org/10.1016/j.cortex.2017.02.018>
- Do, K. T., Prinstein, M. J., & Telzer, E. H. (2020). Neurobiological susceptibility to peer influence in adolescence. In K. C. Kadosh (Ed.), *Handbook of developmental cognitive neuroscience*. Oxford University Press. Online publication. <https://doi.org/10.1093/oxfordhb/9780198827474.013.27>
- Dumontheil, I. (2016). Adolescent brain development. *Current Opinion in Behavioral Sciences*, *10*, 39–44. <https://doi.org/10.1016/j.cobeha.2016.04.012>
- Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science*, *13*, 331–338. <https://doi.org/10.1111/j.1467-7687.2009.00888.x>

- Eisenberger, N. I. (2012). The pain of social disconnection: Examining the shared neural underpinnings of physical and social pain. *Nature Reviews Neuroscience, 13*, 421–434. <https://doi.org/10.1038/nrn3231>
- Eisenberger, N. I., & Lieberman, M. D. (2004). Why rejection hurts: A common neural alarm system for physical and social pain. *Trends in Cognitive Sciences, 8*, 294–300. <https://doi.org/10.1016/j.tics.2004.05.010>
- Falk, E. B., & Bassett, D. S. (2017). Brain and social networks: Fundamental building blocks of human experience. *Trends in Cognitive Sciences, 21*, 674–690. <https://doi.org/10.1016/j.tics.2017.06.009>
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358*, 459–473. <https://doi.org/10.1098/rstb.2002.1218>
- Gabriel, E. T., Oberger, R., Schmoeger, M., Deckert, M., Vockh, S., Auff, E., & Willinger, U. (2021). Cognitive and affective Theory of Mind in adolescence: Developmental aspects and associated neuropsychological variables. *Psychological Research, 85*, 533–553. <https://doi.org/10.1007/s00426-019-01263-6>
- Giletta, M., Slavich, G. M., Rudolph, K. D., Hastings, P. D., Nock, M. K., & Prinstein, M. J. (2018). Peer victimization predicts heightened inflammatory reactivity to social stress in cognitively vulnerable adolescents. *Journal of Child Psychology and Psychiatry, 59*, 129–139. <https://doi.org/10.1111/jcpp.12804>
- Güroğlu, B. (2020). Adolescent brain in a social world: Unravelling the positive power of peers from a neurobehavioral perspective. *European Journal of Developmental Psychology, 18*, 471–493. <https://doi.org/10.1080/17405629.2020.1813101>
- Güroğlu, B., Haselager, G. J. T., Van Lieshout, C. F. M., Takashima, A., Rijpkema, M., & Fernández, G. (2008). Why are friends special? Implementing a social interaction simulation task to probe the neural correlates of friendship. *NeuroImage, 39*, 903–910. <https://doi.org/10.1016/j.neuroimage.2007.09.007>
- Güroğlu, B., Van den Bos, W., Rombouts, S. A. R. B., & Crone, E. A. (2010). Unfair? It depends: Neural correlates of fairness in social context. *Social Cognitive and Affective Neuroscience, 5*, 414–423. <https://doi.org/10.1093/scan/nsq013>
- Guyer, A. E., & Jarcho, J. M. (2018). Neuroscience and peer relations. In W. M. Bukowski, B. Laursen, & K. H. Rubin (Eds.), *Handbook of peer interactions, relationships, and groups* (2nd ed., pp. 177–199). Guilford Press.
- Han, S., & Ma, Y. (2014). Cultural differences in human brain activity: A quantitative meta-analysis. *NeuroImage, 99*, 293–300. <https://doi.org/10.1016/j.neuroimage.2014.05.062>
- Heinrichs, M., Baumgartner, T., Kirschbaum, C., & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses



