

ABSTRACT

Title of Dissertation: DEVELOPMENTAL NEURAL CORRELATES
OF SOCIAL INTERACTION

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Psychology

Children develop in a sea of reciprocal social interaction, but their brain development is predominately studied in non-interactive contexts (e.g., viewing photographs of faces). This dissertation investigated how the developing brain supports social interaction. Specifically, novel paradigms were used to target two facets of social experience—social communication and social motivation—across three studies in children and adults. In Study 1, adults listened to short vignettes—which contained no social information—that they believed to be either prerecorded or presented over an audio-feed by a live social partner. Simply believing that speech was from a live social partner increased activation in the brain’s mentalizing network—a network involved in thinking about others’ thoughts. Study 2 extended this paradigm to middle childhood, a time of increasing social competence and social network complexity, as well as structural and functional social brain development. Results showed that, as in adults, regions of the mentalizing network were engaged by live speech. Taken together, these findings indicate that the mentalizing network may

support the processing of interactive communicative cues across development. Given this established importance of social-interactive context, Study 3 examined children's social motivation when they believed they were engaged in a computer-based chat with a peer. Children initiated interaction via sharing information about their likes and hobbies and received responses from the peer. Compared to a non-social control, in which children chatted with a computer, peer interaction increased activation in mentalizing regions and reward circuitry. Further, within mentalizing regions, responsivity to the peer increased with age. Thus, across all three studies, social cognitive regions associated with mentalizing supported real-time social interaction. In contrast, the specific social context appeared to influence both reward circuitry involvement and age-related changes in neural activity. Future studies should continue to examine how the brain supports interaction across varied real-world social contexts. In addition to illuminating typical development, understanding the neural bases of interaction will offer insight into social disabilities such as autism, where social difficulties are often most acute in interactive situations. Ultimately, to best capture human experience, social neuroscience ought to be embedded in the social world.

DEVELOPMENTAL NEURAL CORRELATES OF SOCIAL INTERACTION

by

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Foreword

This dissertation contains three jointly authored articles for which I made substantial contributions via taking a lead role in design, analysis, data collection, and writing.

The specific articles included are:

Rice, K., & Redcay, E. (2016). Interaction matters: A perceived social partner alters the neural processing of human speech. *NeuroImage*, *129*, 480-488.

Rice, K., Moraczewski, D., & Redcay, E. (under review). Perceived live interaction modulates the developing social brain.

Rice, K., Sadikova, E., & Redcay, E. (in preparation). Let's chat: Developmental neural bases of social motivation during real-time peer interaction.

When necessary, appropriate permission has been granted by the academic journals for inclusion of these articles in this dissertation.

Dedication

To my family.

Acknowledgements

This dissertation exists because of the invaluable help and support of many people. First of all, I would like to thank the families who devoted their time to participate in our research. Some of my favorite moments from the past five years have been interacting with children and parents. It's all too easy to get stuck in academic minutiae in graduate school, but there is nothing like spending time with an eight-year-old to get your mind onto better things. And many thanks as well to the funding agencies that have supported me, including the National Science Foundation for the Graduate Research Fellowship and the University of Maryland Graduate School for the Flagship Fellowship and Graduate Dean's Dissertation Fellowship.

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Chapter 1: Introduction

From an infant playing peek-a-boo to an adolescent navigating peer relationships, children develop in a world filled with reciprocal social interaction. Such interaction is crucial for typical social and cognitive development, and social disabilities such as autism and social anxiety are often most acute during interaction (Heimberg, Brozovich, & Rapee, 2010; Klin, Jones, Schultz, & Volkmar, 2003). Thus, understanding the brain bases of social interaction will provide critical insight into typical and atypical development. Current research examining social brain function, however, almost exclusively employs non-interactive contexts (e.g., looking at photographs of strangers or listening to recordings) that fail to capture real-world social dynamics (Schilbach et al., 2013). Consequently, a key question about the neural correlates of social processing remains unanswered: how does the developing brain support social interaction?

The Importance of an Interactive Approach to Social Neuroscience

From birth, infants are attuned to social stimuli, including faces (Farroni et al., 2005), voices (Vouloumanos, Hauser, Werker, & Martin, 2010), and biological motion (Simion, Regolin, & Bulf, 2008). By two months of age, infants are sensitive to contingent social interaction (Murray & Trevarthen, 1985; Stormark & Braarud, 2004). Reciprocal social interaction plays a foundational role in a variety of social and cognitive domains, including emotion processing (Pollack & Kistler, 2002) and language learning (Goldstein & Schwade, 2008; Kuhl, Tsao, & Liu, 2003; Rosenberry, Hirsh-Pasek & Golinkoff, 2014). As they age, children master

increasingly complex reciprocal social interactions (Jones & Klin, 2009), and this social development continues into adolescence and beyond (Blakemore, 2008). Consistent with the protracted development of social behavior, social regions of the brain show a prolonged developmental trajectory compared to sensory or motor areas (Gogtay et al., 2004), suggesting a potential bidirectional developmental link between changes in social behavior and changes in the social brain.

In spite of the core role of reciprocal social interaction in development, most developmental neuroscience has examined social cognition in detached contexts, contexts that may have limited translational applications. Although developmental cognitive neuroscience has influenced public policy and pediatric care (e.g., Diamond & Amso, 2008), direct applications of neuroimaging research remain limited in many domains, including education (Sala & Anderson, 2012) and psychiatric diagnosis (Giedd & Rapoport, 2010). For the social domain in particular, translational impacts on developmental disabilities such as autism have been limited (Ecker, Spooren, & Murphy, 2013). The gap between basic neuroscience and real-world application is multi-determined, but one potential contributor is that the developing social brain has been primarily studied in non-interactive paradigms that do not capture the child's experience in the social world. Examining brain function in interaction may lead to findings with greater translational relevance.

Evidence from behavioral and brain research with adults corroborates the importance of adding social context to the study of social cognition. Interactive paradigms (e.g., when two participants are playing a game with each other) produce emergent patterns of behavior not reducible to the individual cognitive level (e.g.,

when participants are playing a game with a computer; reviewed in De Jaegher, Di Paolo, & Gallagher, 2010; Gallagher, 2012; Gallotti & Frith, 2013). In part based on these findings, several recent theoretical papers have argued for the incorporation of interactive paradigms in social neuroscience (Risko, Laidlaw, Freeth, Foulsham, & Kingston, 2012; Schilbach et al., 2013). In spite of such efforts, empirical work using interactive neuroimaging paradigms remains limited, in part because of the difficulty of adequate experimental control. The few well-controlled studies that have tackled interactive neuroscience in adults, however, have shown the potency of live interaction, above and beyond third party observation, in activating social brain areas, including temporal parietal junction (TPJ) and dorsal medial prefrontal cortex (dMPFC; Redcay et al., 2010; Redcay et al., 2013), as well as reward regions (ventral striatum; Schilbach et al., 2010). Thus, both behavioral and brain evidence from the adult literature suggests that an interactive neuroscience perspective can fundamentally change the conceptualization of the social brain. Extending this approach to younger populations could yield new insights into typical and atypical development.

Middle Childhood is a Key Time for Interactive Neuroscience

Although social cognition and behavior develop throughout the lifespan, middle childhood (roughly ages 8-12) is a particularly fruitful period for employing social interactive neuroscience. During middle childhood, children begin to spend more time with their peers (Lochman et al., 2010), as new social groups form (Farmer et al., 2015; Feiring & Lewis, 1991), interactions grow more complex (Sroufe et al., 1999), and socio-emotional understanding increases (Carr, 2011). Concurrent with

these changes in social behavior, social cognition also continues developing, as children show improved pragmatic comprehension (Baron-Cohen, O’Riordan, Stone, Jones & Plaisted, 1999; Capelli, Nakagawa, & Madden, 1990; Demorest, Meyer, Phelps, Gardner, & Winner, 1984; Pexman & Glenwright, 2007) and better theory of mind (Devine & Hughes, 2013; Dumontheil, Apperly, & Blakemore, 2010). Perhaps unsurprisingly, during this period of the change, individual variability in children’s social functioning grows, laying the foundation for adolescent outcomes (Monahan & Steinberg, 2011).

Middle childhood also represents a time of structural and functional change in the brain. In particular, multiple studies have indicated that social brain regions show functional specialization during middle childhood, becoming increasingly selective for particular social inputs (cf. Johnson, 2011). For example, posterior superior temporal sulcus (pSTS) shows increased selectivity for biological motion (Carter & Pelphrey, 2006) and bilateral TPJ becomes increasingly selective for processing others’ mental states as opposed to general social information (Gweon et al., 2012). Further, controlling for age, right TPJ specialization correlates with theory of mind ability (Gweon et al., 2012). Structurally, regions of the brain associated with social processing (e.g., dMPFC, TPJ, aSTS) show protracted development into middle childhood and beyond (e.g., Gogtay et al., 2004; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). Thus, although brain development continues into adolescence (Blakemore, 2008), middle childhood represents an important window for targeting neural development using interactive social paradigms.

The constellation of brain and behavior changes in middle childhood make this period foundational for later outcomes, including depression and anxiety (Bress, Smith, Foti, Klein, & Hajack, 2012; Carr, 2011; Eccles, Roeser, Wigfield, & Freedman-Doan, 1999; Meyer, Weinberg, Klein, & Hajack, 2012). Further, the social skills gap between typical children and children with autism significantly widens during this age range as the social world grows more complex (Anderson, Maye & Lord, 2011; Bal et al., 2013; Kanne et al., 2011; Frazier et al., 2014). In spite of the importance of understanding the neural bases of social interaction in middle childhood, however, very few social cognitive neuroscience studies in this age range have involved real-time, socially-interactive paradigms.

A Social-Interactive Approach to Understanding the Developing Social Brain

Real-world social interactions are complex, interpersonal, temporally unfolding events that draw on multiple cognitive processes; studying the neural bases of such phenomena is a challenge. One potential inroad to understanding social interaction is to leverage insights from existing neuroimaging studies that have used offline paradigms. Many well-characterized neural systems are likely also recruited in interaction, including the systems involved in social perception (including both face and body perception; Minnebusch & Daum, 2009), reward (Haber & Knutson, 2010), language processing (Friederici & Gierhan, 2013), attention (Scolari, Seidl-Rathkopf, & Kastner, 2015), action observation (Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014), and mentalizing—or thinking about the thoughts of others (Saxe, 2009). Deconstructing social interaction—via paradigms designed to differentially tap into

these different neural systems—may offer insight into which processes are core to interaction and which processes are more context-dependent.

Assessing the neural bases of social interaction across varied contexts would allow researchers to test multiple hypotheses about the necessary and sufficient processes that constitute social interaction, as well as whether there are emergent properties of social interaction beyond such component parts. For example, recent research has proposed that humans interact with one another because such interaction is intrinsically rewarding (Pfeiffer et al., 2014; Schilbach et al., 2010). This hypothesis would gain support if, across interactive paradigms, even those without ostensibly rewarding components, reward circuitry was reliably recruited. Similarly, it is possible that some neural systems are sensitive to social context, whereas others are not; identifying these sensitive circuits may give insight into the core neurobiological deficits in autism, as this disorder is most severe in interactive contexts (Klin et al., 2003). If viewing a real versus a photographed face does not produce differences between typical children and children with autism in face processing regions, but does produce differences in mentalizing regions, it may suggest that mentalizing deficits are more core to autism. Similarly, perhaps reward circuitry in autism is most impaired in live, but not recorded, contexts, suggesting that this impaired social motivation is fundamental to the disorder (cf. Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Kohls et al., 2014). Finally, well-controlled experiments may yet reveal no difference between live and not-live contexts. That is, the exact same circuitry may be employed in the same way when processing the component pieces of social interaction (e.g., eye gaze, gesture) as when processing

such pieces in an interactive context, indicating social interaction is reducible to its component systems (cf. Redcay, Rice, & Saxe, 2013)

Admittedly, attempts to identify the cognitive components of interaction via neuroimaging are limited by the overlapping nature of these neural systems, both in terms of the roles of specific regions (e.g., the amygdala has been linked to both socio-emotional and reward processing; Pessoa, 2010), and by these systems' co-occurring activation, especially in interactive contexts (e.g., connectivity between mentalizing and mirror neuron regions increases during self-relevant social contexts; Ciaramidaro, Becchio, Colle, Bara, & Walter, 2014). Despite these difficulties in interpreting whole-brain results, systematically deconstructing social interaction across varied contexts—including, but not limited to, varied modalities, social partners, temporal dynamics, attentional demands, and cognitive tasks—will be foundational to a systematic research program that reconstructs the core neural properties of interaction (cf. Schaafsma et al., 2015).

As a first step in building a comprehensive social-interactive research program, this dissertation examines social interaction in two contexts designed to differentially recruit neural circuitry: a social communicative context and a social motivational context. Social communication—the 'shared intentionality' that emerges between a sender and receiver (Tomasello et al., 2005)—and social motivation—the desire to interact and enjoyment of that interaction (Kohls, Chevallier, Troiani, & Schultz, 2012)—represent two early-emerging domains of typical development (e.g., Bigelow, 1998; Murray & Trevarthan, 1985; Rekers, Haun, & Tomasello, 2011; Rochat, Querido, & Striano, 1999) that undergo significant changes during middle

childhood (e.g., Clark & Delia, 1976; Oh et al., 2008; Whalen & Pexman, 2010). Autism is also characterized by core deficits in both domains (Chevalier et al., 2012; Tager-Flusberg, 2007). Further, these two contexts are well suited for assaying the roles of various cognitive systems in social interaction, as previous research suggests strong a priori hypotheses about the neural circuitry that may support social communication (i.e., mentalizing networks) and social motivation (i.e., reward networks) during live interaction.

Social Communication

This dissertation approaches social communication not as a question of creating or processing a specific utterance or gesture, but rather as two individuals' mutual understanding that one wants to transmit information to the other (Clark, 1996; Sperber & Wilson, 1996; Tomasello et al., 2005). Within this framework, social-interactive context may alter the processing of communicative cues (e.g., gesture, speech, written text), via the receiver cognitively representing the social partner's communicative intent or mental state (Tomasello, Carpenter, Call, Behne, & Moll, 2005). That is, interactive context may increase recruitment of the mentalizing network—regions involved in representing the mental states of others (Saxe, 2009). Thus, we aimed to determine whether interactive context alone altered the processing of communicative cues, with specific hypotheses about the brain's mentalizing regions. Specifically, in order to avoid previous confounds in studies of live communication, this dissertation employed a novel, well-controlled social communicative paradigm in which individuals listened to speech that was believed to be either presented over a real-time audio feed or believed to be prerecorded.

We first examined the neural correlates of interactive social communication in adults. Establishing developmental endpoints is a necessary step to contextualize developmental research, especially in novel or understudied fields (cf. Apperly, Samson, & Humphreys, 2009; Cykowicz, Feldman, Snodgrass & Rothstein, 2000; Farrell & Barrett, 2006; Halberda & Feigenson, 2008) More practically, adults could also be in the scanner for longer than children; we could therefore include a theory of mind localizer task designed to isolate, for each individual, the exact regions employed in mental state judgments (Dodell-Feder, Koster-Hale, Bedny, & Saxe, 2011), allowing us to directly test whether the mentalizing network was recruited more during live speech. After establishing the developmental endpoints of processing live speech in the brain, we next extended the same paradigm to middle childhood to examine whether similar social cognitive regions were involved in supporting live interaction.

Social Motivation

We also designed a paradigm to tap into varied facets of social motivation in middle childhood. Specifically, children engaged in a chat in which they initiated interaction via sharing likes and hobbies to a peer and then received contingent and engaged replies. Social initiation and reciprocal engagement have been previously identified as important components of social motivation (Kohls et al., 2012; Tamir & Mitchell, 2012) and sharing with peers may be especially salient in middle childhood (Buhrmester & Prager, 1995). Further, this design separated phases of social reward—desire to initiate interaction and the enjoyment of that interaction—that may have different neural substrates (Haber & Knutson, 2010; Kohls et al., 2012). We

hypothesized that social cognitive and reward circuitry would be more engaged when chatting with a peer as compared to a computer control. Human reward circuitry has been well-characterized across development (e.g., Berridge & Kringelbach, 2008; Knutson & Cooper, 2005; Galván, 2010), and we therefore had strong a priori hypotheses about the involvement of specific anatomical regions. Thus, unlike in the studies of social communication, we examined social motivation in middle childhood without first using an identical paradigm in adults. Further, unlike the social communication studies, this design did not address whether live interaction was processed different from recorded human interaction. Rather we leveraged the insight from those communicative studies—that social interaction matters—to study how social motivation operated in a live context.

Summary of Current Approach

This dissertation presents three fMRI studies (Chapters 2, 3, & 4) that explored the neural bases of how social motivational and social communicative processes unfold in interactive contexts. The aim of Chapter 2 (Rice & Redcay, in press) was determine whether and how social context altered the processing of otherwise matched speech. Specifically, adults ($N=29$) listened to speech that they believed was presented in real-time over an audio-feed and speech that they believed was recorded. We compared activation in each individual's mentalizing network, and hypothesized that a live, interactive context would increase activation in theory of mind regions, even for speech devoid of social content. Using the results of Chapter 2 to establish developmental endpoints in social-interactive processing, Chapter 3 (Rice, Moraczewski, & Redcay, under review) extended the same social

communication paradigm to middle childhood ($N=26$ children aged 7-13). The aim of the study was to investigate whether the developing brain was also sensitive to live context when processing speech and to examine any potential age-related changes during this developmental period. Rather than directly testing the effect of social context, Chapter 4 (Rice, Sadikova, & Redcay, in preparation) leveraged the previous studies' insights about the importance of interactive paradigms in order to assess social motivation in an interactive framework. Children ($N=26$) aged 8-12 believed they were participating in a real-time chat with a peer, and we hypothesized that, as compared to a computer control, this interaction would result in increased engagement of social cognitive and reward circuitry. Additionally, as with Chapter 3, we examined the effects of age on specialization for processing social interaction. Taken together, this set of studies was designed to explore the behavioral and neural bases of multiple facets of on-going social interaction across development.

Importantly, the claim of this dissertation is not that these studies isolate or even perfectly capture the very large constructs of social communication and motivation. Rather, the paradigms are designed to load factors that targeted the certain neurocognitive systems (e.g., previous research has linked self-disclosure and receiving peer approval to reward systems; Guyer, Choate, Pine, & Nelson, 2012; Tamir & Mitchell, 2012) and then to embed these factors in interactive contexts. We acknowledge that although these paradigms were designed to target social communicative and social motivational processes, such processes may span both tasks (e.g., reward circuitry may involved when listening to live speech and mentalizing regions may represent communicative intent when receiving an engaged

reply from a social partner). To that end, in addition to localizer and region of interest analyses, we employed whole-brain analyses in all studies in order to assay the involvement of multiple neural systems. In a research framework designed to target what unites interactive experience, it is important to consider whether, for example, reward or mentalizing circuitry is recruited across different social contexts. Although this dissertation does not explicitly compare across studies, such comparisons within single participants across paradigms represent an important component of future social-interactive research.

A brief note on formatting: although each study is presented as an independent manuscript, the references are included in a single section at the end of the full dissertation, per graduate school guidelines. The appendices contain supplementary materials for each chapter, and Appendix D includes the literature review. Chapter 2 has been accepted and is in press at *NeuroImage*, Chapter 3 is currently under review, and Chapter 4 is ready for submission.

Chapter 2: Interaction Matters: A Perceived Social Partner Alters the Neural Processing of Human Speech

Abstract

Mounting evidence suggests that social interaction changes how communicative behaviors (e.g., spoken language, gaze) are processed, but the precise neural bases by which social-interactive context may alter communication remain unknown. Various perspectives suggest that live interactions are more rewarding, more attention-grabbing, or require increased mentalizing—thinking about the thoughts of others. Dissociating between these possibilities is difficult because most extant neuroimaging paradigms examining social interaction have not directly compared live paradigms to conventional “offline” (or recorded) paradigms. We developed a novel fMRI paradigm to assess whether and how an interactive context changes the processing of speech matched in content and vocal characteristics. Participants listened to short vignettes—which contained no reference to people or mental states—believing that some vignettes were prerecorded and that others were presented over a real-time audio-feed by a live social partner. In actuality, all speech was prerecorded. Simply believing that speech was live increased activation in each participant’s own mentalizing regions, defined using a functional localizer. Contrasting live to recorded speech did not reveal significant differences in attention or reward regions. Further, higher levels of autistic-like traits were associated with altered neural specialization for live interaction. These results suggest that humans engage in ongoing mentalizing about social partners, even when such mentalizing is

not explicitly required, illustrating how social context shapes social cognition.

Understanding communication in social context has important implications for typical and atypical social processing, especially for disorders like autism where social difficulties are more acute in live interaction.

Introduction

Two friends are out for a walk. One turns to the other, points to the sky and says “Look,” and both crane their necks upwards to see a hot air balloon. This interchange, and the thousands of moments of their interaction before and after, can be decomposed into constituent parts: speech processing, gesture, gaze following. Each piece alone, however, is neither necessary nor sufficient to create full, experienced interaction, with its emergent proprieties and attunement between social partners that extends beyond input and output stimuli. During real-time social interactions, social partners create a shared psychological state (Tomasello, Carpenter, Call, Behne, & Moll, 2005) necessary for successful communication. In this framework, communication is defined not by the medium (e.g., language), but by the desire in the sender to create this shared psychological state, a recognition of that desire by the receiver, and the “shared intentionality” that the two partners create together (Clark, 1996; Sperber & Wilson, 1996; Tomasello et al., 2005). Characterizing the neural bases of communication will improve understanding of this core human behavior, with implications for social disabilities such as autism, where impairments are most acute in social interaction (Klin, Jones, Schultz, & Volkmar 2003).

Past neuroimaging research has almost exclusively examined the component pieces of communication (e.g., emotion understanding, language processing, thinking about others’ mental states), despite behavioral evidence that these processes operate differently in interactive, communicative contexts (Gallotti & Frith, 2013; Sebanz, Bekkering, & Knoblich, 2006). For example, infant interaction with an adult

promotes language learning more than observing matched recorded stimuli (Goldstein & Schwade, 2008; Kuhl, Tsao, & Liu, 2003). In adults, even the belief that one is interacting with another person's avatar (versus an otherwise identical computer agent) improves learning (Okita, Bailenson, & Schwartz, 2007; see Fox et al., 2015 for a review of avatar vs. agent literature). Individuals also show different gaze patterns when viewing a potential interactive partner as compared to a video (Freeth, Foulsham, & Kingstone, 2013; Laidlaw, Foulsham, Kuhn, & Kingstone, 2011; Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012), and naturalistic stimuli better distinguish typical and autism groups (Speer, Cook, McMahon, & Clark, 2007). Thus, although extant neuroimaging research has yielded important insight into the social brain, non-interactive methods cannot capture whether and how the social brain functions differently in social interaction (Schilbach et al., 2013).

Although evidence suggests real-time interaction may affect behavior, the question of how real-time interaction alters communication remains unanswered. Several theories suggest that a fundamental aspect of communication is making rapid inferences about a social partner's communicative intentions and mental states even in simple interactions (e.g., gaze following; Teufel et al., 2009), although the exact nature of these inferences is debated (Clark, 1996; Klin et al., 2003; Shintel & Keysar, 2009; Sperber & Wilson, 1996; Teufel et al., 2009; Tomasello et al., 2005). Despite the possibility that communication and mental state inference—or mentalizing—are intertwined, both processes are typically studied separately in non-interactive contexts. For example, fMRI research identifying a “mentalizing network” has predominately focused on explicit reasoning about the mental state contents (e.g.,

beliefs) of characters in stories. The role of this brain network in ongoing interaction is unknown. One possibility is that although not all social interaction contains explicit mentalizing demands, implicit mentalizing processes—including tracking mental state content (Schneider, Slaughter, Becker, & Dux, 2014b; Senju, Southgate, White, & Frith 2009) and monitoring communicative intent (Kampe, Frith, & Frith, 2003)—are more engaged when processing communicative cues from a real-time social partner versus recorded cues.

Greater demand on mentalizing systems is just one theorized difference between processing real-time communication and processing offline, component communicative behaviors. Other possibilities are that live, contingent interactions are more rewarding (Mundy & Neal, 2000; Pfeiffer et al., 2014; Schilbach et al., 2010, 2013), provide unique sources of information compared to recordings (e.g., responsive eye gaze; Kuhl, 2011), or capture more attention (Kuhl, 2007; Risko et al., 2012), perhaps due to increased arousal (Okita et al., 2007), than recorded stimuli. Finally, a tightly controlled experiment may reveal no differences in the processing of matched communicative behaviors in offline versus interactive contexts, suggesting that communication is the sum of its parts. Neuroimaging paradigms may be especially well suited to dissociate these possibilities and to identify the implicit, ongoing processes that are hypothesized to underlie communication and that are difficult to assess via self-report (Schneider, Nott, & Dux, 2014a).

Despite the promise of neuroimaging to illuminate communicative processes, extant interactive neuroimaging paradigms have not directly addressed whether and how interactive context changes the processing of well-matched input stimuli, either

because that is not the direct question of interest or due to methodological limitations (Redcay, Rice, & Saxe, 2013). Past interactive neuroimaging studies have contrasted contingent interaction to non-contingent recordings (Redcay et al., 2010; Redcay, Kleiner, & Saxe, 2012; Schilbach et al., 2010) and compared direct to averted gaze (Holler et al., 2015), but such paradigms do not directly address whether live context alone alters the processing of well-matched input stimuli. Research in which participants play either human or computer opponents in various games (Coricelli & Nagel, 2009; Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe, Houser, Ryan, Smith, & Tourard, 2001) examines engagement with human versus non-human actors, but not how human communication differs in interactive versus non-interactive contexts. Further, such games often demand explicit mentalizing (e.g., deliberate reflection on an actor's motive) and thus cannot determine the extent to which mentalizing is automatically engaged in day-to-day human communication (e.g., pointing to a balloon in the sky). Determining whether and how the neural systems underlying communication differ when communicative acts occur in interactive contexts requires targeted and well-controlled paradigms.

In this study, we employed a novel fMRI paradigm to address the vital gap in our understanding of the neural systems underlying interactive communication. Participants completed trials in which they listened to a short vignette presenting two options, then heard about someone's preference, and made a choice for that person. For some trials, participants believed they were listening to a live social partner over a real-time audio-feed, whereas for other trials they believed they were listening to a recording of another person. Crucially, all stimuli were prerecorded, to ensure

matched stimuli within and across participants. To match contingency and attention across conditions, participants saw contingent positive or negative feedback based on their answer to each question. At the end of the experiment, participants completed ratings of liveness, likeability, and engagement for the live and recorded speakers.

Our main analysis examined neural responses during the short vignette portion (i.e., story), which contained no explicit mentalizing demands. Our aim was to identify the neural systems supporting social interaction beyond the processes supporting the interaction's component parts (e.g., processing human speech). We hypothesized that the brain would be differentially engaged when participants perceived the speaker to be talking to them in real-time (i.e., Live) as compared to a matched recording, specifically in each participant's mentalizing regions. We identified each individual's mentalizing regions using a highly replicated language-based theory of mind localizer, which isolates reasoning about mental states from reasoning about physical inferences that are matched on representational and attentional demands (Dodell-Feder, Koster-Hale, Bedny, & Saxe, 2011). Using a functional localizer is especially important in isolating the regions involved in mentalizing, as portions of the mentalizing network (e.g., TPJ) have also been implicated in more general attentional processes (Decety & Lamm, 2007; Mitchell, 2008) and overlap with portions of the default mode network (Mars et al., 2012; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008; Spreng, Mar, & Kim, 2009). As a control, we also compared two recorded conditions: a friendly, engaging voice (Social, which was contrasted with the Live condition), and a less engaging voice (Standard). This contrast between recorded conditions was designed to ensure

that effects of audio characteristics, likeability, or attention were not driving differences between perceived live and recorded conditions.

Finally, we examined whether autistic-like personality traits were related to neural sensitivity to live interaction, given that autism has been associated with diminished response to live social partners (Klin et al., 2003) and with preserved explicit mentalizing but impaired online implicit mentalizing (Senju et al., 2009). Although all participants in the current study were typical adults, previous research has indicated that typical variability in autistic-like traits is related to behavioral and brain measures of social cognition (e.g., Barman et al., 2015; Bayliss & Tipper, 2005; Hasegawa et al., 2013; Nummenmaa, Engell, Von Dem Hagen, Henson, & Calder, 2012; Miller & Saygin, 2013; Poljac, Poljac, & Wagemans, 2013), and there is evidence that the relation between autistic-like traits and social behavior is stronger in live than recorded contexts (Laidlaw et al., 2011). In particular, we theorized that individuals with higher levels of autistic-like traits would show diminished behavioral responsiveness to the live social partner (as measured by self-report) and diminished sensitivity to live versus recorded speech, especially in regions associated with mentalizing, which would provide evidence that sensitivity to social partners is a core social process.

Methods

Participants

Thirty-one adults (13 males), aged 18–27 years, participated in the neuroimaging study in exchange for course credit or payment. All participants were native English speakers, had normal hearing, normal or corrected-to-normal vision,

no first-degree relatives with autism or schizophrenia, and no personal history of any neurological impairments or psychological disorders. Two participants were excluded because they did not believe that the interaction in the live condition was live, yielding a final sample of 29 adults. A subset ($n = 23$) of the final sample completed a mentalizing localizer task, and analyses with the localizer regions were restricted to this subset. A separate sample of twenty adults (13 males), aged 18–29 years, completed pilot testing of the audio stimuli, and twenty other adults (8 males), aged 18–28 years completed a behavioral version of the social interaction experiment. The local Institutional Review Board approved all study protocols.

Social Interaction Experiment

Creating the live illusion. Participants were told that they would listen to short stories and answer questions, and that sometimes the stories and questions would be presented by a social partner via a real-time audio-feed, and that, for those items, they would receive real-time video feedback from the social partner (e.g., thumbs up). Participants were told that other trials would be prerecorded audio with computer-generated feedback. In actuality, all stimuli were prerecorded.

To maintain the live illusion, the experimenter wore the same clothing and had the same appearance as in the prerecorded feedback videos. Further, before the experiment, participants participated in a truly live video chat (Supplementary Figure S2.1). Participants only met the live speaker. Participants were debriefed at the end of the experiment.

Task design. The task was programmed and presented using the Psychophysics Toolbox Extension for MATLAB 7.6 (PTB-3; Brainard, 1997).

Participants viewed 36 individual trials across 4 runs, 12 from each condition: Live, Social, and Standard (Figure 2.1). Each condition had a different female speaker: Live was the live social partner with a friendly tone; Social was a recorded, friendly voice; and Standard was a recorded, neutral voice. Each trial consisted of the story, answering a question by selecting one of two options and receiving feedback. Live feedback was a silent video of the live speaker, Social feedback was a standardized picture of a happy or sad female (Tottenham et al., 2009), and Standard feedback was a gold star or red “x.” During all audio, and for 2 s before the start of the story, a screen displayed either LIVE VOICE (in green text) or RECORDED (in orange text).

A 2- to 4-s jittered fixation cross was present between the story and the question period and before feedback. There were also 20 s of baseline (fixation cross) at the start, middle, and end of each run. Trial distribution and timing was determined by OptSeq (<http://surfer.nmr.mgh.harvard.edu/optseq/>). The event of interest was the story, and collinearity analysis using AFNI’s 3dDeconvolve (Cox, 1996) revealed that all beta values of interest were estimable.

