School Social Relationships and Brain Functioning

J. Susanne Asscheman and Kirby Deater-Deckard

Decades of research has shown that peer relationships during elementary school are highly influential for children's social and emotional functioning and psychological adjustment (see Chaps. 1 and 2 of this book). With the transition to elementary school and as they develop across middle childhood, children spend more time with their peers and less time with family members. The quantity and quality of social experiences with peers are likely to interact with the developing brain to shape how children respond in peer as well as other social interactions and contexts. With the advancement in neuroimaging techniques, it has become easier to measure brain responses to such environmental input across development. This is an important advancement, because studying how the brains of children respond to social environmental input elucidates the underlying mechanisms by which peer experiences may shape development. In addition to informing the basic scientific literature on child development, this information about the developing nervous system can inform assessment, diagnosis, prevention, and intervention.

Most of the prior studies assessing neural responses to social experiences with peers during development have focused on adolescence, in part because this period of development is characterized by heightened sensitivity to peer acceptance and rejection compared to childhood and adulthood (Guyer & Jarcho, 2018). However, early to middle childhood (spanning the time between infancy and puberty) is also an important period for social development. Compared to early childhood, once children begin schooling (in most countries, by age 5 years), they spend significant amounts of time interacting with peers in formal (e.g., school) and informal (e.g.,

J. S. Asscheman (✉)
Clinical Developmental Psychology, Faculty of Behavioral and Movement Sciences, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

K. Deater-Deckard
Department of Psychological and Brain Sciences, University of Massachusetts, Amherst, MA, USA
e-mail: kdeaterdeck@umass.edu

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sports, neighborhood) social settings. Interactions during this period are mostly focused on peer play in dyads or in larger peer groups (Coplan & Arbeau, 2009). This middle childhood period, as opposed to adolescence, has been relatively understudied in the developmental social neuroscience literature—although recently, there has been an increase in research on brain development in middle childhood. From a developmental neuroscience perspective, middle childhood is just as important to study as adolescence and early childhood, because many brain structures and processes that underlie social behavior undergo major changes across middle childhood and attain a mature form before the start of puberty (Giedd et al., 1999; Gogtay et al., 2004).

Furthermore, individual differences in neural sensitivity to social information during adolescence have their origins earlier in development. Thus, social experiences during middle childhood shape brain development in ways that influence individual differences in social behavior during adolescence (Andersen, 2003; Schriber & Guyer, 2016). In addition, the processes of interest are not limited to social contexts and behaviors; social experiences in childhood can have profound effects on other developmental outcomes, such as academic functioning and achievement. For example, a child who has many negative peer experiences (e.g., victimization, rejection) during childhood may be less motivated to perform well in elementary school or may even drop out of school at some point, which will continue to influence outcomes later in the lifespan (e.g., job opportunities, health literacy).

The goal of the current chapter is to describe the advancement in the field of developmental social neuroscience during childhood with a specific focus on peer experiences. We begin by presenting a theoretical framework designating how peer social experiences, and more specifically social stressors, may impact brain function during development. We then provide an overview of empirical studies assessing brain responses to peer social experiences during childhood. To provide a coherent and detailed overview, we have concentrated on neuroimaging studies describing any sort of social interaction with peers. These studies of brain responses include experimental manipulation of participants receiving feedback and experiencing rejection, as well as naturalistic correlational studies investigating potential influences of prior real-life peer experiences. We included papers that span the preschool and elementary school phases of development, with an age range between 4 and 12 years old. Additionally, to be comprehensive, we included studies that used electroencephalography (EEG) or functional magnetic resonance imaging (fMRI); EEG is more commonly used than MRI with younger children. We conclude by providing directions for future research on peer social experiences and brain development during childhood.

Theoretical Foundations

Social connectedness is fundamental for human survival and developmental thriving. Like other social species, humans are highly motivated to form and maintain social bonds, so they actively search for and engage in social interactions with others. For instance, adults who have experienced exclusion show behaviors that support affiliations with others such as higher levels of prosocial behavior or will adjust their behavior in accordance with others to fit in (i.e., tend and befriend; Taylor, 2011). The socially embedded context for humans has corresponded with the evolutionary emergence of several networks throughout the brain that seem to be involved in detecting and interpreting social information and engaging in sustained social interactions and enduring relationships (Kilford et al., 2016; Nelson et al., 2005; Silston et al., 2018; Stanley & Adolphs, 2013).

Specifically, the *detection node* processes perceptual information to determine whether a stimulus is social (e.g., human or animate) versus nonsocial. The detection node includes the inferior occipital cortex, inferior temporal lobe, intraparietal sulcus, fusiform gyrus (also known as the fusiform face area that is involved in processing facial information), and the superior temporal sulcus. The *affective node* processes detected social information to compute its affective valence and salience. Regions include the amygdala, ventral striatum, septum, bed nucleus of the stria, hypothalamus, orbitofrontal cortex, anterior cingulate cortex, and anterior insula. The *cognitive-regulatory node* is implicated in mentalizing activities (e.g., inferring cause and meaning from social stimuli), inhibiting prepotent responses, and sustaining goal-directed behavior. Mentalizing processes have been associated with activation in the paracingulate cortex and dorsomedial prefrontal cortex; inhibitory control has been associated with activation in the ventral prefrontal cortex; and goal-directed behavior appears to be supported through the dorsal and ventral prefrontal cortex.

Given the importance of social bonds to human development and functioning, being rejected or excluded by others is typically experienced as moderately to highly aversive and causes a stress response characterized by the upregulation of stress hormones (e.g., cortisol) in the body (Dickerson & Zoccola, 2013). At the neural level of analysis, experiences of rejection or exclusion activate the anterior insula, anterior cingulate cortex, posterior cingulate cortex, temporal cortex, and the lateral prefrontal cortex in adolescents and adults (Cacioppo et al., 2013; Vijayakumar et al., 2017; Wang et al., 2017). The anterior insula and anterior cingulate cortex are thought to serve as a "neural alarm" to select behaviors that motivate social connectedness. Structural and functional alterations of the brain networks involved in social interaction and relational behaviors, as well as in detection of social exclusion or inclusion, help explain some of the individual differences observed between children in their psychosocial functioning and adjustment.

From birth to adulthood, the central and peripheral nervous systems undergo substantial structural and functional changes (Gogtay et al., 2004; Mills et al., 2016; Tau & Peterson, 2009). Neural networks of connected clusters of neurons are formed. Over time and development (based in part on experiences), some connections are strengthened while other connections become weaker (Holtmaat & Svoboda, 2009). Moreover, some brain regions first increase in size early in development before showing gray matter volume reductions (i.e., cell bodies, synapses, and dendrites) and increases in white matter (i.e., myelinated and unmyelinated axons) as those regions become more mature, efficient, and specialized in their functions (Lebel & Beaulieu, 2011; Mills et al., 2016). Developmentally, the most posterior parts of the brain (e.g., occipital lobe) mature earliest and fastest, and most anterior regions (e.g., frontal lobe) are the last to show full maturation (Gogtay et al., 2004). Many of these changes during development are influenced by genes, but those genes function in part in response to environmental inputs (Fox et al., 2010; Peper et al., 2007). Thus, individual differences in environmental inputs interact with genetic differences and very likely shape brain development differently across children (even siblings in the same family). Moreover, although environmental inputs may have effects at any point across the life span, these factors may be most powerful in childhood and adolescence, during the rapid and dynamic brain development that occurs in this period of development (Mills et al., 2016; Mills et al., 2014). In light of this consideration, peer experiences may be particularly important in their influences on brain development prior to adulthood.

