



A Social-Interactive Neuroscience Approach to Understanding the Developing Brain

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Abstract

From birth onward, social interaction is central to our everyday lives. Our ability to seek out social partners, flexibly navigate and learn from social interactions, and develop social relationships is critically important for our social and cognitive development and for our mental and physical health. Despite the importance of our social

interactions, the neurodevelopmental bases of such interactions are underexplored, as most research examines social processing in noninteractive contexts. We begin this chapter with evidence from behavioral work and adult neuroimaging studies demonstrating how social-interactive context fundamentally alters cognitive and neural processing. We then highlight four brain networks that play key roles in social interaction and, drawing on existing developmental neuroscience literature, posit the functional roles these networks may play in social-interactive development. We conclude by discussing how a social-interactive neuroscience approach holds great promise for advancing our understanding of both typical and atypical social development.



1. INTRODUCTION

From the first minutes after birth we seek out social partners and our interactions with these social partners shape our social, cognitive, and language development into adulthood. The amount of time infants and toddlers spend engaging with others is related to subsequent language development (Brooks & Meltzoff, 2005; Morales, 2000; Mundy & Newell, 2007) and social development (Nelson, Adamson, & Bakeman, 2008; Vaughan Van Hecke et al., 2007). As children grow older social interactions become more complex and diverse, and children spend increasing amounts of time with peers (Parker, Rubin, Erath, Wojslawowicz, & Buskirk, 2015). These burgeoning social relationships are fundamental to every aspect of our lives, affecting our social and cognitive abilities (Gifford-Smith & Brownell, 2003) and mental and physical health (Achat et al., 1998; Berkman & Syme, 1979). People with stronger social ties may even live longer than those with weaker ties (Holt-Lunstad, Smith, Baker, Harris, & Stephenson, 2015; Seeman, 1996). Though these beneficial social interactions seem automatic and effortless for many, a significant portion of the population struggle to engage with others, including individuals with autism spectrum disorder or social anxiety. These social difficulties cause significant challenges in individual's lives leading to greater feelings of loneliness and fewer friendships (Bauminger & Kasari, 2000), as well as atypical language and cognitive development (Mundy et al., 2007).

Despite the importance of social interaction to our development and everyday functioning, major gaps still exist in our understanding of how the brain supports social interaction and how this brain-behavior relation changes with age and experience. These gaps exist because most of the extant research has relied on noninteractive, often asocial, contexts to

investigate the cognitive and neural bases of social interaction. For example, studies of how the brain responds to social rewards often use a photo of a stranger's smiling face as a social reward, which does not capture the reward of a positive exchange with a friend. This lack of ecological validity is a significant problem because recent theoretical and empirical work demonstrates that participation in a social interaction fundamentally alters cognitive and neural processing (Redcay et al., 2010; Rice & Redcay, 2016; Schilbach et al., 2013).

We argue that developmental social neuroscience researchers should study how the developing brain supports social interaction by situating studies within a social-interactive context, moving from "offline" observational paradigms to "online" interactive paradigms. First, we establish the importance of interactive neuroscience and highlight four social brain systems that demonstrate important roles in social interaction. This section primarily draws on behavioral work and adult neuroscience research, as limited developmental neuroscience data currently exist. Second, we review findings on the roles of these four neural systems in processing social interaction during development. We close by positing that the mentalizing and reward networks may play unique and critical roles in the development of social interaction. However, there are many research questions yet to be addressed in this nascent field.



2. SOCIAL-INTERACTIVE CONTEXT ALTERS BEHAVIOR

Many cognitive and social processes are studied in isolation even though research demonstrates that real-time social interaction with a partner fundamentally changes these behaviors. In adults, effects of live interaction are salient in the domains of language, action, and attention. For example, in real-life dialogue, linguistic production and comprehension processes are tightly interwoven between and within speaker and listener's brains, raising questions about the accuracy of "isolation" models in understanding our everyday conversations (Garrod & Pickering, 2004; Pickering & Garrod, 2013). Similarly, many of our actions are executed collaboratively: from truly joint actions such as carrying a heavy piece of furniture to adjustments in one's own behavior based on others, such as navigating passersby on a busy street, to the subtle mimicry and adjustments in posture we make when engaging with others. Studies of joint action have shown that individuals form shared task representations and adjust their actions and perceptions based on their social partner (review: Sebanz, Bekkering, & Knoblich, 2006).

These studies illustrate that social processes are important to study within an interactive context, but they do not directly test whether live interaction, per se, fundamentally changes behaviors.

Some of the strongest evidence that live context fundamentally alters behavior comes from studies of social attention. Most prior social attention work concluded that people, faces, and especially eyes receive privileged attention. In addition to capturing more viewing time overall, eyes also can automatically capture attention, increase arousal, and guide attention (Emery, 2000). Recently, with mobile eye-tracking technology, researchers have directly compared visual scan patterns during naturalistic real-time social interactions to videos of the exact same stimuli presented from the more standard perspective (e.g., watching recorded videos; Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012). Some similarities exist, but notable differences emerged between laboratory and real-world social attention. Foulsham, Walker, and Kingstone (2011) found that participants wearing a mobile eye-tracker throughout a university campus were *less* likely to look at approaching people as compared to participants viewing recorded videos of those same trips, suggesting the opportunity for interaction affected gaze behavior (Foulsham et al., 2011). Similarly, when wearing a mobile eye-tracker in a waiting room that either had a live confederate sitting across from the participant or a video of the confederate, participants spent more time looking at the video than the live confederate. Even when participants are engaged in an ongoing live interaction (e.g., an interview context), gaze behavior differs when the interviewer is live compared to in a recorded video asking the same questions (Freeth, Foulsham, & Kingstone, 2013). Only in the live context did participants adjust their eye contact based on the interviewer's gaze. In addition to measuring the amount of time spent looking at the eye region, naturalistic eye-tracking also has demonstrated that gaze following in real-world, live contexts is not reflexive and automatic. People follow another's gaze to an object less in a live context than when watching gaze shifts in a video (Gallup, Chong, & Couzin, 2012; Gallup, Hale, et al., 2012). This top-down contextual modulation of gaze is consistent with work showing that participants demonstrate gaze adaptation effects when they believe that a live confederate can see through opaque goggles (and thus are producing intentional gaze shifts; Teufel et al., 2009). The authors argue that these effects can be explained by engagement of the neural mentalizing network during social perception in live contexts (Teufel, Fletcher, & Davis, 2010)—a point we will elaborate on in the next sections of social-interactive neuroscience work in adults.

Similarly, well-controlled comparisons with infants and toddlers indicate that this sensitivity to a real-time social partner, as compared to a recording, emerges early in development. Murray and Trevarthen (1985) demonstrated that by 2 months of age infants are sensitive to the contingency present in online interactions (Murray & Trevarthen, 1985). Young infants detect (and dislike) when a social partner is acting out of sync with their own actions. By 9–10 months infants prefer and show stronger affective responses to live vs video presentations (Diener, Pierrousakos, & Troseth, 2008). This sensitivity to live social partners continues as 24-month-olds are also more likely to imitate live than video models (Nielsen, Simcock, & Jenkins, 2008), and 2- to 4-year-olds adjust their own drumming tempo to a live human partner but not to a drumming machine or drum sound (Kirschner & Tomasello, 2009).

This early sensitivity to live, reciprocal social interaction is critically important to cognitive and social development. In the domain of language learning, infants retain the ability to discriminate nonnative phonetic contrasts when they hear them produced from a live social partner, but not when they view the same engaging speaker via video recording (Kuhl, Tsao, & Liu, 2003). Similarly, toddlers only learn language from others within socially contingent conditions, including both face-to-face interactions and online reciprocal interactions (via Skype) (Roseberry, Hirsh-Pasek, & Golinkoff, 2014). These social learning contexts are important for more than just language learning. When an adult engages an infant in a social-interactive context (e.g., through social cues such as eye contact and “hi baby”), what an infant learns about objects is qualitatively different than when not so engaged (Csibra & Gergely, 2009). Very early in development we engage with and learn from others differently in live, compared to recorded, contexts. Therefore, research on the development of behavioral and neural systems needs to consider the role of social-interactive context.



3. KEY BRAIN NETWORKS FOR SOCIAL INTERACTION IN ADULTS

A growing body of neuroimaging work with adults provides evidence that live context matters. Consistent with behavioral work, live social interaction engages brain networks in qualitatively and quantitatively different ways than offline contexts. Below we briefly highlight the large-scale brain networks that have been identified as central to social interaction from primarily adult functional MRI research.

3.1 Mentalizing Network

The mentalizing, or “theory of mind” network, comprises anterior and posterior midline regions (medial prefrontal cortex, MPFC, and posterior cingulate, PCC) as well as lateral temporal–parietal regions (temporoparietal junction, TPJ, and superior temporal sulcus, STS) (Fig. 1). This network was first identified and characterized through studies in which participants were asked to reason about the beliefs and intentions of story characters, similar to the canonical false belief task (Gallagher & Frith, 2003; Saxe & Kanwisher, 2003). Subsequent studies revealed that this network plays a role in social cognitive processing more broadly, including reflecting on personality characteristics of one’s self and others, emotion processing, and inferring intentions from actions (Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). This research predominantly relied on tasks requiring participants to adopt either a third-person or first-person perspective (i.e., reasoning about one’s self or another but without direct social interaction). The primary function of this network is thought to be reflective or deliberate reasoning about another or one’s own thoughts, beliefs, emotions, or personality characteristics.

