Humans are deeply social beings. Some argue this is the essential characteristic of our species and the primary reason for the large human brain. One of the most fascinating changes in human social development is the shift in focus from family to peers that starts in late childhood and extends through adolescence (Bukowski, Laursen, & Rubin, Chapter 1, this volume; Rubin, Bukowski, & Bowker, 2015). During this phase, social behavior transitions from peer-focused play to extensive integration into social groups with complex peer relations (Nelson, Jarcho, & Guyer, 2016). This shift is accompanied by the adolescent drive to spend more time with friends, weigh peer opinions more heavily, and focus on fitting in, yet standing out, in a new social milieu (Brown & Larson, 2009).

Decades of research show how powerfully peer-related factors can support or compromise adolescent well-being (Bukowski et al., Chapter 1, this volume; Rubin et al., 2015). With this knowledge and an understanding that development unfolds as an interaction between biology and environment, neuroscience-based methods have been used increasingly in developmental and clinical science research to examine how peers “get into” the mind and brain. This area of neuroscience expands existing developmental research by elucidating neural mechanisms engaged by specific features of peer relations, social contexts, and social behavior. In turn, this approach extends theories of adolescent social development by providing new conceptual frameworks for the interplay between peer relations and brain maturation. The insights gained from neuroscience-based research on peers can also inform the design of interventions aimed at limiting the negative impact of peer influence on deviant behavior and substance use, or of experiences of bullying and victimization. Additionally, work in this area holds the promise of translation to clinical applications, which can be designed to treat youth suffering from disorders linked with compromised social development, including social anxiety, depression, and autism.

The main goal of this chapter is to call attention to neuroscience research that has advanced the field toward a more integrative understanding of adolescent peer relations.
and interactions. We begin the chapter by describing three main issues facing research on peers and the brain. We then present theoretical considerations that have helped to guide this work, and follow with a description of the primary methods and measures used in peer-based neuroscience research. Next, we describe key research findings and their implications for our understanding of social development, and then conclude with recommendations about future directions for research on the adolescent brain and peer-based processes.

To achieve an appropriate degree of depth and breadth, we have constrained the focus of this chapter in several ways. First, instead of a comprehensive review of all neuroscientific methods used to study the brain and peers, we concentrate on methods and findings from functional magnetic resonance imaging (fMRI) research. Second, we focus largely on studies that measure brain indices in samples between the ages of 8 and 18, as this age range has been most commonly studied using fMRI and fits squarely within neurodevelopmental frameworks of peer-based processes. Finally, although research on peer relations spans a wide range of relationships, features, and contexts, our emphasis here is guided by the neuroscience-based literature, which has largely focused on how peers treat a target child (e.g., acceptance, rejection, exclusion, and victimization), the influence of a peer’s presence on behavior, and lasting effects of earlier socializing forces exerted by relationships with peers or parents.

**MAIN ISSUES**

The study of peers and the brain has burgeoned in the last decade. Within any burgeoning field, new work can raise new concerns or underscore long-standing issues that must be considered carefully in light of new findings. One issue is that social behavior is complex, full of nuances, and has many dynamic temporal and psychological characteristics. Given this complexity, neuroscience-based investigations of peers and the brain require researchers to strike a delicate balance between reliability and the internal and external validity of the measures under study. On one hand, it is critical to account for adolescents’ real-world experiences with their peers, as these interactions do not occur in a vacuum. On the other hand, because neuroscience research is typically lab-based and requires experimental controls, it has limited ability to precisely mirror peer-based interactions that occur at school, home, or in the community. For example, in fMRI research, participants lie in a scanner and complete tasks while measures of their brain activity are taken. Lying in a scanner is, of course, inherently dissimilar from daily life, with the need to stay very still in a cylindrical tube while the scanner makes loud noises. Quite critically, the tasks used in fMRI research must be designed very carefully in order to accurately sample neural activation according to its biologically based properties, create experimental conditions to probe response from specific brain regions to specific cues (e.g., pictures, words), and represent aspects of social cues and behavior that are relevant to actual peer experiences.

A second issue in the study of peers and the brain is the need to draw on multilevel models that link various aspects of peer experiences and contexts, measures of the brain, and developmental outcomes. For example, normative adolescent behavior varies based on the presence of different peers (e.g., a best friend, unfamiliar peer, rival, or love interest) and the context in which the interaction takes place (e.g., home, classroom, athletic field). The ability to successfully vary behavior based on these social and contextual factors may hinge
on the capacity to flexibly engage different neural circuits (Nelson & Guyer, 2011; Nelson, Lau, & Jarcho, 2014; Schriber & Guyer, 2016). The degree to which neural circuits are fully refined and integrated, and the capacity to engage these circuits, also vary along the adolescent trajectory. This variability, in turn, corresponds with changes in developmentally appropriate and socially adaptive behavior. Thus, it is necessary to integrate multilevel modeling across time, unit of analysis, and context to provide a comprehensive picture of how peer- and brain-based processes unfold across development, and as a function of dynamic systems and various settings.

Finally, a more fundamental question is whether studying the brain adds enough to our understanding of behavior to warrant its high investment of resources. We believe that delineating the neural mechanisms underlying behavior is a valuable endeavor for several reasons. First, brain-based response patterns may reveal unique information that cannot be measured with behavioral observation or questionnaires. For example, two groups of children may utilize distinct neural mechanisms (e.g., cognitive-regulatory circuitry; fear circuitry) to achieve the same behavioral outcome (e.g., social avoidance), and likewise, common neural circuits (e.g., reward circuitry) may contribute to different behavioral phenotypes (e.g., social anxiety, depression, need to achieve). These differences in brain function may provide insight into the pathophysiology of psychopathology or normative development. Second, we are able to measure the brain’s response to factors in the environment that do not have a behavioral corollary. For instance, fMRI has been used to isolate brain function as youth anticipate a forthcoming event. Lastly, measuring brain response has revealed specificity underlying emotional, cognitive, and motivational processes that may have otherwise been unexpected based on behavioral or self-report measures alone. For example, distinct neural circuits are engaged for social processes that elicit similar actions or experiences, such as mimicry (Gallese, Keysers, & Rizzolatti, 2004), thinking about others’ mental states (Saxe & Baron-Cohen, 2006), and joint attention (Happé & Frith, 2014).