- to psychosocial stress. *Biological Psychiatry*, *54*, 1389–1398. [https://doi.org/10.1016/S0006-3223\(03\)00465-7](https://doi.org/10.1016/S0006-3223(03)00465-7)
- Hodges, E. V. E., Boivin, M., Vitaro, F., & Bukowski, W. M. (1999). The power of friendship: Protection against an escalating cycle of peer victimization. *Developmental Psychology*, *35*, 94–101. <https://doi.org/10.1037/0012-1649.35.1.94>
- Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: A meta-analytic review. *PLoS Medicine*, *7*, e1000316. <https://doi.org/10.1371/journal.pmed.1000316>
- Kellij, S., Lodder, G. M. A., van den Bedem, N., Güroğlu, B., & Veenstra, R. (2022). The social cognitions of victims of bullying: A systematic review. *Adolescent Research Review*. <https://doi.org/10.1007/s40894-022-00183-8>
- Lamblin, M., Murawski, C., Whittle, S., & Fornito, A. (2017). Social connectedness, mental health and the adolescent brain. *Neuroscience & Biobehavioral Reviews*, *80*, 57–68. <https://doi.org/10.1016/j.neubiorev.2017.05.010>
- Laursen, B., & Veenstra, R. (2021). Toward understanding the functions of peer influence: A summary and synthesis of recent empirical research. *Journal of Research on Adolescence*, *31*, 889–907. <https://doi.org/10.1111/jora.12606>
- Marion, D., Laursen, B., Zettergren, P., & Bergman, L. R. (2013). Predicting life satisfaction during middle adulthood from peer relationships during mid-adolescence. *Journal of Youth and Adolescence*, *42*, 1299–1307. <https://doi.org/10.1007/s10964-013-9969-6>
- Masten, C. L., Eisenberger, N. I., Borofsky, L. A., McNealy, K., Pfeifer, J. H., & Dapretto, M. (2011a). Subgenual anterior cingulate responses to peer rejection: A marker of adolescents' risk for depression. *Development and Psychopathology*, *23*, 283–292. <https://doi.org/10.1017/S0954579410000799>
- Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011b). An fMRI investigation of empathy for 'social pain' and subsequent prosocial behavior. *NeuroImage*, *55*, 381–388. <https://doi.org/10.1016/j.neuroimage.2010.11.060>
- Masten, C. L., Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Eisenberger, N. I. (2012). Time spent with friends in adolescence relates to less neural sensitivity to later peer rejection. *Social Cognitive and Affective Neuroscience*, *7*, 106–114. <https://doi.org/10.1093/scan/nsq098>
- Mayeux, L., Bellmore, A. D., & Cillessen, A. H. N. (2007). Predicting changes in adjustment using repeated measures of sociometric status. *Journal of Genetic Psychology*, *168*, 401–424. <https://doi.org/10.3200/GNTP.168.4.401-424>
- McIver, T. A., Bosma, R. L., Sandre, A., Goegan, S., Klassen, J. A., Chiarella, J., Booij, L., & Craig, W. (2018). Peer victimization is associated with neural response to social exclusion. *Merrill-Palmer Quarterly*, *64*, 135–161. <https://doi.org/10.13110/merrpalmquar1982.64.1.0135>