A smaller body of work has demonstrated that this network is engaged in contexts that do not explicitly require deliberate reasoning about mental states. Specifically, regions within this network are engaged during social interaction more broadly. For example, the dorsal medial prefrontal cortex (dMPFC) is engaged when a participant hears their name called, makes eye contact with an experimenter, or views communicative facial gestures (Kampe, Frith, & Frith, 2003; Schilbach et al., 2006). Communicative hand and arm gestures also engage regions of this network, including the dMPFC and the STS (Enrici, Adenzato, Cappa, Bara, & Tettamanti, 2011; Redcay, Velnoskey, & Rowe, 2016). Further, the mentalizing network is recruited when two people engage in joint attention and coordinate their visual attention on a common object (Gordon, Eilbott, Feldman, Pelphrey, & Vander Wyk, 2013; Redcay et al., 2010; Redcay, Kleiner, & Saxe, 2012; Schilbach et al., 2010).

These studies of communicative intent and joint attention demonstrate engagement of the mentalizing network in social interaction, but they do not isolate social interaction. That is, social and nonsocial conditions differ across multiple dimensions, including task demands and stimulus characteristics. Such differences leave open the question of whether the mentalizing network is engaged by social interaction per se. Several recent studies have begun to directly test whether simply engaging with a social partner changes

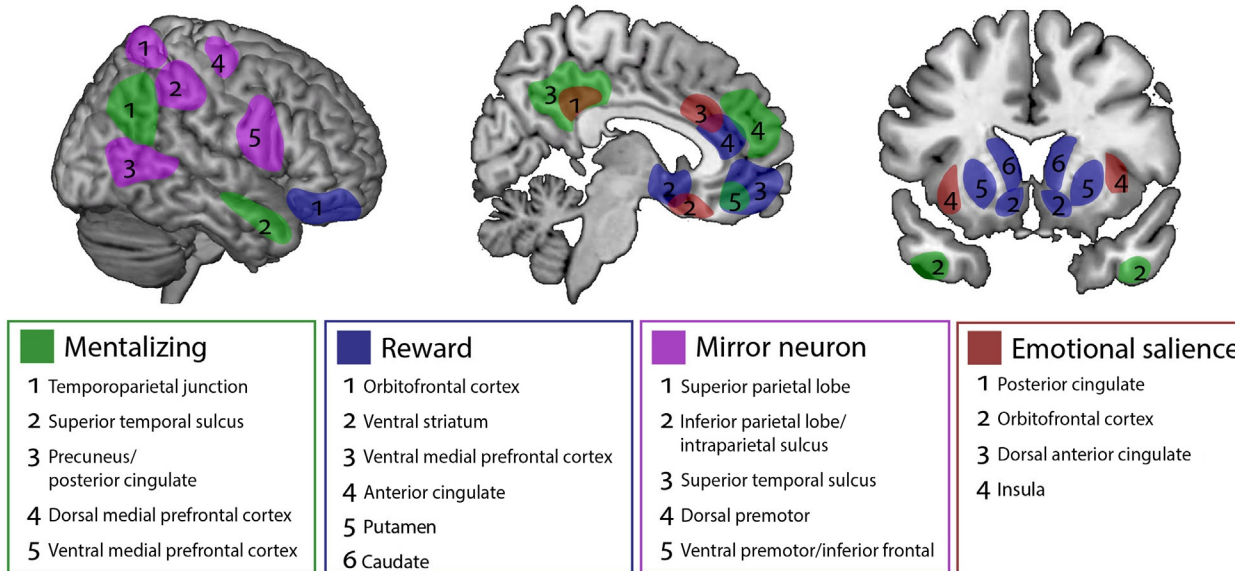


Fig. 1 Key regions of four networks associated with social interaction. Regions of the mentalizing network (*green*), reward network (*blue*), mirror neuron system (*purple*), and emotional salience network (*red*) are displayed on a template brain with numbers corresponding to the label in the boxes for each network. Regions were identified based on the neurosynth meta-analysis tool (<http://neurosynth.org/>, reverse inference maps) using the label of each network as a keyword, with the exception of the emotional salience network. Additionally, the amygdala (not shown) is a key region in both reward and emotional salience networks. Only the right hemisphere is displayed on the rendered brain, but the regions displayed are bilateral.

patterns of brain activation compared to performing a similar task in offline contexts from an observer perspective (Fig. 2A). In one study, we compared real-time social interactions with a live social partner to video playback of the same (or similar but novel) auditory and visual stimuli (Redcay et al., 2010). This paradigm held constant all stimuli demands and characteristics except for the participant's knowledge that they were viewing a recording vs watching a live feed. We found greater engagement of regions of the mentalizing network, as well as attention and reward networks, during live compared to recorded experimenter conditions (Fig. 2A). In a subsequent study, we carefully controlled for potential differences between live and recorded conditions by having participants listen to speech that they were told was from a "live" or a "recorded" speaker. In actuality all stimuli were recorded. Even though stimuli were identical across participants, when participants believed the speech was from a real-time social partner they showed greater engagement of regions of the mentalizing network, specifically the left TPJ and dMPFC (Rice & Redcay, 2016) (Fig. 2B). To determine whether these mentalizing regions were the same as those engaged during deliberate mental state reasoning, we used a mentalizing "localizer" task in which participants performed a standard offline theory of mind task (Dodell-Feder, Koster-Hale, Bedny, & Saxe, 2011). With this localizer, we demonstrated that the same regions that are engaged when explicitly reasoning about the thoughts and beliefs of characters in a story are also engaged when listening to speech from a live social partner, even when such speech does not include explicit mental state demands (Rice & Redcay, 2016) (Fig. 2B). Using a different approach, Schuwerk, Schurz, Mu, Rupperecht, and Sommer (2017) demonstrated that the right TPJ shows greater activation when participants believe a nonsocial cue (arrow) was sent from a confederate outside the scanner compared to when they believed a computer placed it there (Schuwerk et al., 2017). These results are consistent with a separate body of work showing that mentalizing networks are engaged when participants play neuroeconomic games against a human compared to computer (e.g., Rilling et al., 2002). However, unlike in these neuroeconomic games, the three studies described above did not require mentalizing in the live condition, yet participants engaged these regions automatically when they believed they were interacting with a live social partner. Together, these findings suggest that the mentalizing network may play a more primary or fundamental role in social interaction—a point we address in subsequent sections when reviewing the developmental brain bases of social interaction.

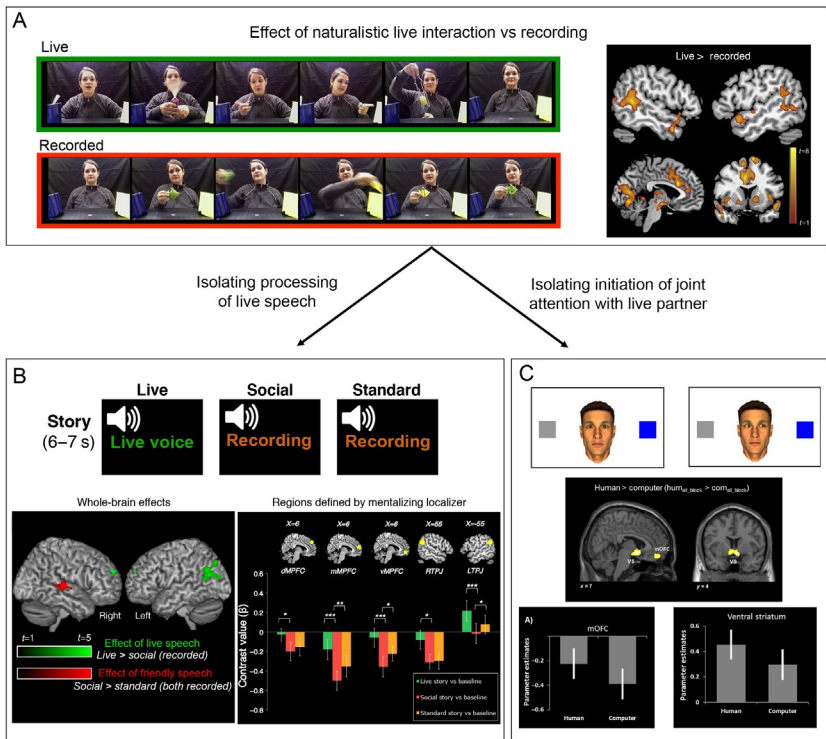


Fig. 2 Neural effects of social-interactive context. (A) Participants either played an interactive game—involving joint attention and speech processing—with the experimenter (Live) or watched recordings of a previous interaction (Recorded). Comparison of these conditions revealed that live interaction significantly activated regions of the mentalizing, reward, and emotional salience networks (Redcay et al., 2010). (B) The effects of listening to live speech were studied when participants listened to speech from a perceived live partner (Live) or recorded speech which was either friendly (Social) or monotone (Standard). The speech consisted of a description of two different objects and did not contain any mental state information. Analysis of the spoken description of the two objects revealed that hearing speech from a perceived live social partner increased activation in each participant’s individually defined mentalizing network (based on a standard localizer) (Rice & Redcay, 2016). (C) In an interactive joint attention experiment, participants directed the gaze of an avatar that they believed either represented a human in another room or was instead a computer program. Simply believing that the partner was human increased activation in ventral striatum and medial orbitofrontal cortex, two regions of the reward network (Pfeiffer et al., 2014). Figures reproduced with permission from Redcay, E., Dodell-Feder, D., Pearrow, M.J., Mavros, P.L., Kleiner, M., Gabrieli, J.D.E., et al. (2010). Live face-to-face interaction during fMRI: A new tool for social cognitive neuroscience. *NeuroImage*, 50 (4), 1639–1647, <https://doi.org/10.1016/j.neuroimage.2010.01.052>; Rice, K., & Redcay, E. (2016). Interaction matters: A perceived social partner alters the neural response to human speech. *NeuroImage*, 129, 480–488, <https://doi.org/10.1016/j.neuroimage.2015.11.041>; Pfeiffer, U.J., Schilbach, L., Timmermans, B., Kuzmanovic, B., Georgescu, A.L., Bente, G., et al. (2014). NeuroImage why we interact: On the functional role of the striatum in the subjective experience of social interaction. *NeuroImage*, 101, 124–137, <https://doi.org/10.1016/j.neuroimage.2014.06.061>.