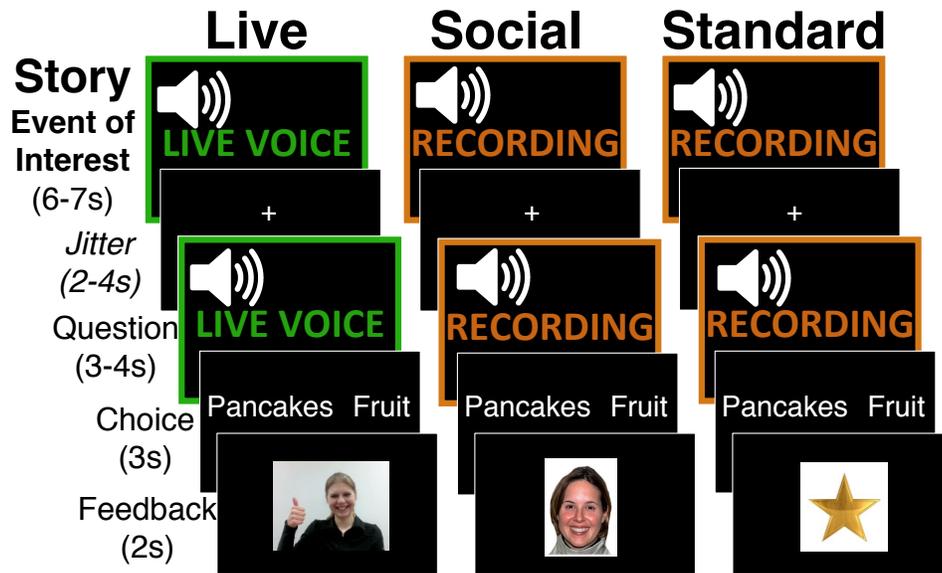


Figure 2.1. Experimental trial structure. The three conditions (Live, Social, and Standard) are depicted in the three columns. Participants believed that audio in the Live condition was presented over a live audio-feed, and the other two conditions were recorded. The Live and Social speakers both had a friendly tone and the Standard speaker had a neutral tone. The content of the story portion was identical across conditions and consisted of a two-sentence description of two different objects that contained no reference to people or mental states (e.g., “There are two things on the breakfast menu. One is pancakes and one is a bowl of fruit.”). For Live trials, participants answered a question about the live social partner and for the Social and Standard conditions, participants answered question about a third party character (e.g., “I/Megan am/is trying to eat healthy. Which food should I/she eat?”). Participants saw contingent feedback based on their answer to the question. Experimental analyses were restricted to the story portion. s = seconds. (See also Supplementary Figure S2.1 & Supplementary Table S2.1).

Post-test procedure. Participants completed a 7-point Likert-scale questionnaire to assess perceptions of each speaker. For each speaker, participants were asked two questions to assess likeability (“How much did you like this speaker?” and “How much do you think you would like interacting in real life with this speaker?”), two questions to assess engagement (“How much did you pay attention when this speaker was talking?” and “How motivated were you to get the questions asked in her voice right?”), and three questions to assess liveness (“How much did your experiences with her feel live?” “How much did it feel like this

speaker was talking directly to you?” and “How much did it feel like this speaker was interacting with you in real-time over a direct connection versus sounding like a recording?”). For each participant, we averaged together these scores on individual items to create composite liveness, likeability, and engagement scores for each speaker.

Participants also completed the Autism Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), which is a self-report measure of autistic-like personality traits. For each item (e.g., “I enjoy social situations”) participants answered on a scale of 1 (definitely agree) to 4 (strongly disagree), such that higher scores indicate more autistic-like traits. The AQ captures variability in ASD traits in the typical population (Baron-Cohen et al., 2001), and in typical individuals, higher AQ scores (more autistic-like traits) are related to diminished or atypical social cognitive abilities (e.g., perception of biological motion; Miller & Saygin, 2013; gaze cueing; Bayliss & Tipper, 2005; emotion perception; Poljac et al., 2013), atypical behavioral response to live but not recorded interaction (Laidlaw et al., 2011), and to neural activity in response to social stimuli (Barman et al., 2015; Hasegawa et al., 2013; Nummenmaa et al., 2012). The current sample showed variability in AQ scores, ranging from 8 to 29 (mean = 16.5, SD = 5.4), with all participants scoring below the conventional cutoff for clinical concern (a score of 32; Baron-Cohen et al., 2001).

Stimuli. Each of the three trial types (i.e., Live, Social, Standard) had a unique speaker. Given the current study’s within-subjects design, it was critical that participants were immediately aware of which condition they were in. To ensure

immediate and reliable recognition of condition, each condition contained both a salient bottom-up cue (speaker voice) and top-down cue (background screen) as to condition.

All audio was normalized to 60 dB. We compared speakers on pitch and length of their audio clips using Praat 5.3 (Boersma, 2002; Supplementary Table 2.1). There were no length differences and, as intended, the Standard speaker was lower-pitched than the other speakers. For the story, the Social speaker had higher pitch than the Live speaker. To determine baseline ratings of liveness, likeability, and engagement for all three speakers, we conducted pilot testing ($N = 20$) in which participants listened to audio but were not told any stimuli were live. Unlike in the main experiment, participants did not meet any of the speakers, only heard third-person audio recordings (e.g., “What should Mary do?”), and saw the same feedback (gold star) for each speaker. There were significant effects of speaker on ratings of liveness, likeability, and engagement ($ps < .01$; Supplementary Table 3C). The Social speaker was rated as more live and likeable than the Live speaker, and the Live speaker and Social speaker were more live, likeable, and engaging than the Standard speaker ($ps < .05$).

Each participant was assigned one of three stimuli sets, which differed on which 12 short vignette and question pairs were assigned to each condition, and ensured that the total amount of time for each condition was matched. The order of the items was randomized within condition and the order of runs was counterbalanced across participants.

Social Interaction Control Behavioral Study

In addition to the Live speaker being presented as live, there were three other differences between the Live and Social conditions: first-person language (e.g., “I like”), video rewards, and meeting the speaker before the experiment. Given that this novel paradigm represents an initial attempt to understand the neural mechanisms of social interaction, we wanted to ensure that the social-interactive context was sufficiently believable (i.e., meeting the live partner before the experiment) and salient (i.e., being visually reminded of the live interaction via short videos of the live social partner, making a choice about the social partner). Although only the content-matched audio portion was analyzed, these three potential confounds were included in this initial study in order to reinforce the live illusion and to create a more ecologically valid social context.

In order to determine if these three factors alone could produce perceived liveness, we conducted a separate behavioral study with $N = 20$ participants (who did not participate in the pilot behavioral experiment or scan) who completed the same task as the fMRI participants, including the post-test questionnaire (Supplementary Table S2.3B), but were told all stimuli were prerecorded.

Mentalizing Localizer

A subset of participants ($n = 23$) completed a mentalizing localizer after the main social interaction experiment, in which they saw written stories about false beliefs and false physical representations (e.g., photographs; Dodell-Feder et al., 2011; <http://saxelab.mit.edu.proxy-um.researchport.umd.edu/superloc.php>).

Participants completed two runs, each with five false belief and five false photograph

stories (presented for 10 s), followed by a true-false question presented for 4 s. The 14-second block was analyzed as one event.

Image Acquisition and Preprocessing

Imaging data were collected using a 12-channel head coil on a single Siemens 3.0-T scanner at the Maryland Neuroimaging Center (MAGNETOM Trio Tim System, Siemens Medical Solutions). The scanning protocol for each participant consisted of four runs of the main experiment (T2-weighted echo-planer gradient-echo; 36 interleaved axial slices; voxel size = $3.0 \times 3.0 \times 3.3$ mm; repetition time = 2200 ms; echo time = 24 ms; flip angle = 90° ; pixel matrix = 64×64), two runs of the theory of mind localizer (T2-weighted echo-planer gradient-echo; 36 interleaved axial slices; voxel size = $3.0 \times 3.0 \times 3.3$ mm; repetition time = 2000 ms; echo time = 24 ms; flip angle = 90° ; pixel matrix = 64×64), and a single structural scan (three-dimensional T1 magnetization-prepared rapid gradient-echo sequence; 176 contiguous sagittal slices, voxel size = $1.0 \times 1.0 \times 1.0$ mm; repetition time = 1900 ms; echo time = 2.52 ms; flip angle = 9° ; pixel matrix = 256×256). The parameters for the functional scans for the social interaction experiment were selected after piloting with four typical adults in order to best allow for signal preservation while maximizing specificity in regions prone to signal dropout.

For both the social interaction experiment and the mentalizing localizer, fMRI preprocessing was performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>). Data were slice-time corrected, realigned to the original volume from the first functional run, and then normalized to the Montreal Neurological Institute (MNI) template brain using both linear and nonlinear transformations. Data were high-pass filtered (1/128

Hz) and spatially smoothed using a 5 mm full-width half-maximum (fwhm) Gaussian kernel.

Outlying volumes (i.e., due to motion or global signal) for each participant were detected using the artifact detection toolbox (http://nitrc.org/projects/artifact_detect). Motion outliers were defined as the difference between two consecutive volumes exceeding 1 mm (across translational and rotational movements), and global signal outliers were defined as being three SD from the mean global signal. For the social interaction experiment, participants were to be excluded if, on two or more runs, their number of motion or global signal outliers exceeded 15% of collected volumes or if total motion exceeded 4 mm. No runs, however, met these criteria. For the theory of mind localizer, two participants had runs with between 15% and 20% outliers, but this motion was not correlated with the task and thus all subjects were included in analyses.

Data Analysis

Social interaction experiment analysis. General linear models were used to estimate parameters for each condition's story event. The model included each story event convolved with the canonical hemodynamic response function, and, as regressors of no interest, the anticipatory periods, the question periods, and the feedback periods. All six motion parameters (roll, pitch, yaw, x, y, and z) and each individual outlier time point were included as regressors.

We analyzed two specific contrasts: first, to examine the effect of live interaction we compared Live Story vs. Social Story; second, to isolate the effects of prosody and likeability, we compared Social Story vs. Standard Story. Given that the

Standard Story was not well matched to the Live Story, that comparison was less theoretically interesting, and we did not analyze that contrast. Contrast maps were thresholded at a two-tailed $p < .001$ and cluster-corrected for multiple comparisons (overall alpha = .05, $k = 93$) using SPM's false discovery rate algorithm. In order to examine individual differences in sensitivity to live interaction, we extracted each individual's contrast value from the clusters identified in the group-level analysis. Specifically, we extracted each individual's Social > Standard contrast values for the clusters showing a significant effect of group for Social > Standard and similarly, Live > Social values for the clusters showing a significant effect of group for Live > Social. We examined the correlations between these individual contrast values and both AQ scores and perceived liveness of the Live speaker. We specifically examined liveness (rather than likeability or engagement) as we designed this rating to quantify the participant's experience of the live illusion.

Mentalizing localizer analysis. The regression model included the same motion and outlier nuisance regressors as the social interaction experiment and additional regressors for the belief and photo story conditions. To identify each individual's regions associated with explicit mentalizing, we examined each participant's whole-brain contrast for false belief vs. false photo stories at $p < .001$, $k = 10$ voxels, and identified peak coordinates for eight regions of interest within each participant (Young, Cushman, Hauser, & Saxe, 2007): bilateral TPJ, bilateral aSTS, precuneus, dMPFC, middle MPFC (mMPFC), and ventral MPFC (vMPFC). All participants with the localizer scan ($n = 23$) had identifiable activation in all regions except for mMPFC ($n = 21$) and vMPFC ($n = 18$). Voxels that were significantly

active within a 9 mm radius sphere surrounding each participant's peak coordinate were used as regions of interest. Again, within each region, we analyzed two specific contrasts: first, Live Story vs. Social Story to examine the effects of live social interaction on activation in mentalizing regions; and second, Social Story vs. Standard Story, to examine the effects of prosody and likeability in mentalizing regions. Given that our specific a priori hypotheses related to these pairwise comparisons, in order to minimize comparisons, we did not compare the effects of Live Story to Standard Story in these regions nor did we conduct a repeated-measures ANOVA across all three conditions.

Results

Perceived Interactive Context Modulates Brain Response to Speech

In order to examine how live interaction modulates the neural correlates of language processing, we compared BOLD activation during the story for the Live condition to the recorded Social condition. Whole-brain results demonstrated that processing speech from a live social partner modulated neural activity compared to processing matched recorded human speech (Figure 2.2A; Supplementary Table S2.2 & Supplementary Figure S2.2), specifically in regions often associated with social cognition (i.e., mentalizing) and social engagement (Frith & Frith, 2006), including dorsomedial prefrontal cortex (dMPFC) and temporal parietal junction (TPJ).

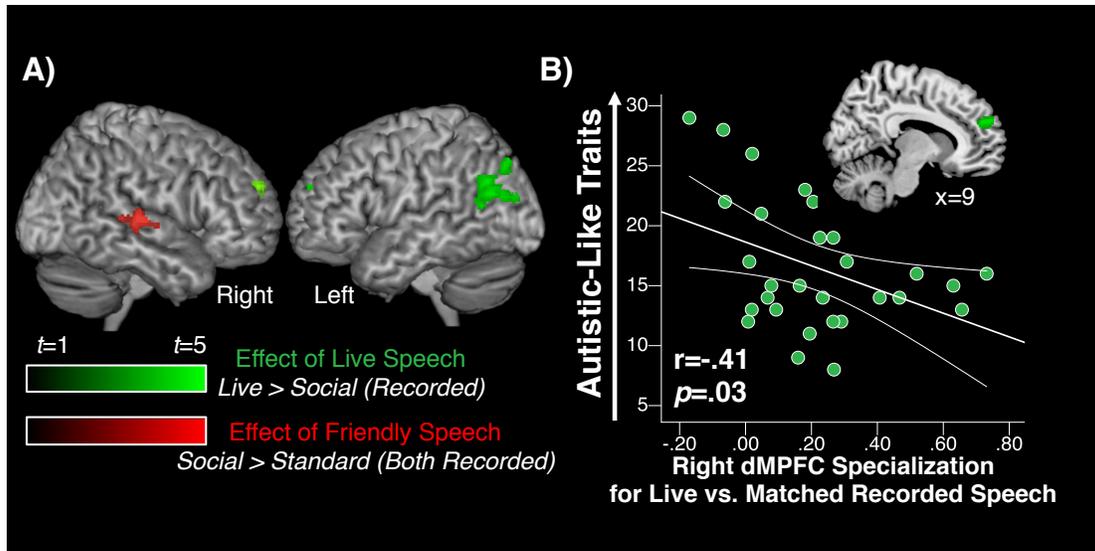


Figure 2.2. Neural correlates of processing live versus recorded speech. (A) Whole-brain comparisons ($N = 29$) of Live Story versus Social Story and Social Story versus Standard Story (corrected $p < .05$). Listening to live speech versus a matched recording activated regions of the brain associated with processing social stimuli, and this activation was dissociable from the effect of listening to a friendly and engaging speaker (Social > Standard). (B) The relation between autistic-like traits, as measured by the Autism Quotient, and individual contrast values for Live Story > Social Story ($N = 29$). Right dorsomedial prefrontal cortex (dMPFC) was defined based on the active voxels for the group-level contrast in (A). Higher levels of autistic-like traits were associated with lower levels of differential activation for live stimuli. (See also Supplementary Table S2.2 and Supplementary Fig. S2.2).

Effects of Live Condition Reflect Perceived Interactive Communication

Perceived liveness is driven by the live illusion. To ensure that these whole-brain effects were due to perceived live interaction and were not reducible to other between-condition differences, we investigated several potential confounds. First, our condition manipulation relied on a participant's belief that the Live condition was live. In order to confirm and quantify belief in the illusion, all participants filled out rating scales after the fMRI session. All participants believed the live illusion. To further check the top-down manipulation of perceived liveness, we examined participant ratings of speaker liveness (e.g., "How much did it feel like this speaker was talking directly to you?"). Participants rated the Live speaker as significantly

more live than the Social speaker ($p < .001$; Figure 2.3A; Supplementary Table S2.3A). Greater perceived liveness of the Live speaker was also marginally correlated with greater activation for Live vs. Social speech in rdMPFC ($r = .34, p = .07$), as measured by individually extracted contrast values from the group-defined cluster, although correlations with perceived liveness were not significant for any of the other identified regions. Further, there was also no correlation between perceived liveness and Social vs. Standard speech activation in right STG, the region defined by that group-level contrast ($r < .1$).

In addition to evidence from the neuroimaging study, an additional behavioral experiment with a separate group of participants ($N = 20$) was conducted to analyze factors that were confounded with the live condition. These potential confounds were included to enhance the illusion of liveness: participants met only the live speaker briefly before the start of the experiment, saw the live speaker give ostensibly live video feedback, and heard the live speaker use first-person language in the unanalyzed question portion. In this separate study, where live stimuli were presented as recorded, these three confounding factors failed to produce significantly higher liveness ratings for the Live compared to Social speaker (Supplementary Table S2.3B). That is, only when participants were told that they were interacting with a live social partner did they actually rate that speaker as feeling significantly more live.

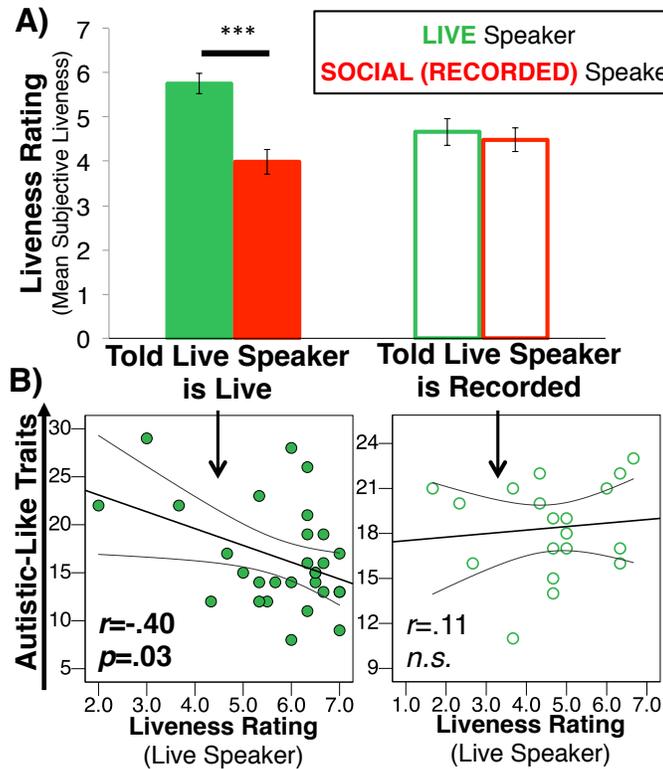


Figure 2.3. Behavioral impressions of speaker liveness. (A) Perceived liveness is driven by the illusion of a live setup. All scanned participants ($N = 29$) were told that the Live condition was live, and they rated the live and matched recorded (i.e., Social) speakers as significantly different on a post-test questionnaire of perceived liveness. Perceived liveness was assessed using a composite of Likert-scale items scored on a 1 to 7 scale (e.g., how direct the speaker seemed, how much it seemed as though the speaker was in the room with the participant). This difference disappeared on an identical behavioral version of the task in which participants ($N = 20$) were told all audio—including audio from the scan’s Live speaker—was prerecorded. (B) Perceptions of liveness for the Live condition speaker were significantly correlated with autistic-like traits (as measured by the Autism Quotient) only for the group that thought they were participating in a live interaction. For both groups, correlations with Autism Quotient scores and perceived liveness of the Social speaker were not significant. *** $p < .001$ (see also Supplementary Table S2.3).

Effects of live context are not reducible to other differences between conditions. One factor that could account for differences between live and recorded interactions is differences in attention. To examine this, we compared reaction time across conditions for the question that followed the story and found no significant differences ($F < 1$, Supplementary Table S2.4). There were also no significant between-condition differences in accuracy, but the very high accuracy for all

questions precludes using that measure to make interpretations about levels of attention across conditions.

Self-reported social engagement and speaker likeability, however, did differ across conditions. Participants rated the Live speaker as more likeable and socially engaging than the Social speaker ($ps < .01$). Thus, to ensure that whole-brain Live > Social effects were not driven by likeability or engagement, we compared Social and Standard speakers, who also differed on likeability and engagement ($ps < .01$). This comparison also helped isolate any low-level effects of audio characteristics, as both Live versus Social and Social versus Standard conditions differed on mean pitch. The comparison of the two not-live conditions (Social > Standard) only implicated regions frequently associated with auditory and speech processing (right superior temporal gyrus), and the specific activation was consistent with pitch responsivity (www.neurosynth.org; posterior probability for pitch = 0.87). There was no overlap in regions identified by the Live > Social and Social > Standard comparisons.

Ongoing Mentalizing Supports Communicative Interaction

Given that additional analyses revealed that the Live > Social effects were driven by the experimental manipulation of a simulated live interaction and not by potential confounding effects, we next examined the Live > Social contrast in each participant's individually identified mentalizing network (defined using an independent localizer; Dodell-Feder et al., 2011). All eight mentalizing regions showed the hypothesized pattern of results: increased activation for live versus recorded social speech. Specifically, this difference was significant in six of the eight identified regions: bilateral TPJ (right: $t(22) = 3.67, p = .001$; left: $t(22) = 4.21, p <$

.001), precuneus ($t(22) = 2.30, p = .032$), dMPFC ($t(22) = 2.33, p = .029$), middle MPFC ($t(20) = 3.97, p < .001$), and ventral MPFC ($t(17) = 4.25, p < .001$). The difference between Live and Social was in the same direction but did not reach significance for the remaining two regions: right ($t(22) = 1.99, p = .059$) and left ($t(22) = 1.82, p = .083$) anterior superior temporal sulcus (aSTS). After applying a Holm–Bonferroni correction for multiple comparisons (Holm, 1979), significant differences between Live and Social remained in bilateral TPJ, middle MPFC, and ventral MPFC (corrected $ps < .01$). Social speech, as compared to Standard speech, did not show significantly greater activation in any of the eight mentalizing regions ($ps > .1$; Supplementary Figure S2.3).

Autistic-Like Personality Traits Relate to Processing Live Stimuli

Autism Quotient (AQ; Baron-Cohen et al., 2001) scores, which measure autistic-like traits, were significantly correlated with perceived liveness for the Live condition (Figure 2.3B), but not the Social ($r(27) = -.27, p = .17$) nor Standard ($r(27) = .13, p = .49$) conditions, such that greater autistic-like personality traits were related to diminished perceptions of live social interaction during the Live condition. This correlation between AQ scores and perceived liveness remained significant after controlling for both engagement and likeability ratings ($r(25) = -.54, p = .003$). AQ scores were not correlated with perceived liveness for any of the speakers in the control behavioral experiment when participants were told that all conditions were prerecorded.

Given that activation in right dMPFC for Live vs. Social speech was correlated with perceived liveness, we next examined the relation between AQ scores

and specialization for live speech in this region. AQ scores were also significantly correlated with specialization in right dMPFC (defined by the group-level contrast) for Live vs. Social speech (Figure 2.2B). Participants with higher levels of autistic-like traits showed diminished neural specialization for live versus matched recorded speech. Additional analyses with the other three group-identified clusters revealed a negative trend in left dMPFC ($r = -.36, p = .06$) and a significant positive relation in left angular gyrus ($r = .37, p = .045$). There was no correlation between AQ scores and activation to Social vs. Standard speech in the right STG cluster defined by the corresponding group-level contrast ($r < .1$).

Discussion

This study used a novel paradigm to isolate the neural systems subserving live human communication. Specifically, this paradigm identified the neural mechanisms underlying the differential processing of otherwise well-matched stimuli in live and recorded contexts. Participants completed an fMRI task in which they listened to two types of prerecorded speech: speech that they believed was being spoken in real-time by the experimenter in another room over a live audio-feed (Live) and matched human speech that participants knew was recorded (Social). Analyses of the content- and prosody-matched story portion revealed that simply believing that a social partner was speaking in real-time more strongly activated social cognitive regions, specifically in each participant's independently identified mentalizing network. Further investigation revealed that this effect was not attributable to low-level differences in audio characteristics, speaker likeability, or attention, and was instead driven by perceptions of speaker liveness. These perceptions of liveness and neural

responses to live interaction were related to Autism Quotient (AQ) scores; individuals with higher levels of autistic-like personality traits were less sensitive to the live context.

In the current paradigm, the analyzed speech segments did not contain any explicit mentalizing demands, and yet live speech still more strongly activated the mentalizing network. This finding indicates that mentalizing may be a critical component of real-time interaction. Live interaction did not increase activation in attention or reward networks, in contrast to some past findings examining social interaction (Pfeiffer et al., 2014; Schilbach et al., 2010). The current paradigm, however, made efforts to control contingency and attention between conditions, and no reaction time differences were found between conditions. Past interactive studies that have found reward system activation have examined interacting with humans versus computers (Pfeiffer et al., 2014) or the effect of directing another person's attention (Schilbach et al., 2010), neither of which was examined in the current paradigm. Importantly, the null finding of the current study does not contradict evidence suggesting that humans are intrinsically motivated to engage with others (Chevallier et al., 2012; Tomasello, 2008) and that motivational brain networks play an important role in social interaction, but rather indicates that real-world, dynamic interaction is likely subserved by several systems, which may be targeted by different contexts.

Activation in regions identified by the mentalizing localizer provides strong evidence that the regions engaged by live stimuli in the current study are part of the network involved in explicit mental state inference. Specifically, although regions

from the broader mentalizing network have also been implicated in more domain-general processes (e.g., attention), this functional localizer matched attentional and other cognitive demands across mentalizing and control items in order to identify, for each individual, the regions associated with mental state reasoning. Further, the regions identified by the localizer revealed no increased activation for the more friendly recorded condition versus the more standard recorded condition, despite the fact that these conditions differed on self-reported engagement and low-level audio characteristics. Thus, although it is possible that other processes support the complex phenomenon of live interaction, these convergent results suggest that the mentalizing network is altered during social interaction.

In the context of the current study, it is unknown how these regions involved in explicit mentalizing subserve interaction. Perhaps most straightforwardly, participants could be engaging in more explicit or even implicit (Schneider et al., 2014a; Schneider et al., 2014b) reasoning about the mental state contents of the live versus recorded speaker within the context of experimental task demands. Three factors, however, argue against this interpretation: first, the analyzed story portion did not contain mentalizing language; second, the mental state content in the unanalyzed question portion of the trial was matched across conditions; and third, there were no behavioral differences between conditions on the questions after each story, which required mental state reasoning to answer.

Given the highly controlled experimental context, increased activation in the mentalizing network may result from tracking belief states beyond task demands. For example, individuals may reflect on the evaluative or interpersonal mental states of

the live social partner (e.g., Does she think I am giving quick enough answers?) but not of the recorded speakers. This ongoing monitoring of the mental states of a social partner, perhaps particularly in regards to how that social partner perceives the interaction, may assist in the creation of a shared psychological state and ensure successful communication. Another possibility is that the mentalizing system is more active not because of ongoing mental state reasoning, but rather because live interaction inherently contains the possibility of suddenly needing to consider another's mental state. That is, the system is primed for activation. Both of these possibilities speak to facets of human interpersonal understanding that may separate live interaction from the sum of its component pieces.

Alternatively, rather than the mentalizing system supporting quantitatively “more” belief state reasoning during live interaction, it is possible that the mentalizing system is engaged in a qualitatively different way. Computationally, the live and recorded conditions are equally demanding in terms of understanding spoken language and making mental state inferences. Thus, perhaps increased activation in these regions during live speech is not driven by differences in representational content, but rather by this network's broader role in social interaction. The exact nature of this role is unknown, but may involve the rapid, ongoing representation of a social partner that underlies phenomena such as social resonance, synchrony, and coordination (Garrod & Pickering, 2009; Kopp, 2010). Interestingly, previous fMRI studies of speech comprehension have implicated regions also involved in mentalizing (e.g., aSTS; Scott, Blank, Rosen, & Wise, 2000, MPFC; Oleser, Wise, Dresner, & Scott, 2007, pSTS; review, Redcay, 2008, and TPJ; review, Mar, 2011),

suggesting a coupling between social and speech processing within this network. Future research should continue to investigate the role of mentalizing systems in speech processing even outside of live contexts.

Due to the constrained and controlled nature of the current paradigm, increased activity in the mentalizing network was necessarily driven by primarily top-down information (i.e., participants were told stimuli were live) as opposed to more bottom-up cues (e.g., real-time contingency, nonverbal synchrony, “interactive alignment”; Garrod & Pickering, 2009; Pfeiffer et al., 2014). This top-down information about speaker liveness affected other judgments about the speaker: as compared to a control experiment where participants knew the live speaker was recorded, simply being told that the speaker was live significantly increased ratings of social engagement and likeability for that speaker. Ontogenetically, in contrast, the perception of live interaction unspools via bottom-up cues and is likely implicit, given that young infants are sensitive to contingent interaction (Murray & Trevarthen, 1985). How these bottom-up processes differ from the top-down experimental manipulation of liveness in the current study is unclear. Understanding factors influencing the perception of social interaction has implications for real-world pedagogical contexts, including listening to and learning from live versus recorded material, and is an important direction for future study.

Differential behavioral and neural response to live social partners has implications for autism. Research suggests that social disability in autism may result from a developmental cascade beginning with early disengagement from social stimuli (Klin et al., 2003; Pelphrey, Shultz, Hudac, & Vander Wyk., 2011). Although

the current study examined typical individuals, higher AQ scores were associated with diminished neural sensitivity to live versus recorded speech in dMPFC, a region linked to atypical ASD activation during live interaction (Redcay et al., 2013), but not during offline, explicit mentalizing (Dufour et al., 2013). The mechanism driving this association in the current sample is unclear, but one possibility is found in the behavioral ratings of speaker liveness. Higher AQ scores were correlated with lower ratings of perceived liveness of the live speaker, but not the recorded speakers, and, further, increased perceived liveness of the live speaker was related to increased activation in dMPFC. Although the current sample size precludes a mediation analysis, the relation between AQ scores and sensitivity to live social partners is concordant with the hypothesis that individuals with autism feel less social resonance with their social partners (Izuma, Matsumoto, Camerer, & Adolphs, 2011; Klin et al., 2003) and suggests that heightened sensitivity for live social partners may characterize typical social development. Interestingly, left angular gyrus specialization for live speech was associated with increased levels of autistic-like traits. This angular gyrus cluster did not overlap with regions identified by the mentalizing localizer, suggesting a nonlinear pattern where reduced sensitivity to live interaction within the mentalizing system, but increased sensitivity outside of this system, may be associated with atypical social processing. Given that the current study had a relatively small number of individuals with high levels of autistic-like traits, however, future work should examine larger typical samples and also test individuals with autism in similar paradigms.

For this initial within-subjects approach to understanding the effect of live interaction on communication, we needed to ensure a believable and salient interactive setup. We thus created an experiment that ensured participants believed the live illusion (i.e., meeting the live partner beforehand) and that reinforced to participants that they were engaging with a real social partner (i.e., “live” videos of the partner, hearing the partner use first-person language, hearing a different speaker for the recorded trials). Indeed, this manipulation had a high success rate as 29 out of 31 adults believed the live illusion. However, interpretations of the current paradigm are limited by the fact that the matched live speech was embedded in this social context. Although our additional analyses indicate that these confounds are not driving the results, future work could employ paradigms with sparser social context. For example, participants could listen to the same speaker, but be told for some trials that the speaker is live and for other trials that the speaker is recorded. If these two conditions do not reveal differences in neural activation, it is possible that with all other factors controlled, belief that speech is presented via a real-time audiofeed is not enough to alter neural processing. However, it is also possible that without a richer social context, participants would find the live stimuli less believable or that, given the sparse, top-down instruction, the live nature of the stimuli would not be salient enough to affect speech processing (cf. Okita et al., 2007). Future studies could manipulate various aspects of social-interactive setups to help isolate the necessary and sufficient conditions to observe the effects found in the current study.

The current study offers important insight into understanding a fundamental human behavior: communication. Regions of the mentalizing network have been

most frequently conceptualized as carrying out specific social cognitive computations (e.g., determining another's beliefs). The current study illustrates that, even when explicit social cognitive demands are held constant, the mentalizing network is sensitive to social interaction. Specifically, this paradigm demonstrates that merely believing that you are listening to a live speaker (versus a matched recording) changes the neural correlates of processing speech, specifically by increasing activation in traditionally defined mentalizing regions. Although the current paradigm only examined spoken language, research suggests that the communicative medium is less important than the creation of a shared psychological state (Noordzij et al., 2009; Stolk et al., 2014). Suggestively, the regions identified in the current study are similar to those identified in studies of interactive but nonverbal joint visual attention (Redcay et al., 2010; Redcay et al., 2012). In addition to illuminating the neural mechanisms underlying interaction, the current findings attest to the necessity of studying communicative cues (e.g., speech) in a communicative context. Future research on disorders characterized by social disabilities that are more acute in live interaction, such as autism and social anxiety, should consider the role of communicative context; interactive paradigms may be more suited to identify these disorders' neural mechanisms. Ultimately, if scientists have the goal of understanding human behavior, such study must take into account human context.