Turning to environmental inputs, but before considering peer experiences, it is worthwhile to highlight the largest literature on environmental factors and brain development in childhood—the effects of exposure to chronic stressors (Chen & Baram, 2015; Lupien et al., 2009). The potential effects of stress on brain development during childhood are studied largely in the context of early-life stressors (e.g., premature birth and low birth weight, insecure attachment, maltreatment, malnutrition). Findings from studies of these kinds of stressors show that severe and long-lasting experiences of early-life stress alter emotional and cognitive brain networks involving regions such as the amygdala, hippocampus, and prefrontal cortex (VanTieghem & Tottenham, 2018). For instance, chronic stress leads to hyperactivation of the amygdala but also impairments in PFC functioning, reductions in PFC volumes, and weakening of cortico-limbic connectivity. These stress-related alterations in networks are thought to lead to higher stress sensitivity and increased risk for psychopathology (Bolton et al., 2017).

Experimental studies using animal and in vitro cell models provide insight into the pathway underlying neural alterations following chronic stress as well as evidence for the causality of this stress-exposure mechanism (Arnsten, 2009). Acute social stressors, such as short periods of maternal deprivation or social instability in the home cage, increase the level of stress hormones (e.g., noradrenaline, corticosteroids) in the brain (de Kloet, 2003). An initial rapid release of (nor)adrenaline mobilizes the body and brain to increase vigilance to respond quickly to stressors. This rapid response is followed by a slower increase in corticosteroids, the end product of the hypothalamic-pituitary-adrenocortical (HPA) axis. These corticosteroids subsequently bind to glucocorticoid (GR) and mineralocorticoid (MR) receptors located on the membrane of neurons. Receptor binding results in changes in intercellular processing such as increased energy consumption, cellular metabolism, cell signaling, neuronal connectivity, and neural transmission (de Kloet et al., 2005). The stress hormones and subsequent cellular changes relocate energy away from higher-order cognitive processing toward emotional processing and memory formation. These changes are suggested to be adaptive and allow individuals to respond adequately to such stressors. However, chronic forms of stress have detrimental effects on neural functioning and architecture (Karatsoreos & McEwen, 2013). Chronic stress has been shown to result in dendritic atrophy and lower spine density in the PFC and hippocampus which leads to impaired memory formation and deficits in cognitive functioning. Moreover, the ability of the hippocampus to generate new neurons necessary for learning and memory is impaired, further hampering memory formation (Lucassen et al., 2016). In contrast to the dendritic impairments in the PFC and hippocampus, the amygdala shows increased dendritic spine growth as well as a hyperactivation to stressors (Karatsoreos & McEwen, 2013). These alterations increase stress sensitivity and may be part of the foundation of anxiety, depression, and aggression problems (Fig. 1).

With respect to peer influences, it is now also widely accepted that negative experiences such as rejection, victimization, or bullying serve as important interpersonal stressors in children's lives (Copeland et al., 2013). Experiences of exclusion, peer rejection, or victimization activate the hypothalamic-pituitary-adrenocortical (HPA) axis (Blackhart et al., 2007), a key system implicated in stress responses. Chronic exposure to peer stressors has been associated with dysregulation of the HPA axis and increased risk for internalizing problems such as anxiety and depression (Ouellet-Morin et al., 2011; Peters et al., 2011). Thus, peer exclusion, rejection, or victimization may also lead to neural alterations in accordance with the previously described neural pathway (Fig. 1). The potential effects of peer stressors on brain development and function have mostly been studied with samples of adolescents (Guyer & Jarcho, 2018). Little is known about the middle childhood period.

Positive social experiences with peers may also contribute to brain development. Being accepted by peers or having several high-quality friendships have been shown to be an important predictor for later mental health (Berndt, 2002; Gifford-Smith & Brownell, 2003; Rubin et al., 2006). On a neural level, animal models show that rat pups exposed to enriched social environments (e.g., social housing, high maternal

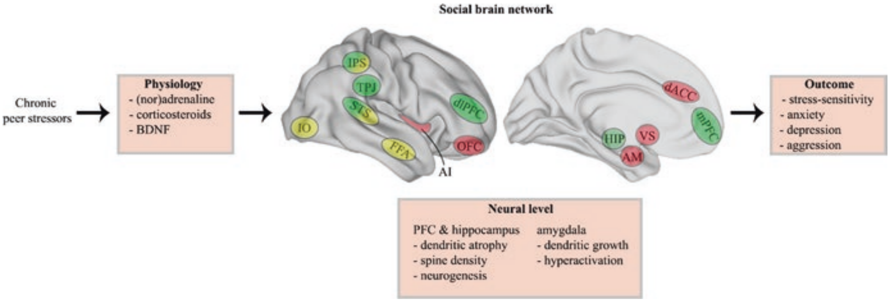

Fig. 1 Theoretical model describing the potential pathway by which chronic peer stressors may lead to negative developmental outcomes via neural alterations in the brain based on results from animal and human studies. Brain regions indicated in yellow indicate regions implicated in the detection node, regions in red are implicated in the affective node, and regions indicated in green are implicated in the cognitive-regulatory node in the social brain network. *BDNF* brain-derived neurotrophic factor, *IO* inferior occipital cortex, *STS* superior temporal sulcus, *TPJ* temporoparietal junction, *IPS* intraparietal sulcus, *FFA* fusiform gyrus, *AI* anterior insula, *OFC* orbitofrontal cortex, *dlFPC* dorsolateral prefrontal cortex, *HIP* hippocampus, *VS* ventral striatum, *AM* amygdala, *dACC* dorsal anterior cingulate cortex, *mPFC* medial prefrontal cortex, *PFC* prefrontal cortex, *TPJ* temporoparietal junction, *STS* superior temporal sulcus

care including sensitivity and secure attachment) show reductions in corticosteroid levels as well as increases in levels of neurotrophins which stimulate neural growth (Curley & Champagne, 2016; van Praag et al., 2000). These growth factors contribute to increased cell survival, growth of new neurons and blood vessels, and increased complexity of the dendritic branches in hippocampal and frontal regions. In humans, the effects of positive experiences on brain development have mostly been studied in the context of positive parenting during childhood. These studies demonstrate associations between positive parenting and total brain volume, hippocampal and amygdala volume, cortical thickness, and brain connectivity (e.g., Kok et al., 2018; Kok et al., 2015; Kopala-Sibley et al., 2018; Wang et al., 2019; Whittle et al., 2014). Behaviorally, exposure to enriched environments or high levels of maternal care may lead to favorable outcomes including lower levels of anxiety and higher levels of social behavior (Baldini et al., 2013; Branchi et al., 2006; Goes et al., 2015; Kok et al., 2018; Lehmann & Herkenham, 2011; Sparling et al., 2018), potentially via neural alterations (Kok et al., 2018). It has yet to be examined how peers during childhood may contribute to children's brain development.