- Meuwese, R., Braams, B. R., & Güroğlu, B. (2018). What lies beneath peer acceptance in adolescence? Exploring the role of Nucleus Accumbens responsivity to self-serving and vicarious rewards. *Developmental Cognitive Neuroscience, 34*, 124–129. <https://doi.org/10.1016/j.dcn.2018.07.004>
- Meyer, M. L., Masten, C. L., Ma, Y., Wang, C., Shi, Z., Eisenberger, N. I., & Han, S. (2013). Empathy for the social suffering of friends and strangers recruits distinct patterns of brain activation. *Social Cognitive and Affective Neuroscience, 8*, 446–454. <https://doi.org/10.1093/scan/nss019>
- Morelli, S. A., Knutson, B., & Zaki, J. (2018). Neural sensitivity to personal and vicarious reward differentially relate to prosociality and well-being. *Social Cognitive and Affective Neuroscience, 13*, 831–839. <https://doi.org/10.1093/scan/nsy056>
- Müller-Pinzler, L., Rademacher, L., Paulus, F. M., & Krach, S. (2016). When your friends make you cringe: Social closeness modulates vicarious embarrassment-related neural activity. *Social Cognitive and Affective Neuroscience, 11*, 466–475. <https://doi.org/10.1093/scan/nsv130>
- Nelson, E. E., Leibenluft, E., McClure, E. B., & Pine, D. S. (2005). The social re-orientation of adolescence: A neuroscience perspective on the process and its relation to psychopathology. *Psychological Medicine, 35*, 163–174. <https://doi.org/10.1017/S0033291704003915>
- Ng, T. H., Alloy, L. B., & Smith, D. V. (2019). Meta-analysis of reward processing in major depressive disorder reveals distinct abnormalities within the reward circuit. *Translational Psychiatry, 9*, 293. <https://doi.org/10.1038/s41398-019-0644-x>
- O'Donnell, M. B., Bayer, J. B., Cascio, C. N., & Falk, E. B. (2017). Neural bases of recommendations differ according to social network structure. *Social Cognitive and Affective Neuroscience, 12*, 61–69. <https://doi.org/10.1093/scan/nsw158>
- Parkinson, C., Kleinbaum, A. M., & Wheatley, T. (2018). Similar neural responses predict friendship. *Nature Communications, 9*, 332. <https://doi.org/10.1038/s41467-017-02722-7>
- Perren, S., Ettekal, I., & Ladd, G. W. (2013). The impact of peer victimization on later maladjustment: Mediating and moderating effects of hostile and self-blaming attributions. *Journal of Child Psychology and Psychiatry, 54*, 46–55. <https://doi.org/10.1111/j.1469-7610.2012.02618.x>
- Platt, B., Kadosh, K. C., & Lau, J. Y. F. (2013). The role of peer rejection in adolescent depression. *Depression and Anxiety, 30*, 809–821. <https://doi.org/10.1002/da.22120>

- Prinstein, M. J., & La Greca, A. M. (2004). Childhood peer rejection and aggression as predictors of adolescent girls' externalizing and health risk behaviors: A 6-year longitudinal study. *Journal of Consulting and Clinical Psychology, 72*, 103–112. <https://doi.org/10.1037/0022-006X.72.1.103>
- Reijntjes, A., Thomaes, S., Kamphuis, J. H., Bushman, B. J., Orobio de Castro, B., & Telch, M. J. (2011). Explaining the paradoxical rejection-aggression link: The mediating effects of hostile intent attributions, anger, and decreases in state self-esteem on peer rejection-induced aggression in youth. *Personality and Social Psychology Bulletin, 37*, 955–963. <https://doi.org/10.1177/0146167211410247>
- Rudolph, K. D., Miernicki, M. E., Troop-Gordon, W., Davis, M. M., & Telzer, E. H. (2016). Adding insult to injury: Neural sensitivity to social exclusion is associated with internalizing symptoms in chronically peer-victimized girls. *Social Cognitive and Affective Neuroscience, 11*, 829–842. <https://doi.org/10.1093/scan/nsw021>
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science, 300*, 1755–1758. <https://doi.org/10.1126/science.1082976>
- Schreuders, E., Braams, B. R., Blankenstein, N. E., Peper, J. S., Güroğlu, B., & Crone, E. A. (2018a). Contributions of reward sensitivity to ventral striatum activity across adolescence and early adulthood. *Child Development, 89*, 797–810. <https://doi.org/10.1111/cdev.13056>
- Schreuders, E., Braams, B. R., Crone, E. A., & Güroğlu, B. (2021). Friendship stability in adolescence is associated with ventral striatum responses to vicarious rewards. *Nature Communications, 12*, 313. <https://doi.org/10.1038/s41467-020-20042-1>
- Schreuders, E., Klapwijk, E. T., Will, G. J., & Güroğlu, B. (2018b). Friend versus foe: Neural correlates of prosocial decisions for liked and disliked peers. *Cognitive, Affective, & Behavioral Neuroscience, 18*, 127–142. <https://doi.org/10.3758/s13415-017-0557-1>
- Schreuders, E., Smeekens, S., Cillessen, A. H. N., & Güroğlu, B. (2019). Friends and foes: Neural correlates of prosocial decisions with peers in adolescence. *Neuropsychologia, 129*, 153–163. <https://doi.org/10.1016/j.neuropsychologia.2019.03.004>
- Schriber, R. A., & Guyer, A. E. (2016). Adolescent neurobiological susceptibility to social context. *Developmental Cognitive Neuroscience, 19*, 1–18. <https://doi.org/10.1016/j.dcn.2015.12.009>
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience, 12*, 154–167. <https://doi.org/10.1038/nrn2994>