Despite these advantages, researchers who use fMRI to probe psychological constructs must remain cautious in their interpretation of their findings. It may be ill advised to make unequivocal inferences about the psychological experience a specific pattern of brain activity supports, as brain function in any one region likely supports a large number of psychological processes. However, new analytic techniques that utilize machine learning methods, and other tools that pool neuroimaging data to generate comprehensive information-processing databases (e.g., Neurosynth), are beginning to provide corroborating evidence to link brain function with psychological experience (Pauli, O’Reilly, Yarkoni, & Wager, 2016).

THEORETICAL CONSIDERATIONS

As a species, our survival is facilitated by behavior that promotes integration and cohesion with others. Because of the dynamic and complex nature of our social world, our brains have evolved with significant neuronal resources to process a wide range of social cues, signals, and intricacies (Dunbar, 2012; Shultz & Dunbar, 2007). Social development, which includes facets of cognition, affect, and behavior, matures slowly, as social demands shift across time and context. Several conceptual frameworks from developmental social neuroscience have begun to guide our understanding of these developmental shifts and to help generate hypotheses about the brain’s role in supporting social maturation, including peer
relations. A core feature of such frameworks is the implicit or explicit assumption that no one brain region or network alone supports social functioning. Instead, social functioning is the product of numerous neural networks that interact to detect, interpret, and engage behavioral responses to social stimuli (Kennedy & Adolphs, 2012; Stanley & Adolphs, 2013). Moreover, accumulating evidence indicates that peer relations and neural circuit interactions reciprocally influence one another.

Remarkably, it is only within the last 25 years that we have come to understand that the brain continues to develop into adulthood (Colby, Van Horn, & Sowell, 2011; Gogtay et al., 2004). Indeed, this understanding led to the inference that social-cognitive processes undergo corresponding changes to support mature social behavior. An influential early account of the neuronal bases of social development is the neurodevelopmental social reorientation model, which suggests that three brain circuits, or nodes, within a social information-processing network (SIPN) work together to support social behavior (Nelson, Leibenluft, McClure, & Pine, 2005). The detection node supports the perception and categorization of basic social properties of stimuli. This node encompasses the superior temporal sulcus, intraparietal sulcus, fusiform face area, as well as the inferior temporal and occipital cortical regions. The affective node imbues stimuli, identified as social by the detection node, with valence and salience based on reward and punishment contingencies. This node encompasses the amygdala, ventral striatum (VS), hypothalamus, bed nucleus of the stria terminalis, and emotion-processing regions within the orbitofrontal cortex (OFC). Finally, the cognitive-regulatory node supports complex aspects of social cognition, such as perceiving others’ mental states, inhibiting prepotent responses, and generating goal-directed behavior. This node encompasses the medial and dorsal prefrontal cortex (PFC) and areas of the ventral PFC, including the OFC (Nelson et al., 2005), and the anterior cingulate cortex (ACC) in an updated model (Nelson et al., 2016).

Variability in the developmental time course for each node may contribute to differences in social behavior during corresponding phases of maturation. For instance, the detection node is well developed early in life and facilitates survival by connecting infants with their caregivers through detection of their facial features and expressions. Although many aspects of the affective node are fully functional in early childhood, the onset of puberty brings heightened engagement to already salient cues when those cues occur in the presence of peers (Chein, Albert, O’Brien, Uckert, & Steinberg, 2011). In contrast, the cognitive-regulatory node follows a more protracted developmental trajectory, taking longer to support more nuanced behavioral patterns, such as the ability to regulate anger elicited by peer-based transgressions or fear elicited by approaching a new social situation. With maturation, inter- and intranode connectivity is strengthened to support greater regulation of social behavior.

Several extensions of Nelson and colleagues’ (2005) initial neurodevelopmental social reorientation framework have been articulated. We built upon the original model by suggesting the prolonged maturation of ventral PFC may support the correspondingly slow emergence of flexible social behavior across adolescence and into adulthood (Nelson & Guyer, 2011). Nelson and colleagues (2014) elaborated on this idea by suggesting that flexible responding to social contexts is an adaptive feature of maturation achieved by neural systems that ascribe affective value to developmentally salient social cues. Attributing emotional value, in turn, promotes motivated learning that facilitates social success most critical to the current phase of development.
In a more recent elaboration, we discuss a range of developmental inflection points, defined by the primary forms and targets of social behavior (Nelson et al., 2016). For example, elicitation and receipt of caregiving behavior from a mother/caregiver is the primary social exchange in infancy. Peer-focused play then becomes increasingly prominent while the mother/caregiver provides a secure base in the juvenile phase. Social behavior then increases in complexity to facilitate integration within larger peer groups in adolescence. An elegant example of the impact of social focus across developmental inflection points is a recent study that demonstrated that the presence of one’s mother can blunt the cortisol stress response in preadolescent children, but has no effect in adolescents, who have shifted their motivated behavior toward peer integration (Hostinar, Johnson, & Gunnar, 2015). Although characterizing maturational phases as based on social motivation is not new, we suggest that the motivation to obtain and maintain certain types of social experiences is constrained by neural development, with neuroendocrine changes adding another layer of influence (Nelson et al., 2016). Collectively, these frameworks articulate how changes in underlying neural circuitry mediate social experiences within different phases of development and can affect peer relations concurrently and prospectively. In the next section, we discuss tests of these theoretical frameworks using neuroscience-based research methods.

**MEASURES AND METHODS**

The two most widely used methodologies in the study of peers and the brain are event-related potentials (ERP) and fMRI, the latter of which is the primary focus of this chapter. Whereas ERP tracks electrical activity on the surface of the brain, fMRI measures changes in blood oxygenation in both cortical and subcortical brain structures. Because they are noninvasive and do not require exposure to radioactivity, as is needed with positron emission tomography (PET), these methods are most commonly used in pediatric neuroscience research.

Three main approaches have been used to isolate brain responses to peers. The most common is to acquire ERP or fMRI data as youth observe and judge visual cues or play simple computer-based games that model discrete aspects of peer contexts. A second approach also draws on experimental manipulation, but varies the presence versus absence of peers *in vivo* to test their impact on brain and behavioral responses to cues or games. A third approach characterizes children based on early life patterns of social behavior or experiences to account for antecedents that may contribute to the brain’s response to social cues and behaviors.