3.2 Reward Network

An extensive set of cortical and subcortical regions have been implicated in reward processing, including the ventral tegmental area, substantia nigra, dorsal and ventral striatum, amygdala, anterior cingulate cortex, insula, orbitofrontal cortex, and MPFC (reviewed in [Haber & Knutson, 2010](#)) ([Fig. 1](#)). In particular, neuroimaging research has frequently identified ventral striatum and orbitofrontal cortex (OFC) as crucial in processing rewards ([Liu, Hairston, Schrier, & Fan, 2011](#)). Although the reward system has predominantly been characterized in nonsocial contexts, recent studies have indicated that similar regions are involved when processing social rewards, such as when receiving positive social feedback, including both non-interactive feedback (seeing a smiling photograph; [Rademacher et al., 2010](#)) and interactive feedback (getting or anticipating a positive evaluation; [Izuma, Saito, & Sadato, 2008](#); [Jones et al., 2011](#); [Wake & Izuma, 2017](#)). Another line of interactive paradigms has found that cooperation and fairness during economic games are linked to increased activity in reward networks ([Rilling & Sanfey, 2011](#); reviewed in [Bellucci, Chernyak, Goodyear, Eickhoff, & Krueger, 2017](#)), but such games necessarily contain nonsocial rewards as well (i.e., money). Even though studies using neuroeconomic games and positive social feedback indicate that social situations *can* activate reward circuitry, they do not answer the question of whether social interaction itself is intrinsically rewarding.

Recently, converging evidence from a variety of paradigms has suggested that simply sharing with others, even without explicit positive feedback, may be sufficient to activate the reward network. [Schilbach et al. \(2010\)](#) employed a joint attention game, in which participants believed they were interacting with a real person (via a digital avatar that was actually computer controlled) and either responded to or initiated joint attention bids. Compared to control trials, joint attention, and specifically initiating joint attention, significantly increased activation in ventral striatum. Reward activation, however, is not consistently seen in joint attention studies ([Caruana, Brock, & Woolgar, 2015](#); [Redcay et al., 2010, 2012](#)) and one potential explanation is that, in the Schilbach paradigm, participants chose which target to look at, whereas in other tasks, participant's gaze was guided by an external cue, suggesting a role for social agency in social-interactive reward.

In tightly controlled studies designed to isolate social interaction, researchers have begun to examine whether simply interacting with a live social partner vs a recording or computer stimulation activates reward

circuitry (Fig. 2C). In a modification of the interactive joint attention paradigm described in the preceding paragraph, Pfeiffer et al. (2014) added a condition where participants believed the partner was a computer, not a live person—even though the partner was a computer in both cases. Simply believing that one was engaged in a real social interaction engaged ventral striatum and OFC. Similarly, in the study by Redcay et al. (2010) discussed in the preceding section—in which participants either interacted with the experimenter over live videofeed or produced the same behaviors while watching recordings of previous interactions—the live interaction significantly increased activation in the reward network. The Rice and Redcay (2016) study, however, in which participants listened to perceived live vs recorded speech revealed no differences in the reward network; merely listening to live speech was not sufficient to activate this system. These findings support the hypothesis that although certain types of social-interactive context are implicitly rewarding—contexts such as sharing with others (Tamir & Mitchell, 2012), receiving positive feedback (Izuma et al., 2008), and knowing that others like the same things you do (Wagner et al., 2015)—the mere presence of a live social partner may not be sufficient to recruit this network, suggesting that areas like ventral striatum might play a more ancillary role in cultivating the subjective feeling of live experience.

3.3 Emotional Salience Network

One key aspect of social interaction is the experienced emotional engagement when one is included (or excluded) from social interaction. The “salience network” (Seeley et al., 2007), encompassing paralimbic structures including the dorsal anterior cingulate (dACC) and frontoinsula cortices, may play a key role in emotional engagement, with the strongest evidence for this possibility coming from studies of social rejection (Fig. 1). Frontoinsula cortices play important roles in interoceptive, autonomic, and emotional processing. For example, these regions are sensitive to physical or emotional pain, pleasurable physical sensations (e.g., touch or “chills”), or faces of loved ones (reviewed in Seeley et al., 2007). Further, the dorsal ACC is sensitive to events that violate one’s expectations. One hypothesis is that this network acts as a salience detector directing attention toward personally relevant and highly salient events—such as the pain of social rejection—through coordination with other large-scale brain networks involved in social or executive processing (Menon, 2011).

Some studies have identified regions of the salience network (dACC and insula) as sensitive to social interaction (Guionnet et al., 2012; Redcay et al., 2010). Specifically, these regions are engaged more when a participant receives a reciprocal, contingent response from a real-time social partner. However, this finding is not consistently seen across studies of social interaction. Instead, the most consistent engagement of the salience network during social interaction is seen in studies of social rejection (review, Wang, Braun, & Enck, 2017). These studies most commonly employ the “Cyberball” task in which participants play a ball tossing game with two other players who, later in the game, consistently exclude the participant. This exclusion elicits feelings of distress and engages the salience network, including the dorsal ACC and insula as well as a broader socioaffective network of regions involved in emotion processing and self-reflection (ventral ACC, MPFC, ventrolateral prefrontal cortex) (reviews: Vijayakumar, Cheng, & Pfeifer, 2017; Wang et al., 2017). These emotion processing regions (e.g., vACC) may even be more reliably activated by social rejection than core salience network regions (e.g., dACC; Vijayakumar et al., 2017). Further evidence for the role of salience and emotional processing regions comes from a study of peer evaluation in which adult participants judged whether they would like or dislike a peer based on a photo and received each peer’s judgment of the participant’s photo (Somerville, Heatherton, & Kelley, 2006). The dorsal ACC was sensitive both to social rejection and to any mismatch between peer and participant ratings (with or without rejection), suggesting the dACC’s role in social rejection is due to a violation of the participant’s default assumptions of inclusion within a social interaction. The ventral ACC, on the other hand, showed greater engagement for peer acceptance compared to rejection. The extent to which the emotional salience network is engaged by social interaction, per se, is unclear given that exclusion from a computer will elicit feelings of rejection to the same extent as a perceived human partner (Zadro & Richardson, 2004). Ultimately, components of real-world interaction appear to engage multiple regions of the broader emotional salience network, but such engagement may not be intrinsic to social interaction.

3.4 Mirror Neuron System

The mirror neuron system (MNS), comprising premotor cortex, inferior parietal lobe, and motor and somatosensory cortex, is engaged when one performs a motor action or views another person perform the same action,

thus providing a potential neural mechanism by which we understand other's action goals (review, [Rizzolatti & Sinigaglia, 2016](#)) ([Fig. 1](#)). This motor resonance may play an important role in social interaction as interaction involves ongoing coordination with and prediction of one's social partner's actions and intentions. However, most neuroimaging research on the MNS involves participants viewing a detached arm reach for an object, with participants sometimes asked to imitate the action. In real-time social interactions actions between partners tend to be complementary, not imitative. Thus, these studies do not directly address the role of the MNS or mirroring mechanisms in live social interaction.

In an early study to address the role of the MNS in social interaction, [Newman-Norlund, van Schie, van Zuijlen, and Bekkering \(2007\)](#) demonstrated that the key portions of the MNS (inferior frontal gyrus and inferior parietal lobe) were engaged more for complementary than imitative actions during an fMRI experiment ([Newman-Norlund et al., 2007](#)). While suggestive, these actions were still performed in a relatively asocial context in which participants viewed a video of a hand performing either a precision or power grip and were told to perform either an imitative or complementary action. More recently, studies have examined coordinated joint actions or communicative actions. For example, in a study of joint action, an experimenter stood next to the fMRI scanner bed and the participant either performed a joint action with experimenter (moving two sticks into the appropriate shape), performed a solo action (moving the sticks alone), or observed the experimenter's solo action. The regions showing greater activation during joint actions only overlapped with the MNS within the superior parietal lobe ([Kokal, Gazzola, & Keysers, 2009](#)). These studies required coordination but not direct communication between social partners. In a clever study of real-time communication in the scanner, [Schippers et al. \(2009, 2010\)](#) had participants play "charades." They found that both the MNS and the mentalizing system showed greater activation when participants decoded observed gestures than when they viewed gestures without decoding them ([Schippers et al., 2009](#)). Further, the neural synchrony between partners was greater during the active guessing task than during passive viewing, both within the MNS and the mentalizing systems ([Schippers, Roebroek, Renken, Nanetti, & Keysers, 2010](#)). Similar to the charades study, when participants perceived actions to be directed toward them with a communicative intent, regions of the MNS and mentalizing systems showed greater coordination (or functional connectivity) than when viewing private or noncommunicative actions ([Ciaramidaro, Becchio, Colle,](#)

Bara, & Walter, 2014). Other work, however, has not identified a role of the MNS in processing communicative gestures (e.g., Redcay et al., 2016). These studies highlight a potential role of the MNS in representing and coordinating action goals with a social partner but further studies need to examine this question within social interactive contexts. Further, when these action goals require inference about a social partner's communicative intent, the MNS works in concert with the mentalizing system.