- Sijtsema, J. J., Lindenberg, S. M., Ojanen, T. J., & Salmivalli, C. (2020). Direct aggression and the balance between status and affection goals in adolescence. *Journal of Youth and Adolescence, 49*, 1481–1491. <https://doi.org/10.1007/s10964-019-01166-0>
- Smith, A. R., Steinberg, L., Strang, N., & Chein, J. (2015). Age differences in the impact of peers on adolescents' and adults' neural response to reward. *Developmental Cognitive Neuroscience, 11*, 75–82. <https://doi.org/10.1016/j.dcn.2014.08.010>
- Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review, 28*, 78–106. <https://doi.org/10.1016/j.dr.2007.08.002>
- Sul, S., Güroğlu, B., Crone, E. A., & Chang, L. J. (2017). Medial prefrontal cortical thinning mediates shifts in other-regarding preferences during adolescence. *Scientific Reports, 7*, 8510. <https://doi.org/10.1038/s41598-017-08692-6>
- Swartz, J. R., Carranza, A. F., & Knodt, A. R. (2020). Amygdala activity to angry and fearful faces relates to bullying and victimization in adolescents. *Social Cognitive and Affective Neuroscience, 14*, 1027–1035. <https://doi.org/10.1093/scan/nsz084>
- Takahashi, H., Kato, M., Matsuura, M., Mobbs, D., Suhara, T., & Okubo, Y. (2009). When your gain is my pain and your pain is my gain: Neural correlates of envy and schadenfreude. *Science, 323*, 937–939. <https://doi.org/10.1126/science.1165604>
- Telzer, E. H. (2016). Dopaminergic reward sensitivity can promote adolescent health: A new perspective on the mechanism of ventral striatum activation. *Developmental Cognitive Neuroscience, 17*, 57–67. <https://doi.org/10.1016/j.dcn.2015.10.010>
- Telzer, E. H., Fuligni, A. J., Lieberman, M. D., Miernicki, M. E., & Galván, A. (2015). The quality of adolescents peer relationships modulates neural sensitivity to risk taking. *Social Cognitive and Affective Neuroscience, 10*, 389–398. <https://doi.org/10.1093/scan/nsu064>
- Telzer, E. H., Miernicki, M. E., & Rudolph, K. D. (2018). Chronic peer victimization heightens neural sensitivity to risk taking. *Development and Psychopathology, 30*, 13–26. <https://doi.org/10.1017/S0954579417000438>
- Tremblay, L. K., Naranjo, C. A., Graham, S. J., Herrmann, N., Mayberg, H. S., Hevenor, S., & Busto, U. E. (2005). Functional neuroanatomical substrates of altered reward processing in major depressive disorder revealed by a dopaminergic probe. *Archives of General Psychiatry, 62*, 1228–1236. <https://doi.org/10.1001/archpsyc.62.11.1228>
- Van de Groep, S., Zanolie, K., & Crone, E. A. (2020). Familiarity and audience effects on giving: A functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience, 32*, 1577–1589. [https://doi.org/10.1162/jocn\\_a\\_01568](https://doi.org/10.1162/jocn_a_01568)