Many of the paradigms implemented with ERP and fMRI require youth to judge features (e.g., “How much do you like this peer?”) or to make choices about cues (e.g., “Press 1 to select the peer on the left, 2 to select the peer on the right”) in the context of a game designed to model youths’ daily experiences. Behavior is often quantified with Likert scale ratings, measures of preferences, bias scores, percent of correct responses, prediction errors, and reaction times. These measures allow researchers to confirm that experimental manipulations induce the intended psychosocial state and ensure that participants followed task instructions. Quantifying participant-generated behaviors, cognitions, and emotions also helps to constrain interpretation of brain-based findings, thereby preventing singular reliance on reverse inference about results.
Despite being a relatively new field, developmental social neuroscience has made great strides toward modeling brain responses to peer-related cues, interactions, and in vivo experiences. In this section, we describe the most commonly implemented tasks paired with fMRI and associated results that link adolescents’ neural and behavioral responses to situations involving peers, as well as their relationship to emerging psychopathology or social competence. We have organized this section according to studies that (1) experimentally manipulate peer cues, (2) experimentally manipulate the physical presence of peers, and (3) account for socializing influences via parents and peers on the brain’s response to peers.

Experimental Manipulations of Peer Cues

Peer Evaluation

Peer evaluation is a common and salient experience for youth. Children and adolescents derive a sense of belonging, identity, and acceptance, or the lack thereof, from peers’ judgments of them. To capture this influential facet of daily social life for youth and adults, several similar tasks have been used to model unique dimensions of socially evaluative feedback experiences (Davey, Allen, Harrison, & Yucel, 2011; Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010; Guyer et al., 2008; Somerville, Heatherton, & Kelley, 2006).

CHATROOM TASK

To leverage the salience of peer evaluation to children and adolescents, Guyer, Nelson, and colleagues designed an ecologically valid paradigm optimized for neuroimaging called the chatroom task. The task design permits integrated measurement of response behaviors, biases in affect and cognition, and associated neural responses in the context of purported peer interaction. Informed by SIPN models (Crick & Dodge, 1994; Lemerise & Arsenio, 2000; Rapee & Heimberg, 1997), the paradigm also captures several phases of the social-evaluative process, including selecting peers for a social interaction (e.g., “Who do you like?”), anticipating feedback (e.g., “Who do you think will like you?”), receipt of feedback (e.g., “Who liked you?”), and memory for feedback (e.g., “Did this person like you?”). Iterations of the chatroom task have been developed that include modifications inspired by sociometric research (Guyer et al., 2014) and for use with neurofeedback training (Platt, Kadosh, & Lau, 2013), as well as for use outside of the scanner such as with eye-tracking methods (Silk et al., 2012) and for use with preschoolers with age-appropriate adaptations (Howarth, Guyer, & Perez-Edgar, 2013).

The chatroom paradigm is typically implemented over two sessions. In the first session, participants are told that they are participating in a national study of teenagers’ Internet-based communication in chatrooms, and at the end of study they will chat online with another teenager who expressed mutual interest in doing so. Participants are informed that “peers” will evaluate and rate them based on the personal profile they complete and a picture taken by the researcher, just as the participants do with their peers. An alleged computer glitch makes peer profiles unavailable, leaving participants to complete the selection phase by indicating their interest in interacting with peers based on their picture alone. Thus, participants provide an index of each peer’s value without the bias of additional peer-based...
information. In the second session (~ 2 weeks later), the anticipation and feedback phases are conducted while participants undergo fMRI scanning, but these phases can also be completed outside of the scanner for behavioral research. The anticipation phase measures neural response as participants view each peer’s picture and rate how much they think that each peer will want to interact with them. The feedback phase measures neural response as participants view each picture again and learn whether each peer was or was not interested in interacting with them.

An initial fMRI study using the chatroom task tested age and sex differences in adolescents’ social metacognition and brain function as they anticipated receiving feedback from peers (Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009). Although no effects of gender or age emerged on their behavior, participants had a bias toward predicting the peers they rated as more desirable would be more interested in interacting with them. When anticipating how much desirable peers would be interested in them, increased activity emerged in a set of regions outlined as part of the affective node in the SIPN model (Nelson et al., 2005), including the nucleus accumbens (drive for reward), hypothalamus (affect engagement), hippocampus (memory and consolidation), and insula (subjective feelings). These neural response patterns were heightened in girls (but not boys) and were strongest among older girls. Thus, whereas self-report measures may not have been sensitive enough to detect gender and age biases in peer-based metacognition, such effects were detected by measures of brain function. Furthermore, these results suggest a potential neural mechanism that could promote female proclivity for social-affiliative behavior (McClure, 2000), while simultaneously increasing risk for psychopathology linked to social competence. Indeed, work using a similar task finds that young adults who are more sensitive to social rejection have greater ventral striatal and dorsal medial PFC responses when anticipating positive versus negative social feedback (Powers, Somerville, Kelley, & Heatherton, 2013). Overall, reward processing and mentalizing brain regions appear highly attuned to awaiting positive feedback when one is overly concerned about negative outcomes.

Other fMRI work has focused on affective and neural response to the receipt of peer feedback. As expected, typically developing adolescents reported more positive affect after being accepted versus rejected by desirable peers (Guyer, Choate, Pine, & Nelson, 2012). Furthermore, acceptance versus rejection feedback elicited greater activity in the caudate and putamen, regions within the striatum that support approach behaviors and social reward processing. This pattern has been replicated in other samples that include typically developing adolescents and young adults (Gunther Moor et al., 2010; Guyer et al., 2014). A study that used a similar social evaluation paradigm documented variation in the activation of regions involved in affect regulation, including an age-related increase in striatal and ventral medial PFC engagement, to receiving expected rejection (Gunther Moor et al., 2010). Taken together, striatal sensitivity to peer feedback supports the idea that during adolescence, peers promote biases toward appetitive, reward-driven behavior. This finding corresponds with the increased salience of, and regulatory reaction to, socially evaluative contexts as one proceeds through the adolescent period. Striatal engagement may reflect a positive affective response to social acceptance, consistent with the increase in positive affect that adolescents report after being accepted by desirable peers, providing evidence for convergence between behavior and this region of the brain.