Chapter 3: Perceived Live Interaction Modulates the Developing Social Brain

Abstract

Although children's social development is embedded in social interaction, most developmental neuroscience studies have examined responses to non-interactive social stimuli (e.g., photographs of faces). The neural mechanisms of real-world social behavior are of special interest during middle childhood (roughly ages 7-13), a time of increased social complexity and competence coinciding with structural and functional social brain development. Evidence from adult neuroscience studies suggests that social interaction may alter neural processing, but no neuroimaging studies in children have directly examined the effects of live social-interactive context on social cognition. In the current study of middle childhood, we compare the processing of two types of speech: speech that children believed was presented over a real-time audio-feed by a social partner and speech that they believed was recorded. Although in reality all speech was prerecorded, perceived live speech resulted in significantly greater neural activation in regions associated with social cognitive processing. These findings underscore the importance of using ecologically-valid and interactive methods to understand the developing social brain.

Introduction

Children develop in a world filled with reciprocal social interaction, but social brain development is almost exclusively measured and understood via non-interactive paradigms that examine component pieces of interaction (e.g., looking at photographs of faces). Behavioral evidence, however, from both adults (e.g., Laidlaw, Foulsham, Kuhn, & Kingstone, 2011; Okita et al., 2007) and children (Goldstein & Schwade, 2008; Kirschner & Tomasello, 2009; Kuhl, Tsao, & Liu, 2003) suggests that live, interactive context significantly alters response to otherwise matched social stimuli. Adult neuroimaging research has begun to identify the neural bases of social interaction (e.g., Pfeiffer et al., 2014; Pönkänen, Alhoniemi, Leppänen, & Hietanen, 2011; Redcay et al., 2010; Rice & Redcay, in press; Schilbach et al., 2010), but few studies have investigated how the developing brain supports social interaction. Understanding the developmental bases of real-world social behaviors will provide insight into both typical and atypical social development, where disorders such as autism and social anxiety are characterized by interpersonal difficulties (e.g., Heimberg, Brozovich, & Rapee, 2010; Klin, Jones, Schultz, & Volkmar, 2003).

Although social interaction is characterized by a variety of properties (e.g., interaction may be intrinsically rewarding; Mundy & Neal, 2000; Pfeiffer et al., 2014; Schilbach et al., 2010, 2013), one component of successful social interaction is the creation of a shared psychological state between partners (Clark, 1996; Sperber & Wilson, 1996; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Consistent with this perspective, recent behavioral (e.g., Teufel et al., 2009) and neural evidence (e.g., Coricelli & Nagel, 2009; Rice & Redcay, in press) from adults suggests that on-going

social interaction involves mental state inference—or mentalizing—about one’s social partner. Specifically, the mentalizing network (e.g., dorsomedial prefrontal cortex [dMPFC], temporal parietal junction [TPJ], posterior superior temporal sulcus [pSTS]; Frith & Frith, 2006) is consistently activated during social interaction, including when individuals process communicative cues (e.g., Kampe, Frith, & Frith, 2003), engage in joint attention (e.g., Redcay, Kleiner, & Saxe, 2012; Schilbach et al., 2010), and play games against a human as opposed to a computer (e.g., Coricelli & Nagel, 2009; Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe, Houser, Ryan, Smith, & Trouard 2001). Such studies, however, often involve either explicit mentalizing, as during strategy games, or do not directly compare stimuli that differ solely on interactive context. In a novel paradigm, Rice and Redcay (in press) isolated the potential role of implicit mentalizing in on-going social interaction. Participants listened to audio clips from live versus recorded speakers that contained no explicit mentalizing demands. Live speech resulted in increased activation in regions identified by a separate mentalizing localizer, including dMPFC and TPJ, suggesting social interaction automatically recruits the mentalizing network. Although these lines of converging evidence suggest a role for spontaneous mentalizing in social interaction, little is known about these processes in children.

Middle childhood (roughly ages 7-13) is an important time for considering the role of mentalizing in social interaction. During this age range, children improve on a variety of social cognitive tasks, including measures of mentalizing (e.g., Apperly, Warren, Andrews, Grant, & Todd, 2011; Dumontheil, Apperly, & Blakemore, 2010). Further, during middle childhood, the brain’s mentalizing network undergoes

functional and structural development. For example, regions involved in mentalizing in adults (including precuneus and bilateral TPJ) become increasingly selective for processing mental states as compared to general social information (Gweon, Dodell-Feder, Bedny, & Saxe., 2012). Further, the degree of mental state specialization in right TPJ correlates with mentalizing ability (Gweon et al., 2012). Both pSTS and TPJ also show protracted structural development (Shaw et al., 2008). Recently, Mills and colleagues (2014) examined the developmental trajectory of three regions involved in mentalizing—pSTS, TPJ and dMPFC—and confirmed that cortical thinning did not begin until middle childhood. These social-cognitive and neural developments coincide with increased complexity of children’s social interactions (Farmer et al., 2015; Feiring & Lewis, 1991) as socio-emotional understanding increases (Carr, 2011) and variability in social competence widens (Monahan & Steinberg, 2011). One possibility is that these changes in real-world social behaviors are supported by behavioral and neural changes in the mentalizing system, making middle childhood an important time to study mentalizing during real-time social interaction.

The developmental role of the mentalizing network during social interaction is unknown because the few developmental neuroimaging studies that have employed interactive paradigms have not directly addressed how live context alters social cognition. For example, researchers have investigated how children respond to potential future interaction (e.g., Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009; Guyer, Choate, Pine, & Nelson, 2012), how adolescents make decisions when observed (Chein, Albert, O’Brien, Uckert, & Steinberg, 2011), and how children

respond to social rejection (e.g., Bolling et al., 2011; Will, van Lier, Crone, & Güroğlu, 2016). Such studies, however, do not isolate whether or how an interactive social context alters the neural processing of that interaction's constituent social stimuli.

In order to characterize the developmental neural response to real-time social interaction, we extended an fMRI paradigm previously used with adults (Rice & Redcay, in press) to children aged 7-13. In this paradigm, children listened to two types of content-matched speech: speech that they believed was coming over a live audio feed from a speaker in another room and speech that they believed was recorded. All stimuli were actually prerecorded. On each trial, children heard a short spoken vignette, which they believed to be either live or recorded, that presented two options (e.g., fruit or pancakes). They then heard about someone's preference (e.g., eating healthy), and finally made a choice for that person based on their preference. After each question, children saw positive or negative feedback, in order to match attention and contingency across conditions. Analyses focused on the short vignette, which contained no mentalizing demands or references to people. This paradigm was chosen both for its experimental control and for the fact that, in adults, the comparison of live versus recorded stimuli resulted in increased activation in each individual's mentalizing network (as defined by a localizer) despite the lack of explicit mentalizing demands. Thus, although regions in the mentalizing network serve a variety of functions, previous findings indicate that this task captures mentalizing specifically.

The current study's comparison between live and recorded speech will help

dissociate between several possible patterns of developmental neural selectivity for social interaction. One possibility is that, even in a task without explicit mentalizing demands, children, like adults, show increased activation in regions associated with mentalizing during live speech. Such activation may be due to implicit, ongoing mentalizing about a social partner (Sperber & Wilson, 1996). Another possibility is that children recruit a more diffuse set of regions during live speech, a pattern consistent with functional specialization seen across other domains (reviewed in Johnson, 2011). Finally, children might show no differential activation to live versus recorded speech, suggesting that—at least for well-matched speech stimuli—similar neural mechanisms support the processing of social stimuli regardless of the live context. Consistent with the first possibility, we hypothesized that live interaction would engage regions of the mentalizing network in children. Specifically, given adult findings (Rice & Redcay, in press), we predicted that sensitivity to live interaction would be strongest in dMPFC and TPJ. Additionally, given evidence that middle childhood corresponds to increased functional specialization within mentalizing regions, we hypothesized that there may be developmental changes in neural sensitivity to live versus recorded speech.

Methods

Participants

Twenty-six typical children aged 7-13 (15 females; average age=10.4 years, SD=1.7) were recruited to participate in the study from a database of local families. All children were full-term, native English speakers, with no history of neurological damage, psychiatric disorders, head trauma, or psychological medications, no

contraindications for MRI scanning, and none had first-degree relatives with autism or schizophrenia, as assessed via parent report. Three of the participants finished one or fewer runs of the experiment, due to general discomfort (1 participant) or discomfort with the headphones (2 participants). Thus, 23 participants (14 females; average age=10.6y, SD= 1.6) completed a sufficient number of runs to examine their behavioral data during the scan (i.e., accuracy and reaction time) and post-test questionnaire ratings.

Of the 23 participants with behavioral data, four participants' neuroimaging data were excluded due to motion (i.e., had more than two runs with over 3.5mm maximum frame displacement or with greater than 10% 1mm outliers). Thus, the final sample with both useable scan and behavioral data included 19 participants aged 7-13 (13 females; average age=10.9y; SD=1.6). Children who provided usable scan data were significantly older than the children who did not (10.9y versus 9.1y; $t(24)=2.57, p=.017$).

Social Interaction Experiment

Creating the live illusion. Although all audio and video stimuli in the experiment were actually prerecorded, a vital component of the design was that children believed that the Live condition was actually live and understood the conceptual difference between live and recorded stimuli. To establish the live illusion before the scan, the main experimenter and the child practiced talking over a truly live video-feed. The main experimenter then explained that the child would hear live and recorded speech during the scan. The child listened to audio clips of the two recorded speakers: a friendly speaker matched to the Live condition (Social

condition) and a more neutral speaker (Standard condition), which was included to ensure that the effect of perceived live speech was not due to differences in likeability or audio characteristics. All children correctly responded to comprehension questions about each speaker (e.g., “Was the speaker talking to you in real life?”).

Task design. Participants viewed 36 individual trials across 4 runs, 12 from each condition: Live, Social, and Standard (Figure 3.1). Each trial began with a silent cue screen: either LIVE VOICE (in green text) or RECORDED (in orange text). After two seconds, the story (i.e., two-sentence vignette) began. In addition to the background cue screen, each condition had a different female speaker, to ensure children quickly understood when they were in a live trial. After a 2-4 second jittered fixation cross, participants were presented with a person’s preference (either that of the live speaker or of a third-party character) and then made a choice for that person by selecting one of two options, and, after another 2-4 second jitter, received feedback. Live feedback was a silent video of the live speaker that children believed was presented live video-feed, Social feedback was a standardized picture of a happy or sad female (Tottenham et al., 2009), and Standard feedback was a gold star or red “x”. Trial distribution and timing was determined by OptSeq (<http://surfer.nmr.mgh.harvard.edu/optseq/>), which optimized the estimation of the main effects of each condition. Further, baseline periods (i.e., fixation cross), each lasting 20 seconds, were added to beginning, middle, and end of each run.

Post-test procedure. Participants completed a post-test questionnaire verbally administered by a separate experimenter that assessed their impressions of the experiment and comprehension of the live setup. For each speaker, participants

answered questions on a 1 to 5 Likert scale that assessed liveness, (i.e., “How much did it feel like this speaker was talking to you in real life?” and “How much did it feel like this speaker was in the room with you?”), likeability (“i.e., How much did you like this speaker?”), and engagement (i.e., “How much did you want to get the questions that the speaker was asking right?”). The two liveness questions were averaged to create a liveness composite. Further, all participants understood that the live speaker was talking directly to the child and could see the child’s answers, and that the recorded speakers were recorded previously and could not see the child’s answers. No children suspected the live stimuli to be recorded. At the end of the experiment, children and their parents were debriefed.

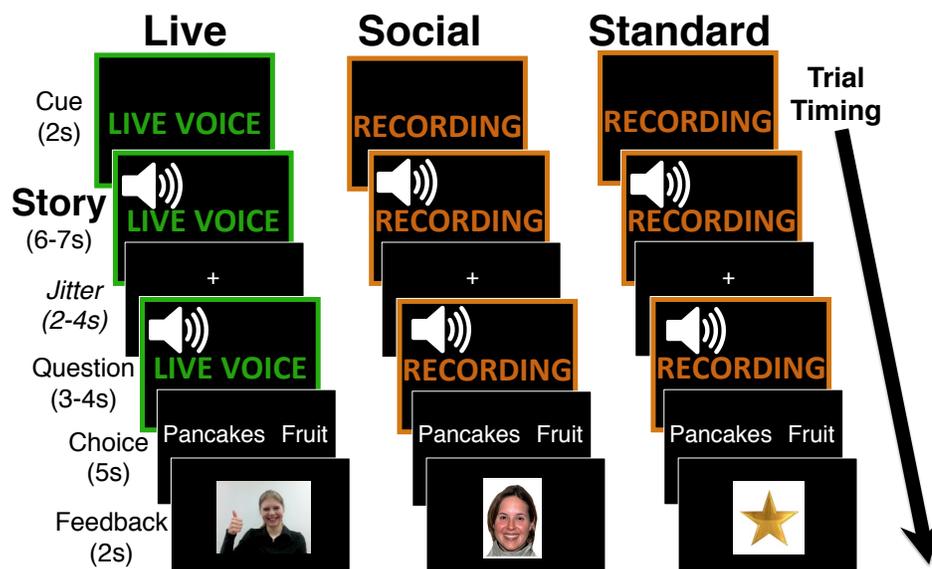


Figure 3.1. Experimental trial structure. Each of the three conditions (Live, Social, Standard) is represented in a column. Children believed that the Live condition was presented via a real-time audio-feed by an experimenter who could see their answers and that the other two conditions were recorded. In each trial, after the Cue screen, children heard a two-sentence Story that presented two options with no mention of social information (e.g., “There are two things on the breakfast menu. One is pancakes and one is a bowl of fruit.”). After this Story, children heard a question, either about the Live speaker or, for the Social and Standard conditions, about a third-party character (“I/Megan am/is trying to eat healthy. Which food should I/she eat?”). After answering the question, children saw feedback dependent on their answer. Analyses focused on the matched Story portion. s=seconds.

Stimuli. We piloted 103 Story-Question pairs on a sample of seven typical children (5 males), aged 8-11 (average=9.52, SD=1.6y). After this testing, 30 easy items were selected (on which accuracy was 100%) and six hard items were selected (on which accuracy ranged from 43% to 72%), in order to ensure that participants would see mostly positive feedback after answering questions.

The resulting 36 items were recorded by each of the three speakers (Live, Social, and Standard). These audio stimuli were identical to those used in the previous adult version of this paradigm (Rice & Redcay, in press). Each child was assigned one of three stimuli sets, which differed on which 12 short vignette and question pairs were assigned to each condition, and ensured that the total amount of time for each condition was matched. The order of the items was randomized within condition and the order of runs was counterbalanced.

Control Behavioral Paradigm

We included several differences between the Live and Social conditions to reinforce the live illusion, increase ecological validity, and ensure that children understood which condition they were in. Specifically, the Live but not Social condition included video feedback, first-person language (e.g., “I like”), and briefly meeting the speaker before the experiment. Although our analysis examined the matched audio portion—and not the video feedback or first-person language—we also investigated whether these other factors could produce perceptions of liveness without being told the speaker was live. We conducted a separate control behavioral-only study with $N=19$ typical child participants (7 males, average age=10.4 years) who completed the same task as the fMRI participants including meeting the “live”

speaker before the experiment. All control participants, however, were told all stimuli were prerecorded. These control participants also completed the same post-test questionnaire. There were no differences between control participants and the scan participants who provided behavioral data ($N=23$) in age ($t(40)=.44$, $p=.66$) or sex ($\chi^2(1)=.023$, $p=.88$).

Image Acquisition and Processing

MRI imaging data were collected using a 12-channel head coil on a single Siemens 3.0-T scanner at the Maryland Neuroimaging Center (MAGNETOM Trio Tim System, Siemens Medical Solutions). The scanning protocol for each participant consisted of four runs of the main experiment (T2-weighted echo-planer gradient-echo; 36 interleaved axial slices; voxel size=3.0 x 3.0 x 3.3 mm; repetition time=2200ms; echo time=24ms; flip angle=90°; pixel matrix=64 x 64) and a single structural scan (three-dimensional T1 magnetization-prepared rapid gradient-echo sequence; 176 contiguous sagittal slices, voxel size=1.0 x 1.0 x 1.0 mm; repetition time=1900ms; echo time=2.52ms; flip angle=9°; pixel matrix= 256 x 256).

fMRI preprocessing was performed using AFNI (Cox, 1996). Data were first slice-time corrected and were aligned to the first volume using a rigid-body transform. The participant's high-resolution anatomical scan was also aligned to the first volume of the first run and then transformed to MNI space using linear and non-linear transforms. The resulting transformation parameters were applied to the functional data. Functional data were spatially smoothed using a 5mm full-width half-maximum (fwhm) Gaussian kernel and then intensity normalized such that each voxel had a mean of 100.

Outliers were defined as volumes in which the difference between two consecutive volumes exceeded 1mm (across translational and rotational movements) and such values were censored in subsequent analyses. Runs were excluded if the number of censored time points exceeded 10% of collected volumes or if total motion exceeded 3.5mm. Participants were included in analyses if they had at least 2 useable runs. The final sample included one child with two runs, five children with three runs, and 13 children with four runs.

Data Analysis

Response to each condition was analyzed using general linear models in AFNI. Given the long events of the current study and the lack of previous work on developmental response to live interaction, we made no assumptions about the shape of the hemodynamic response. We instead estimated responses for each condition using a cubic spline function beginning at the onset of the cue period and lasting for 24.2 seconds (lasting roughly through when participants answered the question). The spline function allows for a smoother estimation of response than ‘stick’ or finite impulse functions, although the two techniques are conceptually similar. Values were estimated at each TR, resulting in 12 estimated (Beta) values for each condition. Modeled events of no interest included the feedback period (due to differences in stimuli characteristics between the conditions), as well as constant, linear, and quadratic polynomial terms to model baseline and drift. To estimate response to speech in the three different conditions, we analyzed the period from Beta 4-6 (Story Window). The Story Window captured 6.8 to 11.2 seconds after story onset, and stories were, on average, around 6 seconds long. Thus, given the hemodynamic

response, this window captured the bulk of the story while minimizing any effect of the initial cue screen before the story or preparation for answering the question.

We analyzed two specific contrasts in this Story Window: first, to examine the effect of live interaction we compared Live versus Social speech; second, to isolate the effects of speaker prosody and likeability, we compared Social versus Standard speech. Given that the Standard Story was not well-matched to the Live Story, that comparison was not of interest. Contrast maps were thresholded at a two-tailed $p < .01$, and cluster-corrected for multiple comparisons (overall $\alpha = .05$, $k = 41$) using AFNI's 3dClustSim.

To examine developmental change, we conducted both region of interest (ROI) analyses and whole-brain analyses. For the whole-brain analyses, we entered age as a covariate in the Live versus Social comparison. For the ROI analyses, we extracted each individual's Live and Social beta values for the Story Window within clusters that showed a significant group-level effect for Live versus Social. We then correlated these individual contrast values with age.

Results

Behavioral Results

Overall accuracy was high (mean=89.4%, SD=8.5%, Range=67-97%) and average reaction time was well within the 5s response window (mean=1.79s, SD=.51s, Range: 1.04-3.10). Although there were no significant differences in accuracy across conditions, comparison of reaction times indicated that children were significantly slower at answering Live items as compared to Social items ($t(22)=2.11$, $p=.046$; Table 3.1A). There was no difference in reaction time between Social and

Standard items ($t(22)=-1.39, p=.18$). Children became faster at answering questions with age, but this effect did not interact with condition type (main effect of age on overall RT: $F(1,21)=7.74, p=.011$; Condition x Age interaction on RT: $F<1$). In contrast, for participants in the control behavioral study—who were told that the Live condition’s stimuli were recorded—there were no between-condition differences in RT (Supplementary Table S3.1).

Table 3.1

Behavioral Performance and Post-test Questionnaire Ratings

	Live	Social	Standard	$F_{(2,44)}$	Pairwise Comparisons
A. BEHAVIORAL PERFORMANCE					
Accuracy (%)	89.61 (12.74)	90.46 (8.8)	88.04 (15.45)	.263	Live=Soc=Std
RT (ms)	1847 (580)	1718 (474)	1811 (601)	1.63	Live>Soc=Std
B. POST-TEST QUESTIONNAIRE RATINGS					
Liveness	4.16 (.70)	2.75 (1.29)	2.39 (1.34)	29.37***	Live>Soc>Std
Likeability	4.46 (.69)	4.01 (.96)	3.44 (1.07)	12.53***	Live>Soc>Std
Engagement	4.74 (.60)	4.38 (.83)	4.17 (.94)	6.42**	Live>Soc=Std

Note: Values are mean (standard deviation). All post-test questionnaire ratings are composites of items scored on a 1 to 5 scale. Post-hoc pairwise comparisons were made using a Tukey’s test with an alpha of .05. **, $p<.01$; ***, $p<.001$. Soc=Social; Std=Standard.

On the post-test questionnaire, children in the scan study perceived the Live condition as significantly more live than the Social condition (Table 3.1B), which in turn was perceived as more live than the Standard condition. There were no relations between any of the post-test rating measures and reaction time or between post-test

ratings and age ($ps > .05$). Among the behavior-only control participants, who were told that the live stimuli were prerecorded, there were no differences in perceived likeability, engagement, or liveness between the Live and Social speaker, although both conditions were rated as more live than the Standard speaker. A repeated-measures ANOVA indicated a significant interaction between whether participants were told the Live speaker was actually live (i.e., whether a child was a control versus scan participant) and perceived liveness ($F(2,80)=5.48, p=.006$). This interaction was not significant for likeability or engagement.

Neuroimaging Results

Main effect of live versus recorded social stimuli. For the Story Window (Betas 4-6), whole-brain analyses revealed significantly greater activation for Live than Social speech in regions often associated with mentalizing (Frith & Frith, 2006), including left TPJ, right pSTS, and precuneus, although no differences in dMPFC activation were observed (Table 3.2, Figure 3.2A). In contrast, comparison of the two recorded conditions, which also differed on subjective engagement and likeability, revealed activation only in superior temporal gyrus, a region associated with pitch processing (e.g., Hyde, Peretz, & Zatorre, 2008; Scott, Blank, Rosen, & Wise, 2000).

For some of the significant Story Window clusters, we noted that differential response to the Live condition began before the analysis window, and thus followed a different time course than response to speech characteristics (i.e., the response when comparing the two recorded conditions; Figure 3.2B). This earlier response may capture cue-related differences between the live and recorded conditions. Thus, we conducted a post-hoc analysis for Betas 2-4 (Cue Window). The Cue Window

corresponded from 4.4 seconds after the beginning of the cue (the two-second screen reading “Live Voice” or “Recording” before the start of the story) through 6.8 seconds after the start of the story. Similar to the Story Window, this analysis revealed significantly increased activation in regions associated with mentalizing, including TPJ and precuneus (Figure 3.2C). Given that the cue screen was identical for both Social and Standard speech, we did not compare those conditions.

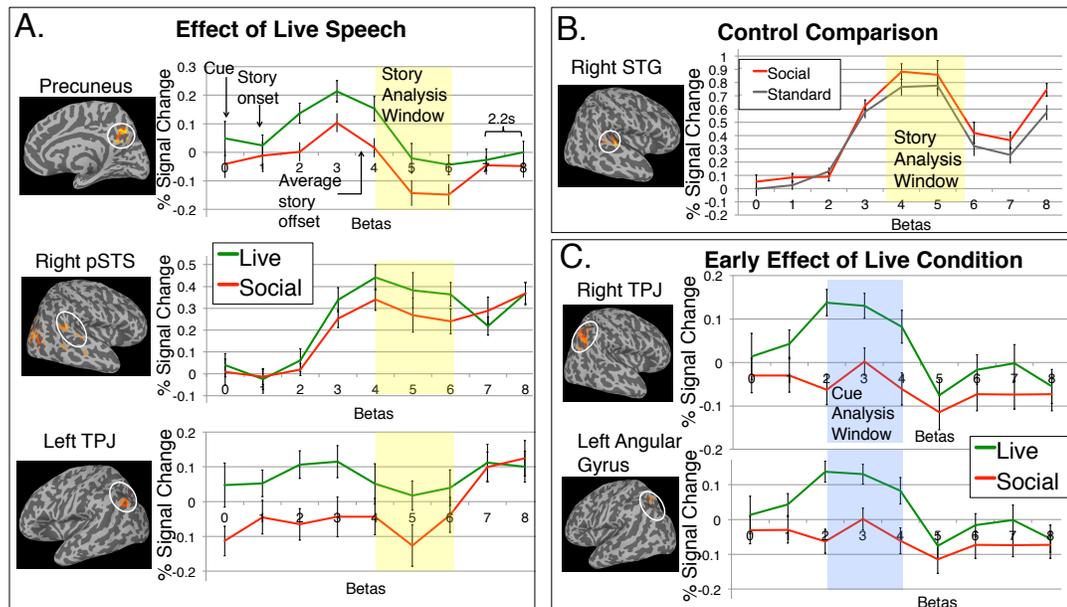


Figure 3.2. Time series plots for selected clusters defined from group-level comparisons. Individual spline estimates for a subset of regions defined by the (A) Live > Social comparison in the Story Analysis Window (Betas 4-6), (B) Social > Standard comparison in the Story Analysis window, and (C) Live > Social comparison in the Cue Analysis window (Betas 2-4). Error bars represent standard error of the mean. s=seconds; TPJ=temporal parietal junction; pSTS=posterior superior temporal sulcus; STG=superior temporal gyrus. (See also Table 3.2).

Table 3.2*Regions Sensitive to Live Interaction*

Region	Side	Peak	Cluster	MNI Coordinates		
		<i>t</i>	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>
A. STORY WINDOW						
1. Effect of live speech (matched content and prosody)						
Live>Social						
Precuneus	L/R	3.15	312	0	-76	38
Occipital gyrus	R	7.32	165	32	-90	20
TPJ	L	4.28	59	-48	-66	44
pSTS	R	4.09	58	66	-46	14
Social>Live						
None						
2. Effect of friendly speech (both recorded)						
Social>Standard						
STG	R	3.43	47	68	-24	0
Lingual gyrus	L/R	3.38	44	-4	-94	-18
Standard>Social						
None						
B. CUE WINDOW						
Effect of live speech (matched content and prosody)						
Live>Social						
Precuneus/PCC	R	2.89	434	2	-54	14
Lingual gyrus	L/R	3.35	196	0	-78	0
TPJ	R	4.28	161	60	-54	36
Angular gyrus	L	4.09	47	-34	-70	50
Social>Live						
None						

Note. TPJ=temporal parietal junction; PCC=posterior cingulate cortex; pSTS=posterior superior temporal sulcus; STG=superior temporal gyrus. Coordinates in Montreal Neurologic Institute (MNI) space. First corrected at $p<.01$ and cluster corrected at $p<.05$ ($k=41$)

Although, as in previous adult work (Rice & Redcay, in press), the TPJ was sensitive to live versus recorded speech, the current study did not employ a

mentalizing localizer to assess whether the region of the TPJ recruited was involved selectively in mentalizing tasks. The TPJ has been implicated in domain-general processes beyond mentalizing, including attention (Decety & Lamm, 2007; Mitchell, 2008); however, previous studies have indicated that the region's roles in attention and mentalizing are spatially separable (Carter & Huettel, 2013; Scholz, Triantafyllou, Whitfield-Gabrieli, Brown, & Saxe, 2009). Thus, we used the meta-analytic database Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011; www.neurosynth.org) to examine the peak TPJ coordinates from both the Story and Cue Window. Both clusters had a strong association with meta-analytic maps of *mentalizing* (Story Window: $z=4.54$, posterior probability=0.82; Cue Window: $z=4.76$, posterior probability=0.83), but not with maps for *attention*, *selective attention*, or *attentional control* ($z=0$ for all terms for both clusters).

Age-related differences in response to live versus recorded social stimuli.

Using regions identified as more sensitive to Live than Social speech during the Story Window, there were no significant relations between age and activation to Live versus Social conditions, nor to Live or Social speech versus baseline. Whole-brain analyses of the Story Window indicated a significant effect of age on Live versus Social speech within left superior frontal gyrus (MNI coordinates=[-24 48 18], $k=42$, $t=-4.15$). Post-hoc analyses examining each condition versus baseline within this cluster indicated that response to recorded speech increased with age (Social: $r=.49$, $p=.03$; Standard: $r=.60$, $p=.007$), but response to Live speech was unchanged ($r=-.17$, $p=.50$). For the Cue Window, whole-brain and ROI analyses for the Live versus Social contrast showed no relation between activity and age.

Given the unexpected whole-brain finding that dMPFC was not more active for Live than Social speech in the Story window, we conducted additional analyses to determine if age-related changes obscured differences in dMPFC activation. Specifically, we used the peak coordinates of right and left dMPFC activation from adults in this same paradigm (Rice & Redcay, in press) in order to create spherical ROIs with 6mm radii. Then, within both dMPFC ROIs, we extracted each child's response to each condition's speech during the Story Window. Left dMPFC activation for *recorded* speech increased with age (Social: $r=.48$, $p=.04$; Standard: $r=.41$, $p=.081$), but sensitivity to live speech did not change ($r=.02$, $p=.94$). Right dMPFC activation, however, was not related to age.

Discussion

This study investigated the neural mechanisms supporting social interaction in middle childhood. Specifically, we used a well-controlled fMRI paradigm—a paradigm that engages the mentalizing network in adults—in order to compare the brain's response to two types of matched speech: speech that children believed was coming from a live social partner (Live) and speech that children believed was recorded (Social). Behavioral results indicate that children understood the distinction between live and recorded speech and perceived the live speaker to be significantly more live (e.g., felt like she was in the same room). Consistent with previous research examining the neural correlates of social interaction (e.g., Hampton, Bossaerts, & O'Doherty, 2008; Kampe et al., 2003; Redcay et al., 2010; Rice & Redcay, in press), simply believing that speech was live resulted in increased activation in social cognitive regions frequently associated with mentalizing, including precuneus, TPJ,

and pSTS. Additional control analyses and experiments suggested that this difference in activation was unlikely to be attributable to differences in low-level audio characteristics, speaker identity, or speaker likeability. These results indicate that neural sensitivity to interactive contexts is present by middle childhood and that mentalizing systems may support on-going social interaction.

Post-hoc examination of neural response to the “cue” screen (which informed participants whether they were about to hear live or recorded speech), also suggested that social cognitive brain regions, including TPJ, were differentially activated by potential live interaction. These findings suggest a possible preparatory response in mentalizing regions, perhaps in anticipation of needing to consider the mental states of a social partner. The current study’s design, however, did not allow for dissociation between response to the cue and the beginning of speech. Future studies should dissociate these mechanisms, to determine if preparatory mentalizing employs different neural substrates than mentalizing during an on-going interaction.

Findings for both the Cue and Story Window provide mixed evidence for developmental continuity in the neural mechanisms supporting social interaction. Like adults, children showed increased activity in regions associated with mentalizing, specifically TPJ, when processing live versus recorded speech—speech with no explicit mentalizing demands—suggesting a role for automatic mentalizing during interaction. Also similar to adults, response to live speech was selective to mentalizing regions (e.g., no differences were seen in attentional or reward regions). Unlike adults, however, children showed no differential response to live versus recorded speech in dMPFC. This null finding is surprising given that dMPFC is

consistently implicated as sensitive to social context across both interactive and ‘offline’ paradigms (reviewed in Van Overwalle, 2011).

One potential explanation for the lack of dMPFC activation is not a lack of response to live stimuli, but rather changes in response to recorded stimuli. In this middle childhood sample, dMPFC response to recorded social stimuli increased with age, whereas response to live stimuli remained constant. The finding of increased activation to recorded stimuli is consistent with past studies of ‘offline’ social cognition, which have found higher dMPFC response to non-interactive social stimuli in adolescence than adulthood (e.g., reviewed in Blakemore, 2008). Thus, one speculative possibility is that dMPFC response to live speech is early-emerging and relatively invariant across age, whereas early adolescence represents a time of peak sensitivity to communicative cues regardless of the interactive context. That is, perhaps the end of middle childhood corresponds to a general increase in social sensitivity that extends broadly to all social stimuli, including recorded human speech. Future work should examine larger samples and compare response to live versus recorded stimuli across a variety of modalities and ages.