4. NEURAL CORRELATES OF SOCIAL INTERACTION IN CHILDHOOD THROUGH ADOLESCENCE

Though the adult literature provides a rich view of the role of key social brain networks in real-time social interaction, these studies cannot speak to how changes in the brain relate to children's developing social-interactive competence. Middle childhood and adolescence are important times to understand how social-interactive contexts modulate neural activity. In middle childhood (roughly aged 7–12), children improve on a variety of laboratory tasks related to social cognition (e.g., Apperly, Warren, Andrews, Grant, & Todd, 2011; Dumontheil, Küster, Apperly, & Blakemore, 2010) and social perception (Rice, Anderson, Veloskey, Thompson, & Redcay, 2016), and they show concordant changes in real-world contexts, including an expansion of social networks (Feiring & Lewis, 1991) and increased autonomy and socioemotional understanding (see Carr, 2011 for review). Further, middle childhood is a time of widening variability in social competence (Monahan & Steinberg, 2011), variability that sets the stage for the time when the social world may be most salient: adolescence (reviewed in Somerville, 2013). Adolescence, signaled by the onset of puberty, brings a host of biological and social changes (reviews: Guyer, Silk, & Nelson, 2017; Herting & Sowell, 2017). Adolescents spend increasing time with peers (Hartup & Stevens, 1997; Lam, Mchale, & Crouter, 2014) and the importance of peer evaluation and acceptance peaks during adolescence (Kloep, 1999; Nelson, Leibenluft, McClure, & Pine, 2004). Indeed, adolescence has been framed as a time of social restructuring, as individuals move away from the family unit to the peer group, precipitated by changes in the social brain (Blakemore, 2012; Nelson et al., 2004). Thus, understanding how the brain supports social interaction in middle childhood and adolescence will offer important insight into these real-world social changes.

4.1 Mentalizing Network

Evidence for developmental changes in the mentalizing network predominantly comes from offline studies in which children reason about characters in stories or make judgments about photographs. [Gweon, Dodell-Feder, Bedny, and Saxe \(2012\)](#) presented adults and children aged 5–11 with stories that involved mental state information, social information, or physical information ([Gweon et al., 2012](#)). Providing all three types of stories allowed researchers to compute a neural selectivity index for mental state information specifically. dMPFC and precuneus were sensitive to mental state information across ages, but bilateral TPJ showed increasing selectivity with age, and right TPJ selectivity for mental state information was related to performance on a behavioral assessment of theory of mind abilities. There is also evidence for age-related changes in the processing of mental states depicted in photographs of an individual's eyes ([Gunther Moor et al., 2012](#)). Younger children (aged 10–12) recruited a wider network of regions when processing such photos, including mPFC and bilateral IFG, than did older adolescents (aged 14–16) and young adults. In general, when compared to adults, children and adolescents also activate a wider network of regions in the mentalizing network—particularly medial prefrontal regions—when making judgments about themselves compared to judgments about a character or about how another person sees them ([Masten et al., 2009](#); [Pfeifer, Lieberman, & Dapretto, 2007](#)). Rather than a lack of specialization, this finding may indicate that adolescents engage in more self-referential processing or more mentalizing about their own traits and how those traits are perceived by others. In sum, evidence from noninteractive paradigms suggests that the engagement of the mentalizing network changes throughout childhood and adolescence.

As in adults, developmental paradigms involving social interaction have also revealed evidence that interaction engages the mentalizing network, even when explicit mentalizing is not required. In a developmental extension of the adult work described previously, Rice and colleagues had children aged 7–13 listen to live vs recorded speech that contained no explicit mental state content ([Rice, Moraczewski, & Redcay, 2016](#)) ([Fig. 3A](#)). Regions involved in mentalizing—including precuneus and TPJ—were more active when participants were listening to live speech, although no age-related changes in activation were found. Similar regions have also been implicated in joint attention. Specifically, an interactive joint attention paradigm with children (aged 8–12) and adolescents (aged 13–18) revealed that

Childhood & adolescence

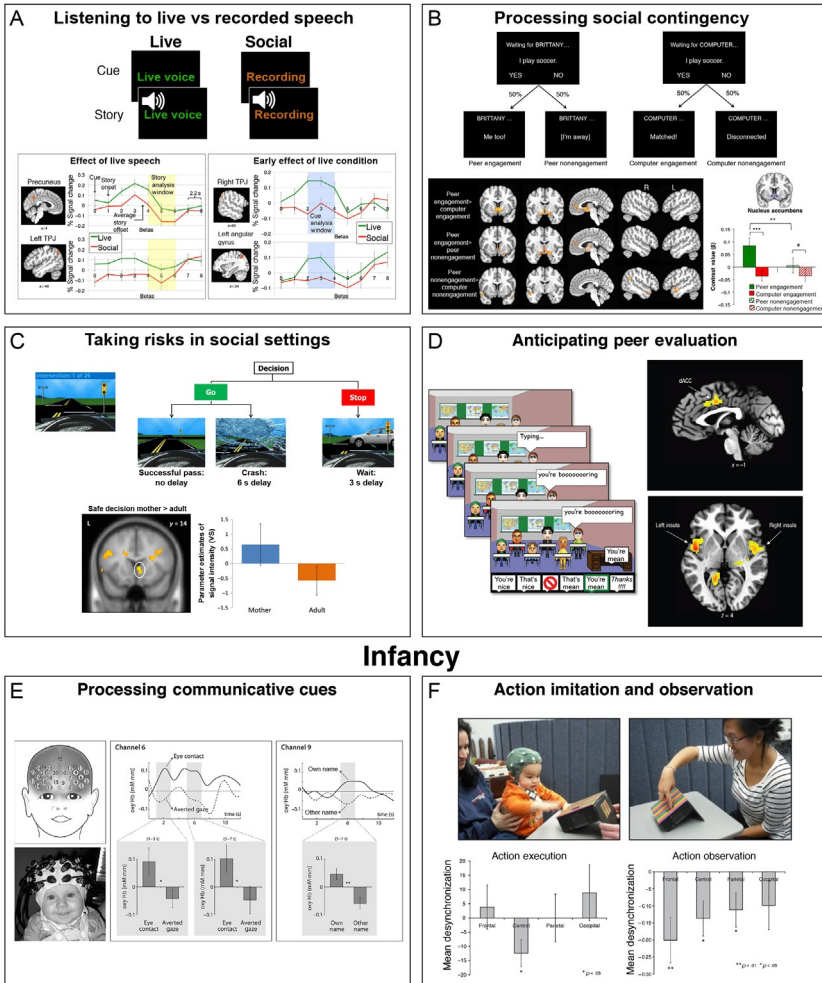


Fig. 3 Survey of social-interactive developmental neuroimaging paradigms. (A) A developmental extension of the paradigm in Fig. 2B, in which children aged 7–13 listened to speech they believed was either live or recorded. Several regions of the mentalizing network showed increased activation during live speech and when anticipating live speech (e.g., during a cue screen) (Rice, Anderson, et al., 2016; Rice, Moraczewski, et al., 2016). (B) An interactive social motivation task in which children aged 8–12 believed they were communicating with a live peer and with a computer control. On each peer trial, children would answer a self-relevant question and then receive either a contingent reply from the peer (e.g., “Me too”) or indication that the peer was unavailable. On computer trials, children also answered self-relevant questions and received contingent and noncontingent replies. Social contingency resulted in the strongest activation of reward regions (e.g., ventral striatum), but a main effect of peer

adolescents, but not children, showed increased bilateral TPJ specialization when initiating vs responding to joint attention (Oberwelland et al., 2016). Intriguingly, across both studies, no main effect emerged in dMPFC for either joint attention or live speech, despite evidence from near-identical adult paradigms that dMPFC activity was modulated by social context.