Furthermore, the deleterious consequences of peer stressors—and the potential positive consequences of good peer relationships—may operate not only through alteration of neural networks and functioning but also through social behavior (i.e., experience-dependent synaptic plasticity; Cicchetti, 2002; Feldman & Knudsen, 1998; Hebb, 1949; Kempermann, 2019). If true, having more opportunities to interact with peers—in positive and negative ways—during childhood could have effects on structural and functional neural specialization in brain regions associated with social cognition. Such effects would likely make children more sensitive to social information and help build a more elaborate repertoire of appropriate behaviors to implement during social interactions with peers. For example, children that have many positive social experiences with peers may become better in interpreting mental states or intentions of other children or learn how to guide their own behavior to achieve positive social interactions with peers (Dodge et al., 2003; Lansford et al., 2010; McDonald & Asher, 2018; Parker & Asher, 1987). This improvement may be reflected in increased specialization of these brain regions responsible for this behavior. In contrast, children that are chronically rejected by their peers or who are socially isolated from peers lack these experiences and do not have as many opportunities to practice their relational skills. As a consequence, the relevant brain regions most important to social behavior may lack valuable inputs that contribute to developmentally appropriate specialization. As a result, chronically rejected and neglected children would be at a social disadvantage in part because of alterations in their brain development and functioning—changes that would likely have its influence into adolescence and adulthood (Fox et al., 2010).

Our aim in the current section was to provide a framework that explains how peer experiences may alter children's neurobiology and affect children's development. We suggest that peer experiences may shape regions important for social behavior. Peer stressors experienced by children may alter neural networks implicated in emotion regulation and cognitive control. These changes may be underlying the developmental trajectories of maladjustment so common among youth who are rejected or neglected by their peers. In the next section, we will summarize the neuroimaging literature examining how the brain responds to different peer experiences during childhood, in an effort to deepen our understanding of how peer experiences may shape brain development and social-emotional functioning.

Empirical Evidence

With foundations in theory described, we next turn to the examination of the empirical evidence. In the following section, we review the neuroimaging studies of preschool or middle childhood periods (4–12 years of age). We review neuroimaging studies that assessed behaviors or skills important during daily interactions with peers and then turn to studies that examined neural responses to either peer feedback or social exclusion specifically (two social stressful situations). We end with a description of correlational studies that have examined whether and how individual differences in temperament or peer experiences were associated with brain responses during experimental manipulations involving social situations with peers.

Peer Interaction

Social interactions with peers are highly complex and dynamic. During peer interactions, children need to observe and interpret actions, understand the intentions of their peers, and decide how to respond to their peers. A few neuroimaging studies have looked at how these processes are represented in the brains of children.

Cooperation is a fundamental skill for children that they use during their daily interactions with peers. For example, building a block tower together with a peer requires a child to coordinate behavior with the actions of the other. The child needs to closely observe and cognitively process the actions of others and align those actions with one's own behavior to achieve a common goal. The neural mirroring system may play an important role in processing actions of others and in motivating cooperation (Sartori et al., 2013). In one study, the involvement of the neural mirroring system in cooperation during early childhood was assessed using EEG (Endedijk et al., 2017). First, at age 3 years, cooperation was assessed by observing children while playing a cooperative game together with a same-sex peer. One year later, neural mirroring was assessed using EEG recordings during the observation of videos in which adults were performing different actions such as driving a toy car around. Children that were more cooperative at age 3 showed higher levels of motor system involvement at age 4 during the observation of actions by others, as was indicated by lower power in the beta-frequency band. Lower power in the beta-frequency reflects increased involvement of the motor cortex as well as error monitoring and action updating. These results may thus suggest that for cooperative actions, high levels of neural mirroring and action updating are needed—capacities already in place by 4 years of age.

Another important aspect for successful peer interactions is understanding the emotions, motivations, and behaviors of others—a process referred to as mentalizing. A few recent studies have tried to understand how the brain's mentalizing network responds during dynamic and realistic peer interactions (Alkire et al., 2018; Warnell et al., 2018). Investigators in one study (Warnell et al., 2018) developed an interactive social motivation task in which children aged 8–12 years were presented with sentences about themselves such as "I play soccer" or "I like French fries" during an fMRI session. Participants were asked to indicate whether these sentences were true or not and then had to wait for a reply. Replies could be either from a peer (peer trial) or from the computer (computer trial). Children were told that this peer was an age- and gender-matched peer, but the replies were simulated. To capture the interactive nature of peer interactions, another manipulation was added such that replies from peers could either be engaged ("Me too" or "I didn't pick that") or nonengaged because they were performing another task ("I'm busy"). Computer replies could also be engaged ("Match" or "Mismatch") or nonengaged ("Disconnected"). Both initiating an interaction and receiving a reply from peers (compared to a computer interaction) resulted in increased activation in the ventral striatum, a region implicated in reward processing. This suggests that interacting with peers is considered rewarding for children. Interestingly, activation in the ventral striatum was not stronger for older children compared to younger children; peer interactions may be equally rewarding across middle childhood. In contrast, receiving an engaged reply from a peer was related to increased activation in the dorsomedial prefrontal cortex—and this response was stronger for older than younger children. The dorsomedial prefrontal cortex is part of the affective node and has been implicated in processing information about self and others (Pfeifer et al., 2007). Other mentalizing areas (i.e., temporoparietal junction, superior temporal sulcus) also showed increased activation when interacting with a peer, relative to a computer—and again, the response was stronger among older children. Thus, socially relevant information about peers is processed by the socio-cognitive and reward network, with some of aspects of the neural activity and socio-cognitive skills continuing to develop across middle childhood.

A different interactive mentalizing fMRI task was used in another study of 8–12-year-olds (Alkire et al., 2018). Children received a hint about a chat partner or a fictional computer character and had to predict what this peer or character would pick as a choice (mental condition) or guess which option would match a certain situation (nonmental condition). For example, "Sue likes to read" would require an answer indicating that she will pick a long novel (mental), while a hint saying "Sue has big feet" would require an answer related to needing bigger shoes (nonmental). After this guess, participants received feedback whether their responses corresponded with those of the peer or character. Results showed that guessing the response of a peer resulted in higher activation in the mentalizing network, compared to guessing the responses to a fictional character. Similar to the study by Warnell et al. (2018), the dorsomedial prefrontal cortex and temporoparietal junction were more engaged in the social interactions with peers and not during mentalizing about a computer character. Moreover, social interactions with peers were considered more rewarding as shown by increased activation in the reward network (e.g., striatum, medial orbitofrontal cortex) compared to guessing reactions to a fictional computer character.

Regarding development, Warnell et al. (2018) found increased activation in the socio-cognitive network with age, but Alkire et al. (2018) found *decreased* activation for older children during mentalizing about peers relative to fictional characters. However, this difference in age effects between studies may be driven by differences in the nonsocial condition. Whereas the nonsocial condition in Warnell et al. (2018) was a computer, the nonsocial condition in Alkire et al. (2018) was a fictional character. The lower activation for older children in the study by Alkire et al. (2018) may be driven by developmental improvements in mentalizing activity for the fictional character compared to the peer, whereas mentalizing about a computer may not improve with age. Despite these distinct age effects, both studies showed that social interactions with peers are considered rewarding during childhood and are processed in socio-cognitive regions important for mentalizing.