- Van Duijvenvoorde, A. C. K., Achterberg, M., Braams, B. R., Peters, S., & Crone, E. A. (2016). Testing a dual-systems model of adolescent brain development using resting-state connectivity analyses. *NeuroImage*, *124*, 409–420. <https://doi.org/10.1016/j.neuroimage.2015.04.069>
- Van Duijvenvoorde, A. C. K., Westhoff, B., De Vos, F., Wierenga, L. M., & Crone, E. A. (2019). A three-wave longitudinal study of subcortical–cortical resting-state connectivity in adolescence: Testing age- and puberty-related changes. *Human Brain Mapping*, *40*, 3769–3783. <https://doi.org/10.1002/hbm.24630>
- 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. <https://doi.org/10.1016/j.cobeha.2016.05.007>
- Van Hoorn, J., Shablack, H., Lindquist, K. A., & Telzer, E. H. (2019). Incorporating the social context into neurocognitive models of adolescent decision-making: A neuroimaging meta-analysis. *Neuroscience & Biobehavioral Reviews*, *101*, 129–142. <https://doi.org/10.1016/j.neubiorev.2018.12.024>
- Wierenga, L. M., Bos, M. G. N., Schreuders, E., Van de Kamp, F., Peper, J. S., Tamnes, C. K., & Crone, E. A. (2018). Unraveling age, puberty and testosterone effects on subcortical brain development across adolescence. *Psychoneuroendocrinology*, *91*, 105–114. <https://doi.org/10.1016/j.psyneuen.2018.02.034>
- Will, G. J., Crone, E. A., Van den Bos, W., & Güroğlu, B. (2013). Acting on observed social exclusion: Developmental perspectives on punishment of excluders and compensation of victims. *Developmental Psychology*, *49*, 2236–2244. <https://doi.org/10.1037/a0032299>
- Will, G. J., Crone, E. A., Van Lier, P. A. C., & Güroğlu, B. (2016a). Neural correlates of retaliatory and prosocial reactions to social exclusion: Associations with chronic peer rejection. *Developmental Cognitive Neuroscience*, *19*, 288–297. <https://doi.org/10.1016/j.dcn.2016.05.004>
- Will, G. J., Crone, E. A., Van Lier, P. A. C., & Güroğlu, B. (2018). Longitudinal links between childhood peer acceptance and the neural correlates of sharing. *Developmental Science*, *21*, e12489. <https://doi.org/10.1111/desc.12489>
- Will, G. J., Van Lier, P. A. C., Crone, E. A., & Güroğlu, B. (2016b). Chronic childhood peer rejection is associated with heightened neural responses to social exclusion during adolescence. *Journal of Abnormal Child Psychology*, *44*, 43–55. <https://doi.org/10.1007/s10802-015-9983-0>
- Williams, K. D., Cheung, C. K. T., & Choi, W. (2000). Cyberostracism: Effects of being ignored over the internet. *Journal of Personality and Social Psychology*, *79*, 748–762. <https://doi.org/10.1037/0022-3514.79.5.748>

### **Appendix. Brain areas, their functions, and the evidence for their relation with peer experiences and interactions**

Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
Amygdala	emotion processing, including arousal, perception, and recognition; emotional learning; motivational salience	Güroğlu (2008) social interactions with friends > all other (familiar or unfamiliar) peers McIver (2018) heightened activation in peer-victimized > defenders and non-victimized adolescents during social exclusion Swartz (2020) higher activity during processing of fear and anger in relation to higher bullying and victimization Telzer (2018) higher activity during risky choices in chronically victimized girls
Anterior insula	intrapersonal experience, including subjective feelings, regulation and internalization of affect; affective response to negative or unexpected (social) behavior (e.g., norm violations, unfairness, errors, social exclusion); behavioral control and response inhibition	Masten (2012) less active during social exclusion when participants have spent more time with friends Meyer (2013) observing exclusion of best friend > exclusion of stranger Rudolph (2016) heightened activity during social exclusion associated with more internalizing symptoms in victimized girls Telzer (2015) higher activity during risk taking in relation to peer conflict Will (2018) higher activity in stably accepted > chronically rejected adolescents during costly sharing decisions
Dorsal anterior cingulate cortex (dACC)	anticipation and detection of affect- or error-related responses; motor control; regulatory response to unexpected (social) behavior (e.g., norm violations, unfairness, errors, social exclusion); assessing the salience of emotion and motivational information; reward-based learning	De Water (2017) more active during social exclusion when participants are more accepted by peers Masten (2012) less active during social exclusion when participants have spent more time with friends Meyer (2013) observing exclusion of best friend > exclusion of stranger Rudolph (2016) heightened activity during social exclusion associated with more internalizing symptoms in victimized girls

*Continued*

Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
		<p>Will (2016b) higher activity in chronically rejected &gt; stably accepted adolescents during (incidental) social exclusion</p> <p>Will (2018) higher activity in stably accepted &gt; chronically rejected adolescents during costly sharing decisions</p>
Dorsal striatum	planning, execution, and automatization of behavior; executive control	Will (2016a) higher activity in chronically rejected > stably accepted adolescents during forgiving excluders
Dorsolateral prefrontal cortex (dlPFC)	executive functions including working memory, selective attention, regulatory control, emotion regulation	Telzer (2018) higher activity during safe (non-risky) decisions in victimized girls
Inferior parietal lobule (IPL)	emotion perception; interpretation of (sensory) information; visuospatial processing; perspective taking	<p>Schreuders (2019) higher activity during prosocial behavior for friends</p> <p>Van de Groep (2020) higher activity when making decisions for friends &gt; unfamiliar peers</p>
Lateral prefrontal cortex (lPFC)	higher-order cognitive control, such as planning, behavioral inhibition, and decision making; integration of cognition and reward/motivation	<p>Asscheman (2019) higher activity in early phases of social exclusion in chronic peer rejected &gt; stably accepted boys</p> <p>Chein (2011) lower activity during risk taking in adolescents (than in adults)</p> <p>Will (2016a) higher activity in chronically rejected &gt; stably accepted adolescents when forgiving excluders</p>

*Continued*

Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
Medial pre-frontal cortex (mPFC)	mentalizing, self- and other-oriented thinking, including understanding other's emotions and self-referential processing	<p>Braams (2014a) processing outcomes for peer &gt; outcomes for self</p> <p>Casement (2014) early peer victimization related to decreased response to rewards, which was positively related to depressive symptoms</p> <p>De Water (2017) more active during social exclusion for more popular participants who were excluded by other popular peers</p> <p>Güroğlu (2008) social interactions with personally familiar &gt; personally unfamiliar peers</p> <p>Meyer (2013) observing exclusion of best friend &gt; exclusion of stranger</p>
Posterior superior temporal sulcus (pSTS)	perspective taking, mentalizing, and social cognition, including higher levels of prosocial behaviors that promote an other-oriented focus and understanding others' minds	Will (2018) higher activity in stably accepted > chronically rejected adolescents during costly sharing decisions
Precuneus	highly integrated cognitive tasks, including visuo-spatial imagery; episodic memory retrieval; self-processing operations, including first-person perspective taking and agency/self-awareness	<p>Braams (2014a) processing outcomes for peer &gt; outcomes for self</p> <p>Braams (2017a) processing outcomes for friends &gt; self in early adolescence</p> <p>Güroğlu (2008) social interactions with personally familiar &gt; personally unfamiliar peers</p>
Putamen	(part of dorsal striatum) reward anticipation and processing; reinforcement learning and habit formation	<p>Schreuders (2018a) higher activity during prosocial behavior for friends</p> <p>Schreuders (2018b) higher activity during selfish decisions for disliked peers</p> <p>Schreuders (2019) higher activity during prosocial behavior for friends; also negatively related to negative friendship quality</p>