also emerged in mentalizing regions; even nonengaged peer replies activated the mentalizing network (Warnell, Sadikova, & Redcay, 2017). (C) A risk-taking task in which adolescents decided whether to run yellow lights while with either their mother or a stranger. Safer decisions resulted in more ventral striatum activation in the presence of their mother, indicating that social context alters the reward circuitry activation in risky contexts (Moreira & Telzer, 2017). (D) An interactive peer evaluation paradigm, in which children believed they were attending a virtual school and chatting with other kids' avatars. Participants learned which avatars were nice, mean, and unpredictable. Compared to typical children, socially reticent preadolescents showed increased activation in regions of the emotional salience network—dACC and insula—when anticipating unpredictable feedback (Jarcho et al., 2016). (E) An fNIRS study of infants that examined response to two different ostensive cues: hearing one's own name and direct gaze. Spatially contiguous channels in prefrontal cortex processed socially relevant visual and auditory information, showing early emerging sensitivity to social interactive cues (Grossmann, Parise, & Friederici, 2010). (F) A study of infants that examined neural response to action execution and observing live actions found evidence of EEG desynchronization, especially in central regions, suggesting continuity with mu suppression found in adult mirror neuron research (Marshall & Meltzoff, 2011; Marshall, Young, & Meltzoff, 2011). Figures reproduced with permission from Rice, K., Anderson, L.C., Velnoskey, K., Thompson, J.C., & Redcay, E. (2016). Biological motion perception links diverse facets of theory of mind during middle childhood. *Journal of Experimental Child Psychology*, 149, 72–80, <https://doi.org/10.1016/j.jecp.2015.09.003>; Rice, K., Moraczewski, D., & Redcay, E. (2016). Perceived live interaction modulates the developing social brain. *Social Cognitive and Affective Neuroscience*, 11, 1354–1362, <https://doi.org/10.1093/scan/nsw060>; Warnell, K.R., Sadikova, E., & Redcay, E. (2017). Let's chat: Developmental neural bases of social motivation during real-time peer interaction. *Developmental Science*, in press, <https://doi.org/10.1111/desc.12581>; Moreira, J.F.G., & Telzer, E.H. (2017). Mother still knows best: Maternal influence uniquely modulates adolescent reward sensitivity during risk taking. *Developmental Science*, in press, <https://doi.org/10.1111/desc.12484>; Jarcho, J.M., Leibenluft, E., Walker, O.L., Fox, N.A., Pine, D.S., & Nelson, E.E. (2013). Neuroimaging studies of pediatric social anxiety: Paradigms, pitfalls and a new direction for investigating the neural mechanisms. *Biology of Mood & Anxiety Disorders*, 3 (1), 14, <https://doi.org/10.1186/2045-5380-3-14>; Grossmann, T., Parise, E., & Friederici, A.D. (2010). The detection of communicative signals directed at the self in infant prefrontal cortex. *Frontiers in Human Neuroscience*, 4, 1–5, <https://doi.org/10.3389/fnhum.2010.00201>; Marshall, P.J., & Meltzoff, A.N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience*, 1 (2), 110–123, <https://doi.org/10.1016/j.dcn.2010.09.001>; Marshall, P.J., Young, T., & Meltzoff, A.N. (2011). Neural correlates of action observation and execution in 14-month-old infants: An event-related EEG desynchronization study. *Developmental Science*, 14 (3), 474–480.

There is some suggestion that dMPFC activation to live speech remains constant throughout middle childhood, but that activation to recorded speech increases with age—perhaps due to overall heightened social awareness (Rice, Anderson, et al., 2016; Rice, Moraczewski, et al., 2016) or a simulated imaginary audience even without explicit peer feedback (Elkind, 1967). Support for the idea of heightened social awareness as children move into adolescence does exist. Somerville et al. (2013) found that when participants aged 8–22 believed that a peer was watching them over a live videofeed, self-reported embarrassment and dMPFC activation peaked in adolescence (Somerville et al., 2013) (Fig. 4A). This dMPFC activity while anticipating observation and while being observed may be due to the region's role in self-reflective processing, mentalizing about others, or their combination. Additional research is needed to determine the exact role of dMPFC in social interactive contexts.

Further support for age-related change in how interaction modulates the mentalizing network comes from paradigms involving real-time peer interaction. In one paradigm, children aged 8–12 believed they were engaged in a real-time chat with a peer vs a computer (Warnell et al., 2017). On some trials, the peer responded contingently, and on others, the peer sent an “away” message. Although peer contingency most strongly activated the mentalizing network, even an “away” message from a peer more robustly engaged the mentalizing network than receiving a contingent reply from the computer (Fig. 3B). Additionally, several regions of the mentalizing network, including right TPJ and dMPFC, showed increased response to peer trials with age (Fig. 4B). One explanation for age-related changes in dMPFC in this study design is that the control condition was nonsocial, whereas the previously discussed speech processing and joint attention paradigms had social controls. Control conditions may also explain why many peer interaction and evaluation paradigms do not engage the mentalizing network; most often, their contrasts compare positive to negative evaluation, both of which involve mentalizing or other real-time social processes.

Developmental studies indicate that regions of the mentalizing network are also engaged when participants play strategic games against a social partner, games in which participants allocate resources to other players with the potential to act in prosocial or selfish manners. This mentalizing network activity may increase from early adolescence to adulthood during these trust games (Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2014; Steinmann et al., 2014; van den Bos, van Dijk, Westenberg,

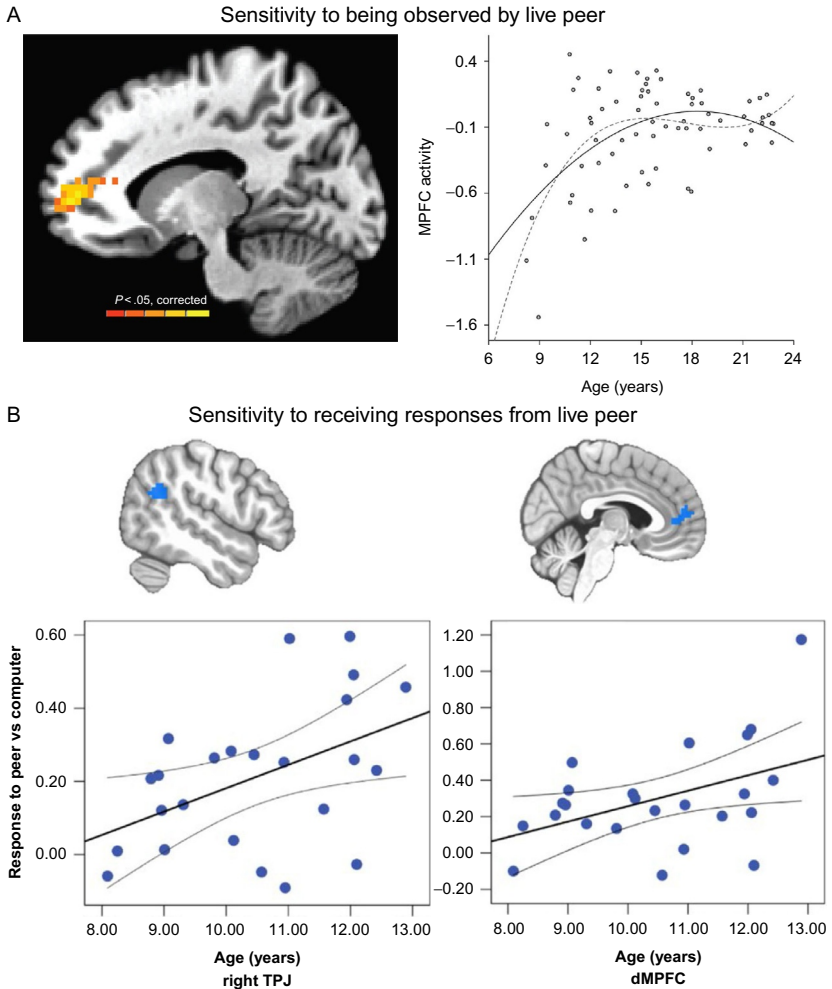


Fig. 4 Age-related effects in the neural processing of social interaction. (A) Compared to children and young adults, adolescents show peak MPFC sensitivity when they believed a peer was watching them through a live videofeed in the scanner (Somerville et al., 2013). (B) Middle childhood sees age-related increases in activation in dMPFC and TPJ when receiving a reply from a peer vs a computer control (see Fig. 3B for paradigm) (Warnell et al., 2017). Figures reproduced with permission Somerville, L.H., Jones, R.M., Ruberry, E.J., Dyke, J.P., Glover, G., & Casey, B.J. (2013). The medial prefrontal cortex and the emergence of self-conscious emotion in adolescence. *Psychological Science*, 24 (8), 1554–1562, <https://doi.org/10.1177/0956797613475633>; Warnell, K.R., Sadikova, E., & Redcay, E. (2017). Let's chat: Developmental neural bases of social motivation during real-time peer interaction, *Developmental Science*, in press, <https://doi.org/10.1111/desc.12581>.

Rombouts, & Crone, 2011), although the exact regions implicated vary across studies and do not always map exactly onto canonical mentalizing regions. Additionally, the developmental changes seen during neuroeconomic games are not always toward increased activation; van den Bos et al. (2011) found that left TPJ recruitment in response to being trusted increased from early adolescence to adulthood, but mPFC activity during reciprocation was highest in early adolescence. This peak in mPFC activation may be consistent with the previously discussed studies revealing that adolescents' self-referential processing engaged a larger prefrontal network, but the exact explanation is unknown. Across studies, however, there is evidence that the mentalizing network is engaged by social interaction and that its recruitment varies across development.

4.2 Reward Network

In adults, social reward engages similar neural circuits as nonsocial rewards (see previous section), but relatively few studies have examined the development of social reward from childhood through adulthood. However, a relatively large body of work has investigated developmental change in reward systems from childhood through adulthood using tasks that primarily involve nonsocial rewards (e.g., money or food). These studies suggest that adolescents demonstrate hyperreactivity to rewards within reward-relevant regions (i.e., striatal, medial, and orbitofrontal cortex; and amygdala) compared to adults which may be due in part to hormonal effects on dopaminergic reward systems associated with puberty (reviews: Galván, 2013; Silverman, Jedd, & Luciana, 2015). However, these findings of hyperreactivity in reward systems during adolescence are not always consistent across studies (Pfeifer & Allen, 2012) and may not always confer a liability in adolescence (Telzer, 2016). A clear explanation of these discrepancies across studies has not yet emerged (for review, see Richards, Plate, & Ernst, 2013).