Neural response to the anticipation and the receipt of peer feedback has also yielded findings that may inform points of intervention for adolescents with psychopathology. Although a heightened focus on social evaluation is normative during adolescence, this
intensification brings with it fear-related symptoms among those with social anxiety, such as the bias to assume that others will evaluate them negatively, even in ambiguous or positive contexts (Rapee & Heimberg, 1997). In line with these symptoms, when anticipating how interested their peers would be in chatting with them, socially anxious versus healthy adolescents showed heightened activation in the amygdala (Guyer et al., 2008; Spielberg et al., 2015). This pattern was specific to when they had previously judged the peers in a negative light, which may reflect a fear of impending negative outcomes such as social retaliation. A stronger pattern of co-activation between the amygdala and the ventrolateral prefrontal cortex (vLPFC; Guyer et al., 2008) during anticipation of peer evaluation has also been found in socially anxious relative to healthy adolescents. Whereas the amygdala directs attention to salient emotional stimuli, signaling the need to avoid or fear a stimulus, the vLPFC, which has strong anatomical connections with the amygdala, inhibits such responses by shifting attention or overriding basic emotional responses (Etkin, Buchel, & Gross, 2015). The role of the vLPFC in regulating the amygdala response to a feared social outcome suggests that socially anxious adolescents need to shift their attention away from, and/or control, their emotional response when anticipating evaluation.

In another study using similar methods, anticipating feedback from peers previously judged in a negative light also elicited a stronger pattern of co-activation between the amygdala and the rostral aspect of the ACC in socially anxious compared to healthy youth; this relationship was potentiated by increased age (Spielberg et al., 2015). This pattern suggests that regulatory neural input increases with age as anxious youth anticipate potentially negative social outcomes. Such patterns of neural co-regulation include regions within the affective and cognitive-regulatory nodes outlined by the SIPN model and suggest functional engagement when youth anticipate outcomes related to salient social cues.

With regard to receiving feedback, another chatroom fMRI study found heightened activation in the amygdala–hippocampal complex in both healthy and socially anxious adolescents just prior to delivery of positive or negative peer feedback (Lau et al., 2011). However, after being rejected by peers, amygdala–hippocampal activation decreased for healthy adolescents but remained elevated for socially anxious youth. Adolescents with depression, relative to healthy controls, also showed more activation to peer rejection than to acceptance in several regions, including the bilateral amygdala, subgenual anterior cingulate, left anterior insula, and left nucleus accumbens (Silk et al., 2013)—all of which are areas within the SIPN affective node thought to ascribe salience and assign value to social cues. Of note, participants further along in pubertal development showed more activation to peer rejection in the bilateral amygdala–parahippocampal gyrus, caudate, and the subgenual area of the ACC (subACC) (Silk et al., 2013). Thus, increased activation of affective node circuitry to peer rejection naturally increases across pubertal development, but adolescents with depression exhibit even higher levels of activation than typical adolescents. Overall, these patterns underscore an overinvolvement of regions within the affective and cognitive-regulatory nodes during a socially distressing experience in adolescents with social anxiety and/or depression.

Finally, we recently used the chatroom fMRI paradigm to test whether socially anxious youth, who may have deficits in social reinforcement learning (Rapee & Heimberg, 1997), exhibit dysregulated neural engagement when experiencing social prediction errors, which typically facilitate such learning. Because they rated how much they thought each peer would want to interact with them during the anticipation phase of their fMRI scan,
participants essentially provided their prediction about the social feedback they expected to receive from each peer. Low ratings (0–50) were coded as a prediction of rejection feedback, whereas high ratings (51–100) were coded as a prediction of acceptance feedback. When participants ultimately received peer feedback, their predictions were either accurate (e.g., predicted and received acceptance feedback) or erroneous (e.g., predicted rejection but received acceptance feedback). Among socially anxious adolescents, relative to anxious and nonanxious adults and adolescents, social prediction errors during peer feedback elicited heightened striatal activity and negative frontostriatal functional connectivity (Jarcho et al., 2015). This relation was specific to unexpected positive feedback from peers judged in a positive light (i.e., those with whom participants most wanted to chat) and corresponded with subsequent impaired memory for feedback. Given the critical role the striatum plays in adolescent social reinforcement learning (Jones et al., 2011), these data suggest that social anxiety in adolescence may relate to altered neural correlates of prediction errors that contribute to impaired learning about social feedback.

Taken together, these findings suggest that alterations in amygdala and striatum engagement during the peer evaluation process may underlie symptoms in youth with social anxiety or depression. First, inflexible amygdala response following a negative peer-related outcome may reflect dysfunctional communication between cognitive control and emotional response circuits involved in inhibition or regulation of the amygdala, or biases about social emotional events (Bishop, Aguirre, Nunez-Elizalde, & Toker, 2015; Etkin et al., 2015). Second, heightened engagement of the striatum during peer evaluation may reflect altered affective response and learning contingencies for appetitive stimuli (Haber & Knutson, 2010). Thus, neural patterns in adolescence that promote the coding of social evaluation as overly important hinder positive social learning and foster inflexible social behavior, thereby suggesting a possible mechanism by which social experiences in one phase of development have lasting effects on social competence in subsequent phases.

VIRTUAL SCHOOL TASK

A second generation of experimental paradigms has enhanced the ecological validity of past fMRI tasks by isolating key features of the social evaluation experience untested by earlier methods. Three such features are (1) the unpredictable nature of social interactions, (2) the experience of bullying, and (3) the ability to generate meaningful behavioral responses. First, during the shift from childhood to adolescence, social situations become increasingly unpredictable due to the growing complexity of peer-based relationships. The ability to successfully navigate such contexts may facilitate normative social development, whereas the failure to do so may have long-term effects on social competence. Yet, few developmental studies of brain function in youth directly manipulate peer-based uncertainty. Second, bullying, another social experience that peaks during adolescence, is now understood to have long-term negative effects on social competence, physical health, and mental health (e.g., Copeland, Wolke, Angold, & Costello, 2013; Takizawa, Maughan, & Arseneault, 2014; Wolke, Copeland, Angold, & Costello, 2013). Although prior fMRI studies have successfully modeled the experience of social evaluation (described above) or acute rejection (see below), none have modeled the experience of bullying, which is defined by repeated acts of aggression, committed with the intent to harm, by perpetrators with greater power than their target (Olweus, 1993; Salmivalli & Peets, Chapter 16, this volume). Third, one way to
successfully navigate challenging social situations is to engage neurocognitive mechanisms that promote adaptive and optimal social behaviors. Yet, few neuroimaging paradigms include design features that allow participants to interact with their peers, in real time or otherwise, beyond simple dichotomous responses.