*Continued*



Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
Superior parietal lobule (SPL)	social cognition, including mental imagery/visuo-spatial perception, recall of personal experiences, mentalizing, and understanding and integration of perspectives	Schreuders (2019) higher activity during prosocial behavior for friends
Superior temporal sulcus (STS)	face processing; audiovisual integration; (biological) motion processing; mental-state attribution	Schreuders (2018b) higher activity during selfish decisions for disliked peers
Temporal parietal junction (TPJ)	other-oriented thinking (perspective taking/mentalizing), including switching attention and perspective, understanding and integration of perspectives and intentionality	Braams (2014a) processing outcomes for peer > outcomes for self Braams (2017a) processing outcomes for friends > self in early adolescence Güroğlu (2008) social interactions with personally familiar > personally unfamiliar peers Schreuders (2019) higher activity during prosocial behavior for friends Van de Groep (2020) higher activity when making decisions for friends > unfamiliar peers
Temporal pole	integration of complex and highly processed perceptual and emotional responses; social and emotional processes, including face recognition and theory of mind	Will (2018) higher activity in stably accepted > chronically rejected adolescents during costly sharing decisions

*Continued*

Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
Ventral striatum	anticipation and processing of rewards (monetary or social); reward-based reinforcement learning; salience processing; processing of positive emotional stimuli	<p>Braams (2014a) win &gt; lose money for best friend (and not for disliked peer)</p> <p>Braams (2014b) win &gt; lose money for best friend, which was positively related to friendship quality</p> <p>Braams &amp; Crone (2017b) age-related increase when winning for the best friend compared with winning for the self or the mother</p> <p>Chein (2011) higher activity in relation to risk-taking behavior in peer context (in adolescents only)</p> <p>De Water (2017) more active during social exclusion for more popular participants who were excluded by other popular peers</p> <p>Güroğlu (2008) social interactions with friends &gt; all other (familiar or unfamiliar) peers</p> <p>Meuwese (2018) less active when winning for self for participants who were more preferred by friends</p> <p>Morelli (2018) higher activity when winning for friends related to more daily prosocial behavior</p> <p>Schreuders (2021) mid-adolescent peak when winning for friends in participants with stable friendships</p> <p>Smith (2015) higher activity for reward processing in peer context (in adolescents only)</p> <p>Telzer (2018) higher activity during risky choices in chronically victimized girls</p>
Ventrolateral prefrontal cortex (vlPFC)	motor inhibition; executive functioning and goal-oriented action planning and regulation; motivational and emotional decision making	<p>Ambrosia (2018) higher activity in adolescents who are more risk taking and show high reciprocal affect or low in risk taking and show low reciprocal affect</p> <p>Telzer (2018) higher activity during safe (i.e., non-risky) decisions in victimized girls</p>

*Continued*

Brain area (abbreviation)	Function: Involved in . . .	Evidence for relation with peer experiences and interactions*
Ventromedial prefrontal cortex (vmPFC)	integration of motivational and emotional information; (emotional) salience processing, reward anticipation, (social) decision making, and goal-directed behavior (i.e., in relation to risks and rewards)	Chein (2011) higher activity in relation to risk-taking behavior (in adolescents only) Güroğlu (2008) social interactions with friends > all other (familiar or unfamiliar) peers Telzer (2018) higher activity during risky choices in chronically victimized girls

\*Referenced by the first author and year. Please see individual author entries in the References for more information.