Social context alters neural sensitivity to the value of nonsocial rewards in adolescence. Specifically, having another person (e.g., a peer) present while participants engage in a risk-taking or reward task alters reward processing. When adolescents play a risky driving game, they show greater ventral striatum (VS) and OFC activation when taking risks if a friend is watching them from the control room than when no one is watching (Chein, Albert, Brien, Uckert, & Steinberg, 2011). Further, the extent of this reward activation is related to the propensity to engage in risk-taking behavior and is context dependent. When a participant's mother was present during a similar driving

game, VS activation increased after participants made *safe* decisions and decreased after risky decisions relative to activation when an unknown adult was watching (Moreira & Telzer, 2017) (Fig. 3C). These studies examined changes to the reward value of risky behavior, but peer presence can affect the value of other types of rewards. Smith, Steinberg, Strang, and Chein (2015) demonstrated that the presence of a peer during a reward task (with no risk involved) led to greater activation within VS, and this effect was specific to adolescents, not adults (Smith et al., 2015). These studies clearly show that the presence of a known social partner can alter sensitivity to reward during adolescence. Further, who is present affects how the reward is processed. While these studies used nonsocial rewards, the altered reward value may be due to the intrinsic reward of implicit approval from a social partner. A peer may think you are cool if you take more risks, whereas a mother will view you more positively when you make a safe decision.

Studies have also directly addressed the effects of peer evaluation on reward systems. Just like the studies examining risk taking when a peer is present, when adolescents reflect on whether their friend will give them a positive evaluation (e.g., does your friend think you are cool?) they engage VS to a greater extent than when they make similar judgments about themselves (Jankowski, Moore, Merchant, Kahn, & Pfeifer, 2014). These rewarding effects of peer evaluation are found even when the peer is a stranger. Several studies of peer evaluation use a similar design in which participants see photos of (perceived real) peers who they believe have evaluated them, either based on seeing the participant's photo or on seeing information participants gave to the experimenters. Feedback that a peer likes you (compared to rejects you) results in greater activation of VS and ventromedial prefrontal cortex (vMPFC) (Davey, Allen, Harrison, Dwyer, & Yücel, 2010; Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010; Guyer, Choate, Pine, & Nelson, 2012). Even the anticipation of a positive evaluation from a peer (e.g., they like or dislike you) engages VS and VMPFC to a greater extent than anticipation of negative evaluation (Gunther Moor et al., 2010; Jones et al., 2014). Between late childhood through adulthood, linear age-related increases in VS activation were seen for peer feedback, both for rejection (Gunther Moor et al., 2010) and acceptance (Guyer et al., 2012).

These studies demonstrate a role of reward systems in social interaction, but all were conducted in offline, noninteractive contexts as participants were not exchanging information in real time with the peer. As reviewed previously, real-time engagement with a social partner can alter brain activation and cognitive processing. Also, these peer evaluation studies focused

on valenced responses (i.e., positive or negative feedback), and thus the extent to which social engagement alone involves reward systems during development is not clear because engagement is present in both positive and negative contexts. To address this question, recent work has examined peer evaluation within online (real-time) contexts without valenced feedback. In the study by [Somerville et al. \(2013\)](#), adolescents reported greater self-conscious emotions when they believed they were being watched in the MRI head coil than either children or adults did, and connectivity between the VS and MPFC was increased during the evaluation period. This finding is consistent with adolescence as a time of heightened sensitivity to peer evaluation or even just the perception of peer evaluation ([Elkind, 1967](#); [Somerville et al., 2013](#)). The real-time chat paradigm discussed previously ([Warnell et al., 2017](#)) separated the effects of social-interactive context (i.e., chatting with a peer or computer) and engagement (contingent or non-contingent response) without the possibility of rejection. Children engaged VS to a greater extent when both sharing information with a peer and when receiving contingent feedback from that peer, compared to receiving the peer's away message ([Fig. 3B](#)). Further, this VS response was greatest when the contingent response came from a peer, compared to the computer response. In this study, however, reward region sensitivity to peer engagement did not differ across age (8–12 years). The lack of age-related differences may be because the age range did not extend into the adolescent age that typically shows a peak in reward sensitivity (e.g., [Galván, 2013](#)) or because the age-related change in reward sensitivity is specific to peer evaluation, rather than social engagement. Future studies should investigate these developmental changes.

In sum, extant studies demonstrate that the reward system plays a role in important facets of social interaction during development. These include learning who is a preferred or positive social partner, thinking about a peer's opinion of oneself, sharing information with peers, and receiving a reciprocal response during online social interactions. Further, adolescence appears to be a time of heightened sensitivity of reward systems to the presence of peers and to peer evaluation.

4.3 Emotional Salience Network

The developmental role of the emotional salience network in social interactions is not yet clear. In adults, social rejection engages both the salience network and additional socioaffective processing regions. During

development, however, social exclusion studies do not reliably identify the dACC and insula (core salience network regions). However, socioaffective regions (vACC, MPFC, and posterior cingulate) are recruited (Vijayakumar et al., 2017). Additionally, adolescents engage the ventral striatum during exclusion, but adults do not. This engagement of VS is consistent with findings reviewed previously of VS hyperreactivity during adolescence, and may reflect increased sensitivity to and learning from peer rejection during this period (review, Vijayakumar et al., 2017) or be due to domain-general maturational effects of puberty on reward systems (e.g., Op de Macks et al., 2011).

In studies of peer evaluation in which participants receive positive or negative feedback from an unfamiliar peer, the insula and ventral ACC are engaged more for *positive* evaluations than negative (Davey et al., 2010; Guyer et al., 2012). A study of social reinforcement learning demonstrated a role of the insula in participants' learning in which peers would consistently provide positive peer approval (compared to inconsistent or negative feedback). Further, this insula activity was an inverted U-shaped across development, with a peak in adolescence (Jones et al., 2014). Thus, adolescence may be a unique time of heightened sensitivity and salience of *positive* peer approval. Importantly, this conclusion is based on data from typically developing children. In a novel interactive paradigm, Jarcho et al. (2016) led both typical and socially reticent children to believe they were interacting with virtual peers who were predictably mean, predictably nice, or unpredictable (Jarcho et al., 2016) (Fig. 3D). The dorsal ACC and bilateral insula (regions of the salience network) were engaged more in socially reticent vs typical children when anticipating social evaluation from unpredictable peers during an online social interaction (Jarcho et al., 2016). These findings suggest a developmental role for the salience network, but the developmental literature does not yet provide a clear picture of whether and how the salience network is involved in peer acceptance and rejection during social interaction. However, a broader socioaffective network including vACC, mPFC, insula, and VS clearly plays important roles in navigating the type of response (inclusion or exclusion) that one may receive from a peer.

4.4 Mirror Neuron System

Studies of adults and younger children and infants have begun to examine the role of the MNS in social interactions, although relatively few studies

have examined this system in school-aged children and adolescents. Those that have examined school-aged children have generally relied on paradigms featuring the passive observation of hand and arm actions toward objects (Biagi et al., 2015; Pokorny et al., 2015; Shaw, Grosbras, Leonard, & Pike, 2012), and thus focused on only the action observation component of the MNS. In a longitudinal study of 9- to 14-year-old children, age-related decreases were seen across multiple regions of the action observation system, as identified from previous meta-analyses (Shaw et al., 2012). A cross-sectional study of 7- to 15-year-olds found increasing laterality with age within action observation regions (Biagi et al., 2015), whereas a second study found no evidence of age-related differences between 9 and 17 years (Pokorny et al., 2015). Thus, how the MNS changes with age from childhood through adulthood remains unclear. Further, to understand the contribution of the MNS in the development of social interactive competence, there is a need for studies to probe how the MNS is engaged in online social interactions in older children.



5. NEURAL CORRELATES OF SOCIAL INTERACTION IN INFANCY

Given the difficulty of using fMRI with awake infants (although see Deen et al., 2017 for a recent exception), almost all studies that examine the social-interactive brain during in the first 2 years of life have employed EEG and fNIRS (see Lloyd-Fox, Blasi, & Elwell, 2010 for a review of fNIRS). Such techniques have limited spatial resolution, especially for subcortical regions, and thus it is difficult to map findings in infants onto the four brain networks discussed in the previous sections. Nevertheless, research on early human development broadly suggests some continuity in the regions involved in processing social interaction. Evidence for developmental continuity predominately comes from paradigms that have examined constituent components of social interaction, including eye contact, speech processing, joint attention, and action observation and imitation, rather than from studies directly comparing the processing of live vs recorded interaction. We do not extensively review the brain bases of infant social cognition here (see Grossmann, 2015 for a review). Rather, we focus on the paradigms that are most relevant to understanding whether the infant brain is sensitive to social-interactive context, and, if so, whether the neural processing of social interactive cues in infancy can be mapped onto the neural systems hypothesized to underlie social interaction at later ages.

5.1 Communicative Cues

One particularly important component of social interaction is communicative or ostensive cueing—signals from a social partner that he or she is engaging in a communicative act. These cues can include the establishment of direct gaze and infant-directed speech, and behavioral sensitivity to such cues emerges in early infancy (Senju & Csibra, 2008). In one of the first fNIRS studies of direct gaze, Grossmann et al. (2008) presented 4-month-old infants with computer-animated adult faces that established direct or averted gaze and found increased activity in frontal and temporal regions in response to direct gaze (Grossmann et al., 2008). Similar prefrontal regions appear to also be engaged in live contexts. In a paradigm involving face-to-face real-time interaction, mPFC activation was increased during social play that contained direct gaze as opposed to social play with averted gaze (Urakawa, Takamoto, Ishikawa, Ono, & Nishijo, 2015). Thus, although the literature is still relatively sparse, there is some evidence that mPFC may index direct gaze cues (see Grossmann, 2013; Grossmann & Johnson, 2013 for review). PFC, particularly mPFC, may also be sensitive to ostensive auditory cues. A study examining the auditory ostensive cue of hearing one's name found that 6-month-olds showed increased mPFC activation when hearing their own name, and this effect was largest when that name was spoken by their mother (Imafuku, Hakuno, Uchida-ota, Yamamoto, & Minagawa, 2014). Though additional studies have also found evidence for frontal cortex engagement during infant-directed speech (Saito et al., 2007), others have found temporal lobe activation for this contrast and that frontal cortex is more engaged by the contrast of maternal vs non-maternal infant-directed speech (Naoi, Minagawa-Kawai, Kobayashi, Takeuchi, & Nakamura, 2012). Thus, across studies, ostensive cues engage the infant's frontal and temporal regions, regions that have been identified to be a key part of the mentalizing system in children and adults.