The rewarding nature of social interactions with peers may influence how children behave. Prior studies in adolescents showed that the mere presence of a peer results in increased risky behavior and enhanced activation in the reward network (striatum) of the brain (Albert et al., 2013; Chein et al., 2011). Yet, this phenomenon has received relatively little attention during childhood. One study of 10–14 year olds ($M = 12$ yrs.; Hoffmann et al., 2017) demonstrated that peer presence may also influence how the brain reacts to risk-taking situations. Children completed a computerized risk-taking task (Balloon Analogue Risk Task; Lejuez et al., 2002) in the fMRI scanner while being observed by a peer. Youth took fewer risks and showed increased activation in the amygdala and medial temporal lobe during peer observation compared to completing the task alone. The amygdala has been implicated in processing affective salient information and loss aversion (Janak & Tye, 2015). Thus, when children are observed by peers, risks may become more salient and aversive which may reduce risk-taking behavior.

A different condition in Hoffmann et al. (2017) involved peers encouraging the child to take more risk in the next trial. Peer encouragement resulted in higher levels of risk and greater activation in the inferior frontal gyrus (IFG), compared to trials in which the participants was only being observed by peers. The increased IFG activation may relate to integrating the information from peers in deciding and executing a behavioral response (Dippel & Beste, 2015). Results from Hoffmann et al. are distinct from studies of adolescents. That is, while adolescents took more risks during the mere presence of peers (Chein et al., 2011; Gardner & Steinberg, 2005), children actually became more risk-aversive when being observed by peers and only took more risks when peers verbally motivated them to take more risks. Furthermore, while the mere presence of peers elicited activation in the brain's reward regions (i.e., ventral striatum) (Chein et al., 2011), this childhood sample showed increased activation in a region implicated in salience processing. Thus, the effects of peers appear to be different across childhood and adolescence both on a behavioral and neural level, thereby underscoring the importance of studying peer processes across different developmental periods.

In sum, neural evidence for children's motivation to interact with peers is shown by increased activation in brain reward regions during peer interactions. In addition, the brain imaging evidence shows neural activation patterns that correspond with children actively monitoring the actions of others, trying to infer mental states of their peers, and adapting their behavior based on input from their peers. The literature long ago established the salience of peer interactions based on behavioral evidence; the more recent neuroimaging findings deepen that evidence by including neural indicators.

Peer Feedback

One of the most salient and important peer experiences—in middle childhood as well as adolescence and adulthood—is being socially evaluated by peers and receiving feedback on attributes, behaviors, or beliefs (Somerville, 2013; Westenberg et al., 2004). This feedback can be rewarding or aversive. Receiving negative feedback from peers is one of the most frequent peer stressors in childhood and adolescence. Examples include a peer saying that he or she does not like the child's clothes or a teenager receiving no "likes" on their social media post. These events can be highly salient for children and adolescents, as part of the social information being gathered to determine their social inclusion within a peer group.

Neural processing to peer feedback has been examined in adolescence (Gunther Moor et al., 2010; Guyer et al., 2011; Guyer et al., 2009; Somerville, 2013) and young adulthood (Davey et al., 2010; Somerville et al., 2006), but investigation of these processes in middle childhood has only begun recently. Typically, neural responses to peer feedback are elicited using a social feedback task. Days or weeks prior to the fMRI session, participants are asked to fill out a form with personal information about their favorite movie or sport, and other likes and dislikes. The participants are then led to believe that their profiles will be reviewed by other peers. During the fMRI session a few days or weeks later, participants are shown pictures of age-matched peers and are also presented with feedback about how that peer felt about the participant's profile. This peer feedback can be positive, negative, or neutral. Among adolescents, negative feedback is associated with increased activation in the salience network including the amygdala, anterior insula, and medial prefrontal cortex (Somerville, 2013). Positive feedback is rewarding, indicated by increased activation in the striatum.

Social feedback tasks are now being used in brain imaging research in middle childhood. In one study, 7–10-year-olds completed a social network aggression task (Achterberg et al., 2018; Achterberg et al., 2017). Children filled out profiles at home prior to the fMRI session. During the fMRI session, children received positive, negative, or neutral feedback from peers. However, in contrast to the social evaluation task described previously, this task allowed children to respond to the peer feedback with a loud noise blast that would be presented to the peer. The length of the noise blast was used as an indication of the level of aggression toward that peer.

Results of this study (Achterberg et al., 2018; Achterberg et al., 2017) showed that noise blasts were longer after negative feedback, followed by neutral feedback, and the shortest noise blasts were given after positive feedback. With regard to neural activity, peer feedback—regardless of valence—resulted in activation in the anterior cingulate cortex. In contrast, only negative feedback was associated with increased activation in the medial prefrontal cortex, and only positive feedback was associated with increased activation in the caudate. One interpretation is that the anterior cingulate cortex is involved in processing all socially salient information, the medial prefrontal cortex is more specific in its processing of socially threatening information, and the caudate region is more specific in its processing of socially rewarding information. Interestingly, the neural patterns in the studies in middle childhood are similar to those reported in adolescence (Davey et al., 2010; Gunther Moor et al., 2010; Guyer et al., 2011; Guyer et al., 2009). Thus, the neural components of processing salient social information from peers already are in place by middle childhood.

But is it possible that those processes are evident even earlier in development? One study examined this question in a sample of 4–6-year-olds, using an adapted, age-appropriate version of the social aggression network task (van Wijk et al., 2019). Two weeks before the EEG lab visit, children were asked to pick one out of five cuddly animal toys as their favorite and received this toy at home to become highly familiar with it. During the lab visit, EEG was recorded while children received feedback from hypothetical peers on their cuddly animal (e.g., "Your cuddly animal is stupid"). Instead of delivering a noise blast to the peer, children were told that the peer had ten balloons and the target child could destroy balloons by pressing a button. Longer button presses resulted in more destroyed balloons and were used as a measure of individual differences in aggression. Neural processing of feedback was assessed by examining EEG alpha power frontal lobe asymmetry, an indicator of approach and avoidance motivation and behavior (Kelley et al., 2017). Negative feedback resulted in longer button pressing compared to neutral and positive feedback, suggesting that these young children were aware of and affected by negative peer evaluation. However, there were no associations (direct or indirect, i.e., mediating) between asymmetry and feedback condition or button pressing. Thus, evidence of behavioral responses to peer negative evaluation were evident among 4–6-year olds, but the null finding using EEG leaves open questions about whether and how neural processing is involved at this young age.

In sum, studies of adults and adolescents have established neural response patterns to negative and positive peer evaluative feedback. Although results from studies of children are preliminary, similar patterns are evident in middle childhood. It remains to be seen whether those patterns are established even earlier in development (e.g., during the toddler or preschooler years).