In contrast to dMPFC, the current study did not find age-related changes in selectivity for live interaction in TPJ, STS, or precuneus—regions associated with the mentalizing network that were more active for live versus recorded speech. This null result is in contrast to research finding increased middle childhood specialization for explicit mentalizing in similar regions (Gweon et al., 2012). One possible explanation for this discrepancy is although similar brain regions are implicated in explicit and implicit mentalizing (Kovács, Kühn, Gergely, Csibra, & Brass, 2014; Schneider,

Slaughter, Becker, & Dux, 2014), specialization for the more implicit mentalizing required by on-going interaction—the type displayed in interactive contexts even by very young children—happens before explicit specialization. Perhaps regions implicated in explicit mentalizing have an ontogenetically-prior role in supporting social interaction more broadly (e.g., Grossmann & Johnson, 2010) and, later in development, become loci of explicit mentalizing (e.g., false belief tasks) due to children’s cumulative experiences employing mental state reasoning during social interaction. The current data, however, cannot speak directly to these possibilities.

The behavioral data also indicated that children were sensitive to the distinction between live and recorded stimuli and were slower to respond to questions from the live speaker. Although the exact mechanism spurring slower responses to a live partner is unknown, one possibility—consistent with the brain data—is that children engaged in more mentalizing or different mentalizing about the live social partner. Consistent with this explanation, no difference in reaction time emerged when participants in a control study were told that the live stimuli were recorded. Future research involving interference tasks could help determine if increased mentalizing is the predominant cognitive mechanism driving behavioral differences in responding to live versus recorded partners (e.g., Kiesel et al., 2010).

Interpretation of the current results is complicated by the fact that regions in the mentalizing network are involved in processes beyond mentalizing, spanning both social (e.g., animacy detection, Shultz & McCarthy, 2014; narrative processing; Mar, 2011) and non-social (e.g., attention; Decety & Lamm, 2007; Mitchell, 2008) domains. Although comparison of this study’s pattern of results to a meta-analytic

database show strong overlap with other studies of mentalizing, future developmental research could adopt a localizer approach in order to isolate, for each individual, regions involved in mentalizing or language processing (see Rice & Redcay, in press). Additionally, although the live and recorded speech was content-matched, the current paradigm did have several differences between conditions, designed to heighten the saliency of the live social partner. Although both the comparison between the two recorded conditions and the results from the control behavioral study suggest that differences in audio characteristics or speaker likeability are not responsible for the observed results, future research should develop even more well-controlled paradigms. Ultimately, however, it is possible that isolating the effect of social interaction will be difficult, as attentional or motivational processes may be inextricably linked to the emergent properties of real-world social interaction.

Overall, the current study provides some of the first developmental evidence that neural response to otherwise matched social stimuli is modulated by social-interactive context. The brain regions sensitive to a live social partner in children are similar, but not identical, to those identified in adult studies of social interaction (e.g., Kampe et al., 2003; Redcay et al., 2010; Rice & Redcay, in press), indicating that mentalizing supports social interaction across development. Specialization for live interaction did not increase with age in this sample, but paradigms with more complex dyadic interaction may yet reveal specialization. Although future research should more finely parse the components of live interaction that may be driving the current findings, the current study is a novel first step in embedding developmental social neuroscience in the social world.

Chapter 4: Let's Chat: Developmental Neural Bases of Social Motivation During Real-time Peer Interaction

Abstract

Humans are motivated to interact with each other, but the neural bases of social motivation have been predominately examined in non-interactive contexts. Understanding real-world social motivation is of special importance during middle childhood (ages 8-12), a period when social skills are improving, social networks are growing, and social brain networks are specializing. To assess social motivation in an interactive context, the current study used a novel fMRI paradigm in which children believed they were chatting with a peer. Specifically, the design targeted two phases of interaction: (1) Initiation, in which children engaged in a social bid via sharing a like or hobby, and (2) Reply, in which children received either an engaged (“Me too”) or non-engaged (“I’m away”) reply from the peer. On control trials, children were told that their answers were not shared and that they would receive either engaged (“Matched”) or non-engaged (“Disconnected”) replies from the computer. Results indicated that during both Initiation and Reply, key components of reward circuitry (e.g., ventral striatum) were more active for Peer than Computer trials. Additionally, during Reply, social-cognitive regions were more engaged by the peer, and this social cognitive specialization increased with age. Finally, the effect of engagement type on reward circuitry activation was larger for social than non-social trials, indicating developmental sensitivity to social contingency. These findings demonstrate that both reward and social cognitive networks support real-time social interaction in middle

childhood. An interactive approach to understanding social reward has implications for social disabilities such as autism, where social motivation is more affected in real-world contexts.

Introduction

Throughout the lifespan, humans are motivated to interact with each other—a construct referred to as social motivation (Baumeister & Leary, 1995; Chevallier, Kohls, Troiani, Brodtkin & Schultz, 2012; Tomasello, 1999). From early infancy, humans preferentially attend to human faces (Farroni et al., 2005; Morton & Johnson, 1991) and voices (Vouloumanos, Hauser, Werker, & Martin, 2010), and prefer contingent to non-contingent social stimuli (Bigelow, 1998; Murray & Trevarthan, 1985). As children grow, they actively initiate social interaction and attempt to maintain social relationships (Rekers, Haun, & Tomasello, 2011), a drive that continues into adulthood (Baumeister & Leary, 1995). Furthermore, diminished social motivation is theorized to be a core feature of autism spectrum disorders (see Chevallier et al., 2012 for review). Mapping the neurobiological bases of social motivation will improve understanding of both typical and atypical development.

Recent attempts to understand the neural bases of social motivation have leveraged existing research on the brain's reward system (see Berridge & Kringelbach, 2008; Haber & Knutson, 2010; Fareri, Martin, & Delgado, 2008; Taber, Black, Porrino, & Hurley, 2012 for reviews of reward processing). Broadly, reward circuitry involves a network of brain regions, including ventral tegmental area, substantia nigra, amygdala, portions of medial prefrontal cortex (including orbitofrontal cortex; OFC), insula, anterior cingulate cortex, and ventral striatum (VS). In particular, VS is often considered a 'hub' of reward processing (Sesack & Grace, 2010; Kohls et al., 2012), as its nuclei are connected to many other dopaminergic regions involved in reward (reviewed in Haber & Knutson, 2010).

Mounting evidence suggests that this reward circuitry may index a ‘common currency’ across different types of reward (cf. Montague & Berns, 2002). Recent studies have tested this theory by presenting the same participants both social and monetary rewards and have found evidence that these disparate reward types implicate overlapping regions (Izuma, Saito, & Sadato, 2008; Lin, Rangel, & Adolphs, 2011). Importantly, however, although some similar reward circuitry appears to be responsive to both non-social and social rewards, social rewards also tend to engage the broader social cognitive network (see Ruff & Fehr, 2014 for review), including temporoparietal junction (TPJ), dorsomedial prefrontal cortex (dMPFC), and superior temporal sulcus (STS).

Based on the evidence that more general reward circuitry contributes to social motivation, a growing literature has investigated the role of such circuitry across varied types of social motivation paradigms (see Báez-Mendoza & Shultz, 2013 and Bhanji & Delgado, 2014 for review). For example, VS has been implicated across wide-ranging social contexts, from anticipating or receiving a positive evaluation (e.g., Gunther Moor et al., 2010; Jankowski, Moore, Merchant, Khan, & Pfeifer, 2014; Guyer, Choate, Pine, & Nelson, 2012; see Izuma, 2012 for review), to sharing information or perceptual experiences with a social partner (Tamir & Mitchell, 2012; Wagner et al., 2015), to tracking the probability that a particular social partner will give positive feedback (Jones et al., 2011; 2014). Although such paradigms have targeted multiple aspects of social reward, these studies have not examined social motivation in the context of a dynamic, back-and-forth interaction (e.g., instead participants are told that they are seeing the results of an evaluation that occurred

some days previously). Thus, such studies do not examine social motivation in the context of directly sharing or engaging with a social partner, which may be the deficit most core to disorders like autism (Kohls et al., 2012).

A separate set of studies has directly investigated the neural bases of such real-time social engagement, finding evidence that reward circuitry is responsive to interaction. For example, studies in which participants play cooperative games with humans have found increased VS activation as compared to playing such games with a computer (Rilling et al., 2002), although reward circuitry is not consistently implicated in competitive contexts (e.g., Coricelli & Nagel, 2009; Kircher et al., 2009) or in a context when participants were passively receiving live versus recorded input (i.e., listening to speech; Rice & Redcay, in press). A growing set of studies have investigated cooperation in the context of joint attention, in which a participant responds to another's gaze shifts or directs another's gaze (either that of a real person or of an avatar; e.g., Caruana, Brock, & Woolgar, 2015; Koike et al., 2016; Schilbach et al., 2010). Such paradigms frequently recruit reward circuitry, in addition to robustly activating social cognitive regions (Schilbach et al., 2010; Pfeiffer et al., 2014; Preller et al., 2014; Redcay et al., 2010; but see Redcay et al., 2012). These studies, however, have two limitations when addressing the neural bases of social motivation. First, such cooperative paradigms frequently confound the processes of contingency (e.g., receiving a response to a gaze shift) and social context (e.g., being in the presence of a social actor). Given substantial evidence that both contingency (e.g., Balleine & Dickinson, 1998; Muhle-Karbe & Krebs, 2012; Stefani & Moghaddam, 2006; Yin, Knowlton, & Balleine, 2006) and social context (e.g.,

viewing an attractive face; Aharon et al., 2001; Cloutier, Heatherton, Whalen, & Kelley, 2008; O'Doherty et al., 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007) involve reward systems, disambiguating these two components of social motivation will yield insight into the mechanisms driving social reward. Second, most existing studies of real-time engagement analyze a joint attention event as a single trial, failing to separate out one's social bid from the partner's response. Given evidence that reward circuitry, especially in autism, may differentially respond to different phases of interaction (e.g., the desire to initiate versus the enjoyment of the resultant interaction; Chevallier et al., 2012; Kohls, Chevallier, Troiani, & Schultz, 2012), it is necessary to separate out such multiple components of social motivation.

The most common paradigm employed to examine distinct phases of social reward is a social incentive delay paradigm, which dissociates between reward anticipation and outcome (e.g., Spreckelmeyer et al., 2009; Rademacher et al., 2010; Richey et al., 2014). In such paradigms, the participant first sees a cue indicating what reward they can earn (e.g., a triangle indicating that they can see a smiling face), after which a target appears and, if the participant presses the button quickly enough, a photograph of a smiling face—the social reward—is then displayed. In contrast to established behavioral research about the power of real-world social rewards (e.g., Handgraaf, de Jeude, & Appelt, 2013; Heyman & Ariely, 2004), social incentive delay paradigms have found that social rewards are less effective than monetary rewards in changing behavior (Gossen et al., 2014; Kohls, Peltzer, Herpertz-Dahlmann, & Konrad, 2009; Lin et al., 2011), that social rewards produce equal or diminished VS activation compared to monetary rewards (Lin et al., 2011;

Rademacher, Salama, Grunder, & Spreckelmeyer, 2014; Spreckelmeyer et al., 2009), and that individuals with ASD do not show unique dysfunction in processing social rewards (Delmonte et al., 2012; Dichter, Richey, Rittenberg, Sabatino, & Bodfish, 2012). The finding that these social reward stimuli have limited reward value, even in incentive delay tasks that use video rewards instead of photographs (Cox et al., 2015; Kohls et al., 2013), may be because such stimuli fail to capture the motivational components of real-world back-and-forth interaction with a social partner. Thus, the precise role of social cognitive and reward systems during distinct phases of naturalistic, reciprocal interaction remains unknown. In particular, although social motivation is a broad construct, two complementary components have special developmental and clinical relevance: the desire to initiate social interaction and the enjoyment of the resultant reciprocal interaction. These components may follow different developmental trajectories, show different neural bases, and be differentially affected by disorders such as autism (cf. Kohls et al., 2012).

Understanding the neural bases of these two processes—social initiation and the resultant social engagement—is especially important during middle childhood (ages 8-12). This age range is characterized by rapid behavioral social development, as peers grow increasingly salient (Sroufe, Egeland, & Carlson, 1999), and by structural (Mills et al., 2014; Urošević, Collins, Muetzel, Lim, & Luciana, 2012) and functional (Carter & Pelphrey, 2006; Gweon, Dodell-Feder, Bedny, & Saxe, 2012) development of social brain regions and reward circuitry. Specifically, middle childhood is a time when regions of the social cognitive network, including regions implicated in previous studies of social reward (e.g., STS, TPJ) specialize for social

stimuli (Carter et al., 2006; Gweon et al., 2012). In spite of the importance of this period, however, most developmental reward research has focused on adolescence (see Spear, 2011 for review). The limited research examining reward processing in middle childhood has primarily employed monetary rewards (e.g., Gotlib et al., 2010, Forbes et al., 2009; Helfinstein et al., 2013) or non-interactive social rewards (e.g., Kohls et al., 2014). More interactive neurodevelopmental studies have examined social feedback and exclusion (e.g., Bolling et al., 2011; Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen 2010; Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009; Guyer et al., 2012), but such research primarily focuses on the neural correlates of the child's response to their peers' actions, not on the child's initial motivation to engage or the reward salience of mutual engagement. Thus, for middle childhood—a crucial period of social and brain development—the neural bases of social motivation are underexplored.

The current study employed a novel, social-interactive fMRI paradigm with children aged 8-12 in order to examine both the desire to initiate interaction with a peer and the enjoyment of the resultant interaction. Children believed they were chatting online with an age- and gender-matched peer about likes and hobbies, although in reality the peer was a simulated computer program. As opposed to previous interactive paradigms, which have examined constructs such as visual joint attention (e.g., Pfeiffer et al., 2014, Redcay et al., 2012), the current paradigm's use of reciprocal sharing about real-world interests was designed to increase children's attention and interest in a setting more aligned to conversation, especially as sharing self-relevant information is a cornerstone of normative social development

(Buhrmester & Prager, 1995; Collins & Miller, 1994; Sprecher, Treger, Wondra, Hilaire, & Wallpe, 2013). Specifically, on each trial, children engaged in a social bid to the peer, via revealing a like or hobby (e.g., letting the peer know “I like soccer”), and then received a reply about the peer’s interest in the same subject (e.g., the peer replying “Me too”). On control trials, children still answered self-relevant questions, but believed they were chatting with a computer who would answer with “Matched” if the child’s answer matched a randomly selected answer.

Importantly, the paradigm was designed to assess the intrinsic reward of mutual social engagement, not to address social exclusion or social disagreement. Thus, the peer and the computer were programmed to rarely disagree with the child. Social engagement (i.e., agreement) was instead contrasted with non-engagement; on peer non-engagement trials, children believed the social partner wanted to chat, but could not because he or she needed to complete another task. Crucially, both the peer and the computer gave engaged replies (Peer: “Me too/neither”; Computer: “Matched”) and non-engaged replies (Peer: “I’m away”; Computer: “Disconnected”), allowing for separation of the effects of contingency and social context.

Our hypotheses related to the two independently analyzed phases of each trial: the initial period in which children responded to a prompt (i.e., Initiation), knowing that their answer would either be shared with the peer or with a computer control (cf. Tamir & Mitchell, 2012), and the period in which children received an engaged or non-engaged reply from either the peer or the computer (i.e., Reply). We first predicted that, for both Initiation and Reply, the brain’s reward circuitry—specifically VS—would be more active in the peer conditions. Additionally, given evidence that

social reward (reviewed in Ruff & Fehr, 2014) and social interaction (Rice & Redcay, in press) both engage the social cognitive network, we also hypothesized that the peer conditions would increase activation in regions associated with social processing (e.g., dMPFC, TPJ; Van Overwalle, 2009). We also predicted an interaction for the Reply phase, such that the effect of contingency (i.e., engagement versus non-engagement) on reward circuitry would be greater for the social (i.e., peer) than the non-social (i.e., computer) trials. Finally, given evidence for age-related functional specialization in the social cognitive network during middle childhood, especially in TPJ (e.g., Gweon et al., 2012), we hypothesized that social cognitive regions identified in the whole-brain comparison of peer versus computer replies would show increased activation to peer response with age.

Methods

Participants

Twenty-six children (11 males) aged 8-12 years (mean age=10.36y, SD=1.45y) participated in the study. Children were recruited from a database of local families. All children were full-term, native English speakers, and, as assessed via parent report, had no history of neurological damage, psychiatric disorders, psychological medications, first-degree relatives with autism or schizophrenia, nor any other characteristics that would prevent MRI scanning. Behavioral data from all twenty-six children were analyzed. Data from two children were excluded from the fMRI analyses due to excessive motion, yielding a final sample of 24 children in the neuroimaging sample (10 males, average age=10.47y, SD=1.44y).

Task Procedures

Setting up the chat. Before the scan, the experimenter explained to the child that they would be chatting with a peer on the computer. Children were told that they would not be able to have a regular typed conversation because they would only have a “yes” button and a “no” button. Thus, to initiate interaction with the peer, children learned that they would answer “Yes” or “No” to a statement about likes or hobbies (e.g., “I play soccer”). The experimenter explained this answer would start the conversation with the peer, who would see the child’s start of the exchange, and would be able to send his or her own answer to the question back (“Me too/neither!” or “That’s not what I picked”). Additionally, the children were told that the peer would sometimes be unable to respond, as he or she would have to play another game, and that, for these trials, an away message would be displayed as the peer response (“I’m away”; Supplementary Figure S4.1A). Crucially, children understood that even on these trials, the peer was still able to see the child’s own answer, but could not respond. Thus, each time the child shared an answer with the peer, he or she was initiating a social bid that would be received by the partner but could either be responded to or not responded to by the partner.

The experimenter next explained that, for some trials, the child would just be connected to a computer and that no one would see his or her answer. For these computer trials, children believed that after they answered Yes-No question that the computer would randomly pick either “Yes” or “No” (Supplementary Figure S4.1B) and that the subsequent screen would display either “Matched!” or “Mismatched,” depending on whether the randomly-selected answer matched the child’s. Further,

children were told that the computer would sometimes lose the connection and be unable to generate a random answer, resulting in the word “Disconnected”.

After the experimenter verified that all participants understood the directions, children were told that it was time to find their chat partner. The experimenter took a photograph of the child (ostensibly to be sent to the chat partner), and then showed children a preprogrammed series of screens creating the chat illusion (Supplementary Figure.1C). Specifically, children saw two photos of age- and gender-matched peers (smiling, direct gaze photos from the NIMH Child Emotional Faces Pictures Set; Egger et al., 2011). These photos have been successfully used to assess peer perception in middle childhood (e.g., Guyer et al., 2009, 2012, 2014). To increase motivation, children selected the peer they would rather chat with, as research has shown that feedback is more salient when coming from a desirable peer (cf. Guyer et al., 2009).

Stimuli characteristics. To select the 104 self-relevant statements (e.g., “I like French fries”) that children responded to, 168 candidate items were piloted on a separate sample of 12 typical children aged 7-12. Out of the 168 piloted items, items that were most difficult for children to answer within the response window (i.e., lowest response rates) were excluded. Of the remaining 115 items, eight were selected to be Disagreement items, based on the fact that roughly 50% of children answered “Yes” and 50% answered “No,” making the peer’s disagreement plausible. Disagreement items were included to increase the realism of the peer chat, but given the low frequency of such items, neural data were not analyzed for disagreement

trials. The final 96 items were chosen such that average reaction time, response rate, and answer (i.e., “yes” versus “no”) could be matched between conditions.

Stimuli presentation. The task was programmed and presented using the Psychophysics Toolbox Extension for MATLAB 7.6 (PTB-3; Brainard, 1997). Each trial consisted of two phases: Initiation, in which children answered a Yes-No self-relevant question believing their answer would be viewed by a peer (Peer Initiation) or no one (Computer Initiation), and Reply, in which children receive either engaged or non-engaged feedback from the peer (“Me too/neither!” vs. “I’m away”) or computer (“Matched!” vs. “Disconnected”); see Figure 4.1 for design and timing information). For each run, children also viewed two Disagreement trials (i.e., “That’s not what I picked” for the Peer or “Mismatched” for the Computer). These trials were designed to increase verisimilitude but were not analyzed. Thus, children viewed 52 trials of each initiation type and 24 individual trials of each analyzed reply type (Peer Engagement, Peer Non-engagement, Computer Engagement, Computer Non-engagement). If participants did not respond to the question within the response second window, they saw a non-engaged reply and these trials were not analyzed. All children responded to at least 80% of trials, with an average response rate of 96%.

The distribution of the trial types and the timing of the jitters and inter-trial intervals were determined by the program OptSeq (<http://surfer.nmr.mgh.harvard.edu/optseq/>), to ensure the optimal timing in order to allow for independent analysis of the events versus baseline. Specifically, Initiation and Reply types were counted together as one trial for event spacing and ordering (e.g., Peer Engagement was one trial type). This model was further tested for

colinearity using AFNI's 3dDeconvolve (Cox, 1996; <http://afni.nimh.nih.gov/>), ensuring that all beta values of interest were estimable.

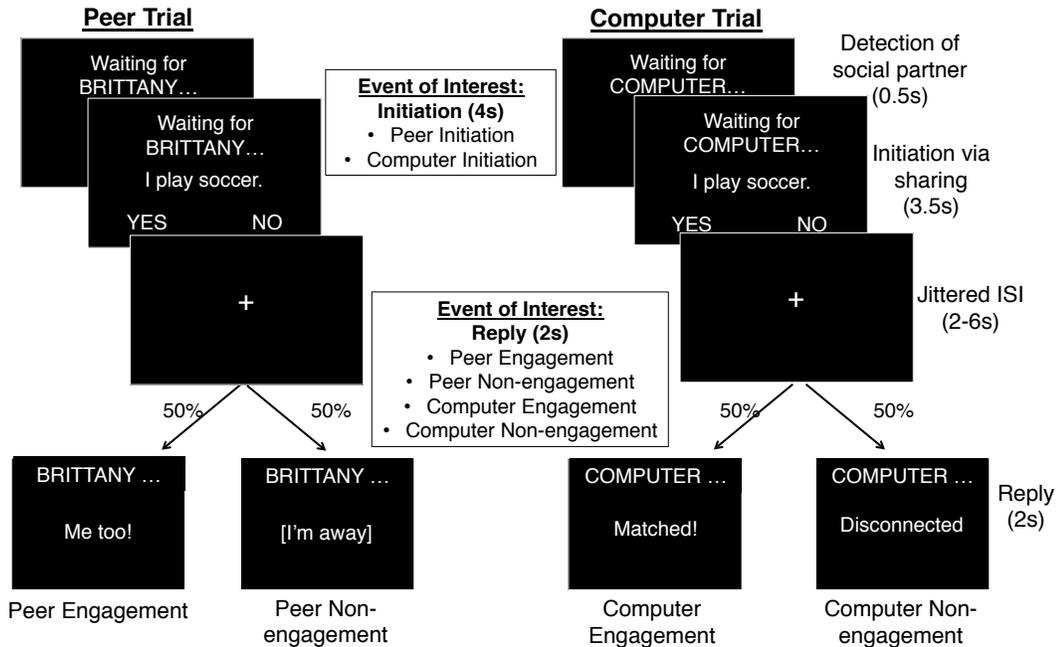


Figure 4.1. The interactive social motivation task. Children completed 24 trials of each condition (Peer Engagement, Peer Non-engagement, Computer Engagement, Computer Non-engagement) in an event-related design. All Peer Engagement trials expressed agreement with the child. Participants believed that the peer was a live child participating in another experiment and that on certain trials (Non-engagement) he or she was busy playing another game and was unable to respond. Thus, trials of social non-engagement did not contain elements of deliberate social exclusion. Participants also believed that the computer generated a random answer and when that answer matched the participant's, the screen read "Matched!" Children were also told that if the computer lost its connection, the screen would read "Disconnected."

A 2-6s jittered fixation cross, distributed exponentially and centered around 3.5s, was present between the Initiation and Reply portions, as well as in-between each trial. Additionally, a baseline fixation cross was present for the first 15s and last 10s of each run. Further, to reinforce the live illusion, in-between each run, children were shown the smiling, direct photo of the age- and gender-matched peer that was they selected in the portion of the experiment before entering the scanner (Egger et

al., 2011), along with a message about the chat (e.g., “That was fun!”; Supplementary Figure S1.D).

Each participant was assigned one of four stimuli sets, which differed based on which of the 96 items were assigned to Peer Engagement, Peer Non-Engagement, Computer Engagement, and Computer Non-Engagement. Within each run, the timing and order of the trial types was predetermined. Based on these constraints, trials were randomly assigned to different positions within the runs (e.g., the Peer Engagement item selected could be any of the 24 possibilities). The participant’s stimuli set (i.e., which items are assigned to which condition) and run order were predetermined to ensure that all possibilities were represented over the course of the study and to ensure that reaction time and response rates were matched for the peer versus computer conditions.

Post-test questionnaire. The experimenter verbally administered a post-test questionnaire to children, assessing how enjoyable participants found the two Initiation types (Peer vs. Computer) and the four Reply types (Peer Engagement, Peer Non-engagement, Computer Engagement, Computer Non-engagement). Additionally, children were asked about how much attention they paid when initiating, as well as how much they wanted to see the answers of the peer versus the computer. Questions were presented on a 1 to 5 point Likert scale. Participants’ belief in the live illusion was also assessed. All children believed that the peer was real and chatting with them in real-time.

Image Acquisition & Preprocessing

fMRI imaging data were collected using a 32-channel head coil on a single Siemens 3.0-T scanner at the Maryland Neuroimaging Center (MAGNETOM Trio Tim System, Siemens Medical Solutions). The scanning protocol for each participant consisted of four runs of the experiment (T2-weighted echo-planar gradient-echo; 40 interleaved axial slices; voxel size=3.0 x 3.0 x 3.0 mm; repetition time=2200ms; echo time=24ms; flip angle=78°; pixel matrix=64 x 64), and a single structural scan (three-dimensional T1 magnetization-prepared rapid gradient-echo sequence; 176 contiguous sagittal slices, voxel size=1.0 x 1.0 x 1.0 mm; repetition time=1900ms; echo time=2.52ms; flip angle=9°; pixel matrix= 256 x 256).

fMRI preprocessing was performed using AFNI (Cox, 1996). Data were slice time corrected and then, using a rigid-body transform, aligned to the first volume. The anatomical scan was also aligned to the first volume and then transformed to MNI space via linear and non-linear transformations. The functional data were then normalized using these same transformation parameters, and were spatially smoothed with a 5mm full-width half-maximum (fwhm) Gaussian kernel. Finally, functional data were intensity normalized in order for each voxel to have a mean of 100.

Outliers—defined as volumes in which the difference between two consecutive volumes exceeded 1mm (across translational and rotational movements)—were censored in subsequent analyses. Runs were excluded if total motion was greater than 4mm, or if greater than 10% of collected volumes were excluded. Participants with at least three usable runs were included in the final analyses. Two children had fewer than three usable runs, six children had three runs,

and 18 children had four runs, resulting in a final sample of 24 children with greater than two useable runs.

Data Analysis

General linear models were constructed in order to estimate the response parameters for both the Initiation and Reply events. Models included the events of interest (Peer Initiation, Computer Initiation, Peer Engagement, Peer Non-engagement, Computer Engagement, Computer Non-engagement) convolved with the canonical hemodynamic response function, as well as constant, linear, and quadratic polynomial terms to account for baseline and drift. Six motion parameters (x, y, z, roll, pitch, and yaw) and outlying time points were also included as regressors.

For the Initiation event, we analyzed the Peer Initiation versus Computer Initiation contrast. For the Reply event, we analyzed the main effect of partner type ([Peer Engagement + Peer Non-engagement] versus [Computer Engagement+Computer Non-engagement]), and the main effect of engagement type ([Peer Engagement+Computer Engagement] versus [Peer Non-engagement+Computer Non-engagement]), as well as the interaction between the two. We also planned a priori comparisons to isolate the effects of engagement in social contexts (Peer Engagement versus Peer Non-engagement), the effects of social engagement with matched contingency (Peer Engagement versus Computer Engagement), the effects of social context without contingency (Peer Non-engagement versus Computer Non-engagement), and the effects of contingency without social context (Computer Engagement versus Computer Non-engagement). Across comparisons, all contrast

maps were thresholded at $p < .001$ and cluster corrected at $p < .05$ ($k=19$, using the updated version of AFNI's 3dClusStim, cf. Eklund, Nichols, & Knutsson, 2015).

In addition to whole-brain comparisons, we also conducted ROI analyses. Specifically, given our a priori hypotheses about the role of VS in social motivation and engagement, we selected two VS ROIs for analysis: inferior VS (corresponding to NAcc) and superior VS (corresponding to ventral caudate). The specific ROIs were selected from a study by Di Martino and colleagues (2008), in which the authors identified anatomically-based regions of VS with distinct patterns of functional connectivity. These particular ROIs have been used in other studies of VS activation (e.g., Kelly et al., 2009; Kolla et al., in press; Padmanabhan et al., 2013), and represent a focused examination of VS activity. The focus on ventral, as opposed to dorsal, striatum was driven by past research indicating a key role for VS in processing social rewards (Izuma, Saito, & Sadato, 2010; Pfeiffer et al., 2014; Schilbach et al., 2010; Tamir & Mitchell, 2012).

Finally, to explore age-related changes in the processing of social stimuli, we examined regions of the social cognitive network (specifically dMPFC, TPJ, and aSTS; Saxe, 2009), as this network had been previously identified as undergoing functional specialization in middle childhood. Given the difficulty of anatomically defining these regions, we instead identified these clusters by selecting regions of the social cognitive network that showed a significant group effect for the Peer Reply > Computer Reply contrast, and extracted each individual's beta value for that same contrast in each cluster. For left aSTS, two separate peaks were identified at the group level. Given our interest in the role of these regions in social cognition, we

selected the cluster that was identified by the meta-analytic database Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011; www.neurosynth.org) as showing the stronger association with the terms “social cognitive” and “theory of mind.” We then correlated these extracted beta values with age. We did not examine the Initiation period, as the whole-brain Peer > Computer contrast did not reveal any significant clusters in that window.

Results

Behavioral

As assessed via the post-test questionnaire, all children believed they were chatting with a real peer and, further, children’s ratings indicated that they found the peer likeable. On a 1-5 scale, children’s average rating of how much they would like the peer in ‘real life’ was 4.23 (SD=.71), with no child giving a score lower than 3. Further, children believed that these feelings toward the peer were reciprocal; when asked how much the peer would like them in real life, children’s responses again ranged from 3-5, with an average score of 4.19 (SD=.75). Additionally, children’s opinions about whether they would like the peer in real life were higher after the experimental social interaction than when they first saw the peer at the beginning of the study (mean pre-test=3.69, mean post-test=4.23, $t(25)=-4.24$, $p<.001$).

For the post-test questions about the Initiation period, children rated initiating with the peer as significantly more likeable than initiating with the computer (mean peer=4.54, mean computer=2.38, $t(25)=8.75$, $p<.001$). Children also reported paying more attention to the peer condition (mean peer=4.08, mean computer=3.31, $t(25)=3.95$, $p<.001$) and rated their desire to see the peer’s answers as significantly

higher than their desire to see the computer's responses (mean peer=4.35, mean computer=2.88, $t(25)=5.47, p<.001$).

For the Reply period, a two-way repeated measures ANOVA examining the effect on self-reported enjoyment of partner type (Peer vs. Computer) and engagement type (Engagement vs. Non-engagement), indicated a significant main effect of partner ($F(1,25)=17.52, p<.001$; Figure 4.2) and engagement ($F(1,25)=59.69, p<.001$). Additionally, the interaction was significant, ($F(1,25)=11.21, p=.003$), such that ratings for the Peer responses were more affected by engagement status than the ratings for the Computer responses.