To our knowledge, no studies with infants have directly compared live interaction to recorded social cues, but there is some evidence that live context alters neural activation. Specifically, paradigms that combine auditory and visual ostensive cues have found different effects in live vs recorded contexts. Two such paradigms involved computer-presented stimuli. In one, infants listened to their own name or another name and, in a separate condition, viewed either direct or averted gaze (Grossmann et al., 2010). Adjacent, but not overlapping, regions of dorsolateral PFC were engaged by both types of ostensive cues (Fig. 3E). In another EEG/ERP study involving recorded stimuli, both infant-directed speech and direct gaze

showed similar neural effects (specifically in frontal regions), and when the cues were combined, ERP data indicated that these effects were not additive (Parise & Csibra, 2013). In contrast to these two studies, an fNIRS study involving real-time interaction found that direct gaze and infant-directed speech only altered brain activity in combination and did not show effects in MPFC—although effects were seen in inferior frontal, temporal, and temporal–parietal regions (Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015). The authors suggest that the naturalistic situation of the study, in which there were two infants present, required additional ostensive cues to generate a neural response. That is, in rich, chaotic, real-world settings, adults may use infant-directed speech, but in the absence of another communicative cue, infants may not assume that the adult is attempting to deliberately communicate with him or her. Future studies should continue to address whether context affects neural engagement in response to ostensive cues by directly comparing live and recorded conditions.

5.2 Joint Attention

Ostensive cues often serve as the foundation for sustained interactions, interactions that can move from dyadic (i.e., between two people) to triadic (i.e., referring to objects or events). At least by the second half of the first year of life, the infant brain is sensitive to joint attention and engages similar regions to those engaged by adults. Two EEG/ERP studies of live social contexts found that establishing direct gaze with an infant before engaging in joint attention altered neural activity (Hoehl, Michel, Reid, Parise, & Striano, 2014; Parise, Reid, Stets, & Striano, 2008), and similar results have been found in an ERP study that used computer-based stimuli (Senju, Johnson, & Csibra, 2006). More recent fNIRS studies have pinpointed which regions show this sensitivity. In one paradigm, Grossmann and Johnson (2010) compared neural responses to a full joint attention event (smiling, making eye contact with the infant, turning toward an object) to control events that lacked either turning toward an object or the establishment of communicative cues (Grossmann & Johnson, 2010). The left medial prefrontal cortex (specifically dMPFC) was more active during joint attention. A follow-up study examined infant-initiated joint attention (Grossmann, Lloyd-Fox, & Johnson, 2013) in a paradigm where the computer avatar smiled, established direct gaze, and then either turned toward the object the infant had just looked at (congruent) or toward the other object (incongruent). Congruent trials elicited a larger response in a similar

left-lateralized prefrontal region to that seen in the response to joint attention paradigm. Thus, joint attention appears to activate prefrontal regions in the first year of life. Joint attention paradigms in adults also engage medial prefrontal regions (e.g., Redcay et al., 2012; Schilbach et al., 2010), suggesting developmental continuity in the use of mentalizing network regions during joint attention. Given the methodological limitations of infant research methods, however, the role of the subcortical reward network that has been associated with joint attention (Schilbach et al., 2010) has not been systematically investigated.

5.3 Action Imitation and Observation

Research on action observation and imitation primarily relies on EEG paradigms that use mu suppression as an index of MNS engagement. Although a full consideration of the MNS in infancy is outside the scope of this review, the general pattern of findings also suggests developmental continuity; mu desynchronization is seen in both action observation and action imitation in infants and adults (see Fox et al., 2016; Marshall & Meltzoff, 2011, 2014 for review; Fig. 3F). The mirror neuron literature also provides, to our knowledge, the only direct comparisons of how the infant brain processes live vs recorded stimuli. One study comparing action observation and imitation for recorded videos vs a live presentation found stronger mu suppression for live stimuli in 18- to 36-month-old infants (Ruysschaert, Warreyn, Wiersema, Metin, & Roeyers, 2013). In particular, during the observation condition, mu suppression was only seen during live presentation. An fNIRS study also employed live and recorded stimuli to examine responses to an actor moving an object vs a control condition where an object moved by invisible means (Shimada & Hiraki, 2006). For both adults and 6- to 7-month-old infants, the live context elicited a greater difference between conditions in motor cortex, although the effect was weaker in infants. These results are consistent with other evidence that social-interactive context changes neural activity. For example, Reid, Striano, and Iacoboni (2011) found that mu suppression was greater when 14-month-olds engaged in real-time dyadic interaction with a live experimenter compared to a condition where the same experimenter completed motor activities without engaging the infant (Reid et al., 2011). Evidence from young children (3-year-olds) also suggests that engaging with a social partner in a joint action task produces greater mu suppression than when observing the same joint action between two other people

(Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011). Thus, there is additional evidence from the mirror neuron literature that, in the first years of life, humans differentially process live, interactive stimuli.

In sum, across the wide variety of studies, there is broad continuity in the regions engaged by social-interactive context within the systems studied: Mentalizing and MNS. For example, mu suppression is seen in action observation and imitation paradigms in both infants and adults. In paradigms in which infants process ostensive cues and engage in joint attention, medial prefrontal and posterior temporal regions show greater engagement. Broadly, these regions coincide with those of the mentalizing network identified in older children and adults.



6. CONCLUSIONS: THE DEVELOPMENTAL ROLE OF KEY BRAIN NETWORKS IN SOCIAL INTERACTION

In the introduction, we presented the hypothesis that interaction with a social partner produces fundamentally different patterns of attention, cognition, and brain activation than simple observation of similarly complex stimuli (cf. Schilbach et al., 2013). For the four networks reviewed here, we provided research evidence that each have clear roles in social interaction across development. However, only the mentalizing and reward networks (and to some extent mirror neuron) showed modulation by live context alone. While some studies have suggested that the MNS shows differential response to live contexts in infants and young children, almost no research has examined this question in older children and adults. Thus, the question of how the MNS is modulated by live, interactive contexts is one that remains to be answered by future research as current evidence is too limited to draw conclusions. The fourth network reviewed—the emotional salience network—may play a role in the emotional response to peer inclusion but does not appear to be altered solely by interactive context. Thus, given the core role of mentalizing and reward networks in real-time social interaction, in this section we discuss the potential social-interactive functions of these two networks and address continuity and change in these functions across development.

6.1 Core Role for Mentalizing Network in Social Interaction

Of the four networks reviewed, the most consistent evidence for modulation by real-time social interaction was seen within the mentalizing network. However, the exact role this network plays in children's and

adolescents' social interactions is presently unknown. In both children and adults, the mentalizing network is engaged even when explicit mentalizing is not required by the paradigm. One possibility is that the presence of a live social partner engages either explicit or implicit mentalizing not strictly necessary for task performance (e.g., "I wonder what she thinks of my answer"; "Why did he say that?"). Another is that this increased activation is anticipatory, as most live interactions will require mentalizing about a social partner at some point. This anticipatory mentalizing activity may serve as a social readiness potential, preparing the mentalizing system to rapidly and flexibly infer and predict a social partner's goals and actions. Indeed, in the paradigm involving children listening to live compared to recorded speech, increased activation was seen in right TPJ during a cue screen indicating that live speech was about to start (Rice, Anderson, et al., 2016; Rice, Moraczewski, et al., 2016).

Another possibility is that live interaction does not induce a greater amount of mentalizing, but rather that the mentalizing network is engaged in a fundamentally different way during interactive contexts. Support for this comes from the remarkable developmental continuity in the regions involved in social interaction, even in infancy. Key regions of the mentalizing network (dMPFC and pSTS) show early and continued sensitivity to interactive contexts. There is ongoing debate about the mentalizing capacities of infants (e.g., Butterfill & Apperly, 2013; Ruffman, 2014; Sodian, 2016), but it seems evident that preverbal infants do not yet possess the full, explicit representational capacities of older individuals. Thus, this frontal-temporal network cannot be explicitly tracking belief states. Instead, the same regions that come to explicitly process theory of mind stories may serve an ontogenetically prior and broader role in representing the complexities of real-time social interaction, complexities that include social resonance, detection of self-relevance, and rapid coordination between partners (Garrod & Pickering, 2004; Grossmann, 2015; Kopp, 2010). In this framework, engagement of the mentalizing system during social interaction may help shape the system to be sensitive to explicit mental state representation. That is, this "social readiness" activation is increasingly paired with mentalizing as children engage in more complex social interactions. Behaviorally, there are strong developmental links between engagement in social interaction and later development of the mentalizing system (Brooks & Meltzoff, 2015; Nelson et al., 2008). However, current neuroscience research does not dissociate between these different accounts to explain why the mentalizing network is more engaged during live interaction.

Regardless of the specific mechanism driving developmental change, neural sensitivity to social interaction begins in the first year of life and appears specialized to similar mentalizing regions as in adults, suggesting continuity in the core role of social interaction across development.