The “virtual school” paradigm was developed to study these three key features of social interactions by modeling brain function during real-time anticipation and receipt of feedback from purported peers with a reputation for being unpredictable, a bully, or nice, to whom participants provide psychologically meaningful behavioral responses (Jarcho et al., 2013, 2016). At a first visit, participants are told that they are the “new kid” at the virtual school they will attend while undergoing an fMRI scan. They create a cartoon avatar and personal profile they believe will be shown to “other students,” described as real peers participating in the study at other testing sites. Other students’ characteristics and behaviors have, in fact, been preprogrammed for experimental control. At a second visit, subjects learn that two of the other students have a reputation for being “nice,” two for being “unpredictable,” and two for being “mean.” Reputation comprehension is assessed prior to completing the virtual school task in the scanner. During the fMRI task, subjects enter virtual classrooms populated by virtual renditions of the other students. To model bullying, a power imbalance is created whereby the other students evaluate the subject based on their profile information, whereas the subject, who is a new kid, can only respond to this feedback. For each trial, subjects are cued to anticipate social feedback when the word “Typing . . . “ appears above one of the virtual other students. Because students have an established reputation, subjects have been primed to anticipate different types of feedback from each peer. Subjects then receive positive feedback (100% from nice peers, 50% from unpredictable peers) or negative feedback (100% from bullies, 50% from unpredictable peers), and respond with one of six options, which are positive (“You’re nice,” “That’s nice”), negative (“That’s mean,” “You’re mean”), sarcastic (“Thanks!!”), or avoidant (∅).

Two studies have been published using the virtual school paradigm. The first was a behavioral study that demonstrated the validity of the task (Jarcho et al., 2013). The second was an fMRI study implemented with preadolescents characterized as high or low in childhood social reticence (SR; Jarcho et al., 2016). While anticipating unpredictable compared with predictable peer feedback, high relative to low childhood SR was associated with greater activity in the dorsal area of the ACC (dACC) and bilateral insula, brain regions implicated in processing salience and distress, and consistent with results from the studies using the chatroom and cyberball (see below) tasks. In addition, a functional connectivity analysis showed that in high versus low SR youth, insula activation was high when medial PFC activation was low, a region commonly implicated in affect regulation. Although still early, these data suggest that the virtual school paradigm may be a valuable tool for investigating more complex peer-based interactions, despite the methodological and physical constraints of neuroimaging.

Social Exclusion

Another frequently used approach to manipulating peer cues in neuroimaging research focuses specifically on measuring behavioral and brain responses to the experience of being excluded by peers, a common and distressing form of social stress. One of the most
commonly used paradigms for inducing social exclusion during fMRI scanning is the cyberball task (Eisenberger, Lieberman, & Williams, 2003; Williams & Jarvis, 2006). In cyberball, participants play a virtual ball-tossing game with two unfamiliar peers represented by cartoon figures. In some versions of the task, photographs of peers accompany these figures. Participants are led to believe that they are playing this game with actual peers, and are told that on some turns they will receive the ball and have to throw it to another player, and on other turns, another player will make that decision. In actuality, the game is rigged via a computer program so that the participant is systematically included and excluded from the game.

Social exclusion delivered via the cyberball task has consistently engaged the dACC and insula in adults, areas implicated in the experience of physical pain and distress processing (e.g., Eisenberger, 2015) as well as cognitive-regulatory functions such as conflict monitoring, expectancy violation, and decision-making errors (Carter & van Veen, 2007; Somerville et al., 2006). Two fMRI studies of neural response to the experience of social exclusion in healthy youth have shown that social exclusion versus inclusion generally elicits greater activation in the subACC and VS (Masten et al., 2009; Sebastian, Viding, Williams, & Blakemore, 2010), areas involved in emotion regulation and depression. Indeed, subsequent work found that subACC activation to social exclusion prospectively predicted increases in depressive symptoms from early- to mid-adolescence (Masten, Telzer, Fuligni, Lieberman, & Eisenberger, 2012). Moreover, greater activity in the subACC and anterior insula during exclusion was associated with higher self-reported distress (Masten et al., 2009). Conversely, youth who were less distressed exhibited greater activity in vlPFC and VS. Involvement of the insula suggests that exclusion may invoke feelings of pain and negative affect, but that the vlPFC may play a role in regulating feelings of distress following exclusion. Whereas past work in adults implicates the dACC, in contrast, this study in adolescents found heightened activity in the subACC. The established role of the subACC in clinical depression, however, suggests that adolescents for whom exclusion causes extreme distress may have greater emotional reactivity than adults in this context, and may be vulnerable to social stress-related depression.

The cyberball task has also been used to examine the neural mechanisms that promote adolescents’ risk-taking behavior following social exclusion (Peake, Dishion, Stormshak, Moore, & Pfeifer, 2013). During fMRI scanning, adolescents played the stoplight task, a computerized driving game that requires making decisions in the face of risk (see the next section, “Experimental Manipulation of Peer Presence,” for more detail). Participants completed this decision-making task prior to and following cyberball-based exclusion, while purportedly being observed by the same peers who excluded them. Adolescents who reported being more susceptible to the influence of their peers engaged in more risk-taking behavior after social exclusion. Furthermore, these adolescents had greater activation in the rostral temporoparietal junction (rTPJ), which mediated the link between peer influence susceptibility and risk-taking behavior. Finally, adolescents who were more susceptible to peer influence showed less activation in dlPFC when experiencing the negative consequence of risk taking (i.e., car crash), again specifically after they were socially excluded. These findings suggest that the negative impact of peer interactions on subsequent risk-taking behavior, particularly in youth who are very sensitive to peer influence, may be mediated by neural circuits involved in mentalizing (e.g., rTPJ) (Gweon, Dodell-Feder, Bedny, & Saxe,
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2012; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011) and attention and self-regulation (e.g., dLPFC) (Cohen, Berkman, & Lieberman, 2013). Returning to the SIPN framework, these findings provide support for the idea that adolescents have a strong orientation to peer influence that fuels the engagement of both the affective and detection nodes. Even further, peer influence dampens the ability or requires the overrecruitment of the cognitive-regulatory node to regulate affect-driven behavior. These propositions need to be further tested through longitudinal work and with task-based modifications to facilitate assessment of the influence of more fine-grained conditions and contexts.