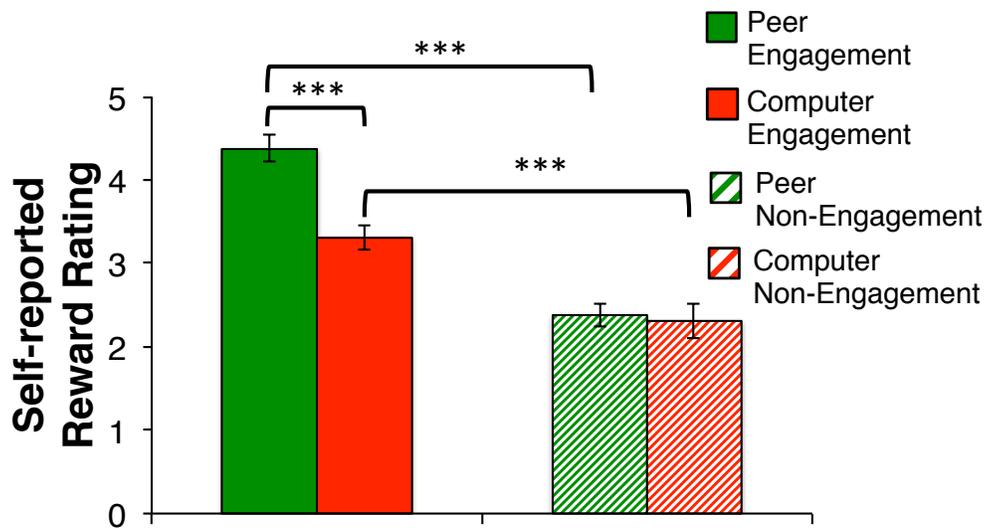


Figure 4.2. Effects of contingency and social context on subjective reward value. On a 1 to 5 Likert scale, children rated how they felt when receiving different types of replies from both peer and computer partners. Both contingency (i.e., engagement) and social context (i.e., peer) produced higher ratings of reward, with a significant interaction between the two terms. ***, $p<.001$.

Post-hoc pairwise comparisons of behavioral data indicated that Peer Engagement had significantly higher enjoyment ratings than both Computer Engagement ($t(25)=5.87, p<.001$) and Peer Non-engagement ($t(25)=8.27, p<.001$)

and that Computer Engagement was more highly rated than Computer Non-engagement ($t(25)=4.03, p<.001$). The contrast between Peer Non-engagement and Computer Non-engagement was not significant ($t(25)=.348, p=.73$).

Although children did not complete enough Disagreement trials for the corresponding fMRI data to be analyzed, behavioral ratings indicated that Peer Disagreement was preferred to Peer Non-engagement ($t(25)=-4.12, p<.001$), although not to Peer Engagement ($t(25)=6.91, p<.001$). For the Computer trials, Engagement was preferred to Disagreement ($t(25)=2.96, p<.01$), but there was no difference in ratings of Non-engagement and Disagreement.

Finally, although there were significant differences on post-test ratings, children self-disclosed equally quickly in both the Peer and Computer conditions (peer mean=1.71s; computer mean=1.73s, $t(25)=-1.28, p=.21$). There was also no difference between conditions in the percentage of statements skipped (peer mean=3.8%; computer mean=4.4%, $t(25)=-.77, p=.45$) or in the proportion of statements for which children answered with ‘yes’ (peer mean=68.7%; computer mean=69.4%, $t(25)=-.44, p=.65$).

Neuroimaging

Effect of social initiation. Whole-brain analyses revealed no significant differences between sharing with a peer versus sharing with the computer (i.e., Initiation period). Higher-power ROI analyses, however, indicated that NAcc (Mean Peer=.083; Mean Computer=.052; $t(23)=2.16, p=.042$) and ventral caudate (Mean Peer=.13; Mean Computer=.089; $t(23)=2.02, p=.055$) were more active when sharing with a peer.

Effect of mutual engagement. For the Reply period, we first examined the whole-brain main effect of partner type ([Peer Engagement + Peer Non-Engagement] > [Computer Engagement + Computer Non-Engagement]; Supplementary Table S4.1; Figure 4.3; Supplementary Figure S4.2). Receiving a reply from a peer resulted in significantly higher activation in many regions, including bilateral NAcc, OFC, dMPFC, right TPJ, and bilateral aSTS. In contrast, whole-brain analyses of the main effect of engagement type ([Peer Engagement + Computer Engagement] > [Peer Non-engagement + Computer Non-Engagement]) revealed a more limited set of regions including OFC and dMPFC, with no striatal activation and no activation in more lateral social-cognitive regions. Analysis of the interaction term ([Peer Engagement > Peer Non-engagement] > [Computer Engagement > Peer-Non engagement]) did not reveal any significant clusters.

We also conducted additional pairwise comparisons for contrasts of interest. For Peer replies, Engagement resulted in significantly greater activation than Non-engagement in several regions, including NAcc, dMPFC, and amygdala, but no difference in lateral regions associated with social cognition. Similarly, the comparison of the engaged peer to the engaged computer also indicated increased response in NAcc and dMPFC. In contrast, for trials without a contingent response (i.e., Non-engagement), the differences between Peer and Computer trials did not implicate striatal regions and instead revealed differential activation in regions such as TPJ and STS. For trials without a social component (i.e., Computer), differential Engagement was indexed only by a cluster in left superior frontal gyrus.

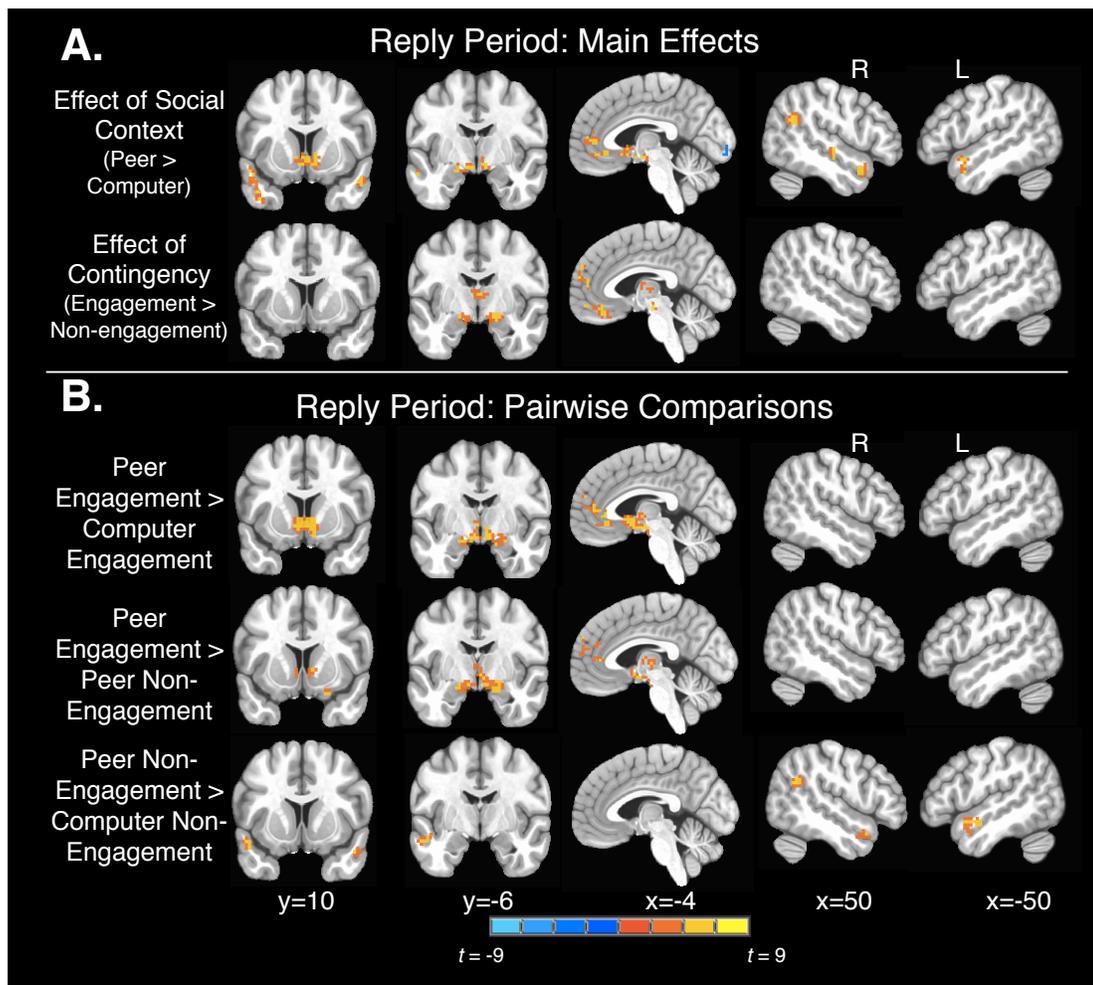


Figure 4.3. Whole-brain analyses examining the neural bases of social engagement (cluster corrected $p < .05$). (A) Regions sensitive to the main effects of social context (receiving a reply from a social partner versus a computer) and the main effects of contingency (receiving a reply based on one's own answer versus receiving a reply indicating the peer or computer is unavailable). Social context activated regions involved in both reward (e.g., VS, OFC) and social processing (e.g., TPJ, STS). Contingency activated a smaller subset of reward regions (e.g., OFC). (B) Pairwise comparisons between several conditions. Peer Engagement resulted in greater reward circuitry recruitment than Peer Non-engagement or Computer Engagement. The comparison between Peer Non-engagement and Computer Non-engagement, however, activated only social cognitive regions (e.g., TPJ).

In order to further explore the effects of social context and contingency on VS activity, we next examined interactions between partner type and reply type in the VS ROIs. For the NAcc ROI, a 2 (Computer vs. Peer) x 2 (Engagement vs. Non-engagement) repeated measures ANOVA revealed a significant effect of partner type

($F(1,23)=26.75, p<.001$; Figure 4.4), as well as evidence for an interaction ($F(1,23)=7.23, p=.013$), although the effect of engagement type did not reach significance ($F(1,23)=3.69, p=.067$). Pairwise comparisons revealed that NAcc response was significantly greater for Peer Engagement than both Computer Engagement ($t(23)=5.57, p<.001$) and Peer Non-engagement ($t(23)=2.81, p<.01$), but there was not a significant difference between the two types of computer engagement ($t(23)=-.072, p=.94$). The difference between a non-engaged peer and non-engaged computer reply was marginally significant ($t(23)=1.91, p=.069$).

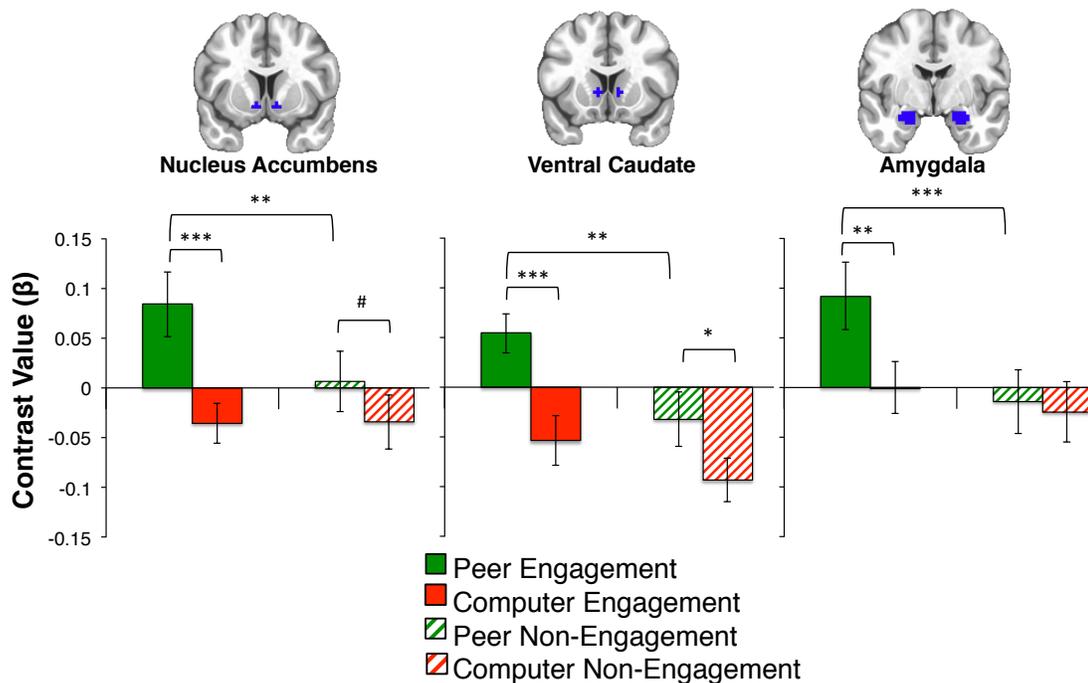


Figure 4.4. Region of interest analyses for the effects of social context and contingency during the reply period. Paired t -tests were used to test 1) Peer Engagement vs. Computer Engagement, 2) Peer Engagement vs. Peer Non-engagement, 3) Peer Non-engagement vs. Computer Engagement, and 4) Computer Engagement vs. Computer Non-engagement. #, $p<.1$; *, $p<.05$; **, $p<.01$; ***, $p<.001$. Error bars represent ± 1 standard error. Results of 2×2 repeated-measures ANOVA are reported in the text.

Analyses of the ventral caudate ROI revealed similar, but not identical patterns to the NAcc. Again, there was a significant effect of partner type ($F(1,23)=26.29, p<.001$), but unlike for the NAcc, the effect of engagement type was significant ($F(1,23)=12.82, p=.002$) and the interaction was not ($F(1,23)=1.31, p=.26$). That is, the sensitivity of NAcc to Engagement type was dependent on partner type, but the ventral caudate was equally responsive to differences in Engagement across conditions. For ventral caudate, pairwise comparisons again revealed significant differences between Peer Engagement and both Peer Non-engagement ($t(23)=2.93, p<.01$) and Computer Engagement ($t(23)=4.05, p<.001$), as well as a significant difference between Peer Non-engagement and Computer Non-engagement ($t(23)=2.34, p=.028$).

Comparing across Reply and Initiation, Reply showed the larger difference between Peer and Computer stimuli in both NAcc ($t(23)=4.81, p<.001$) and ventral caudate ($t(23)=4.90, p<.001$).

Finally, given whole-brain evidence of differential activation across conditions in a cluster that extended into the amygdala, we conducted additional analyses within an anatomically-defined bilateral amygdala ROI (Maldjian et al., 2003). A 2 (Peer vs. Computer) x 2 (Engagement vs. Non-engagement) repeated measures ANOVA revealed significant main effects of partner ($F(1,23)=6.45, p=.018$) and engagement type ($F(1,23)=16.02, p=.001$), as well as a significant interaction ($F(1,23)=5.71, p=.026$), such that the effect of engagement type on amygdala activation was larger for peer than computer trials. Pairwise comparisons

indicated a significant difference between Peer Engagement and both Computer Engagement ($t(23)=3.66, p=.001$) and Peer Non-Engagement ($t(23)=4.41, p<.001$).

Age-related effects. Given that middle childhood is a time of increased sensitivity to peers and neural specialization for social stimuli in the social-cognitive network (Carter & Pelphrey, 2008; Gweon et al., 2012), we conducted additional analyses examining the relation between age and response to Peer vs. Computer replies in this network. Specifically, for the clusters identified by the whole-brain (Peer Engagement + Peer Non-Engagement) > (Computer Engagement + Computer Non-Engagement) comparison, we identified the significant activation clusters corresponding to dMPFC, right TPJ, and bilateral aSTS (there was no significant left TPJ cluster). For each individual, we extracted their contrast values within each cluster for the main effect of partner type and then examined the correlation between these values and age. The difference between Peer and Computer trials increased with age for dMPFC ($r(22)=.44, p=.033$), right TPJ ($r(22)=.46, p=.023$) and left aSTS ($r(22)=.45, p=.027$). Post-hoc analyses revealed that this effect was driven by increased response to both Peer Engagement and Peer Non-Engagement in all three regions, with no significant difference between peer engagement types and no significant changes in response to either Computer Engagement or Computer Non-engagement. In contrast to these social cognitive regions, neither the anatomical VS ROIs nor a VS ROI that was functionally defined based on the main effect of partner type showed any relation between age and the main effect of partner ($r(22)=.12$ for the functionally-defined ROI; $r(22)=.16$ for NAcc, and $r(22)=.25$ for ventral caudate). Finally, the correlations between social cognitive specialization and age were not

reducible to pubertal status; even when controlling for pubertal status, as measured by the self-report Pubertal Development Scale (Carskadon & Acebo, 1993), the relation between right TPJ specialization and age remained significant ($r(21)=.43, p=.043$), and the correlations with dMPFC and left aSTS were marginally significant ($r(21)=.36, p=.089$; $r(21)=.39, p=.063$). Correlations between pubertal status and functional specialization were not significant for any of the social cognitive or reward regions ($ps>.05$).

Although an initial goal of this study was to examine the link between subjective self-report measures of reward and neural indices of reward, the post-test questionnaire produced insufficient variability to be analyzed as a measure of individual differences.

Discussion

The current study investigated the role of social-cognitive and reward regions in supporting naturalistic peer interaction during a real-time interactive task. Specifically, children aged 8-12 completed a real-time chat with a perceived live peer in which trials had two phases: Initiation, when children initiated interaction via discussion of their own likes and hobbies, and Reply, when children received either engaged (“Me too!”) or non-engaged (“I’m away”) replies from the peer. In control trials, children disclosed to a computer and received either engaged (“Matched!”) or non-engaged (“Disconnected”) replies. This design allowed us to test our hypotheses that (1) reward and social cognitive regions would be involved across multiple phases of social interaction, (2) social-cognitive regions would show increased selectivity for social stimuli with age, and (3) although both contingency (i.e., engagement) and

social context (i.e., peer vs. computer) would contribute to reward system activation, they would show a significant interaction such that reward regions would be more sensitive to contingency in a social contexts.

Broadly, our hypotheses were supported. Consistent with behavioral ratings indicating that children preferred initiating to the peer versus a computer control and preferred peer to computer replies, fMRI data indicated increased VS recruitment both for initiating interaction with the peer versus the computer and for receiving replies from the peer versus the computer. In addition to recruiting reward regions, peer replies resulted in increased activation in social cognitive regions, including right TPJ. Further, within these social cognitive regions, the difference between peer and computer activation increased with age, such that older children showed greater response to both engaged and non-engaged peer replies. Finally, analysis of the Reply period indicated an interaction between partner type and engagement type: for both behavioral ratings and VS activation, the effect of contingency (i.e., engagement type) was greater for the social than non-social condition. That is, although children preferred both social replies and contingent replies, the difference in reward value between a contingent and non-contingent social partner was significantly larger than the difference between the contingent and non-contingent computer control.

Social Interaction is Rewarding

The current paradigm provides converging evidence, from both behavioral and fMRI data, that social engagement is rewarding across multiple phases of interaction. Although both social initiation and the resulting social engagement significantly activated VS, the effects were larger during the peer's reply. One

possible explanation for reduced differential engagement of VS during initiation is that the self-disclosure during the initiation period was so intrinsically rewarding that between-condition differences were minimized, an explanation which is supported by the high activation relative to baseline for both peer and computer initiation (cf. (Tamir & Mitchell, 2012). Another possibility is that the rewarding aspects of social initiation come from making an active choice to approach a social partner. Future paradigms could employ a design in which children choose whether and when to approach social partners in order to determine the role of active choice in social motivation. Understanding what makes social initiation rewarding is especially important in autism, as the desire to initiate social interaction may be the component of social motivation that is most impaired (Kohls et al., 2012).

In addition to the brain and behavioral evidence attesting to the rewarding nature of interaction more broadly, both levels of analysis also indicate a significant interaction between contingency and social context in reward processing. A main effect of contingency did emerge, indicating that contingent replies were more rewarding than their non-contingent counterparts. Interestingly, behavior and neural indices of reward were larger when this contingency was embedded in a social context; although children preferred contingency in both conditions, they preferred it even more when a peer was agreeing with them as opposed to the computer. Attesting to the power of social contingency, children even rated trials on which the peer disagreed as more enjoyable than trials on which the peer failed to respond. Given that social context and contingency unfold together in most real-world situations, this

combination may underscore the uniquely rewarding nature of interaction, potentially beginning very early in development (cf. Murray & Trevarthen, 1985).

The current study is limited, however, in its use of a single social partner who agreed with the child on almost all trials. Although this design was successful in separating social non-engagement from social exclusion, future studies should investigate how varied ratios of agreement to disagreement, or intentional to unintentional non-engagement (e.g., Bolling et al., 2011), affect self-reported reward value and reward circuitry activation. One possibility is that non-engagement becomes more desirable than disagreement when the peer frequently disagrees with the child. More involved studies of peer relations may be especially fruitful if they examine how children simultaneously learn about multiple social partners who vary in their response rates, especially given evidence for the role of VS in real-time social learning (e.g., Jones et al., 2011).

In addition to the analyses of ventral striatum, the current paradigm indicated that OFC was sensitive to the main effect of contingent outcomes, which were also behaviorally rated as more rewarding. OFC has been repeatedly linked to processing rewarding outcomes (see Liu, Hairston, Schrier, & Fan, 2011 for a meta-analysis), with several studies finding relations between OFC and subjective perceptions of reward value (e.g., Elliott, Agnew, & Deakin, 2008; Knutson, Fong, Bennett, Adams, & Hommer, 2003; see Levy & Glimcher, 2012 for review). Although the behavioral ratings in the current study had insufficient range to assess the relation between OFC activation and perceived reward, understanding how perceived reward relates to

neural activity in real-world contexts is an important future direction (c.f. Berridge, Robinson, & Aldridge, 2009; Peters & Büchel, 2010).

In contrast to the main effect of contingency on OFC activation, NAcc was modulated by contingency only when the contingent reply came from a social partner. This broader sensitivity of NAcc to social context is consistent with literature implicating NAcc in a host of social behaviors, including pair bonding and learning about conspecifics (see Báez-Mendoza & Shultz, 2013 and Bhanji & Delgado, 2014 for review). In contrast, and more similarly to OFC, ventral caudate showed a significant effect of contingency, indicating that even within VS, different regions may be sensitive to different components of social interaction. These results indicate the importance of precision when discussing reward circuitry and the utility of conducting quantitative meta-analysis across paradigms (cf. Pfeifer & Allen, 2016). Ultimately, despite some differences between regions, reward circuitry was most responsive to real-time social engagement from a peer.

Finally, post-hoc examinations of bilateral amygdala indicated that the region was also sensitive to engagement and social context, producing the greatest response to engaged replies from a peer. Previously studies of social reward have also found amygdala activation, particularly during rewarding outcomes (e.g., Rademacher et al., 2010; Tabibnia, Satpute, & Lieberman, 2008; Trezza et al., 2012), but the precise function of the region in social motivation is unclear. The amygdala plays complex, and perhaps interconnected, roles in both reward processing (see Baxter & Murray, 2002 and Murray, 2007 for reviews), specifically in representing and indexing reward value (e.g., Belova, Paton, & Salzman, 2008; Bermudez & Schultz, 2010), and in

social cognition (see Adolphs, 2010 for review), including in higher order processes like theory of mind (Rice, Viscomi, Riggins, & Redcay, 2014; Shaw et al., 2004; Stone, Baron-Cohen, Calder, Keane, & Young, 2003, but see Spunt et al., 2015). Several recent models of amygdala function have suggested that these different processes may overlap in the structure's role in assessing both stimulus value and influencing resultant behavioral responses (Adolphs, 2010; Pessoa, 2010).

Intriguingly, unlike for NAcc and ventral caudate, the amygdala was only sensitive to the distinction between peer and computer replies when the replies were contingent, suggesting that the region may be most sensitive to social contexts that require a response. Ultimately, even though much literature considers reward circuitry and social cognitive regions separately, social motivation and social cognition are likely overlapping and mutually informative systems.

Social Cognitive Systems Support On-going Interaction

In addition to the role of reward circuitry in processing social information, social cognitive regions (e.g., dMPFC, TPJ, STS) were also involved in supporting ongoing peer interaction. Interestingly, TPJ and STS did not show the same interaction between contingency and social context present in reward circuitry; these regions were still engaged even when the child viewed messages indicating that the peer was unavailable to chat. One possible explanation is that these regions of the social-cognitive network are involved when processing any socially-relevant information, perhaps due to cognitive elaboration about why the social partner was away or due to anticipated future interaction (e.g., non-engagement can often quickly turn into engagement in real-world contexts). Indeed, previous studies with children

have indicated that similar regions are active simply when listening to speech from a perceived social partner, even without any explicit social cognitive demands (Rice, Morczewski, & Redcay, under review).

In contrast to the role of TPJ and STS in processing all peer replies (even when non-engaged), dMPFC was sensitive to the type of social reply, with increased activation to engaged replies. One potential explanation for increased dMPFC activity to engaged replies is that such replies included information about the peer in relation to the child (i.e., “Me too/neither”). dMPFC has been consistently linked to processing trait judgments about the self and others, including in middle childhood (Decety & Sommerville, 2003; Schurz, Radua, Aichhorn, Richlan & Perner, 2014; Pfeifer, Lieberman, & Dapretto, 2007). Interestingly, no differences were found in social cognitive regions during Initiation, perhaps because self-disclosure was so socially salient regardless of interactive context, or because the social cognitive system was less engaged when the child wasn’t receiving a direct message from the peer. To help address the varied roles of these regions during both social initiation and social reciprocity, future research should use functional connectivity analyses to examine how social context and contingency both modulate links within and between reward and social cognitive networks.

Social Cognitive, but not Reward, Systems Show Developmental Change in Middle Childhood

Reward circuitry and social cognitive regions showed differential patterns of age-related changes. For both contingent and non-contingent peer responses, activation in social cognitive regions increased with age as compared to the computer

control. This age-related change is consistent with previous work indicating the middle childhood functional specialization of similar regions in other social contexts, such as mental state reasoning (Gweon et al., 2012) and perceiving biological motion (Carter & Pelphrey, 2008). Although previous research has not found increasing dMPFC specialization to mental state information in this age range (Gweon et al., 2012), it is possible that specialization unfolds differently in more interactive contexts.

In contrast to age-related changes in social cognitive regions, the current sample did not provide evidence for any age-related changes in reward regions. This finding is somewhat surprising given evidence that adolescence is a time of hyperactivity in reward circuitry, particularly in ventral striatum (see Galván, 2010 for a review). One possible reason for the lack of age-related changes in the current study is that adolescent changes in reward sensitivity may rely in part on hormonal changes (e.g., Blakemore, Burnett, & Dahl, 2010; de Macks et al., 2011; Galván 2013) that are not present during middle childhood. Interestingly, the social cognitive specialization in the current paradigm was predicted by age, not pubertal status. Thus, speculatively, the mechanisms driving social cognitive specialization may be less biological and more sociocultural (e.g., increased social network complexity, increased social autonomy). The current study cannot offer insight into the mechanisms driving age- or puberty-related changes, but future research should continue to disambiguate these patterns longitudinally and over larger age ranges.

Reconceptualizing Social Reward

Although reward is most typically discussed in terms of anticipation and outcome (e.g., Dichter et al., 2012; Hoogendam, Kahn, Hillegers, van Buuren, & Vink, 2013; Knutson & Cooper, 2005), such framing may be more applicable to non-social reward than dynamic, back-and-forth interactive contexts. In an ongoing interaction, aspects that could be construed as rewarding outcomes (e.g., smiling, laughter, verbal approval, physical contact) are embedded in a larger, temporally-unfolding structure. Indeed, these ostensible outcomes—such as a partner’s smile—help shape the future trajectory of that interaction and thus may also serve as anticipatory cues about other rewarding events to come. Employing paradigms with multiple embedded and dynamic phases that target multiple components of reward circuitry will help disambiguate the roles of different regions in real-world contexts. Further, such studies should continue to investigate both canonical reward circuitry, as well as more traditional social cognitive networks, as the real-time interplay between these systems is likely necessary to support real-world social behaviors.

Overall, the current study provides behavioral and neural evidence for the roles of social cognitive and social motivational systems in on-going peer interaction. Although both systems support social interaction in middle childhood, they may specialize at different rates and be sensitive to different components of interaction. Ultimately, however, real-world social interaction contains many components not assessed in this study—including multimodal sensory perception, volitional control, and the emergent properties a social dyad—which may also play key roles in the interplay between social motivation and other social cognitive systems. Continued

efforts to embed social neuroscience in real-world social contexts will yield greater insight into both in typical development and social disabilities such as autism, building on the current study's insights into the neurobiological bases of one of the most fundamental human motivations: the drive to interact with others.

Chapter 5: Discussion

This dissertation investigated the developmental neural bases of social interaction via novel fMRI paradigms that targeted two different components of social experience: social communication and social motivation. Taken together, the included studies provide evidence that (1) listening to communicative cues from a perceived live social partner—versus listening to a recording—increases the recruitment of social cognitive brain regions in children and adults and (2) social motivational and social cognitive systems support reciprocal peer interaction in middle childhood. Beyond these specific findings, the general approach taken in this dissertation represents an important step forward in characterizing the neural bases of real-world social behaviors.

Summary

Chapter 2 examined how a social-interactive context affected adult processing of communicative cues. We used a novel paradigm to compare how the brain processed speech believed to be coming from a live social partner versus recorded speech. Unlike previous socially-interactive neuroimaging studies—in which participants played human versus computer opponents (Coricelli & Nagel, 2009; Gallagher et al., 2002; McCabe, Houser, Ryan, Smith, & Trouard, 2001), processed contingent versus non-contingent cues (Redcay et al., 2010, 2012; Schilbach et al., 2010; Caruana, Brock, & Woolgar, 2015), or experienced social exclusion (Eisenberger, Lieberman, & Williams, 2003)—this new paradigm targeted a

fundamental claim of interactive neuroscience: that an interactive social context alters the neural processing of otherwise identical communicative cues (Schilbach et al., 2013). Our results supported this claim, as the mentalizing network—which was defined in each individual using a functional localizer— was strongly recruited in response to live speech. Although evidence from other paradigms had suggested a potential role for reward (Pfeiffer et al., 2014) or attentional networks (Kuhl, 2007; Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012) in processing interactive stimuli, these networks were not differentially recruited when processing live versus recorded speech.

Chapter 3 extended the interactive paradigm of Chapter 2 to middle childhood, a key developmental period for social behavior (e.g., Farmer et al., 2015; Feiring & Lewis, 1991; Sroufe et al., 1999) and the social brain (e.g., Carter & Pelphrey, 2006; Gweon et al., 2012). Results indicated that, by middle childhood, the brain is sensitive to social context: social cognitive regions were more heavily recruited when children believed they were listening to live speech. Although children did not complete a mentalizing localizer, regions frequently associated with mentalizing were more recruited for live speech, including precuneus, superior temporal sulcus (STS), and bilateral temporoparietal junction (TPJ; Frith & Frith, 2006; Saxe, 2009). Unlike adults, however, children did not recruit dorsomedial prefrontal cortex (dMPFC). Thus, children showed similar, but not identical, activation patterns to the adult sample in terms of sensitivity to live speech.

Given that the previous two chapters established the importance of social-interactive context, Chapter 4 employed an interactive paradigm to study social

motivation, a construct typically examined in either offline, detached paradigms (e.g., Spreckelmeyer et al., 2009; Rademacher et al., 2010; Richey et al., 2014) or in paradigms that conflate social context with contingent responses (e.g., Schilbach et al., 2010). In our novel paradigm, children interacted in real-time computer-based chat with a peer that they believed to be a real social partner. The paradigm isolated two phases of this interaction: (1) initiation, in which children made a social bid to the peer via disclosing likes and hobbies, and (2) reply, in which children received either an engaged or non-engaged response from the peer. Additionally, children completed control computer trials, in which they disclosed to a computer and received computer replies that were either engaged or non-engaged. Unlike Chapters 2 and 3, Chapter 4 did not directly compare social reward from a live social partner to a recorded, human control. Rather, the aim of the study was to determine which neural systems supported social motivation during a real-time interaction with a peer. We found that reward systems (e.g., ventral striatum; Haber & Knutson, 2010) were more engaged by peer interaction during both initiation and reply, and that peer replies also significantly increased activity in social cognitive regions. Further, for these social cognitive regions, the difference between peer and computer conditions increased with age.