Current evidence for developmental change in the mentalizing system during social interaction is sparse. Offline studies of theory of mind have found increased TPJ specialization when processing mental state information (Gweon et al., 2012), and there is some evidence that TPJ also shows increasing response to social interaction from childhood into early adolescence (Oberwelland et al., 2016; Warnell et al., 2017; but see Rice, Anderson, et al., 2016; Rice, Moraczewski, et al., 2016). These age-related changes may indicate that, as children get older, live social interaction elicits greater mentalizing about a social partner. Complicating this narrative, however, are mixed findings of dMPFC activity in response to social interaction. Although infant and adult paradigms consistently find that dMPFC is responsive to ostensive cues and social context (e.g., Grossmann et al., 2010; Rice & Redcay, 2016; Schilbach et al., 2010), recent developmental extensions of two such studies—listening to live vs recorded speech and processing joint attention—failed to find dMPFC activation in middle childhood and adolescence (Oberwelland et al., 2016; Rice, Anderson, et al., 2016; Rice, Moraczewski, et al., 2016). In contrast, two paradigms comparing social interaction to a nonsocial control found dMPFC activation, with evidence for activity peaking in late childhood or adolescence (Somerville et al., 2013; Warnell et al., 2017). Such apparently contradictory findings may be explained by the specific experimental contrasts utilized; if adolescence is a time of peak social sensitivity, then it is possible that contrasting two social conditions (e.g., listening to two types of friendly speech) will obscure dMPFC activity, even though the region's sensitivity to social interaction has been present since infancy. This explanation, however, is necessarily speculative until research is conducted with more targeted paradigms with a variety of appropriate control conditions.

To better understand developmental change in mentalizing networks during social interaction, future developmental research should directly examine mentalizing within social-interactive contexts from childhood through adolescence. Additionally, combining neural data with rich, real-world behavioral measures of social interaction may help clarify the role of the mentalizing system in social interaction (e.g., Lee, Miernicki, & Telzer, 2017). Additionally, the extent of developmental continuity should

be more clearly established. Specifically, the methods used with infants (EEG/ERP, fNIRS) have limited spatial resolution, which makes it difficult to map findings onto adult research or even to compare across studies. Although the infancy literature discusses prefrontal and temporal cortex broadly, these are very heterogeneous regions, and improvements in neuroimaging technology will better isolate whether a region such as mPFC is consistently involved in live social-interactive contexts. Assuming that there is evidence for continuity in the regions involved, one possibility is that changing connectivity between regions drives social-cognitive changes (cf. Grossmann, 2015), and thus more studies should investigate changes in network connectivity throughout development.

6.2 Context-Dependent Role for Reward Network in Social Interaction

In studies that isolate interaction with an online peer compared to an offline peer or computer control, reward network activation is seen when engaging in joint attention eliciting games (Pfeiffer et al., 2014; Redcay et al., 2010), but not when hearing speech from a live (or perceived live) social partner (Rice, Moraczewski, et al., 2016; Rice & Redcay, 2016). Thus, unlike for the mentalizing network, the presence of a social partner alone may not be sufficient to engage reward network activity. Rather, reward activation during social interactions may be more context dependent.

Which social-interactive contexts do and do not elicit reward activation remains unclear. Offline studies of peer evaluation, in which there is no opportunity for back-and-forth interaction, demonstrate an important role of the reward network in learning about social partners—particularly whether the partner will respond favorably and whether they share similar interests (Gunther Moor et al., 2010; Jones et al., 2014). Such offline studies leave open the question of whether online social interaction differentially engages reward circuitry. One possibility is that live interaction modulates reward system activity differently in online compared to offline contexts, similar to the findings for the mentalizing system.

Studies that do employ real-time peer interactions demonstrate reward network activation when participants share self-relevant information or attention with a peer during a reciprocal interaction (Schilbach et al., 2010; Tamir & Mitchell, 2012; Warnell et al., 2017). This reward activity is seen both during sharing and when receiving a reciprocal, contingent response from a peer, suggesting a role for reward brain regions in tracking

how another person feels about what you like (Warnell et al., 2017) or whether a person follows your lead (e.g., in joint attention studies) (Schilbach et al., 2010). Putting together the peer evaluation and reciprocal social interaction studies, one possibility is that the VS and other components of the reward network are engaged during social interaction but only in contexts that provide an opportunity to learn about one's social partner (e.g., "Are they like me?"; "Will they like me?"). Learning that a peer thinks or behaves similarly to you and/or thinks highly of you is itself intrinsically rewarding and motivating, and such approval is missing in studies of simply listening to live vs recorded speech. Further, reward regions may only be engaged when the participant feels a sense of social agency. For example, the only joint attention paradigms that do find reward system activity allow participants to choose where to direct the partner's gaze. To determine whether and how social interaction alters the role of the reward system in social processing, studies should compare different types of social reward (e.g., positive evaluation, sharing with a peer) within online interactive contexts to the same rewards in offline contexts.

To understand developmental continuity and change in reward activation, more studies are needed that examine social interaction in infancy through adulthood. For example, the age and familiarity of the peer likely influence engagement of reward circuitry and the influence of these factors may change with age. Studies of peer evaluation demonstrate a peak in reward system engagement for positive evaluation during adolescence (Gunther Moor et al., 2010; Guyer et al., 2012), consistent with developmental change in reward systems for nonsocial rewards. However, age-related changes are not seen for social reciprocity in middle childhood (though studies are very limited) (Warnell et al., 2017). It is unknown whether sharing information with a peer and receiving a reciprocal response would result in similar inverted U-shaped reward activation in adolescence. Additionally, there is a major gap in our understanding of social reward in infants and young children due to methodological challenges. Although key components of the reward circuit are subcortical, ERP components in older children and adults have been identified that index social reward (e.g., Cox et al., 2015; Rolison, Naples, Rutherford, & McPartland, 2017). Similar components may be sensitive to social reward earlier in development and could be tested within social-interactive contexts so as to determine if some of the same continuity in social cognitive processing underlies the processing of social reward.

6.3 Connections Within Networks and Between Social Partners

Although this chapter has focused predominantly on the separate roles of each of the four networks, these networks have structural and functional connections. Future research should examine how connectivity within and between networks—particularly the mentalizing and reward networks—supports social interaction across development. For example, the mentalizing network could provide early and sustained activation during an online interaction representing both a preparatory signal and ongoing updating about a social partner's mental state. This system may alert the reward system about the opportunity to learn about one's social partner, and the reward system may provide reciprocal information to the mentalizing system about that learning. These suggestions remain speculative until investigations are conducted into functional connectivity within and between these two systems during ongoing social interaction. Studies of functional connectivity during a "resting state" have demonstrated that these large-scale social brain networks undergo significant change in functional network organization during development (Gu et al., 2015; Power, Fair, Schlaggar, & Petersen, 2010; Uddin, Supekar, Ryali, & Menon, 2011), but limited work has addressed how social-interactive context modulates network connectivity or how these changes are related to real-world social development.

In addition to understanding the connections between these networks within one participant, researchers should examine how changes in network activation unfold in multiple social partners. The studies discussed in this review focus on how engaging in a social interaction alters specific brain networks within one social partner. In addition to modulating these social brain networks, engaging with a social partner can lead to one's brain becoming aligned or coupled with one's social partner. This alignment has been studied through hyperscanning methods in which two participants are imaged at the same time using MRI, EEG, or fNIRS while performing interactive tasks (reviews: Babiloni & Astolfi, 2014; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). Synchrony is typically measured by examining which brain regions (in fMRI) or scalp sensors (in EEG or fNIRS) are more correlated between brains during the interaction task than during solo performance. This synchrony between social partners can increase when the listener is more engaged with the speaker. In a pioneering study, Dikker et al. (2017) recorded portable EEG from a group of students and their teacher in a classroom. They found that the higher the postsemester ratings

of the teacher, the greater the brain-to-brain synchrony between student and teacher during class (Dikker et al., 2017). Thus, some compelling evidence suggests greater alignment between brains during social interaction, but further work is still needed to disentangle the role this neural synchrony may play in facilitating or maintaining ongoing face-to-face social interactions, and whether such synchrony is disproportionately present in particular neural systems. A fascinating extension of this neural synchrony method would be to examine infant–caregiver neural synchrony given the importance of physiological and behavioral synchrony in social development (Feldman, 2012). However, research is just beginning to extend these brain-to-brain synchrony methods to infants (Leong, Byrne, Clackson, Lam, & Wass, 2017).

6.4 Overall Summary and Clinical Implications

The behavioral and neuroscience studies reviewed demonstrate compelling evidence for the importance of social-interactive context. Engaging with a live social partner alters the cognitive and neural mechanisms employed when processing social information. This is especially true within the mentalizing and reward networks. Although both networks are sensitive to online, real-time social interactions, the role of each network appears to differ. While the mentalizing network is most consistently and automatically engaged by the presence of a social partner, the reward network's engagement may be more context dependent. To better understand the interplay between these neural systems, future research should investigate the extent to which these networks work together during social interaction. Current findings suggest both continuity and discontinuity in the processing of social interaction, and future research should conduct longitudinal studies to examine the development of the networks and their patterns of connectivity. Finally, while this review has focused primarily on typical development, understanding how the brain supports social interactions is fundamentally important in understanding disorders of social interaction, such as autism spectrum disorder and social anxiety. While this work is still in its infancy, early evidence suggests that discrepancies between offline and online social processing may be even greater within these disorders than in typical development (Jarcho et al., 2013; Redcay, Rice, & Saxe, 2013; Rolison, Naples, & McPartland, 2015; Schilbach et al., 2013). The world we develop in is a socially interactive one, and, to better understand that development, social neuroscience research ought to be interactive as well.

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