**Experimental Manipulation of Peer Presence**

Another dimension to consider in capturing the influence of peers on adolescent brain function is the physical presence or absence of peers. For example, risky behaviors, such as substance use and unsafe driving, often occur in the presence of other adolescents, suggesting that peers contribute to adolescents’ decisions to take risks (Chassin, Hussong, & Beltran, 2009). A powerful paradigm for testing this relation during fMRI scanning is the stoplight task (Steinberg et al., 2008). In this task, participants are instructed to drive across 20 intersections as quickly as possible to receive a cash prize. At each intersection, there is a stoplight that could change from green to yellow or red. Participants are given the option of braking before the intersection, which causes a short delay, or not braking, which saves time. If participants choose not to brake, then their car could be hit by another car traversing the intersection, causing a longer delay than if they had stopped to wait for the light.

The stoplight task has been used to study brain function in adolescents, young adults, and adults, with an important manipulation of playing alone and while being observed by a peer (Chein et al., 2011). With peers watching, adolescents relative to young adults had greater activation in the VS and OFC, which further predicted greater risk-taking behavior during the game. Additionally, the more susceptible adolescents reported being to peer influences, the greater their VS activation when playing the game with peers watching. This finding aligns with the theory that adolescents’ risk-taking behavior is influenced by the presence of peers, and highlights the engagement of the striatum as a neural mechanism that may support this relationship. Similarly, among adolescent males, greater neural reactivity in social-affective networks (e.g., anterior insula, dACC, subACC, and mentalizing: the dorsomedial PFC [dmPFC], TPJ, and posterior cingulate cortex [PCC]) during social exclusion predicted greater subsequent risk-taking behavior in the presence of a peer (Falk et al., 2014). Thus, consistent with behavioral observations, the actual presence of peers increases adolescent risk taking, potentially by reducing attention to the consequences of engaging in risky behavior, an effect amplified among youth with a proclivity to be susceptible to peer influences.

Another line of research demonstrates that peer presence, even without a behavioral challenge, is sufficient to induce changes in brain function unique to adolescents. A clever study demonstrated that the mere belief that peers were watching them as they passively lay in an fMRI scanner elicited more self-conscious emotions, autonomic arousal, engagement of the mPFC, and striatum–mPFC connectivity among adolescents compared with children or adults (Powers et al., 2013). Taken together, these data suggest a neural mechanism by which peer-related self-consciousness may bias-motivated social behavior.
Socializing Influences on Neural Response to Peers

Experiences with parents/caregivers and peers early in life lay the foundation for individual differences in behavior; data now reveal that these differences emerge in neural sensitivities that influence how adolescents engage with peers.

Parenting Experiences

Parenting style may be more influential on the brain than peer experiences in some developmental phases, under specific contexts, and for certain outcomes (Nelson et al., 2016). For example, Tan and colleagues (2014) had adolescents discuss a problem with their mothers that the adolescents hoped their mothers could help them solve. Two weeks later, participants completed the chatroom task. Youth whose mothers maintained a negative affect for longer periods of time during their discussion had a dampened neural response to the positive context of peer acceptance. This effect emerged in the amygdala, left anterior insula, subACC, and left nucleus accumbens (NAcc), all regions within affective circuitry of the SIPN model. The finding that affective tones modeled for youth by their parents can impact adolescents’ neural response to a socially rewarding experience has important implications for adolescents’ ability to develop social competence with peers.

Associations between parenting and neural response to peers have also been observed within cognitive-regulatory circuits that follow a more protracted path of development. In youth with versus without an early childhood temperament of behavioral inhibition, higher levels of harsh parenting in middle childhood were associated with diminished vlPFC response to peer rejection in late adolescence, suggesting less, or less flexible, regulation of responses to peer rejection as a function of adverse parenting in the behaviorally inhibited group (Guyer et al., 2015). These results were complemented by data suggesting that youth with high levels of warm parenting in middle childhood showed a decreased caudate response to peer rejection in adolescence.

Aside from parenting style, maternal mental health also shapes neural processing of peer cues. Youth whose mothers had a history of depression showed reduced VS and ACC activity in response to peer acceptance, but regardless of depression risk status, youth with high social affiliation had greater VS response to acceptance (Olino, Silk, Osterritter, & Forbes, 2015). These findings suggest that maternal depression may dampen adolescents’ neural response to a social reward through altering their tendency toward social affiliation. Overall, we have begun to see how earlier socialization experiences with parents shape how adolescents’ brains respond to peers in ways that are valence-specific and that show moderation of parenting influences by individual differences.

Peer Experiences

The quality and types of past experiences one has with peers, both positive and negative, are also likely to have a cumulative effect in shaping neural function. To capture adolescents’ peer experiences across childhood, an innovative study combined neuroimaging with peer nomination data (Will, van Lier, Crone, & Guroglu, 2015). Specifically, participants indicated which peers in their class were most and least liked every year from first to sixth grades. These nominations were used to classify participants as chronically rejected or accepted in childhood. The adolescents then played inclusion and exclusion rounds of
cyberball. Although the groups reported similar levels of distress immediately following social exclusion, chronically rejected adolescents showed higher levels of activation than accepted adolescents in the dACC when excluded versus included. Furthermore, chronically rejected adolescents also showed higher activity than accepted adolescents in the dACC and anterior PFC when they were incidentally “excluded” in the course of an inclusion round, where the ball was tossed a similar number of times among all purported players in the game. This finding suggests that chronically rejected youth may be hypervigilant to being excluded, even when the overall social context is one of inclusion. These results underscore the power of one’s past peer experiences in shaping neural response patterns to later peer experiences.

Conversely, positive past peer relationships may differentially sensitize the adolescent brain to social stress. For example, adolescents completed a diary every night for 2 weeks in which they reported the amount of time they spent with friends outside of school. Two years later, they played cyberball during an fMRI scan. Adolescents who reported spending more time with their friends in the past showed dampened activity in the dACC and anterior insula during social exclusion (Masten et al., 2012). Because these regions are consistently linked with the experience of distress in this context (Eisenberger et al., 2003; Masten et al., 2009), these data suggest that maintaining positive relationships (e.g., spending time with friends) may attenuate neural hypersensitivity to negative peer interactions later in life.