Social-Interactive Context Matters

Significant behavioral (e.g., Goldstein & Schwade, 2008; Kuhl, Tsao, & Liu, 2003; Laidlaw, Foulsham, Kuhn, & Kingstone, 2011) and theoretical literature (e.g., Gallotti & Frith, 2013; Schilbach et al., 2013) has suggested that social-interactive context changes cognitive processing; it is possible, however, that well-controlled

neuroimaging paradigms would have found no effect of social-interactive context on neural activity. For example, previous findings indicating that interaction is fundamentally distinct from observation could have been instead attributable to lower-level differences in contingency or other stimuli characteristics rather than interaction per se (cf. Redcay, Rice, & Saxe, 2013). The results from this dissertation, however, speak directly against this possibility.

Attesting to the importance of interactive context, activation in mentalizing regions was increased simply by listening to live versus recorded speech—speech with no mental state information or other overt social content—both in children and adults. Similarly, the results from Chapter 4 indicate that believing that one’s responses would be seen by a social partner increased reward circuitry activation. Although, by design, this social motivational paradigm does not speak directly to the question of processing live versus not-live social cues, the results still show the importance of social context. Future social motivation paradigms could more directly compare live versus recorded reward stimuli, perhaps by having children view real-time responses from a live peer versus viewing the stored answers from a peer who participated the day before. Such paradigms would help further identify the sensitivity of reward circuitry to live versus not-live contexts. Overall, and across paradigms, the neuroimaging results indicate that social-interactive context alters neural processing.

In addition to our neuroimaging findings, behavioral data also indicate that children and adults are sensitive to social context. For example, in Chapters 2 and 3, both children and adults rated the live speaker as more likeable and engaging than the

recorded speaker—an effect that disappeared in control behavior experiments in which participants were told the live speaker was prerecorded. Importantly, in addition to the live and matched recorded speakers, the paradigm from Chapters 2 and 3 employed an additional recorded speaker with lower levels of prosody. This speaker was included as a control to assess whether differences in likeability or engagement alone could be responsible for differences between the live and matched recorded speech. We found that, as intended, the two recorded speakers did differ on ratings of engagement and enjoyment, but that this contrast did not produce differences in the mentalizing network. This lack of neural difference between the recorded conditions suggests that motivation or likeability differences alone cannot explain the current findings, but that such factors may be a part of interactive experience. Supporting this idea, in Chapter 4, children rated chatting with the peer as much more enjoyable and motivating than chatting with the computer control.

Although the current paradigms showed large effects of live context on self-report ratings, effects of social context on implicit behavioral measures were mixed. Adults showed no difference in reaction time (RT) when answering questions from the live versus not-live speaker, although this may have been due to the ease of the questions. In Chapter 3, in contrast, children showed significant slowing when responding to questions from a live versus a recorded social partner. This finding, paired with increased activation in social cognitive regions, may suggest additional cognitive deliberation when children believed their answer would be viewed by a live partner. RT, however, is multi-determined. For example, RT is often used as an index of reward salience in social contexts (Jones et al., 2011; Rademacher et al., 2010), a

finding that suggests that faster RT may have been expected in the social motivational context of Chapter 4. In that study, however, no RT difference emerged when making social bids to the peer versus computer. This null finding could be explained by any motivationally-driven RT decrease being balanced out by increased cognitive deliberation in the social context (e.g., will she think it's cool that I like Taylor Swift?), similar to the potential elaborative processes occurring in Chapter 3's social communicative paradigm. In sum, evidence across studies suggests that the effects of social context on implicit measures of behavior are likely influenced by the interplay of specific task demands, which complicates any interpretations of RT findings.

In spite of this dissertation's strong evidence for the effects of social context on both brain and behavior, links between the two domains were less clear. Some evidence from adults suggests a correlation between perceived liveness of the live speaker (e.g., how much it seemed like the speaker was in same room) and neural specialization for live speech, but no similar correlations emerged in the developmental sample. One reason for limited brain-behavior relations for children is that the self-report Likert scale measures of Chapters 3 and 4 produced a limited range that made investigating individual differences difficult. Future research should examine more fine-grained self-report measures in order to track the relation between subjective perception and neural activation (e.g., the link between perceived reward and OFC activation; Levy & Glimcher, 2012).

Ultimately, there may be certain emergent properties of live interaction that cannot be controlled for in studies that target the core properties that separate interaction from observation. For example, in Chapters 2 and 3, we found that

believing that one was interacting with a live partner increased self-reported motivation and attention. One perspective is that these are confounds that could be addressed by improving study design. In contrast, it is possible that simply believing that one is interacting with a real person may alter motivational or attentional processes in a fundamental way, perhaps in concert with increased mentalizing (Krach, Paulus, Bodden, & Kircher, 2010). These two possibilities may be disambiguated by paradigms that employ cognitive interference tasks or which continuously vary perceptions of ‘liveness’ and simultaneously examine continuous changes in self-reports of motivation or attention. For example, if participants’ levels of motivation monotonically increase while interacting with an avatar behaving in increasingly agentive ways, it would suggest that simply perceiving a social partner affects engagement levels. Although unlikely given the current findings, it is possible that, as social-interactive paradigms become increasingly well controlled, differences between live and not-live conditions would fail to emerge. Such potential null findings, however, could be due to the fact that in such highly controlled paradigms (e.g., with no visual or audio cues that one has a real social partner), the interactive experience becomes wholly top-down without any of the bottom-up cues that typically signal interaction. Having to consciously remember that one is in an interaction may be too demanding for young children or clinical populations, and such top-down interactive paradigms may not capture emergent properties of real-world interaction. Future research employing paradigms that cue interaction in multiple ways will help answer the question of what is core to social-interactive experience.

Developmental Change in Middle Childhood

This dissertation targeted middle childhood both because it represents a time of important change in social behavior (Farmer et al., 2015; Feiring & Lewis, 1991; Sroufe et al., 1999) and because several recent studies have found middle childhood to be a period of functional specialization in the social brain (Carter & Pelphrey, 2006; Gweon et al., 2012; Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey 2009). The results from Chapter 4 are consistent with these prior studies finding functional specialization, as they indicate that—for several regions of the brain’s social cognitive network (i.e., TPJ, dMPFC, aSTS)—the difference between response to peers and response to non-social controls increases with age. This increasing gap between conditions is driven not by a change to non-social stimuli, but by an increase in the response to the peer. Interestingly, this increased response to the peer is not only found on trials in which the peer engages with the child, but even on trials on which the peer is unavailable to chat. Thus, the results from Chapter 4 suggest that between the ages of 8-12, social cognitive regions become more sensitive to social interaction.

In contrast, the results from Chapter 3 do not show increased sensitivity to social-interactive stimuli in this same network. Although children show increased activation in social cognitive regions (e.g., TPJ, STS) during live versus recorded speech, none of these regions showed age-related changes, either when examining the magnitude of live or recorded speech to baseline activation or when comparing the conditions to one another. Thus, unlike in the social motivational context, the social

communicative paradigm did not indicate middle childhood to be a time of changes in neural sensitivity for interactive stimuli.

Taken together, these different patterns of specialization suggest that developmental changes in neural selectivity may be context dependent. For example, in Chapter 4's motivational paradigm, children were interacting with a peer about self-relevant topics (i.e., likes and hobbies). Thus, rather than increased social cognitive sensitivity to live interaction more broadly, observed age-related changes may indicate increased salience of or attention to socially-relevant information about peers. Increased attention to peers or self-relevant traits would also be consistent with behavioral findings about developmental changes in middle childhood (Buhrmester & Prager, 1995; Lochman et al., 2010). To test this hypothesis, researchers could examine whether a relation between age and neural selectivity of the social cognitive network emerges if children answer factual (versus self-relevant) questions or if they chat with an adult (versus a peer). Similarly, modifying Chapter 3's social communicative paradigm in order to examine peer speech or more socially-relevant speech may yet reveal evidence of age-related changes in the social cognitive network. Examining the conditions under which neural activation increases would help dissociate whether our results indicate a general increase in functional specialization for social contexts, or a more context-dependent sensitivity to particular types of social interactions. As a preliminary hypothesis—and one supported by the lack of age-related specialization in Chapter 3—it is likely that some components of the brain's social-interactive system have already specialized by

middle childhood, whereas sensitivity to components of interaction other than a simple live versus not-live distinction may still be developing.

The results from the current studies do not address whether behavioral, cognitive, or biological processes are driving the increased activation to peer responses seen in Chapter 4. Limited evidence from a self-report pubertal scale suggests that age, more than pubertal status, is responsible for those effects, but age is likely confounded with changes in social network size, transitions to middle school, and changing levels of social autonomy, which all may play a role in changes in neural activity. Future studies could include more nuanced measures of social development (e.g., size and diversity of social networks; Cohen, Doyle, Skoner, Rabin, & Gawltney, 1997), in order to pinpoint the factors leading to specialization. Further, it is possible that these neural changes have a bidirectional influence on peer relationships; children with increased neural sensitivity to peer contexts may have more successful peer interactions. Ultimately, longitudinal studies will be the most informative in uncovering the reasons behind developmental change, as such paradigms will be able to better separate the causal relations among middle childhood's complex constellation of pubertal, social, and neurobiological changes.

Roles for Social Motivational and Social Cognitive Systems

As laid out in the introduction, we aimed to understand the brain bases of live interaction via measuring how different interactive contexts affected different neural systems. Across both social communicative and social motivational contexts, social cognitive circuitry—and, in particular, TPJ—was activated by social interaction. Although these social cognitive regions have been linked to a variety of processes

(e.g., TPJ plays a domain-general role in attention; Decety & Lamm, 2007; Mitchell, 2008), both localizer analyses and meta-analytic findings (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) indicate that these engaged regions are part of the mentalizing network.

These converging findings raise the possibility that increased engagement of mentalizing regions may be intrinsic to social interaction. The exact role of this network in supporting interaction, however, is not known. One possibility is that these mentalizing differences across live and not-live contexts are quantitative, such that the mentalizing network does “more” mental state representation when dealing with a real social partner. For example, even when receiving a peer’s “I’m away” message, children may be simulating the cognitive states of their peer (e.g., “I wonder what he would have said to that question”). Another possibility is that, although regions such as TPJ are often conceived of as “mental state computation” regions, such regions could play more a global role in supporting social-interactive processes, such as interactive alignment and synchrony (Garrod & Pickering, 2009; Kopp, 2010). Further, different regions of the larger mentalizing network may be involved in different components of interaction (e.g., TPJ, more than dMPFC, may be involved in representing a live social partner across task contexts). Future research should continue to interrogate the role of the mentalizing network across development and across interactive contexts to determine if its activation is core to supporting interactive experience, even absent any overt or explicit mentalizing demands.

In contrast to the increased activation in social cognitive regions across tasks, and contrary to theories suggesting that social interaction is intrinsically rewarding

(e.g., Pfeiffer et al., 2014), Chapters 2 and 3 found no differences in reward circuitry activation when processing live versus recorded speech. Although both behavioral and neural evidence have suggested that social interaction is rewarding, such paradigms frequently confound contingency or choice with social context. For example, in social paradigms that have produced reward circuitry activation, participants answered a self-disclosure question (Tamir & Mitchell, 2012), pressed a button to see a smiling face (Spreckelmeyer et al., 2010), or initiated joint attention by choosing which box to look at (Schilbach et al., 2010). In contrast, when participants initiated joint attention, but were guided by external cues about where to direct their partner's gaze, reward circuitry was not activated (Redcay et al., 2012). Thus, it is possible that live context alone is not sufficient to produce reward system activation, and that more contingent social interaction is necessary to tap into motivational processes.

Our results from Chapter 4 further support the role of contingency in social reward. We found an interaction between partner type (peer versus computer) and contingent reply type (engaged versus non-engaged), such that nucleus accumbens was significantly more engaged for social contingency than non-social contingency, but there was no difference for the non-contingent events. Indeed, for non-contingent social events, activation in ventral striatum was not significantly greater than baseline activation. Thus, the social communicative paradigm from Chapters 2 and 3, in which participants merely listened to several sentences of speech, may not have been sufficient to engage the reward system. Additionally, it is also possible that these long speech events failed to capture more transient reward circuitry responses. Future

research should continue to disambiguate the necessary and sufficient conditions for social interaction to elicit reward circuitry activation.

Ultimately, any discussion of the roles of different neural systems should occur in the context of connectivity and overlap between networks. For example, diminished functional connectivity between reward circuitry and pSTS has been linked to symptom severity in autism (Abrams et al., 2013). Speculatively, perhaps such underconnectivity may be especially acute during live interaction and functional connectivity during interactions, as compared to offline paradigms, may better predict current and future symptomatology. Similarly, although the paradigms in this dissertation did not find effects of live interaction on attention network activation, it may be that interaction changes the connectivity patterns of the attention network with other cognitive systems. Pairing functional connectivity and localizer analyses across a variety of paradigms will help provide sharper insight into the constituent systems supporting social interaction.

Social Neuroscience Going Forward

Although this dissertation employed two well-controlled paradigms to study interactive context, neither paradigm fully captured the dynamics of real-world interaction. For example, for experimental control, all live partners were actually simulated. Participants were convinced by these simulations, but real partners will likely be necessary to understand the temporally fine-grained “interactive alignment” that unfolds between two individuals (Garrod & Pickering, 2009). True social interaction is also a multisensory experience that most often involves concurrent audio, visual, olfactory, and tactile cues. To date, however, these sensory domains

have most often been investigated in isolation (e.g., Gordon et al., 2013); future multisensory studies may offer better insight into real-world social processing. In another dissimilarity between real-world interaction and laboratory experiments, most neuroimaging studies are designed such that a single trial type is repeated multiple times. In Chapter 4 for example, each trial follows the same pattern, and the child's growing knowledge about the peer does not change the subsequent questions asked. True back-and-forth interaction, in contrast, unfolds over time such that what happened previously affects subsequent events. This temporal unfolding may be what fosters the emergent properties of interaction, or, in the words of De Jaegher and colleagues (2010), what allows the interaction to "take on a life of its own" (p. 442). Thus, although it will be an enormous methodological challenge, future interactive neuroscience paradigms should attempt to embrace more dyadic, temporally unfolding approaches.

Given the temporal dynamics of interaction and the limited temporal resolution of fMRI, a multi-method approach will be necessary to fully understand the neural bases of social interaction. For example, EEG has offered insight into how typical adults process information from real social partners, including direct versus averted gaze (Pönkänen, Peltola, & Hietanen, 2011) and joint action cues (Kourtis, Sebanz, & Knoblich, 2010), and investigators have begun to use fNIRS to examine response to real-time social exclusion (Ruocco et al., 2010). Pairing these neuroimaging methods with eye-tracking will also be fruitful, as social attention may be differentially affected by live contexts (Laidlaw et al., 2011; Pfeiffer, Vogeley, & Schilbach, 2013). Additionally, hyperscanning paradigms employing fMRI, EEG or

fNIRS in which multiple individuals are scanned simultaneously may offer a unique perspective on interaction (e.g., Cui, Bryant, & Reiss, 2012; Koike et al., 2016; Krill & Platek, 2012; reviewed in Babiloni & Astolfi, 2014). Although hyperscanning data are difficult to interpret and analyze (Burgess et al., 2013), such paradigms do offer insight into the neural activity of both initiator and responder and can involve participants flexibly switching between roles. In the end, no single method is likely to untangle the complex neural bases of social interaction, but using multiple methods will move the field forward.

Using a greater range of tools to study interaction is also necessary to provide greater insight into the neural bases of social interaction in young children and infants. Given that infants as young as two months are sensitive to contingent versus non-contingent social interaction (Murray & Trevarthen, 1985), neonates may show neural sensitivity to the cues that indicate live interaction, with neural specialization for these cues increasing over time. Recent evidence indicates that infants show neural selectivity for one such interactive cue—human speech—beginning by one month of age, with increasing specialization over the next three months (Shultz, Vouloumanos, Bennett, & Pelphrey 2014). Similarly, EEG evidence suggests specialization over the first year of life for social versus non-social audiovisual stimuli, with live social stimuli eliciting larger neural effects than recorded social stimuli (Jones, Venema, Lowy, Earl, & Webb, 2015). Intriguingly, some of the same regions implicated in explicit mental state computation in adults have been linked to processing social-interactive cues (i.e., joint attention) in infancy (Grossmann & Johnson, 2010). One potential explanation for this overlap is that these mentalizing

regions may support social-interactive processes more broadly earlier in life, and then later come to specialize for mental state computation, as such computation occurs most frequently during interaction. Longitudinal research examining how specialization for social interaction unfolds over time will not only map out a normative developmental trajectory, but will also help illuminate the how particular neural networks subserve adult social interactions.

Mapping the development of the neural response to live interaction will also improve understanding of psychiatric disorders with social components, including autism, schizophrenia, and social anxiety. Individuals with these disorders often show the largest functional impairments in interactive contexts, and some preliminary research has begun to indicate that interactive neuroimaging paradigms may better aid the search for psychiatric biomarkers (Assaf et al., 2013; Billeke et al., 2015). Indeed, in Chapter 2, we found that the activation difference between live and recorded speech in dMPFC was correlated with a measure of autistic-like traits designed to capture variability in the typical population (Autism Quotient; Baron-Cohen et al., 2001); adults with more autistic-like traits showed diminished sensitivity to live speech. Downward extending such paradigms may allow for earlier detection of autism, as group differences may be more robust in interactive than non-interactive contexts (e.g., Merin et al., 2007).

Conclusions

This dissertation embeds social neuroscience in the social world. Across paradigms that examined both social communication and social motivation in children and adults, we found that social-interactive context alters neural processing.

In particular, interactive context increased activity in regions associated with mentalizing, suggesting a core role for this system in social interaction. The precise cognitive processes subserved by these regions, however, are not yet known. Although the mentalizing network was recruited across tasks, the levels of both reward circuitry engagement and age-related neural specialization were dependent on the specific paradigm. Thus, different neural systems are likely differentially recruited across the heterogeneous landscape of real-world social-interactive contexts. Future studies examining how the brain supports social interaction across both varied contexts and varied developmental time points will illuminate the core and ancillary processes of social experience. Ultimately, this dissertation provides a launching pad for understanding how social-interactive context affects individuals, dyads, and groups at behavioral, cognitive, and neurobiological levels. Or, put more plainly, for understanding a fundamental part of what makes us human: how we relate to one another.

Appendix A: Chapter 2 Supplementary Materials

Supplementary Table S2.1

Audio Characteristics of the Three Experimental Conditions

	Live	Social	Standard	$F_{(2,105)}$	Pairwise Comparisons
STORY AUDIO FEATURES					
Length (s)	6.26 (.38)	6.25 (.39)	6.26 (.39)	.089	Live=Soc=Std
Volume (dB)	60.00 (.01)	60.00 (.01)	60.00 (.01)	.062	Live=Soc=Std
Pitch (Hz)	235.3 (8.5)	259.0 (14.4)	180.9 (5.7)	555.29***	Soc>Live>Std
QUESTION AUDIO FEATURES					
Length (s)	3.53 (.39)	3.85 (.40)	3.66 (.37)	5.79**	Std=Soc>Live=Std
Volume (dB)	60.00 (.01)	60.00 (.01)	60.00 (.01)	.027	Live=Soc=Std
Pitch (Hz)	288.6 (46.3)	295.7 (35.6)	173.9 (7.7)	290.82***	Std>Live=Soc

Note. Values are mean (standard deviation). Post-hoc pairwise comparisons were made using a Tukey's test of multiple comparisons with an alpha of .05.

Abbreviations: s=seconds; dB=decibels; Hz=Hertz. **, $p < .01$; ***, $p < .001$.

Supplementary Table S2.2

Regions Showing Differences between Conditions for the Content-Matched Story Portion

Region	Side	Peak <i>t</i>	Cluster <i>k</i>	MNI Coordinates		
				<i>x</i>	<i>y</i>	<i>z</i>
EFFECT OF LIVE INTERACTION (MATCHING PROSODY)						
Live>Social						
Angular gyrus	L	4.54	93	-34	-78	42
TPJ	L	5.09	382	-38	-56	32
dMPFC	L	5.08	108	-8	50	28
dMPFC	R	5.39	152	12	56	28
Social>Live						
Lingual gyrus	L	-5.56	482	-18	-94	-4
Lingual gyrus	R	-4.82	164	22	-94	4
EFFECT OF FRIENDLINESS (MATCHED ON RECORDED CONTEXT)						
Social>Standard						
STG	R	5.72	184	64	-22	6
Standard>Social						
None						

Note. TPJ=temporal parietal junction; dMPFC=dorsomedial prefrontal cortex; pSTS=posterior superior temporal sulcus; STG=superior temporal gyrus. All coordinates are in Montreal Neurological Institute (MNI) space.

Supplementary Table S2.3

Participant Ratings of the Speakers Across Experimental Conditions

	Live	Social	Standard	$F_{(2,56)}$	Pairwise Comparisons
A. SCAN SUBJECTS (BELIEVED LIVE SPEAKER WAS LIVE)					
Liveness	5.76 (1.23)	3.99 (1.50)	2.61 (1.51)	39.99** *	Live>Soc>Std
Likeability	6.45 (.69)	4.76 (1.52)	3.52 (1.27)	46.07** *	Live>Soc>Std
Engagement	6.50 (.81)	5.60 (1.21)	4.76 (1.50)	27.98** *	Live>Soc>Std
B. BEHAVIORAL SUBJECTS (LIVE SPEAKER WAS PRESENTED AS RECORDED)					
Liveness	4.67 (1.37)	4.48 (1.22)	2.62 (1.25)	17.60** *	Soc=Live>Std
Likeability	5.43 (.85)	5.08 (1.30)	3.03 (1.26)	28.22** *	Soc=Live>Std
Engagement	5.58 (.89)	5.30 (1.04)	4.13 (1.43)	15.23** *	Soc=Live>Std
C. PILOT SUBJECTS (HEARD AUDIO CLIPS WITHOUT CONTEXT)					
Liveness	3.43 (1.27)	4.00 (1.75)	2.52 (1.06)	13.14**	Soc>Live>Std
Likeability	4.08 (.99)	4.73 (1.35)	3.20 (1.11)	13.13** *	Soc>Live>Std
Engagement	4.53 (.98)	4.70 (1.07)	3.88 (1.11)	6.50*	Soc=Live>Std

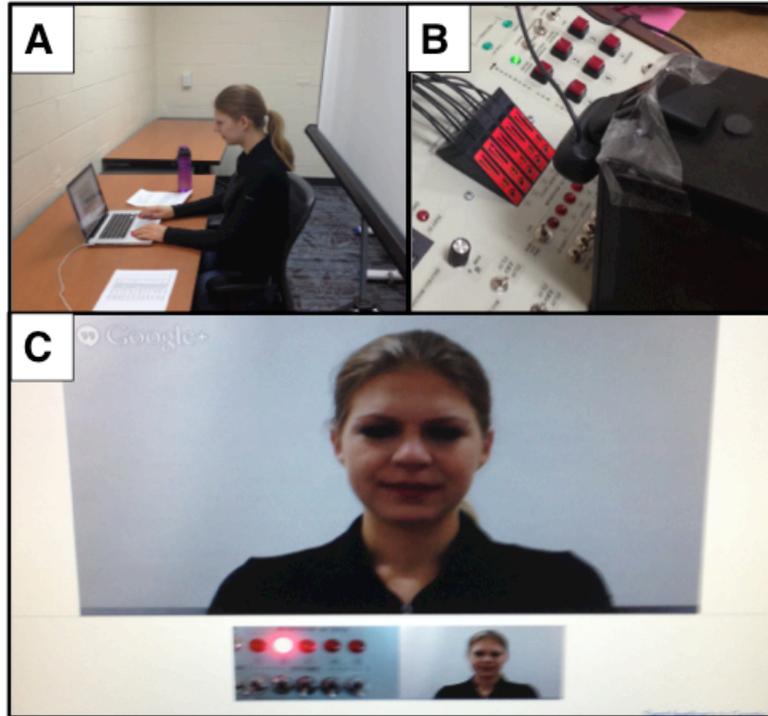
Note: Values are mean (standard deviation). Post-hoc pairwise comparisons were made using a Sidak correction for multiple comparisons at an alpha of .05. All post-test questionnaire ratings are composites of items scored on a 1 to 7 scale. When assumptions of sphericity were violated, a Greenhouse-Geisser correction was employed. *, $p < .05$; **, $p < .01$; ***, $p < .001$. Soc=social; Std=standard.

Supplementary Table S2.4

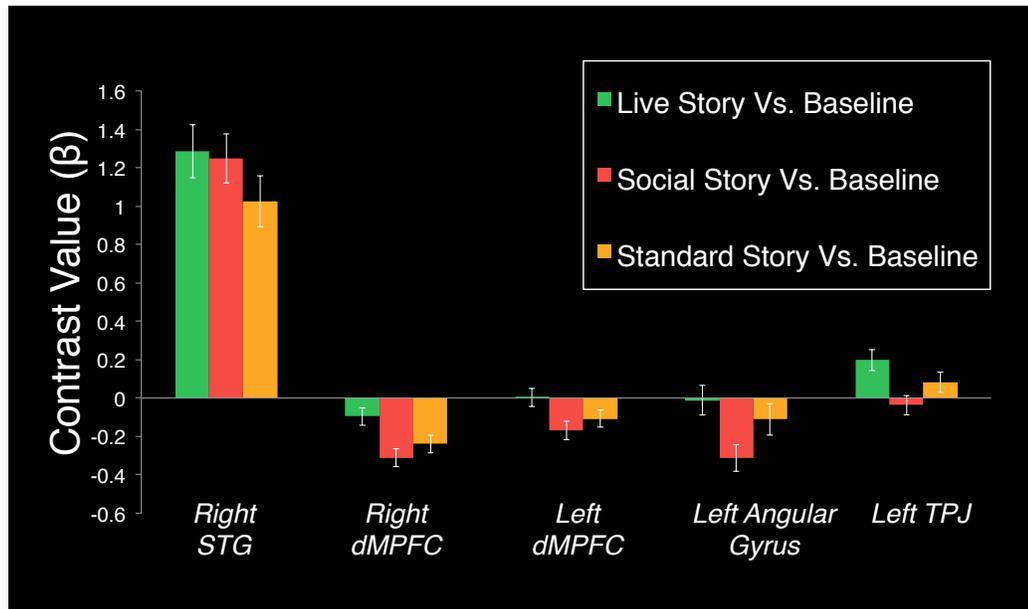
Behavioral Performance Across Experimental Conditions

	Live	Social	Standard	$F_{(2,56)}$	Pairwise Comparisons
Accuracy (%)	95.66 (.06)	94.25 (.08)	94.20 (.08)	.395	Live=Soc=Std
RT (ms)	1088 (199)	1121 (188)	1133 (242)	.520	Live=Soc=Std

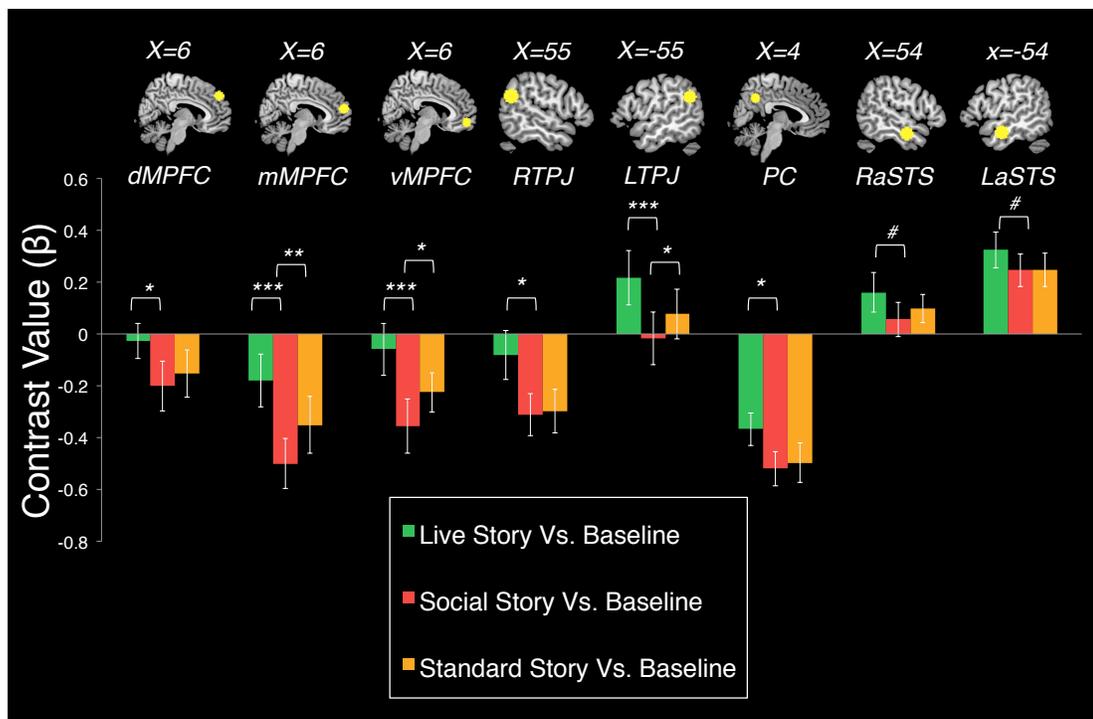
Note. Values are mean (standard deviation). Post-hoc pairwise comparisons were made using a Sidak correction for multiple comparisons at an alpha of .05. Untransformed RTs are reported in the table, but statistical tests were performed on inverse transformed RTs. Abbreviations: RT=reaction time; ms=milliseconds; Soc=social; Std=standard.



Supplementary Figure S2.1. Experimental setup to assist in creating the live illusion. Before the study began, the participant viewed the experimenter room (A), where the live speaker had set up a live video chat. The webcam on the laptop in the experimenter room was trained on her face. The second webcam in the video chat (B) was trained on a button display, which lit up when the participant inside the scanner pressed a button. When inside the scanner, before the main experiment began, the participant viewed the screen depicted in (C). The participant saw the live experimenter's face and heard her talking to him or her. The live speaker asked the participant a question (e.g., "Press 1 if it is summer and 2 if it is winter"). Immediately after pressing the button (in the case of (C), the button is 2), the participant saw their choice illuminated and thus knew that the live experimenter had also seen their choice. The live partner then gave live contingent feedback (e.g., thumbs up). After this live chat, the main experiment began, in which prerecorded stimuli were presented as live.



Supplementary Figure S2.2. Comparison of contrast values within regions defined by group-level analysis (see Supplementary Table 2). Right STG was defined by Social > Standard and all other regions were defined by Live > Social. Contrast values are averages of each individual's average beta weights for each condition's story versus baseline. Error bars represent +/- 1 standard error. Abbreviations: dMPFC=dorsomedial prefrontal cortex; STG=superior temporal gyrus, TPJ=temporal parietal junction.



Supplementary Figure S2.3. Comparison of contrast values within individually-defined regions activated by the mentalizing localizer. Each individual's regions were defined by intersecting a 9mm sphere with voxels active at $p < .001$, $k = 10$. Contrast values are averages of each individual's average beta weights for each condition's Story versus baseline. The brain images represent 9mm spheres around group average coordinates, but each individual's own regions were used in analysis. Paired t-tests were used to test 1) Live vs. Social and 2) Social vs. Standard. #, $p < .1$; *, $p < .05$; **, $p < .01$; ***, $p < .001$. Error bars represent ± 1 standard error. Abbreviations: dMPFC=dorsomedial prefrontal cortex; mMPFC=middle medial prefrontal cortex; vMPFC= ventromedial prefrontal cortex; TPJ=temporal parietal junction; PC=precuneus; aSTS= anterior superior temporal sulcus; R=right; L=left.