Peer Exclusion

Another peer stressor that some children may experience during their interactions with peers in school is exclusion from social activities. Examples include the following: when a child does not receive an invitation to a party of a classmate, but all the others are invited, and when a group of children is playing a game at the schoolyard and one child is not asked to join and is even ignored when asking to be part of the game. These experiences can be very stressful and emotionally painful for children and may be evident in changes at the neural level as well. However, there is sparse research in childhood on neural processing of peer social exclusion—most of the available research has included adolescent and adult participants.

One common paradigm employed by peer exclusion studies that measure neural responses to social exclusion is the Cyberball, an "online" ball-tossing game (Williams & Jarvis, 2006). Participants are led to believe that they are playing this ballgame with two other players. In reality, the game is preprogrammed by the experimenter. During the Cyberball game, participants first participate in a fair play round in which all players receive the ball as often as the others. However, as the play proceeds, the participant becomes excluded from the game by the two other players and no longer receives the ball. Neuroimaging studies in adolescence and adulthood have shown that being excluded from this ballgame is experienced as distressing, as shown by temporary decreases in mood and need satisfaction levels and increased activation in the medial prefrontal cortex, insula, anterior cingulate cortex, precuneus, and lateral prefrontal cortex (Cacioppo et al., 2013; Vijayakumar et al., 2017; Wang et al., 2017). Whereas the activity in the insula, medial prefrontal cortex, and anterior cingulate have been related to the negative affect induced by social exclusion, the activity in the lateral prefrontal cortex has been implicated in regulation of this negative affect (Eisenberger et al., 2003; Masten et al., 2009). Interestingly, studies have adapted parts of this game by using shorter durations and alternating social inclusion and exclusion rounds, and yet, the neural processes observed during social exclusion have been very similar across the game variants (Vijayakumar et al., 2017). Thus, neural processing of social exclusion in Cyberball appears to be very robust.

The Cyberball task has also been used in a few EEG studies to examine neural sensitivity to social exclusion in preadolescent children (Crowley et al., 2010; van Noordt et al., 2015). Results showed that early and later stages of social exclusion elicited increased neural activity among children aged 8–12 years old. During early periods (264–656 ms), an enhanced positive ERP component, resembling the P300 component, was found at the posterior site (Crowley et al., 2010) and higher theta oscillations in medial frontal sites (van Noordt et al., 2015). These findings were interpreted to reflect signaling conflict and salience of the exclusion experience. During later periods of social exclusion, Crowley et al. and van Noordt et al. also both reported larger ERP negativity and increased theta oscillations in medial frontal regions. Also, in both studies, the later ERP components were associated with the amount of distress children reported. Together, these findings show that by age

8–12 years, children show increased neural sensitivity during social exclusion that reflects detection of exclusion and neural modulation of emotional responses.

Differences in neural processing of social exclusion by strangers versus friends have also been studied. In an EEG study by Baddam et al. (2016), children aged 8–12 years and their best friends were invited for participation. Both the child and best friend played the Cyberball task in a separate room. Participants were told that they would play the Cyberball task together with their best friend and a stranger, but in reality the task was preprogrammed by the experimenter. Children first played a social inclusion round in which the ball was tossed fairly toward all players (child, best friend, and stranger). In the second round, the child was for the most part excluded by the stranger and best friend. Tosses from the friend toward the stranger during the exclusion block were considered as an exclusion trial by a friend, and tosses from the stranger to the friend were considered an exclusion trial by a stranger. Results showed that exclusion by a stranger was associated with larger P2 responses and higher slow wave activity in medial frontal sites compared to exclusion by a friend. The larger P2 responses may indicate higher attentional allocation to rejection by strangers compared to friends. Increased slow wave activity may indicate processing of aversive stimuli, arising from the aversive nature of exclusion by strangers compared to friends.

One potential explanation for the increased sensitivity to social exclusion from strangers may relate to the social competition between peers and the instability of friendships during middle childhood (Hartup, 1996; Schneider et al., 2005). In this Cyberball task, strangers threw the ball toward participant's best friends and excluded the participant. As such, strangers may intrude in the friendship, which is a highly salient experience that may lead to distressed feelings and increased neural sensitivity to exclusion among the participants.

Social exclusion experiences also include passively observing other individuals being excluded, which also may be very distressing for children (Saylor et al., 2013). A child can decide to compensate for the exclusion by including the excluded child. Compensation for peer exclusion may be socially challenging and may influence the participant's own inclusionary status. To examine this prosocial compensation behavior, the Prosocial Cyberball Game (PCG) was developed and tested (Riem et al., 2013). In the PCG, the participant is playing an online ball-tossing game with three other virtual players. During the first round, all players receive the ball an equal amount of time (i.e., fair play). During the second round, during the unfair round, one player is excluded by the two other players—but in contrast to the original Cyberball, the participant still receives the ball from the other players. The participant can decide whether to include the excluded player by tossing the ball toward the excluded one (the so-called prosocial compensation). Prosocial compensating behavior is assessed by comparing trials in which the participant tosses the ball toward the excluded player, with trials in which the participant is tossing the ball toward the excluders. Higher percentages of tosses toward the excluded player during the unfair round compared to the fair round are considered compensating behavior. Two recent studies examined the behavioral and neural responses of this compensating behavior among 7–11-year-olds (van der Meulen et al., 2017; van der

Meulen et al., 2018). Results of both studies showed that children compensate for the social exclusion by tossing the ball toward the excluded player during the exclusion round more often than during the fair round. The neural correlates were less clear, however. In the 2017 study, no neural correlates were found, but in the subsequent 2018 study, compensating behavior was associated with increased activation in the posterior cingulate cortex/precuneus and with lower insula activity. Activation changes in these brain regions suggest that children who show stronger compensating behavior are striving to infer the mental states of others and are modulating affective responses while observing the peer exclusion.

When observing a peer being excluded, a child may also worry or be concerned about becoming excluded themselves. This concern about becoming excluded also was examined in van der Meulen et al. (2017), and (2018), by comparing trials in which the other players excluded the participant with trials in which the participant *did* receive the ball from the other players (referred to as *self-exclusion*). Self-exclusion resulted in increased activation in the inferior frontal gyrus, insula, hippocampus, caudate, amygdala, and occipital gyrus. These neural correlates overlap partly with previously described neural correlates of social exclusion in adolescents and adults and are linked to affective responses (Cacioppo et al., 2013; Vijayakumar et al., 2017; Wang et al., 2017). Also, being included by the excluders relative to self-exclusion resulted in increased activation in the supplementary motor area, precentral gyrus, middle frontal gyrus, anterior cingulate cortex, supramarginal gyrus, middle cingulate gyrus, and caudate. Again, results only partly overlap with findings in adult studies such as the anterior cingulate cortex and caudate (Dalgleish et al., 2017; Perini et al., 2018). These regions are implicated in attentional processing, appraisal of events, and reward processing thereby indicating the importance of being included in childhood (Delgado, 2007; Shenhav et al., 2013). Heritability analysis showed that the neural responses to self-exclusion and prosocial compensating behavior were related to nonshared environment and measurement error. This was surprising, given that prosocial behavior has been shown to be heritable in childhood (Gregory et al., 2009; Knafo & Plomin, 2006). However, prosocial behavior in prior behavior genetic studies has usually been measured with questionnaires; in contrast, the prosocial compensating behavior being examined in the studies by van der Meulen et al. (2017, 2018) may reflect state-like responses to social exclusion. In other words, variation between youth in prosocial compensating behavior may be less genetically influenced than overall prosocial tendencies. In addition, the blood-oxygen-level-dependent (BOLD) response underlying the fMRI signal is quantitatively “noisy”. Heritability studies using BOLD have not yet been able to separate out specific measured environmental influences from measurement error. More research is necessary to interpret the nonshared environment finding.