Negative peer relationships have also been found to modulate adolescents’ subsequent behavior and engagement of brain regions assessed within nonsocial contexts that pertain to risk taking and reward processing. Specifically, adolescents who previously reported high levels of conflict with their peers engaged in more risk-taking behavior and showed heightened activation in the striatum and insula when completing a risk-taking task; these associations were attenuated for adolescents who reported high levels of peer support (Telzer, Fuligni, Lieberman, Miernicki, & Galván, 2015). Moreover, adolescent girls with higher levels of peer victimization in early adolescence demonstrated a decreased response in the dorsal and rostral portions of the mPFC when anticipating monetary rewards in mid-adolescence (Casement et al., 2014). These findings suggest that past negative peer experiences may disrupt a broad range of neural circuits across different classes of stimuli that require rule learning and motivation.

Overall, neuroimaging research that focuses on past socializing experiences suggests that familial and peer influences may moderate neurobiological attunement to threat and reward cues in social contexts. The weighting of these different socialization influences may have particular import over one another at different times in development and in different contexts. An exciting line of research has begun to parse common and distinct neural networks implicated in peer- and parent-based influences on adolescent attitudes to corresponding brain function (Welborn et al., 2016). Such research lays the groundwork needed for researchers to isolate contexts in which the adolescent brain is more susceptible to specific forms of social influence.

**IMPLICATIONS**

Key results from this work have far-reaching implications. First, although the idea that peers have a profound influence on each other’s thoughts and behavior during adolescence has
been commonplace for centuries, it is only in the last 25 years that researchers have begun to isolate the neural mechanisms that promote this relationship. In this relatively short amount of time, great strides have been made toward isolating neural correlates of distinct behavioral and psychological responses to peers during specific phases of development. This work has demonstrated that the brain is responsive to social cues imbued with maturational relevance; such research also provides a mechanism by which social experiences at each stage of development may impact social competence during subsequent phases of maturation.

Second, despite their similarity in expression, some forms of peer-related behavior may be supported by distinct patterns of brain function. For instance, neuroimaging has revealed that for some forms of stable behavior, such as the expression of social reticence and social anxiety during adolescence, similar peer contexts evoke distinct patterns of engagement in cognitive and affective processing nodes of the brain. Thus, although such forms of behavior may appear as an expression of symptoms along a single continuum, they may be grounded in distinct neural mechanisms. This possibility has important implications for interventions aimed at targeting adolescents at risk for developing psychopathology in adulthood.

Third, the key findings discussed in this chapter suggest the potential for the translation of the brain’s role in cognition and emotion into treatments for adolescent problems involving peers. Although the behavioral manifestations of such problems inform treatment needs, some forms of dysregulation may be inaccessible to self-report or lack behavioral corollaries. For instance, youth who exhibit altered brain function during anticipated social evaluation may benefit from specific types of social skills training, whereby adaptive interpretation and valuation of social cues could help promote positive social competence. Moreover, children who fail to exhibit social competence in peer contexts could suffer from impaired engagement of executive node function or hyperreactivity in the affective processing node. Isolating the circuit, or interplay of circuits, implicated in poor social responding could help determine if interventions that provide youth with skills linked to inhibitory control or reward processing are needed. Moreover, as the effects of social interactions on brain function become more well established, greater efforts may be made to guide youth with social problems to reevaluate the social cues they attend to and remember or when, and when not, to attend to certain peer-based social cues.

Finally, research has revealed how social experiences in early life can powerfully shape later responding at the level of the brain. A growing body of literature suggests that early experiences with parents or peers may influence brain function across a variety of contexts. To that end, isolating the neural circuits responsive to particular contexts and cues and delineating when they are more or less influential in development, will be necessary for improving social competence and treating youth with social problems.

**FUTURE DIRECTIONS**

As highlighted in our review of the literature, a great deal of progress has been made in our understanding of how peer contexts intersect with brain development, particularly in late childhood and adolescence. In this section, we discuss several future directions in research that we hope will extend our knowledge about peer experiences and neurobiological development, and inform the design of intervention strategies aimed at youth who encounter peer-related difficulties. Of course, it will be critical to formulate clear theories and testable
hypotheses to unify our current understanding of brain development and peer experiences and to shape future research through a theory-based approach.

First, a great deal of the literature linking adolescent brain function with peer-related social cognition aims to isolate neural mechanisms implicated in social anxiety disorder. However, deficits in social functioning are a diagnostic criterion for the vast majority of mental health disorders included in the DSM-5 (American Psychiatric Association, 2013). Although inroads have been made into studying social-processing deficits in many of these disorders, tests of the relation between brain function and peer-based acceptance or rejection across a range of disorders are rare. For example, many studies with adolescents with autism spectrum disorder assess neurocognitive deficits associated with processing emotional faces, theory of mind, and empathy, but few have explored how the brain responds to peer acceptance and rejection (Masten et al., 2011). Likewise, adolescents with disruptive, impulse control, or conduct disorder often have high levels of rejection sensitivity (Downey, Lebolt, Rincon, & Freitas, 1998; London, Downey, & Bonica, 2007). Yet neuroimaging studies of social rejection in populations with externalizing behavior problems are exceedingly rare. Although there is still a great deal to learn about the neural mechanisms of peer-based processing in adolescents with, and at risk for, social anxiety, it is important to expand the scope of this research to isolate shared and distinct mechanisms that contribute to social-processing deficits across multiple disorders. The National Institute of Mental Health’s (NIMH) Research Domain Criteria initiative (Insel et al., 2010) provides a framework for this type of work. However, utilizing such a framework requires careful consideration of how social competence is operationalized in the absence of diagnostic categorization. One way to define social competence is by quantifying positive peer relationships attained through effective social behaviors. Varying levels of social competence, regardless of corresponding diagnoses, could then be related to the brain function elicited by social information processing during peer-based experiences of rejection and acceptance—which, in turn, maps on closely to real-world experiences tied to social competence.