Appendix B: Chapter 3 Supplementary Materials

Supplementary Table S3.1

Behavioral Performance and Post-Test Questionnaire Ratings for the Control Behavioral Experiment

	Live	Social	Standard	$F_{(2,36)}$	Pairwise Comparisons
BEHAVIORAL PERFORMANCE					
Accuracy (%)	84.72 (11.16)	82.87 (19.3)	86.57 (11.12)	.442	Live=Soc=Std
RT (ms)	1384 (244)	1421 (360)	1438 (312)	.348	Live=Soc=Std
POST-TEST QUESTIONNAIRE RATINGS					
Liveness	3.42 (.95)	3.13 (.85)	2.39 (.88)	9.89***	Live=Soc>Std
Likeability	3.84 (1.07)	4.00 (1.20)	3.39 (1.12)	2.02	Live=Soc=Std
Engagement	4.58 (.61)	4.47 (.77)	4.16 (.83)	2.11	Live=Soc=Std

Note: Values are mean (standard deviation). Due to a technical error, task data were not recorded for one participant, resulting in N=18 for accuracy and reaction time (RT) measures and N=19 for post-test ratings. All post-test questionnaire ratings are composites of items scored on a 1 to 5 scale. The control study had a 3s response window due to timing constraints at the behavioral session. Post-hoc pairwise comparisons were made using a Tukey's test with an alpha of .05. **, $p < .01$; ***, $p < .001$. Soc=Social; Std=Standard.

Appendix C: Chapter 4 Supplementary Materials

Supplementary Table S4.1

Regions Showing Differences During Social Interaction

Region	Side	Peak	Cluster	MNI Coordinates		
		<i>t</i>	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>
A. INITIATION PERIOD						
Peer > Computer						
None						
Computer > Peer						
None						
B. REPLY PERIOD						
Main Effect of Partner						
Peer > Computer						
NAcc	L/R	5.35	206	0	6	-12
dMPFC	L/R	5.22	97	0	48	6
Insula	R	4.94	63	32	14	-16
mid-STG	R	4.30	54	50	-18	-10
aSTS	L	4.04	52	-54	6	-18
vMPFC	R	4.53	45	2	48	-12
IFG	L	6.21	41	-42	24	-12
TPJ	R	6.16	35	50	-54	24
Insula	L	5.26	32	-30	12	-18
aSTS	R	4.43	20	54	14	-18
aSTS	L	4.22	20	-64	-10	-18
Computer > Peer						
Lingual gyrus	R	4.03	131	20	-76	-12

Cuneus	R	4.11	49	24	-94	26
Lingual Gyrus	L	4.48	31	-4	-96	-10
IPS	R	3.82	19	8	-64	60

Main Effect of Engagement

Engagement > Non-engagement

OFC	R/L	6.31	80	0	26	-28
Amygdala	R	4.62	45	14	-6	-12
Amygdala	L	4.07	42	-12	-6	-12
Thalamus	R/L	4.00	41	0	-6	12
dMPFC	L	4.60	39	-4	60	18
Sub. Nigra	R	4.55	31	2	-12	-16
SFG	L	4.88	31	-12	32	56

Non-engagement > Engagement

None

Interaction Effect (Partner x Engagement)

None

Effect of Peer Engagement vs. Computer Engagement

Peer Engagement > Computer Engagement

Amygdala	R	4.99	300	14	-4	-16
NAcc*		5.54		0	6	-12
dMPFC	L/R	4.97	259	0	44	6
vMPFC*				4	42	-6
Insula	R	3.86	74	30	14	-18
Insula	L	3.82	34	-28	12	-22

Computer Engagement > Peer Engagement

None

Effect of Peer Engagement vs. Peer Non-Engagement

Peer Engagement > Peer Non-Engagement

Amygdala	R	4.01	139	14	-4	-12
NAcc		3.80		10	6	-6
Amygdala	L	4.16	77	-12	-6	-16
dMFPC	L	3.85	57	-4	60	12
ACC	L/R	3.77	25	0	38	8
Thalamus	L/R	4.36	21	0	-10	8

Peer Non-Engagement > Peer Engagement

None

Effect of Peer Non-Engagement vs. Computer Non-Engagement

Peer Non-engagement > Computer Non-engagement

aSTS	L	4.38	55	-52	8	-22
TPJ	R	5.07	32	50	-54	24
aSTS	R	4.18	24	50	12	-28

Computer Non-engagement > Peer non-engagement

Lingual gyrus	R	4.37	34	14	-78	-12
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Effect of Computer Engagement vs. Computer Non-Engagement

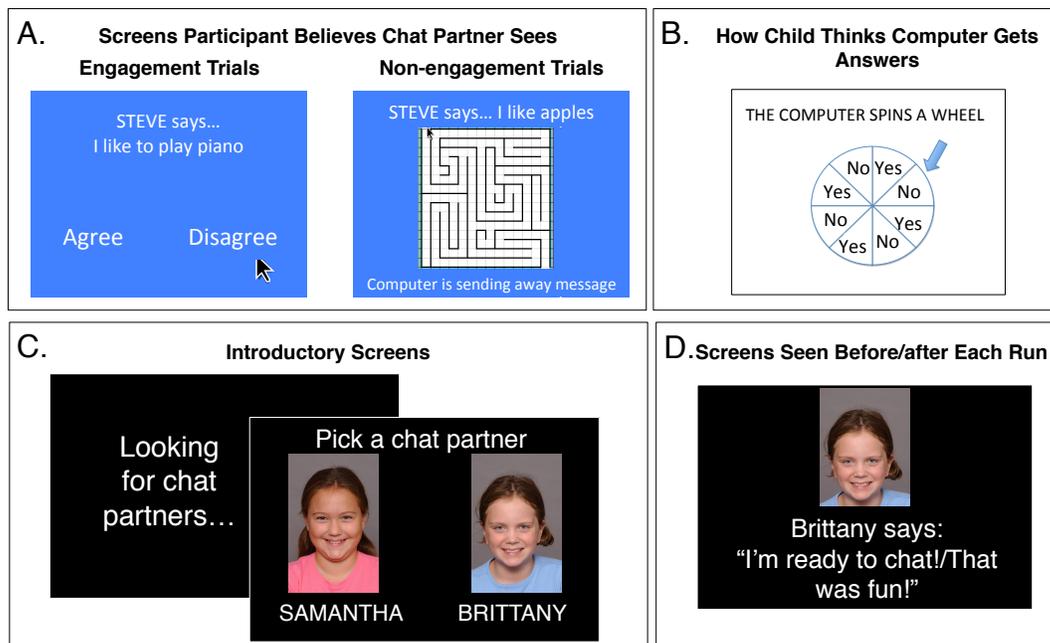
Computer Engagement > Computer Non-engagement

SFG	L	4.65	23	-16	30	56
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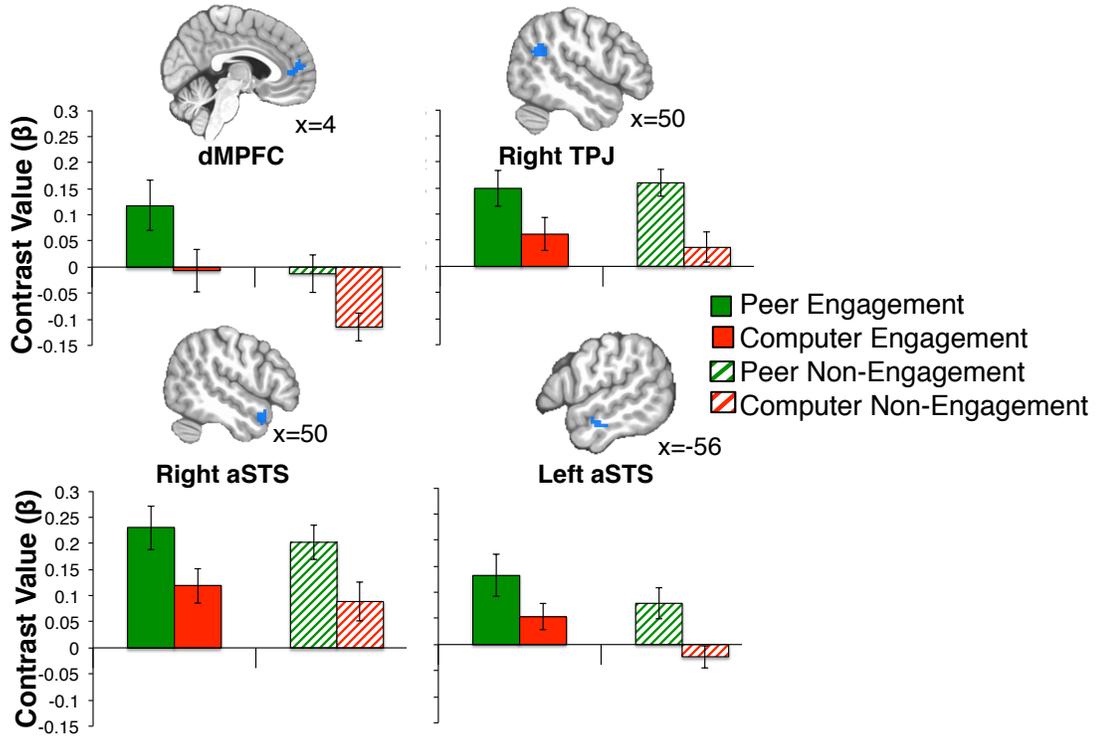
Computer Engagement > Computer Non-engagement

None

Note. NAcc=nucleus accumbens; TPJ=temporal parietal junction; dMPFC=dorsomedial prefrontal cortex; aSTS=anterior superior temporal sulcus; SFG=superior frontal gyrus; ACC=anterior cingulate cortex; vMPFC=ventromedial prefrontal cortex; OFC=orbitofrontal cortex; IPS=intraparietal sulcus; IFG=inferior frontal gyrus; STG=superior temporal gyrus. All coordinates are in Montreal Neurologic Institute (MNI) space. Data were voxel corrected at $p<.001$ and cluster corrected at $p<.05$ ($k=19$). *; subpeaks within clusters.



Supplementary Figure S4.1. Explanatory materials and stimuli for the interactive chat task. (A) Children believed that their answer (e.g., “Steve says I like to play piano” if the participant’s name was Steve) was always displayed to the chat partner, and that for some trials the partner would be able to respond (e.g., clicking “Don’t agree”). For other trials, however, the partner would be busy solving a maze and thus the computer would send an away message. (B) Children were told that when they were chatting with the computer, the computer randomly generated an answer (either “yes” or “no”). This process was explained before the task via an animation of a spinning wheel. (C) After children learned the chat game, they chose their partner. The child’s photo was also taken and the experimenter explained that photo would be sent to the chat partner. (D) Before and after each run, the photo of the child’s chat partner was displayed in order to increase the live illusion. The specific messages displayed changed with each run. No imaging data were collected while this screen was displayed.



Supplementary Figure S4.2. Regions of the social cognitive network respond to social context during an interactive chat. Regions were defined from Main Effect of Partner Type contrast ($[\text{Peer Engagement} + \text{Peer Non-Engagement}] > [\text{Computer Engagement} + \text{Computer Non-Engagement}]$). Contrast values are the average of each participant's own contrast value versus baseline for each condition. Error bars represent ± 1 standard error. No significance testing was conducted as these regions were selected based on the existence of certain significant contrasts.

Appendix D: Literature Review

Toward a Taxonomy of Social Reward: A Synthesis of Behavioral and Neural Evidence from Humans and Animals

Introduction

Neural circuitry underlying reward processing has been extensively studied and characterized across multiple levels of analysis (see Berridge & Kringelbach, 2008; Haber & Knutson, 2010; Fareri, Martin, & Delgado, 2008; Taber, Black, Porrino, & Hurley, 2012 for reviews). To interrogate reward circuitry, researchers typically use non-social rewards, such as food, money, or tokens. The past few decades, however, have seen an increased focus on the rewarding aspects of social stimuli, or *social reward*. From 1970 to 2000, roughly 1500 articles indexed on Google Scholar used the phrase “social reward.” Since 2000, over 5500 articles have been published that use the term. In spite of this upsurge of interest in social reward, the field remains fragmented, employing diverse paradigms rooted in different traditions, from neuroeconomics to attachment theory.

The goal for the current review is to begin to synthesize this vast body of literature into a common taxonomy that spans disciplines and paradigms. After briefly reviewing reward circuitry, this review discusses five potential categories of social reward: (1) observational (i.e., viewing detached social stimuli, such as a photograph of a stranger); (2) interactive (i.e., simple dyadic interaction, such a joint attention game), (3) evaluative (i.e., reputation, such as learning another thinks you are trustworthy), (4) vicarious (i.e., watching another receive a reward), and (5)

cultural (i.e., following social norms, such as conforming to group opinion). This review also considers the construct of affiliative reward (i.e., the rewarding nature of relationships with specific people, such as attachment figure), which can interact with any of the five previous paradigms (e.g., viewing a photograph of one's mother). Within each of these sections, findings from neural and behavioral work in both animals and humans are discussed. The review ends by discussing future directions for social reward research, with a special focus on those directions inspired by this taxonomy, such as investigating the potential common and distinct components of social reward categories.

Reward Circuitry

Rewards guide behavior (Delgado, 2007). Animal behavioral research has often examined reaction time, approach behaviors, and effort as proxies for measuring the rewarding value of a stimulus. For example, in rodent samples, researchers will frequently employ place conditioning or mazes to assess rewarding motivation and learning (e.g., measuring time to extinction; e.g., Humphreys & Einon, 1981; Peartree et al., 2012; Thiel, Okun, & Neisewander, 2008). Both implicit and explicit measures are used in humans, including measuring facial expressions, reaction time, and subjective ratings of reward value. Such behavioral measures, however, may not fully explain the cognitive mechanisms underlying reward-seeking behavior; investigation into the neural bases of reward may provide valuable insight (Berridge, Robinson, & Aldridge, 2009).

Over the past several decades, scientists have gained an increasingly fine-grained understanding of the neural circuitry supporting multiple components of

reward. Much of the original work on reward circuitry involved lesion studies in monkeys (e.g., Divac, Rosvold, & Szwachart, 1967) and rats (e.g., Glick, Cox, & Crane, 1975), as well as studies of electrical self-stimulation in rats (e.g., Justesen, Sharp, & Porter, 1963; Olds & Milner, 1954). Such studies isolated striatal and midbrain areas—specifically nucleus accumbens (NAcc) and ventral tegmental area (VTA)—as involved in reward-seeking behaviors. The core role of these regions was supported by pharmacological (e.g., Yeomans & Baptista, 1992) and electrophysiological (e.g., Bowman, Aigner, & Richmond, 1996; Schultz, Apicella, Scarnati, & Ljungberg, 1992) research.

Although these striatal areas, specifically NAcc, are often considered a hub of reward processing (e.g., Sesack & Grace, 2010; Kohls et al., 2012), striatal regions receive input from and project to several other parts of the brain (reviewed in Haber & Knutson, 2010). Ventral striatum (VS; which consists of NAcc, caudate, and putamen) receives input from orbital frontal cortex (OFC), anterior cingulate cortex (ACC), amygdala, hippocampus, and midbrain, and projects to VTA and ventral pallidum. VTA also sends input back to frontal cortex via the thalamus. Many of these projections involve dopamine, which is involved in several aspects of reward (Schultz, 2010).

Initial studies of reward implicated dopamine as the primary neurotransmitter underlying reward prediction and learning (e.g., Lippa, Antelman, Fisher, & Canfield, 1973). For example, dopaminergic neurons in VTA and substantia nigra (SN) respond to desirable outcomes (e.g., receiving juice) and eventually come to respond to the cue that precedes the juice (reviewed in Schultz, Dayan, & Montague, 1997).

Dopamine is also involved in coding prediction error, which occurs when the expected outcome and predicted outcome differ (reviewed in Schultz & Dickinson, 2000). Specifically, if the neural response to prediction error (i.e., activation of midbrain dopamine neurons) is artificially induced in rodents, cued reward-seeking will increase (Steinberg et al., 2013). Similarly, in humans, enhancing dopaminergic function increases the magnitude of neural prediction error as measured by striatal BOLD signal, and the magnitude of this signal change corresponds to learning reward cues (Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006). Addictive drugs increase dopamine expression in NAcc (Koob, 1992), and greater dopamine increase has been linked to both drug-seeking and subjective reward, although extensive use relates to diminished response during consumption (reviewed in Volkow, Wang, Fowler, Tomasi, & Telang, 2011). More recent research has also begun to consider the roles of other neurotransmitters, including opioids, glutamate, and endocannabinoids, (e.g., Trezza et al., 2012; Volkow et al., 2011), and reward processing mostly likely results from an interplay between several different neurotransmitters (Dolen, Darvishzadeh, Huang, & Malenka, 2013).

Importantly, reward processing is not a unitary construct. One common framework for understanding reward is to consider *liking*, *wanting*, and *learning* to be dissociable constructs (Berridge et al., 2009). Colloquially, something that is rewarding is something that is enjoyable; this intuition maps closely on to the idea of liking. This construct can be measured by subjective ratings or implicit measures (e.g., facial expressions). In contrast, wanting refers to motivation or *incentive salience*, which can also be measured explicitly (e.g., expressed goals) or implicitly

(e.g., conditioned response to cues). Perhaps surprisingly, dopamine is not core to the ‘liking’ response, and although wanting behaviors can be altered via artificially increased dopamine expression, this change has no effect on liking (Wyvell & Berridge, 2000). The final component, learning, involves a host of behaviors, including anticipation, cue-reward pairings, and prediction error. In reviewing the literature, Berridge and colleagues (2009) concluded that more neural circuitry (e.g., amygdala, VTA) was related to wanting, although certain ‘hotspots’ within NAcc affect liking. Parsing the different components of reward processing is important as they relate to different neural processes and are differentially affected in psychopathology (e.g., addiction; Volkow et al., 2011).

In humans, however, paradigms that dissociate the anticipation of a reward from its consumption have produced mixed results. Although some literature has associated NAcc with ‘wanting’ or anticipation and medial OFC with ‘liking’ or consumption (e.g., Chevallier et al., 2012), a recent meta-analysis of 142 fMRI reward studies (Liu, Hairston, Schrier, & Fan, 2012) concluded that although both mOFC and NAcc responded more to positive than negative rewards, mOFC was most sensitive to reward consumption and NAcc tracked both anticipation and outcome. These findings may suggest a stronger role of NAcc in learning. Amygdala was found to be more active during outcome and was especially active to negative rewards.

In a separate meta-analysis, Diekhof and colleagues (2012) examined how VS and mOFC/VMPFC (the authors’ term) tracked reward magnitude during different phases of reward. VS was sensitive to expected reward magnitude (i.e., during anticipation), even at the level of individual participants. Further, VS activation

during outcome was also linked to reward magnitude, and was stronger for unpredictable or unexpected rewards, consistent with the hypothesized role of VS in prediction error. Given the fact that most experiments, however, contain some degree of uncertainty, it is difficult to determine the extent to which VS is tracking uncertainty vs. magnitude (e.g., larger unpredictable rewards do result in larger positive prediction errors). In contrast, mOFC/VMPFC was sensitive to reward magnitude only during consumption. Intriguingly, the few studies that found mOFC/VMPFC activation during anticipation had either long delay periods or highly certain rewards, which may result in simulated reward value before the reward is actually obtained. Finally, VS, but not mOFC/VMPFC, also indexed changes in reward type during an experiment.

In sum, the multiple phases of reward processing rely on a complicated neural circuitry involving connections between cortical and subcortical regions, with mOFC and VS playing major roles. For the purposes of this current review, the main focus is on identifying and classifying paradigms that have been used to study social reward. Given the vast array of paradigms, it is difficult to conduct a fine-grained analysis of the specific regions involved processing different reward types. Thus, for this initial overview, the bulk of the discussion on the neural correlates of social reward will focus on how VS and mOFC support social reward processing, as these are the two regions most frequently examined in social reward studies, and their roles have been well-characterized for non-social reward processing.

Categories of Social Reward

The principle goal of this review is categorize social reward. Although this categorization schema is predominately based on the human literature, such literature is often limited in terms of direct interrogation of cellular mechanisms. Thus, selected animal literature is incorporated when appropriate. Importantly, this review is not exhaustive in terms of reviewing the behavioral, animal, and neural evidence within each category of reward, especially in the cases where recent meta-analyses or reviews have specifically targeted a reward type. Nor is this review designed to explicitly compare across non-social and social rewards in order to compare and contrast mechanisms (see Ruff & Fehr, 2014 for review of this topic). Rather, the hope of this review is to provide a novel framework for considering categories of social reward and social motivation, with a special focus on development and psychopathology, in order to inspire a more systematic investigation of facets of social behavior.

Two recent reviews have focused on the role of ventral striatum in human social behavior. In one, Bhanji and Delgado (2014) reviewed research across four categories: responses to social reward that appear identical to those of non-social reward; neural responses that influence social decisions (e.g., following advice); neural responses that underlie cooperation, competition, and learning about others; and the neural responses of conforming to social norms. The review, however, was more focused on discussing the broad role of striatum in extant neuroimaging studies rather than providing an exhaustive categorization of social reward based on both behavioral and neural literature. In a more precise categorization scheme, Baez-

Mendoza and Schultz (2013) divided up two axes of social behavior: first, who acts (i.e., self or other) and second, who receives (i.e., self or other). Consistent with prior literature, the authors concluded that ventral striatum was involved in a host of social behaviors. Although a helpful beginning, these two axes did not include important dimensions of social reward, such as whether or not the reward was tangible, whether it involved dyadic interaction (cf. Schilbach et al., 2013), whether activation was associated with different phases of reward processing (e.g., anticipation vs. outcome), and did not include instances of social aversion (e.g., exclusion). Additionally, the review did not consider changes across the lifespan or across psychopathologies. Classifying social reward types by starting with types of reward rather than reviewing ventral striatum activity per se may provide a more complete characterization of human reward, especially in cases where the neural underpinnings involve more complex circuitries.

In a more expansive review, Ruff and Fehr (2014) considered the neurobiological similarities and differences in processing social and non-social rewards. The authors considered three categories of social rewards: rewards from others (a broad category spanning both reward and punishment as well as learning about other people), vicarious reward, and social norms (e.g., cooperation). Broadly, the authors concluded that much of the same neural circuitry is involved in both social and non-social reward processing (e.g., VS, mOFC) across both anticipation and outcome evaluation, with one exception being the open question of whether learning social norms proceeds along similar routes to other value-based (i.e., non-social) learning. Importantly, the authors note that there may be fine-grained

differences in the processing of non-social versus social stimuli that cannot be detected by BOLD the bold signal, and that these differences may be accentuated by connections with regions outside of reward circuitry (e.g., the involvement of social cognitive regions such as TPJ). The goal of that review, however, was not to construct categories of social reward, but to compare social and non-social evaluation processes.

This taxonomy thus builds on these previous reviews by attempting to explicitly categorize social reward. The initial categories are constructed based on human behavioral literature. This approach is similar to a recent review of theory of mind—a similarly broad concept with an expansive and growing literature—which had the goal of “deconstructing” theory of mind into constituent parts (e.g., interpreting facial expressions, gaze following; Schaafsma, Pfaff, Spunt, & Adolphs, 2015). This review’s attempt at an explicit taxonomy will better enable future research to consider commonalities and distinctions across reward paradigms. Such precision may result in studies that target more exact mechanisms on both behavioral and cellular levels. Importantly, this taxonomy is not intended to be final, and indeed, one hope is that future investigation spurred by this taxonomy leads to better insight into types of social reward.

Specifically, this review considers six categories of social reward: observational, interactive, evaluative, vicarious, cultural, and affiliative. Such categories are not mutually exclusive, but are typically studied separately. For each category, the relevant human behavioral literature will be briefly considered in order to establish that a particular set of behaviors appear to be rewarding. After introducing

the particular type of social reward, each section includes a more in-depth review of the animal literature and human neuroimaging evidence. Finally, across reward types, broader implications for development and psychopathology are discussed, as are future directions integrating across categories. For categories in which there has been a recent review or meta-analysis, the focus of this review is less focus on recounting individual studies, and more on emphasizing commonalities and differences across paradigms.

Observational Reward

Behavioral manifestation. This category is the simplest—the observation of conspecific stimuli. From early infancy, humans preferentially attend to conspecific faces (Farroni et al., 2005; Morton & Johnson, 1991), voices (Vouloumanos, Hauser, Werker, & Martin, 2010), and biological motion (Simion, Regolin, & Bulf, 2008). These preferences continue into throughout development; for example, adults are willing to pay more money to see more attractive faces (Smith et al., 2010). Additionally, social stimuli are perceptually privileged in variety of ways, including being easier to detect when presented subliminally (Jiang, Costello, & He, 2007), a construct that has been referred to as ‘social orienting’ (reviewed in Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012). Finally, there is evidence that social stimuli can change behavior. For example, using photographs of faces as reward can decrease reaction times (e.g., Rademacher et al., 2010; Delmonte et al., 2012) and improve learning (e.g., Van Zeeland et al., 2010). In sum, children and adults like social stimuli, and often prefer social to non-social stimuli, and these stimuli can serve as reinforcers.

An important consideration throughout this review, however, is that ‘liking’ is only one facet of reward. For example, in a behavioral study with children and adolescents, participants rated a series of smiling faces in terms of their subjective value (i.e. ratings of liking; Demurie, Roeyers, Baeyens, & Sonuga-Barke, 2012). These faces were then used as a reinforcer in a reaction time task. Results indicated that although faces with broader smiles were significantly more likeable than more neutral faces, they did not differentially affect RT. In contrast, receiving points paired with social stimuli did influence RT. Given that other studies have found that social stimuli can affect behavior, review of social reward paradigms must include consideration of what aspects of reward are being measured.

Animal evidence. Given the primacy of olfactory cues in rodent social behavior, most behavioral studies of observational social reward in rodents have focused on the animals’ response to smell. Evidence indicates that rats have a preference for certain conspecific odors (Galef & Kaner, 1980) and that the odors produced by other rats can influence food choice (Galef, 1996). Most rodent research, however, has focused on the physical preference of conspecifics as reward stimuli, and as such, is reviewed in the following section on interactive reward.

In contrast, reward from simply observing social stimuli has been more extensively investigated in non-human primates. Much of the early work measured the extent to which primates would complete specific actions, such as pressing a lever, pulling a rope, or moving a joystick, in order to view photographs or videos of conspecifics (reviewed in Anderews, 1998). More recent research has quantified the particular value associated with different types of observational reward. In these

“monkey pay-per-view” paradigms, rhesus macaques are given the choice between two stimulus pairs: first, some quantity of juice and second, another quantity of juice paired with a photograph. Results indicate that male monkeys require more juice to see a low status male and less juice to view a high status male or female perinea (Deaner, Khera, & Platt, 2005). This behavioral research has been replicated in several subsequent paradigms that have examined the neural mechanisms underlying the behavioral choice.

Researchers have interrogated several cortical and subcortical areas during this pay-per-view task. Electrophysiological recordings in OFC have indicated that firing rate is related to image value (i.e., status), but this relation is weaker than simply encoding image category (Watson & Platt, 2012). Further, more neurons were sensitive to image category than the size of the fluid reward—despite the fact that fluid amount, more than image type, dictated the monkey’s behavioral choice. This finding, in addition to the fact that many neurons fired in response to both forced and free-choice outcomes, indicate that OFC may be involved in coding social value in addition to decisions. Finally, investigations of anterior striatum indicated that different neurons were responsive to fluid versus social rewards, with socially-responsive neurons located more medially (Klein & Platt, 2013). Interestingly, in this study, reaction times were faster the more juice the monkey could obtain, but were slower for both the most and least preferred social images. Striatal neurons responded to both anticipation and outcome and, unlike many human fMRI studies (reviewed subsequently), this firing did not correlate with the reward value for either social (status level) or non-social (juice amount) reward. In sum, these findings indicate

that, at least for observational reward, that different neural regions process different aspects of reward, with mixed evidence for whether social and non-social rewards are computed in the same neural regions.

Although the bulk of this research has examined group-level effects in male macaques, recent behavioral work with females has indicated that they too distinguish between social stimuli (Watson, Ghodasra, Furlong, & Platt, 2012). Additionally, there is evidence that variability in serotonin transporter genes can influence response to observing social stimuli (Watson, Ghodasra, & Platt, 2009). Future animal work should continue to investigate individual differences in both the behavioral and neural mechanism of observational social reward.

Human neural evidence

Viewing social stimuli. In one of the most straightforward explorations of the reward value of observing social stimuli, researchers have employed viewing paradigms in which individuals see faces of variable levels of attractiveness. In a paradigm with adult male participants, NAcc responded more strongly to more attractive female faces (Aharon et al., 2001), although the study design could not disentangle reward and outcome. Further, participants were willing to expend more effort (i.e., press a key more) to view more attractive females. In addition to NAcc, mOFC has also been found to track increasing attractiveness (Cloutier, Heatherton, Whalen, & Kelley, 2008; O'Doherty et al., 2003; Winston et al., 2007), with smiling versus neutral faces also producing more OFC activation (O'Doherty et al., 2003).

Findings become more complicated when comparing across demographic variables and considering a wider range of face stimuli. Heterosexual females have

shown less mOFC sensitivity to attractive opposite-sex faces than males (Cloutier et al., 2008; O'Doherty et al., 2003), although differences in NAcc recruitment between males and females were not observed (Cloutier et al., 2008). There is suggestion that although OFC was found to increase in activation for more attractive faces, ventral striatum shows a non-linear response, with greater activation to both rewarding and aversive (i.e., deformed) face stimuli (Liang, Zebrowitz, & Zhang, 2010). The authors argue that these findings imply that striatum may serve as a general salience detector, although, intriguingly, male and female participants showed different patterns of activation. Additionally, the social status of both the participant and the observed stimuli affects VS response (Ly, Haynes, Barter, Weinberg, & Zink, 2011). When viewing images and learning information about both low- and high-status individuals, VS activity was higher in participants who matched the observed stimuli in status. Finally, VS sensitivity to facial attractiveness appears to be moderated by gaze: when a face is gazing directly at a participant, increased attractiveness is related to increased VS activity, but during averted gaze, the opposite relation holds (Kampe, Frith, Dolan, & Frith, 2001). Such findings indicate the importance of considering the full social context, even in observational studies.

Additionally, although initial studies concluded that reward circuitry activation to attractive faces indicated common processing of social and non-social reward, more fine-grained analyses have revealed that monetary rewards versus erotic photos are processed in separate regions of OFC, despite receiving similar hedonic ratings (Sescousse, Redoute, & Dreher, 2010)—this study, however, only examined outcome and not anticipation, so it is possible that neural similarities vary depending

on the phase of reward processing. Additionally, particular OFC subregions may show non-linear response to attractiveness (Winston et al., 2007). Finally, in a paradigm in which people paid to view faces, separate regions of VMPFC tracked the amount people were willing to pay versus individuals' ratings of experienced value (i.e., attractiveness). Thus, brain-behavioral mapping in reward is complicated by the many different behavioral ways in which reward can be manifest. More fine-grained imaging analyses may reveal a more complex story about the reward of attractive faces.

Social incentive delay paradigms. One of the most robust paradigms used to examine response to rewards in the Social Incentive Delay (SID) paradigm. This is a modification of the traditional Monetary Incentive Delay (MID) task in which the anticipation phase and the outcome phase are dissociated. These paradigms present the participant with a cue indicating the reward that could be earned on that trial (Anticipation), present some task (e.g., a button that the participant must press as quickly as possible), and finally present the reward (e.g., photo indicating the participant pressed the button quickly enough to earn money; Outcome). In the SID paradigm, participants typically have two cues: one which indicates that the participant could earn a social reward (e.g., photograph of a smiling face) and one that indicates the participant could earn a monetary reward. A cue indicating that the participant cannot receive a reward on that trial typically serves as the control.

The initial SID studies found that similar regions were involved in processing social and monetary reward, although the response tended to be stronger for monetary reward. The original paradigm, by Rademacher and colleagues (2010), used multiple

'levels' of each reward (e.g., the social cue indicated whether the participant could earn would see a very happy, moderately happy, or only slightly happy face). Results indicated that RT got faster for greater rewards across both monetary and social conditions. This magnitude-dependent effect of behavior was mirrored in the fMRI findings—NAcc, putamen and caudate activation increased with greater reward magnitude for anticipation of both monetary and social reward. Intriguingly, the only differences appeared during consumption, where social reward increased amygdala activation and monetary reward increased thalamic activation, although neither reward activated VS. The authors concluded that given the dopaminergic projections in the thalamus, this increased activation reflects that money is a stronger reward.