Together, results from the studies described in the current section demonstrate that children between 7 and 12 years of age show neural sensitivity to social exclusion. These neural correlates overlap to some degree with the neural correlates found in adolescent studies (e.g., inferior frontal gyrus, insula). Furthermore, social exclusion by strangers seems to be more distressing and salient (in terms of neural sensitivity and processing) than social exclusion by friends. In addition, some children who observed someone else being excluded compensated for the exclusion by behaving prosocially toward the target; this variation was associated with increased activation in social-affective and mentalizing brain regions. Although the neural correlates of compensating behavior in childhood were inconsistent across studies, this new line of research lays a foundation for future imaging studies that will allow us to deepen our understanding of how social exclusion experiences are processed and responded to, by children.

Individual Differences in Temperament or Prior Peer Experiences

The studies described so far have shown that children are sensitive to peer stressors, and these peer stressors elicit brain activation in affective and cognitive control regions. However, those studies have not considered individual differences in children's and adolescents' temperament and peer experiences prior to the studies' assessments, yet these may matter a great deal. Not all children are sensitive to peer social experiences to the same extent. According to the differential-susceptibility hypothesis (Belsky & Pluess, 2009) and the diathesis-stress model (Boyce & Ellis, 2005), some children show higher sensitivity to stressors (such as negative peer experiences), whereas other children may be relatively unaffected by the presence of (chronic) stressors. The differential-susceptibility hypothesis further states that children who are more sensitive to negative social contexts may flourish in very supportive and positive contexts (Belsky & Pluess, 2009). Thus, there are likely to be subgroups of children who benefit in particular from both the absence of stressors (e.g., peer rejection) and the presence of positive enriching factors (e.g., having strong friendships). It is important to consider these individual differences in sensitivity to peer environmental factors to understand possible resilience factors that can be targeted for interventions or preventions. Therefore, we next consider recent fMRI studies that have examined how individual differences in prior temperament or peer experiences during childhood are associated with sensitivity to peer interactions.

In one neuroimaging study of 11-year-olds (Jarcho et al. (2016), children who were either high or low in social reticence (i.e., silent, withdrawn) participated in a fMRI session while performing a peer feedback task called the virtual school paradigm (Jarcho et al., 2013). The virtual school paradigm was developed as a feedback task that would be similar to situations in classrooms and capture the dynamic nature of social feedback processing involving anticipating and receiving peer feedback from others who have reputations as being nice, mean, or unpredictable. Anticipating feedback from peers with a mean or unpredictable social reputation may be even more distressing than anticipating peer feedback from anonymous peers whose reputations are unknown (as is the case in the Cyberball studies described earlier). The virtual school paradigm consists of two sessions. Days prior to the experiment, participants are told that they will participate in a game in which they are placed in a virtual school environment. To increase the salience of this experience, children are asked to create their own avatar and also fill out a personal profile with their interests. During the second visit, prior to the fMRI assessment, children are introduced to several virtual classmates and receive information on their social status—two who are nice, two who are mean, and two who are unpredictable in their behavior. Children complete the virtual school paradigm inside the scanner. Every trial starts with the image of a virtual classroom with the different peers (nice, mean, or unpredictable). One peer starts typing a feedback response and participants see the text ("Is typing…") in a text balloon close to this virtual peer (the "anticipation" phase). Children then see the feedback of the peer which is either from a set of pre-generated responses (e.g., "you're lame") or containing information specific to the child's previously completed personal profile. Following feedback, children can respond to the feedback from predetermined responses that are either nice, mean, or avoidant (no response).

Results showed that children who were high in social reticence showed increased activation in the dorsal anterior cingulate cortex and mid-to-anterior insula during the anticipation of feedback from an unpredictable peer (Jarcho et al., 2016). Given the role of these regions in salience and affective processing, these findings suggest that children high in social reticence find anticipating unpredictable feedback more salient and distressing than children lower in social reticence. Moreover, a weaker functional coupling was found between the insula and regions involved in inhibitory control (ventromedial prefrontal cortex, premotor cortex) for children high in social reticence. During negative feedback from unpredictable peers compared to mean peers, amygdala activation decreased for reticent children but increased for non-reticent children. The amygdala may serve a role in valence signaling, which may interact with the level of predictability of peer feedback (McHugh et al., 2014). Furthermore, non-reticent children may process unpredictable negative feedback as more salient as it was not expected, while children high in social reticence may exhibit abnormal processing during these situations.

The virtual school paradigm was also used in another study examining how childhood wariness (i.e., fearful or passive behavior in social situations) and victimization in school relate to neural activation during peer feedback, in a sample of 11-year-olds (Jarcho et al., 2019). No behavioral differences in responses to feedback were observed for children that were victimized or scored high on wariness. However, highly victimized children that scored high on childhood wariness showed greater activation in the amygdala, striatum, and left insula during positive feedback from unpredictable peers. In addition, the degree of amygdala activation in highly victimized, highly wary children was positively associated with self-reported levels of social anxiety. These effects were found for *positive* feedback, and the study by Jarcho et al. (2016) showed *dampened* amygdala activation for unpredictable *negative* feedback among reticent children. The amygdala may play a role in valence signaling, novelty processing, and reinforcement learning in unpredictable social situations (Janak & Tye, 2015). Children high on social reticence may frequently experience negative feedback from unpredictable peers, and positive feedback from others may be less common for youth high on victimization and wariness. Findings from these studies show the importance of considering both personal risk factors (i.e., wariness) and social contextual risk factors (i.e., victimization) to understand differential sensitivity to peer interactions and potential links with maladjustment (i.e., social anxiety).

Besides showing correlations with differential brain activation during peer feedback situations, behavioral inhibition and social reticence may also relate to the child's behavior during socially stressful situations. In a study by Lahat et al. (2014), 7-year-olds performed a cognitive control task (i.e., Flanker) while EEG was recorded to assess cognitive conflict using the N2 component. Following the EEG recordings, participants played a real-life ball-tossing game with an unfamiliar experimenter during which the child was excluded after a few minutes. Children's behavior in response to the social exclusion was observed and coded. Children that were behaviorally inhibited and had higher N2 amplitudes during the cognitive control task showed higher socially withdrawn behavior and lower assertiveness in response to a social exclusion experience. Behaviorally inhibited children with lower N2 components did *not* show this withdrawal behavior. In general, higher levels of executive function have been linked to better peer relationships from early childhood through adolescence (Holmes et al., 2016). However, results from Lahat et al. show again that personal risk factors (e.g., behavioral inhibition, social reticence) may influence social behavior in response to peer feedback. Children who are highly inhibited may not be able to adaptively and flexibly respond to socially stressful situations when they also show high levels of cognitive control over their behavior. This may contribute to maintaining socially withdrawn behavior that influences subsequent social-emotional development.