Second, the literature we reviewed largely focused on adolescence. In part, this focus reflects methodological constraints; young children are often unable to understand and perform somewhat complex tasks of social cognition and metacognition while remaining still in an fMRI scanner. Unfortunately, this developmental limitation has hindered peer-based fMRI research in early childhood, despite the fact that tracking how the young brain reacts to peers is fundamental to understanding how neural pathways critical to social cognition are initially established. Our field would benefit from implementation of peer-based fMRI tasks that are developmentally appropriate for a younger population. To that end, as a promising variant of the chatroom task, the playdate task has been used with preschoolers. The playdate task draws on events similar to those in the chatroom task and is compatible with concurrent ERP and cardiophysiological data acquisition. Results from an initial behavioral study show that preschoolers can successfully complete the playdate task, and that the task elicits meaningful variability in behavior that relates to individual differences in socially oriented temperamental tendencies (Howarth et al., 2013). Specifically, shy versus nonshy boys reported higher levels of sadness when a child with whom they wanted to play rejected them, but lower levels of sadness when a child with whom they did not want to play rejected them. The initial peer preferences of boys who are shy appeared to moderate their emotional responses to rejection, and may reflect emotional difficulty or avoidance of processing socially awkward situations. Probing these patterns further would be
advanced through the development of peer-based paradigms that can be paired with ERP to assess cortical brain activity as a more child-friendly alternative to fMRI. ERP studies may also provide better temporal resolution than fMRI, which may be important for measuring moment-to-moment neural responses to peer cues in certain neural circuits.

Third, much existing work focuses on brain responses to thinking about or experiencing peer-based acceptance or rejection, being included or excluded in a game with peers, and having a peer present or absent. However, there are many more facets to peer contexts that have been well studied in behavioral and observational research; this work should be used to guide future research questions. New paradigms such as the virtual school have been developed and tested to expand these contexts by incorporating the experience of being bullied, the importance of a peer’s reputation, and the dynamics underlying the influence of different types of peers. Certainly there are ethical constraints on the types of experiences that can be simulated within the laboratory, but it will be important for future work to delineate how both chronic and acute peer victimization and bullying, as the target or the perpetrator, relate to brain development. Doing so can better elucidate how these social stressors create negative neurodevelopmental trajectories and the biological mechanisms that underlie offenders’ negative social behaviors. It will also be critical to examine whether positive peer exchanges and peer support might foster more positive trajectories for social competence across childhood and adolescence. For example, peer support in early adolescence buffers the neural response to social rejection in later adolescence (Masten et al., 2012), and neighborhood quality during adolescence has a similar buffering effect that lasts into adulthood (Gonzalez, Beckes, Chango, Allen, & Coan, 2015). Furthermore, other characteristics of the peer system will be important to translate within developmental cognitive neuroscience approaches, such as capturing the effects of youths’ membership in cliques and crowds or the significance of youths’ actual friends (for better or worse) on brain function and structure. Finally, we know little about romantic relationships and the role of the brain during adolescence (Suleiman & Harden, 2016). Yet, as youth move into adulthood, the peer group becomes less salient and romantic relationships become more established, suggesting that this is another important relational context in which to study brain development (Furman & Rose, 2015).

Fourth, future work is needed to broaden the array of brain indices studied in conjunction with peer influences. For example, a dearth of research examines the relation between brain structure and peer systems. Little is known about whether the volume of neural structures or the integrity and pattern of structural connectivity vary as a function of past peer experiences. One initial study suggests a relation between amygdala volume and social network complexity in both adolescence and adulthood (Von Der Heide, Vyas, & Olson, 2014), highlighting the role of social networks in establishing connections across the brain with regions important for emotional learning (Nelson et al., 2014). Corroborating evidence for the import of brain structure on peer systems has also begun to emerge from studies of traumatic brain injury (TBI) in childhood. Childhood TBI is associated with profound deficits in social competence that may be linked to alterations in executive function; social behaviors that encompass affiliation, aggression, and withdrawal; as well as adjustment to peer-based expression of acceptance and rejection (Heverly-Fitt et al., 2016; Yeates et al., 2013, 2014). Location and extent of injury are likely to differentially influence each of these processes, and thereby impact social competence in potentially unique ways (Bigler et al., 2013). Given the high incidence rate of childhood TBI (Centers for Disease Control
and Prevention, 2011), there is a critical need for further work in this area, which has been largely overlooked by developmental psychologists and by those who use fMRI to study the interplay between peer influences and the brain. Yet another recommendation for expansion of the current literature on peers and neuroscience would be to draw on animal models, which may offer a way to more precisely account for peer-based influences on neural mechanisms related to structural plasticity.

Finally, the extant literature on the brain’s response to peer experiences is largely limited to studies of youth raised in Western societies. Understanding how the brain responds to peers in other cultures will be an important future direction. For example, implementing the type of research reviewed here in societies that emphasize collectivism over individualism may reveal a different neural signature of peer evaluation and social exclusion. Furthermore, it will be important to determine if aspects of the neurodevelopmental reorientation framework are universal across cultures, or whether the social emphasis engendered by specific cultures gives rise to variation in neurodevelopment.

CONCLUSION

In this chapter we have reviewed current theory and empirical research on the relations between peers and brain function. In doing so, we described neurodevelopmental frameworks that have guided research on brain function and peer interactions and relations in childhood and adolescence. This material provided a backdrop for interpreting the key findings we have reviewed. We also presented main issues and methods within the field, which highlight the complexity of rigorously testing hypotheses about how peers get into the brain. We reviewed seminal and emerging research on the neural correlates of peer evaluation, social exclusion, peer presence, and earlier socializing experiences with parents and peers.

A common thread that runs through this work is an appreciation of the fine balance between reconstructing what transpires in adolescents’ social lives and maintaining scientific control to test the impact of those events on the brain. We challenge the field to continue pushing this balance further to bring more of the real world into the laboratory (or the laboratory into the real world through the use of technological advances). Given the importance of peer-related experiences to well-being and optimal functioning, we have argued that the human brain is designed to promote social learning and affiliation across development to facilitate adaption to age-appropriate social demands. Thus, the most promising yet difficult task facing our field is to more explicitly leverage the knowledge we gain from this research to inform the development of interventions that promote social competence and emotion regulation. Finally, we are hopeful that the knowledge we gain about how children’s social lives with their peers infiltrate their neurobiological functioning, and vice versa, will constrain brain-based developmental theories about peer influence.

REFERENCES


Neuroscience and Peer Relations