Prior experiences with peers may also sensitize children to expect new rejection events—sometimes called *rejection sensitivity* (London et al., 2007). Behavioral evidence has shown that children high in rejection sensitivity demonstrate an increased vigilance for hostile rejection cues and respond more aggressively to new rejection experiences (Dodge et al., 2003; Lansford et al., 2010). Adolescents with a history of peer rejection or victimization also show this sensitivity, including distinct neural changes that reflect greater rejection sensitivity to new rejection events (Rudolph et al., 2016; Will et al., 2016). Specifically, youth with a history of peer rejection or victimization show increased activation in the dorsal anterior cingulate cortex during new rejection events, compared to those without such history. However, as mentioned in the previous section, neural correlates of social exclusion experiences only partly overlap when comparing childhood and adolescent samples (Cacioppo et al., 2013; van der Meulen et al., 2017, 2018; Vijayakumar et al., 2017; Wang et al., 2017)—thus, the neural patterns associated with exclusion experiences for those with histories of peer problems may be distinct for children and teenagers.

There have been only two studies we know of that have examined whether and how long-term prior experiences of peer rejection associate with neural rejection sensitivity in childhood. In an interpersonal feedback brain imaging study with 11-year-olds who had, or had not, experienced chronic peer rejection (Lee et al., 2014), children were asked to provide answers to unsolvable puzzles inside the MRI scanner. They then received interpersonal feedback in the form of photos of facial expressions of others (i.e., positive, negative, neutral). Peer-rejected children showed increased activation in the "social pain" network (Eisenberger, 2012) including the orbitofrontal cortex, ventrolateral prefrontal cortex, hippocampus, and amygdala during negative feedback. During positive and neutral facial feedback, increased activation in the inferior occipital gyrus was found for these rejected children. Thus, peer rejection in school was associated with heightened sensitivity to negative feedback after trying to solve an unsolvable puzzle; this was *not* the case for 11-year-olds without a peer rejection history. As found in other studies described earlier, increased amygdala activation was found during negative peer feedback, showing the importance of this region in processing stressful peer experiences during childhood. It is possible that children who experience peer rejection in school may be more socially vigilant and anxious, which may underlie the observed increase in amygdala activation. Again, results from this study align with other studies on social reticence, behavioral inhibition, and victimization showing how prior experiences with peers pertain to individual differences in neural sensitivity to peer interactions during childhood.

In another study, Asscheman et al. (2019) examined how prior experiences of peer rejection were associated with neural sensitivity to a new peer stressor, among 8–12-year-old boys. Children's history of peer rejection was determined based on peer nomination measures assessed in elementary school 3 years before the fMRI study. Boys with stable levels of low or high peer rejection and peer acceptance over these 3 years participated in a fMRI study in which participants were excluded during the Cyberball. Peer-rejected boys showed increased activation in bilateral dorsolateral prefrontal cortex as well as supramarginal gyrus compared to peer-accepted boys. These results thus show that chronic peer rejection during middle childhood is associated with increased activity in regions associated with emotion regulation, attentional control, and social cognition. Like Lee et al. (2014), there was no associated change in dorsal anterior cingulate cortex activation—a brain region that has been linked with peer exclusion experiences in prior imaging studies of rejected or victimized adolescents (Rudolph et al., 2016; Will et al., 2016).

In sum, the relevant childhood brain imaging literature shows that child characteristics as well as prior real-life peer rejection experiences are associated with differential sensitivity to stressful peer feedback and exclusion behavior. Although these studies are cross-sectional, if future research demonstrates stronger causal evidence, it would mean that prior peer experiences and behavioral risk factors may shape how the brain responds to new peer experiences and influence the pathway between peer stressors and psychopathology (e.g., social anxiety). Although some similarities in neural correlates were found with the imaging studies of adolescents, some neural correlates were not found in childhood samples (i.e., dorsal anterior cingulate cortex). Thus, peer stressors may be processed differently in childhood, compared to during and after puberty. More research is necessary in middle childhood and especially in early childhood when peer relationships and social skills are first emerging—a developmental period when prevention and intervention may be most effective (Fox et al., 2010; Shonkoff & Levitt, 2010; Wachs et al., 2014).

Future Directions

The studies presented in the current chapter demonstrate that progress is being made in our understanding of peer influences on brain function and development during childhood. However, many outstanding questions remain. In closing, we provide some directions for future research to advance the field.

First, longitudinal studies are needed, but there are challenges to be overcome for that work to proceed. Environmental influences such as peer relationship histories may alter how the brain responds to new social information, but the empirical studies to date are cross-sectional; as a result, we were not able to interpret likely neural changes over time and development. It remains to be seen how individual differences in brain responses to social information emerge and change with development and how these individual differences may explain longer-term developmental outcomes such as behavioral and emotional problems in later childhood, adolescence, and early adulthood. Longitudinal fMRI studies will give invaluable insight into the variability of the BOLD signal on different time points across development. This could address questions related to trait- and state-like brain activation patterns that might permit stronger inferences from the existing cross-sectional literature (i.e., ruling out cohort effects). Moreover, longitudinal studies allow mapping of the dynamic features of developmental trajectories (e.g., timing of nonlinear changes; rate of changes) of brain function. It may be individual differences in those dynamics (i.e., delays, velocity), rather than more general variance in functional and structural brain differences that are most predictive of outcomes (Shaw et al., 2010). For example, children with ADHD show delayed and slower cortical maturation across childhood, which may result in the cognitive control deficits found in these children (Shaw et al., 2007). Although longitudinal brain imaging studies with children are challenging, there remains a need for such studies to elucidate likely causal effects of peer experiences on brain development and developmental outcomes.

Another issue to address in future research concerns whether the tasks (and resulting scores) used in imaging studies meet the standard of invariant measurement required for comparing means and variances across multiple time points in development (Telzer et al., 2018). For example, brain activation in specific regions of the brain during a cognitive control task may show an average increase with age across development in childhood. However, this increase could indicate an improvement in cognitive functioning or simply reflect an improvement in neural signal-to-noise ratio in BOLD signal at later ages when behavioral performance is better (i.e., less noise and therefore improved signal estimation). One potential solution is to adapt tasks over development, so that the overall level of difficulty (i.e., error rates) for each age point remains constant over time. An even more fundamental measurement issue in longitudinal brain imaging studies is the lack of evidence for strong test-retest reliability of BOLD scores from fMRI (Herting et al., 2018). The solution likely will require establishing estimates of short-term test-retest reliability over the course of weeks and then adjusting longitudinal stability estimates for reliability of measurement. This statistical approach has been shown to be useful in other fields

(Heise, 1969). Applying this approach to fMRI will be time-consuming and expensive, yet the field would benefit from more extensive collaborations to assess neural measures with large samples of children across shorter intervals. Finally, there are measurement issues for social behavioral tasks such as Cyberball. Debriefing is essential because of the deception that is involved, making repeated assessments intrinsically different from the initial deception assessment. Future research will need to address this and other measurement challenges when conducting longitudinal studies.

Second, our knowledge on peer socialization and brain development requires studying not only brain function but underlying anatomical structure and connectivity (Wang & Olson, 2018). Changes in brain function may already occur after a single experience. Repeated and enduring co-activation of neurons results in structural connectivity changes (“neurons that fire together, wire together”; Hebb, 1949). Therefore, changes in gray and white matter structures and connectivity during development will reveal more useful information about the long-lasting changes arising from prior experiences. A recent cross-sectional study showed that victimized adolescent boys exhibited lower ventrolateral prefrontal cortex volumes (du Plessis et al., 2019). In addition, social interactions are highly complex and dynamic and require fast real-time processing and integration of information that depends heavily on white matter structures (Kennedy & Adolphs, 2012). Studying white matter connectivity may reveal some of the underlying deficits in social competence that may help explain peer difficulties. For example, social anxiety symptoms may be better explained by individual differences in white matter structures compared to gray matter structures (Whitfield-Gabrieli et al., 2015). Furthermore, it has been theorized that stress during early life accelerates structural brain changes in emotion networks (i.e., stress acceleration hypothesis; Callaghan & Tottenham, 2016). Faster structural brain changes may be detrimental for children and adolescents, as this acceleration may affect how much time these children have to learn and refine behavioral skills necessary for the psychosocial challenges found during adolescence (Ge & Natsuaki, 2009). Rapid brain maturation may thus increase children’s vulnerability for psychopathology. Thus, future studies should assess structural brain maturation in relation to peer environmental factors and adjustment outcomes.

Third, future research will benefit from inclusion of positive peer experiences as potential “buffers” of peer stressors in development. For example, one brain imaging study of adolescents (Telzer et al. (2015) showed that adolescents who experience high levels of peer conflict during their daily lives also showed higher levels of risk-taking behavior and increased brain activity in regions associated with affective processing (e.g., insula, ventral striatum). However, having supportive peer relationships had a buffering effect. Similarly, in a study of adults, neural responses to a social exclusion experience were dampened when participants were reminded of their attachment figure (Karremans et al., 2011).

Fourth, social relationships in childhood go well beyond peer relations at school. Social interactions with peers are not static and do not occur in a vacuum; children’s social lives are dynamic and intersect with social lives involving siblings and adults. Children continue to have attachment relationships with parents beyond early childhood, and nonparental adults (e.g., teachers) play an important role in children's social and emotional development. In addition, children spend time with their peers and siblings outside of school settings, in their homes, neighborhoods, and other settings. According to the stress-buffering hypothesis, social support from multiple relationships with other children and with adults may mitigate the impact that stressors have on health and functioning (Cohen et al., 2000). Future research would benefit from considering how these other social relationships interact with negative and positive peer relationships in school.

Fifth, future studies should take advantage of progress in the use of functional near infrared spectroscopy (fNIRS) (Wilcox & Biondi, 2015). This imaging technique has several advantages over other neuroimaging techniques such as EEG and fMRI (Ferreri et al., 2014). Movement artifacts can better be dealt with in fNIRS than with fMRI which is a great advantage when measuring brain activity in physically active and "fidgety" children (Lloyd-Fox et al., 2010). Relatedly, most EEG studies use event-related potentials (ERP) to understand the neural processing of peer stressors in young children. However, ERP signals require many trials with high-quality signals which may be very challenging to collect in these young children due to high motion. Another advantage of fNIRS is that, like ambulatory EEG hardware, fNIRS hardware can be used in ecologically valid settings (e.g., schools) so the data that are collected can be more natural for children compared to the confined setting of MRI scanners. However, there are limitations with fNIRS. fNIRS has better spatial resolution but poorer temporal resolution than EEG. Also, fNIRS has better temporal resolution than fMRI, but unlike fMRI, it can only measure about 1 cm into the surface of the cortex. Peer environmental experiences may be associated with emotional and reward systems deep in the brain, and fNIRS cannot measure those responses. With advantages and disadvantages compared to EEG and fMRI, fNIRS is highly suitable for use with infants, children, and adolescents in cross-sectional and longitudinal designs.

Sixth and finally, an interesting and novel approach is to investigate a potential role of the gut microbiota in the link between peer experiences and brain development. Gut microbiota may modulate brain function and development via the microbiota-gut-brain axis (Brett & de Weerth, 2019), and bidirectional links exist between intestinal microbiota composition and brain function (Collins et al., 2012). Dysbiosis in the gut microbiome has been linked to alterations in brain development (Rogers et al., 2016). Moreover, pre- and postnatal stress may alter the composition of the gut microbiome (O'Mahony et al., 2017; Zijlmans et al., 2015). It has yet to be investigated but peer stressors during development may also potentially influence the gut microbiome.

Implications and Conclusions

The research presented in the current chapter will one day inform prevention and intervention practices as well as public policy. Increasing our understanding of how various risk factors differently influence brain development and psychosocial adjustment in childhood (as opposed to adolescence or adulthood) may allow earlier identification of those individuals who are most sensitive to peer stressors and are at most risk to develop behavioral and emotional problems. Relatedly, knowledge about the buffering effects of positive features of other social relationships (e.g., parents, teachers, friends) on neural sensitivity to peer stressors could be used to prevent some of the negative outcomes for children as well as adolescents who are experiencing peer difficulties.

Moreover, new avenues of research arising from neurocognitive studies may provide new opportunities for affordable and simple interventions. For example, although the research is new and requires much more study, there is mounting evidence of bidirectional links between brain development and gut microbiota. This may be an effective target for interventions for promoting healthy brain development in the presence of peer stressors, such as changing the composition of the gut microbiota with probiotics (Brett & de Weerth, 2019; Wang et al., 2018). Lastly, longitudinal studies provide more conclusive evidence than cross-sectional studies of links between peer stressors and brain development. That growing literature suggests that prior peer experiences can become “embedded” in children’s (neuro)biology and may influence subsequent brain development as well as behavioral, cognitive, and emotional functioning. The transactional process between peer problems and brain development may lead to significant neural alterations that set the stage for psychopathology. Schools will do well to include social and emotional learning as part of their curricula (in addition to standard academic subjects) from kindergarten onward, to promote healthy development of the brain and body during childhood and beyond (Greenberg et al., 2017).

In conclusion, our goal in the current chapter was to outline the progress being made in the field of social developmental neuroscience by reviewing the literature on neural responses to peer experiences (i.e., interactions, feedback, exclusion) during the elementary school period (4–12 years old) as a comparison to the more extensive literature on adolescents. The theoretical framework is that peer experiences may lead to specific and long-lasting changes in neural structures and functioning across development—changes that may enhance risk for psychosocial and health problems later. The literature suggests that children show neural processing during peer interactions and in response to peer stressors in affective, socio-cognitive, and control networks—patterns that include some features that are similar to those found in adolescents and some features that are distinct in childhood. Furthermore, not all children respond in similar ways to peer stressors. Already by 7 years of age, prior real-life experiences with peers (e.g., peer rejection) as well as personal attributes that increment risk (e.g., social reticence) interact with neural processing of peer stressors. Much remains to be done, with a need for longitudinal multimodal functional and structural imaging research that situates children’s school-based peer experiences in a broader social context. Our hope is that this review and suggestions for future research in this rapidly developing field serve to strengthen the empirical literature and inform the development of even more effective prevention and intervention programs designed to alleviate the effects of stress in peer relations in childhood.

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