Replications of this paradigm have also indicated that monetary rewards may be more effective than social rewards. Two studies found faster RT to money than social rewards, as well as stronger NAcc during the anticipation period—although with some evidence for equivalent VMPFC activation to outcome (Dichter, Richey, Rittenberg, Sabatino, & Bodfish, 2012; Richey et al., 2014). Both studies used neutral faces as feedback and did not show varied levels of social reward. A study which varied levels of social reward also found increased VS activation during the anticipation of monetary versus social rewards, but found certain that dorsal caudate was equally responsive to both reward types (Delmonte et al., 2012). Thus, although there may be effects of the specific type of observational social stimuli used in the study, evidence indicates that monetary rewards are more effective at soliciting behavioral and neural responses than simply viewing static social stimuli.

Several SID studies have also investigated sex and age-related changes in response to social reward. Spreckelmeyer and colleagues (2009) found that only men showed an effect of monetary and social (mixed-sex) reward magnitude on RT. Although women did not show a behavior distinction between levels of social reward, their neural activity during anticipation reflected sensitivity to increasing values of both monetary and social reward in regions including NAcc, caudate and putamen. In contrast, men were much more responsive to monetary than social reward, and showed no VS activation to social anticipation. The same group found that, in a comparison of younger (20-28 years) and older (60-78 years) adults, older individuals showed greater NAcc activation to social rewards, whereas younger individuals showed greater activation to monetary rewards (Rademacher, Salama, Grunder, & Spreckelmeyer, 2014). Unfortunately, however, the authors did not obtain subjective reward ratings, making it difficult to isolate whether findings were due to biological age-related changes or diminished salience of money in the older population. In general however, these findings suggest that sex and age are important factors to consider in social reward studies.

In addition to general demographic effects on sensitivity to social reward, recent research has explored whether individual differences in social ability track neural differences in response to social reward. Using social videos (rather than photographs), Gossen and colleagues (2014) found that anticipatory NAcc activation for social videos was diminished in individuals with low Empathizing Quotient scores. This finding, however, did not seem related to general VS dysfunction, as these participants had higher activation for monetary rewards. All participants,

however, were faster to respond to monetary than social trials. In a similar ERP study, researchers separated participants into two groups: those who scored high on the Autism Quotient (indicating more autistic-like traits) and those who scored lower (Cox et al., 2015). Participants also viewed a video during the social reward condition, but were told that the videos were actually presented via a live feed from another room. Researchers found attenuated P300 response during the anticipatory period for social reward for individuals with high versus low level of ASD-like traits, but no difference in groups in response to non-social reward cues. Additionally, unlike in some previous studies, subjective incentive ratings were higher for the social than non-social cues. The non-social cues in this paradigm, however, represented the chance to win candy—as opposed to conventional monetary rewards—making it difficult to dissociate whether the ‘live’ videos were increasing response to social rewards or whether the non-monetary rewards were decreasing response. Additionally, no study has yet directly compared response to more dynamic versus more static social rewards in the SID paradigm, although a recent review argued that dynamic rewards may better capture real-world social processing (Kohls et al., 2012a).

In addition to studies examining dynamic or even live social reward, other investigators using the SID paradigm have explored the effect of other variations in social reward, including the stimulus gender and pairing the face with other feedback. Initial results indicate increased reward system (i.e., VTA, NAcc, VMPFC) activity when viewing anticipatory cues for opposite sex faces (Spreckelmeyer, Rademacher, Paulus, & Grunder, 2013). Women also showed increased recruitment of social

cognitive regions (i.e., TPJ) for opposite- versus same-sex faces, although men did not show this pattern. Based on these findings, the authors concluded that in a SID paradigm that did not explicitly cue facial attractiveness, men and women show equal anticipatory neural activity for opposite-sex faces. In another SID variant that did cue different levels of facial attractiveness, researchers found increased NAcc activation in response to larger reward cues for monetary, but not social rewards (Libedinsky et al., 2011). In contrast, in the outcome phase, VMPFC tracked facial attractiveness, but not magnitude of monetary rewards. In a SID behavioral study, researchers used a cartoon drawing of a thumbs up paired with verbal compliments of increasing intensity, along with the number of points a child earned of that trial (where, for example, larger point amounts were always paired with larger verbal praise and indicated by a particular cue; Demurie, Roeyers, Baeyens, & Sonuga-Barke, 2011). Disentangling the effects of the praise versus the points was not possible in that particular study, but a later follow-up indicated that sans points, the stimuli did not alter RT (Demurie et al., 2012). Finally, in a study without photographs, researchers compared minimal verbal feedback (the word ‘fast’ or ‘slow’) to money and found stronger RT and neural effects for monetary rewards (Kirsch et al., 2003), concluding that verbal praise was less rewarding than money.

Another important direction in SID paradigms is the incorporation of social punishment. In a recent study, Kohls and colleagues (2013) used dynamic videos of both social reward and punishment and found that anticipation of a punishment led to stronger VS activation, as well as faster reaction time. In contrast, a paradigm using photos as reward and punishment found no effect on RT, in spite of significant

differences in subjective ratings (Cremers, Veer, Spinhoven, Rombouts, & Roelofs, 2014). Further, an ROI analysis indicated that left putamen responded equally to neutral and reward cues, with decreased response for punishment cues, but otherwise there was no difference between conditions. Another SID study involving both reward (photo of smiling face) and punishment (photo of angry face) examined the effects of intranasal oxytocin (OT) administration on neural response to anticipatory cues (Groppe et al., 2013; see section on Affiliative Reward for more on OT). Specifically, OT administration increased neural activation to both social reward and social punishment cue, but no effect was seen in behavioral data; both groups had faster RT for high levels of reward and punishment. Additionally, VTA activation only related to performance in the placebo group, indicating that OT may change reward processing mechanisms.

Finally, there have been slight variations on the SID incorporating go/no-go paradigms. In the original ERP paradigm, larger P300 responses were observed during the anticipatory period for both social (smiling face) and monetary (picture of wallet) rewards (Kohls et al., 2011). Monetary rewards, however, did have a larger effect on RT than social rewards did. In a follow-up fMRI study, Kohls and colleagues (2012b) found that participants gave higher subjective ratings to monetary than social rewards, and that although social rewards lead to higher activation in ‘social’ brain regions (e.g., STS), monetary rewards led to higher activation in caudate and putamen (although there was no difference in NAcc or amygdala activation). Further, striatal activation was consistently weaker on no-go blocks,

consistent with the idea that reward circuitry is less engaged when no active response is required.

Learning from observing social feedback. Although the SID is a robust measure of motivation, separating out the anticipation and outcome phases, this reaction-time based paradigm does not directly measure learning. Other paradigms have used social stimuli to reinforce learning, an approach which yields insight into another facet of reward. In one recent paradigm, Lin and colleagues (2012a) used photographs of smiling faces as a reinforcer in a probabilistic gambling task. Participants were presented with different ‘slot machines’ associated with different probabilities of winning (either a monetary reward or seeing a face). Participants were faster to learn the probabilities associated with each slot machine when the machines dispensed monetary versus social reward, but ultimately learned from both conditions—a finding replicated in a subsequent behavioral extension (Lin, Rangel, & Adolphs, 2012b). Further, during the outcome phase, participants showed similar VMPFC activation to both types of reward and common striatal activity to prediction error.

In a similar task with children, researchers presented a task in which children had to learn the classifications associated with a random set of pictures (Van Zeeland et al., 2010). Social rewards for correct performance were smiling faces paired with feedback (i.e., “That’s right”) and non-social rewards were monetary. Additionally, children saw sad faces and crossed out coins for incorrect performance. Both types of feedback increased accuracy in children. Additionally, VS was more active for positive versus negative feedback for both conditions. In a follow-up analysis, the

authors examined response to outcome for deterministic vs. random trials (i.e., trials where it was possible to learn a contingency versus ones where it was not). Although the authors did not directly compare across monetary and social conditions, general findings indicated increased VS involvement across conditions, with increased OFC involvement specific to the monetary condition.

All the previous paradigms, however, did not pair a tangible reward with the social reward (even the study that used points did not concretely connect those to a real-world reward). In an innovative ERP paradigm, Stavropoulos and Carver (2014a; 2014b) paired both social (smiling vs. frowning face) and non-social (upwards or downwards arrow) feedback with images of goldfish crackers (either crossed out or not). Children had to choose between two boxes, and if they chose correctly, they received both the visual reward and an indication that they would receive goldfish. In this way, the authors attempted to match tangible reward value across social and non-social conditions to isolate response to social reward. Children showed a larger stimulus preceding negativity (SPN) during anticipation for social than non-social trials and larger feedback related negativity (FRN) for social outcomes. In this task, there was no way to learn which box would produce a correct response, so researchers could not directly measure learning. The authors noted however that, unlike in many previous studies, social feedback actually elicited a larger response than non-social. Given the design however, it is unknown if this was due to pairing social reward with tangible feedback or do to the absence of a monetary reward (cf. Cox et al., 2015). This paradigm does raise important questions about how to make observing a social stimulus more tangible. One potential solution is to increase the

interactive nature of the social stimulus (e.g., dyadic interaction), a line of research explored in the following section on interactive reward.

Interactive Reward

Behavioral manifestation. In a recent review of translational neuroscience, Insel (2010) drew a distinction between *receptive* and *expressive* processing. Studies of social reception are focused on the unique ways that sensory social stimuli are encoded and processed—a construct that dovetails with the observational reward category delineated above. In contrast, social expression involves social interaction, and appears to be supported by different neural mechanisms than reception alone. Insel argues that the “dark matter” of social neuroscience lies at the intersection of these two constructs. Schilbach and colleagues (2013) also use the phrase dark matter to refer to *second-person neuroscience*—a theoretical and methodological approach designed to isolate the neural mechanisms supporting social interaction. Thus, examining the rewarding nature of such interaction is an important facet of categorizing social reward.

Behavioral evidence suggests that humans possess an intrinsic drive for social interaction. From early infancy, two-month-olds prefer contingent to non-contingent social interaction (Bigelow, 1998; Murray & Trevarthan, 1985). As children grow, they actively initiate social interaction and attempt to maintain social relationships (Chevallier et al., 2012; Rekers, Haun, & Tomasello, 2011). For example, preschoolers prefer to collaborate with an adult on a task than to complete the task alone, even when the adult’s presence is not necessary for the task (Gräfenhain, Behne, Carpenter, & Tomasello, 2009; Warneken, Chen, & Tomasello, 2006).

Children also perform more quickly on computer games when they believe they are playing against peers versus the computer (Geurts, Luman, & Van Meel, 2008), suggesting a strong motivational component of interaction. This drive for social interaction is found in adults as well, who report increased satisfaction after playing games against other people (Fehr & Camerer, 2007; Rilling et al., 2002) versus non-social controls. In sum, interaction appears to be a category of social reward.

Animal evidence. Decades of behavioral research have indicated that conspecific interaction is rewarding for rodents (reviewed in Trezza, Baarendse, & Vanderschuren, 2010; Trezza, Campolongo, & Vanderschuren, 2011). Specific behavioral paradigms used with rodents include place conditioning paradigms and T or Y mazes. In a place conditioning paradigm, rats are conditioned to associate a particular location (e.g., the left-hand side of a cage) with social interaction (e.g., the presence of other rats). Measuring place preference before and after the conditioning provides a quantitative index of reward. In a T or Y maze, rats are exposed to an apparatus with multiple arms. To study social reward, scientists place another rat at the end of one arm and measure both preference and the length of time to extinction once the rewarding stimulus is removed. Results from both paradigms indicate that social interaction is a reward (e.g., Calcagnetti & Schechter, 1992; Normansell & Panksepp, 1990). Further, social interaction with a human can also condition behavior, as long as the rat had prior interaction with the person before the experiment (Davis & Perusse, 1988). Additional evidence that social interaction is rewarding comes from studies of rat vocalizations; particular frequency vocalizations are associated with pleasurable behaviors, including social play (Burgdorf et al.,

2008). More titrated examinations of social preference in rats indicate that even contact with a partner through a mesh barrier is will induce place conditioning (Peartree et al., 2012), but that the effects are stronger with a reciprocal social partner than with a partner who cannot play (e.g., due to drugs or being physically confined; Humphreys & Finon, 1981).

Although such precise quantitative studies (e.g., place conditioning) have not been conducted with non-human primates, the evidence still suggests that primates find social interaction rewarding. Chimps will learn task with chance to groom human experimenter (Falk, 1958) and both play and grooming are reinforcers for young chimps, with play as a stronger reinforcer (Mason, Sharpe, & Saxon, 1963). Even when tested hungry, chimpanzees chose play over food roughly half the time.

Several studies have probed the neural bases of these social reward mechanisms. Unlike in observational reward studies, however, separating out different phases or components of reward processing is difficult during ongoing play. A growing body of rodent literature, however, has begun to dissociate neural mechanisms underlying different components of social interaction. For example, opioid-targeting drugs differentially affect play motivation versus the amount of play that happens at the end of the Y maze, and do not appear to affect learning (Normansell & Panksepp, 1990). Specifically, morphine increased play behavior and naloxone decreased play compared to controls, and extinction was slower for morphine-treated rats than naloxone-treated rats. Neither drug, however, altered the choice to play or running time, indicating that liking and motivation may be dissociable in the arena of social play. Although that study did not examine opioid

expression in particular neural regions, more specific investigation of NAcc has revealed that, post-play, rats exhibit increased opioids in NAcc (Vanderschuren, Stein, Wiegant, & Van Ree, 1995), and artificially altering opioid expression in NAcc has a direct role in changing play behaviors (Trezza, Damsteegt, Achterberg, & Vanderschuren, 2011). Recent research has also examined dopamine, finding that dopamine antagonists reduce social play, although agonists have less effect, perhaps because signaling is already maximum during play (Trezza & Vanderschuren, 2009). In addition to opioids and dopamine, endocannabinoids also play a complex role in social behavior (reviewed in Solinas, Goldberg, & Piomelli, 2008; Trezza & Vanderschuren, 2008). Additional research has begun to explore the connection between different neurotransmitter systems, finding that coordination between dopamine and endocannabinoid affects reward processing, although that question has primarily been investigated in terms of non-social reward (Gardner, 2005). In terms of social reward, a recent study indicates that social reward depends on joint action between oxytocin and serotonin in NAcc (Dolen, Darvishzadeh, Huang, & Malenka, 2013). Play-based studies however, have not investigated real-time activity of individual neurons, in part because of the unconstrained nature of social play.

Finally, an additional line of animal research examines how non-social rewards and social rewards interact. For example, cocaine (a non-social reinforcer) reduces play behavior but increases socially-conditioned place preference (Thiel, Okun, & Neisewander, 2008). These findings indicate that there may be portions of social interaction that are rewarding besides play, and also further support the dissociation between motivation and enjoyment.

Human neural evidence

Interaction with a human versus computer. One body of literature has examined the neural correlates of playing a game with a human versus computer opponent. During game play, activation in the mentalizing network is reliably increased (e.g., dMPFC, TPJ, STS), but reward network activation is less consistent (e.g., Corcelli & Nagel, 2009; Kircher et al., 2009). Some research, however, has found that VS may track performance, perhaps indexing strategic thinking (Bhatt & Camerer, 2005). In terms of the outcome of the game (e.g., winning vs. losing), a first-person shooter study found stronger DS and VMPFC activation when defeating a human opponent (Katsyri, Hari, Ravaja, & Nummenmaa, 2013). Behaviorally, however, no difference in reported reward. Crucially, these studies control for stimuli differences between computer and human partners (as the human partner is almost always simulated), and therefore any observed differences are due to additional processing in participants. Thus, any difference in processing is brought to bear by the participants. But, these studies unfold in the context of competition, which may be fundamentally different in the context of cooperation (Le Bouc & Pessiglioni, 2013). For example, in a prisoner's dilemma study, Rilling and colleagues (2002) found that, cooperation reliably increased NAcc activity. Further, even in the studies that do find increased reward activity, the increased activity in social cognitive and mentalizing regions more broadly suggests that reward may be interacting with other aspects of social signaling.

Joint attention. A separate line of research has directly investigated the question of whether mutual engagement is rewarding. Specifically, several paradigms

have targeted joint attention, a phenomenon in which two individuals coordinate and communicate about a third object (e.g., via mutual gaze; Tomasello et al., 2005). Schilbach and colleagues (2010) developed an interactive joint attention paradigm, in which participants believed the avatar on the screen corresponded to a real participant in another game. Over the course of the game, participants either congruently responded to gaze shifts from the avatar (i.e., looking at the same block that the avatar looked at), responded incongruently to gaze shifts, successfully initiated joint attention with the avatar (i.e., looked at a block after which the avatar looked at the same block) or unsuccessfully initiated joint attention (i.e., the avatar looked at another block). Successful initiation of joint attention resulted in significantly higher VS activation than the other three conditions. Further, this VS activation correlated with subjective reports of enjoyment during initiation, despite evidence from non-social paradigms that OFC may be more involved in tracking reward value (Diekhof et al., 2012; Peters & Buchel, 2010).

In a later study by the same group, Pfeiffer and colleagues (2014) created a paradigm in which participants believed they were either playing a joint attention game with a human or a computer. In this way, the authors could control stimuli characteristics while only varying the perception of human interaction. During the first portion of the game, participants were told that the other player was merely told to respond, and in the second phases, participants were told that the other player was explicitly instructed to cooperate. Overall, human interactions were rated as more pleasant and when participants believed they were interacting with a human partner, VS and mOFC activation increased as compared to computer trials, regardless of the specific

events unfolding in the experiment. Additionally, early VS response in the first phase of the game (i.e., without cooperative instruction) was the strongest predictor of whether participants rated the interaction as human, whereas in the cooperative phases, VS activation increased over the course of cooperative trials. The authors suggest that the rewarding nature of social interaction might motivate conspecific cooperation.

The interactive joint attention paradigm has recently been extended to compare habitual cocaine users and control participants (Preller et al., 2014). Behaviorally, cocaine users report less enjoyment during self-initiated joint attention, concordant with decreased mOFC activation during these trials. In contrast, ventral striatum activation was similar between groups. Arousal, however, was higher for cocaine users during joint attention, whereas controls were more aroused by trials in which the avatar did not respond to their gaze shift. Such results suggest that drugs operating on reward circuitry may affect responses to social rewards, but conclusions are tentative in the absence of experimental work (although see Thiel et al., 2008 for experimental rodent evidence that cocaine administration decreases social play but not social conditioning).

Importantly, not all joint attention paradigms have revealed increased striatal activity. Redcay and colleagues (2010; 2012) examined true face-to-face interaction via video feed, in which a participant in the scanner played a live joint attention game with an experimenter outside of the scanner. Each individual could see the other's eye movements, and, depending on the trial, either initiated or responded to joint attention cues. The control involved participants responding to non-social attention cues. Live

joint attention, as compared to the control, differentially activated regions involved in mentalizing—namely the posterior superior temporal sulcus (pSTS) and temporal parietal junction (TPJ), but no difference was found in VS. Interestingly, in the analysis of full blocks of live interaction (without isolating joint attention events), Redcay and colleagues (2010) did report increased VS activation. Although the reason for this discrepancy is not clear, one possibility is that in the Redcay paradigm, participants' self-initiated joint attention was guided by the presence of a cue on the screen, whereas in the Schilbach paradigms, participants chose which item on the screen to gaze at. Perhaps the aspect of volitional control in social interaction (and a social partner congruently responding to that decision) is an important part of social reward.

Sharing information. Sharing information with others, as opposed to privately answering questions, increases activation in NAcc (Tamir & Mitchell, 2012). Specifically, adults completed a paradigm in which they answered either self- or other-relevant questions (e.g., “I like to snowboard” vs. “Obama likes to snowboard”), and were told that their answers would either be shared after the session with a chosen friend or family member, or would be kept private. The authors found increased VS activation for both self-relevant and shared items, although there was no interaction between the two conditions. These results indicate that even outside of the context of real-time interaction, the potential of social engagement may be rewarding.

In a separate paradigm, Jones and colleagues (2011) examined the neural response to reciprocated self-disclosure. Specifically, they had participants fill out questionnaires indicating a series of hobbies and preferences. Participants were told

that these responses were shared with three social partners, and then, during an fMRI experiment, participants learned if these three partners wanted to engage with the participant based on that information. Each of the three partners was programmed to respond at different rates, and results indicated that VS tracked the probability of reciprocal social engagement. Additionally, a follow-up developmental study found that children and adolescents also engage VS during social reinforcement learning, although adolescents seemed to show diminished sensitivity to the differential rates of response across social partners (Jones et al., 2014). These findings suggest that perhaps adolescence is a time of heightened sensitivity to social feedback.

Sharing advice with others has also been linked to reward system activation (Mobbs et al., 2015). Specifically, in an advisor-advisee game, participants gave advice to another player, who was also receiving advice from a confederate. Advisor VS activation was greater when their advice was followed (versus rejected), and VS only activated to the other player's winnings when those winnings were a result of the advisor's (versus the confederate's) advice. The advisor's MPFC, in contrast, tracked both the other player's wins and losses in response to the advisor's suggestions, suggesting a more general role for MPFC—consistent with other social cognitive literature (Saxe, 2006)—in monitoring social information.

The precise cognitive mechanism underlying the rewarding nature of social interaction is unknown. Social interaction is multifaceted, with a large set of constituent component processes (e.g., contingency, reciprocity, dynamicity), and any particular combination may be necessary or sufficient to result in reward system activation. One recently advanced explanation is that social interaction entails theory

of mind, and that engaging in theory of mind is rewarding (Krach, Paulus, Bodden, & Kircher, 2010). This theory, however, does not explain the studies of social interaction that have found activation in mentalizing, but not reward, regions (e.g., Redcay et al., 2010; 2012). Deconstructing the component pieces of social interaction in a series of highly-controlled experiments may help isolate the rewarding components of interaction, although it is possible that reward is an emergent property of the interaction.

Finally, although the reviewed paradigms have predominantly been visually-based, animal research suggests that other types of social engagement are also rewarding. In humans, limited research has examined the neural correlates of affective or social conspecific touch (e.g., Gordon et al., 2013; Loken, Wessberg, McGlone, & Olausson, 2009), although such research has not implicated reward circuitry. Future paradigms, however, should target multimodal social engagement, especially as social interaction may have properties not captured by a single modality.

Evaluative Reward

Behavioral manifestation. Evidence from both social and developmental psychology suggests that others' opinions matter—social approval functions as a rewarding stimulus that alters behavior (for a review of human impression management see Leary & Kowalski, 1990). For example, social rewards (e.g., receiving a public grade) can increase pro-social behavior whereas monetary rewards can decrease such behaviors (Benabou & Tirole, 2006; Handgraaf, de Jeude, & Appelt, 2013; Heyman & Ariely, 2004). Simply viewing pictures of others' eyes (priming the feeling of being watched) causes humans to act more prosocially (e.g.,

Ernest-Jones, Nettle, & Bateson, 2011; Pfattheicher & Keller, 2015). Self-reputation management emerges early in development (Engelmann, Hermann, & Tomasello, 2012) and has been argued to serve an important evolutionary purpose (Milinski, Semmann, & Krambeck, 2002). Consistent with this theory that social belonging and reputation are important or even rewarding to humans, ostracism has been linked to varied negative outcomes (reviewed in Williams, 2007). Thus, behavioral evidence suggests that both gaining and maintaining a positive reputation are important motivators for humans. For the purposes of this taxonomy, these evaluative types of reward are distinct from simple positive feedback from a social partner (e.g., seeing a smiling face in response to pushing a button quickly enough)—evaluative reward involves the participant feeling as though he or she is being evaluated as a person (e.g., as trustworthy, as a worthy friend, etc.).

Animal evidence. Although social status is certainly present in some groups of non-human primates (e.g., chimpanzees: Newton-Fisher, 2004), no research has indicated that animals are sensitive to reputation or social evaluation in the same way as humans. For example, unlike five-year-old human, chimpanzees behave in the same way whether or not they are observed by a group mate (Engelmann et al., 2012). Crucially, such findings do not indicate that conspecific feedback does not shape animal behavior. Especially among non-human primates, social feedback is involved in shaping many behaviors, including vocalizations (Koda et al., 2013). Rather, animals do not appear to represent such feedback as reflecting how they represented in the mind of another individual. As such, although interesting research has explored how primates respond to different facial expressions (e.g., anger; Watson et al., 2009)

that send social signals, such studies are likely not examining the cognitive representation of that anger as ‘this is what another thinks of me.’ Thus, evidence for the rewarding nature of social evaluations is limited to human research.

Human neural evidence

Positive social evaluation. In one of the first human fMRI studies of response to social feedback, Izuma and colleagues (2008) had participants fill out a series of questionnaires and record an introductory video and then told participants that they would receive feedback on these materials from real social partners. In reality, participants viewed preset feedback while in the scanner. In some blocks, participants learned that observers thought they possessed highly valuable traits (e.g., “trustworthy”, whereas in others, observers gave more lukewarm evaluations (e.g., “modest”). In a control “Other” condition, participants also saw the same target words, but were told they were being applied to other people. In a separate session, participants won monetary rewards in blocks of both high and low value. Researchers masked social reward activation (defined as areas that were more active for positive feedback for the self versus another) based on monetary reward activation, and found that bilateral caudate and putamen were active for both social and monetary rewards. Additionally, left caudate appeared to be sensitive to reward magnitude, regardless of reward type. Similar to many of the previously reviewed SID paradigm studies, the authors argue for a ‘common currency’ of social reward. MPFC, however, was uniquely responsive to social feedback about the self, and this effect was not moderated by how positive the feedback was, suggesting potential dissociation

between systems associated with computing the value of social reward versus the processing of social information.

Subsequent research has examined the neural correlates of social acceptance more generally. Somerville and colleagues (2006) had participants decide if they would like to interact with a person and then learned whether that person wanted to interact with them. Dorsal anterior cingulate cortex (dACC) was more sensitive to expectancy violations (e.g., the social partner picked that they did not want to interact when the participant did not), whereas ventral ACC tracked acceptance and rejection, with elevated activation to acceptance. Further, subsequent research indicated that self-esteem may influence neural activation to feedback, as vACC activation is not as affected in individuals with high self-esteem (Somerville, Kelley, & Heatherton, 2010). Neither study, however, found activation in OFC or striatum.

Similarly, developmental research has indicated increased VS activation in response to acceptance from others. In the Chatroom task, children were told they were going to be chatting with various peers, and when children and adolescents received feedback that a peer wanted to interact with them (versus rejected them), activation increased in caudate and putamen (Guyer, Choate, Pine, & Nelson, 2012). In contrast, precuneus and medial temporal gyrus (MTG) were sensitive to whether the child rated the peer as desirable, with increased activity when feedback was inconsistent with the child's own ratings. Additionally, many social cognitive regions, including TPJ, became more active to acceptance with age, which the authors suggest reflects an increase in self-referential processing in response to social feedback. Interestingly, other research has suggested increased VS activation in response to

adolescents thinking about what their best friend thinks about them in terms of social (versus academic or physical) domains (Jankowski, Moore, Merchant, Khan, & Pfeifer, 2014). Further, this sensitivity to peer evaluation increases with age and pubertal status. The analysis, however, did not consider whether or not the adolescent felt that they would be viewed positively—merely that they were reflecting on a peer evaluation. Thus, interesting future work could investigate the role of positive versus negative peer evaluations across adolescence versus adulthood. One possibility is that merely reflecting on one's social status or reputation is more rewarding in adolescence than adulthood.

The previously reviewed social evaluation research examined the outcome phase, but several studies have examined the anticipation phase of these same paradigms. In the Chatroom task, the anticipation phase was operationalized as children's ratings of how much they believed each peer would want to interact with them (Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009). For girls, but not boys, NAcc activation to anticipating feedback from desirable versus non-desirable peers increased with age. In a developmental extension of the Somerville et al. (2006) paradigm, anticipation of positive feedback was associated with increased VS and vMPFC activation, and increased with age (Gunter Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010). Additionally, positive feedback itself was only associated with increased reward circuitry activation when it came from liked peers. Further age groups responded differentially to positive versus negative feedback from desirable peers: striatal and VMPFC activity was similar to positive feedback, but was greater in adults to negative feedback. These findings may explain the lack of

striatal activation in the original Somerville et al. (2006) study, as that study collapsed across desirable and non-desirable social partners. Thus, evidence suggests that both anticipating and observing feedback activates reward circuitry, and these effects are greater for positive feedback, feedback from desirable partners, and increase with age.

A separate body of literature has investigated neural response to active social exclusion. For example, an extensive set of studies have investigated response to Cyberball, a virtual ball-tossing game in which participants believe they are being excluded by two confederates (e.g., Eisenberger, Lieberman, & Williams, 2003; Masten et al., 2009). In general, dACC and ventral lateral PFC (VLPFC) are more active during exclusion, with some evidence that dACC tracks subjective exclusion experience whereas VLPFC is involved in regulating the emotional effects of rejection (reviewed in Premkumar, 2012). Further, the effects of rejection may be greater in adolescents, both in terms of behavioral distress and in neural activation (Sebastian, Viding, William, & Blakemore, 2010). These findings indicate that social exclusion is not merely the absence of social reward, and rather involves a more complex circuitry including regions involved in pain perception and affect regulation.

Acting while observed. In contrast to studying direct social evaluation, another line of research has examined how individuals respond when being observed by others. VS activity in response to non-social feedback was greater when being observed (Simon, Becker, Mothes-Lasch, Miltner, & Straube, 2014). Additionally, performing a charitable act in the presence (versus absence) of observers increased VS activation both before the donation choice was made and during the donation (Izuma, Saito, & Sadato, 2010a). Further, prosocial behavior increased when

observed. In spite of behavioral and neural effects, however, all but one participant denied that the observers had any effect, indicating that acknowledging the role of reputation may be seen as socially undesirable. Similarly, when participants answer questions about whether they follow social norms (e.g., “I am not punctual for appointments”), VS activation is greater when observers are present. Additionally, mPFC activity was greater when answering questions about the self (versus general social statements), and this increase was accentuated by observers. The authors concluded that MPFC and VS may play a role in promoting cooperative behaviors and societal order. This contention could be further investigated by examining whether individual differences in neural response to being observed are related to cooperative behaviors.

In a review of neuroimaging research on reputation, Izuma (2012) concluded that in addition to reward circuitry tracking the value of others’ opinions, there were roles for MPFC in tracking the content of reputation and TPJ in monitoring others’ mental states. Indeed, in moving from more simple observational paradigms (e.g., viewing attractive faces) to capturing multiple facets of naturalistic human experience, it becomes increasingly important to characterize activity not only in single regions, but in the complicated interplay between the multiple networks underlying social value.

Vicarious Reward

Behavioral manifestation. Observing others receive rewards intersects with multiple facets of reward. In terms of learning, early research on vicarious reward found that merely observing others receive rewards was a powerful tool for shaping

behavior (reviewed in Deguchi, Fujita, & Sato, 1988). Helping others, either directly or via sharing rewards, is subjectively rewarding (e.g., Dunn, Aknin, & Norton, 2014), especially when the other is a friend (e.g., Fareri, Niznikiewicz, Lee, & Delgado, 2012). Prosocial and altruistic behaviors emerge early in development (reviewed in Brownell, 2013), as does sensitivity to fair allocation of resources (e.g., Schmidt & Sommerville, 2011). Thus, the reward of sharing or viewing others receive reward appears to be an important component of human behavior.

Animal evidence. Vicarious reward also shapes animal learning. Vicarious learning is an especially salient mechanism for learning fear (reviewed in Askew & Field, 2008). For example, rats can be fear conditioned via watching other rats receive shock (Jeon et al., 2010). In addition to fear, animals can learn a wide variety of tasks via conspecific observation (e.g., rats, Zentall et al., 1996; non-human primates: Subiaul, Cantlon, Holloway, & Terrace, 2004). Macaques can even learn token economies by watching humans (Bevacqua et al., 2013). Such social or observational learning paradigms, however, does not directly assay whether watching conspecifics receive rewards is intrinsically rewarding for animals, or whether such learning may operate via different mechanisms than animals being conditioned themselves.

In a more direct test of the value of rewards to conspecifics versus oneself, Chang and colleagues (2011) presented macaques with a series of decisions in which they could allocate juice. Monkeys were always presented with two choices out of the set of giving juice to themselves, a conspecific, themselves and a conspecific, or no one. Monkeys preferred giving a reward to the other monkey than to no one receiving a reward, but preferred rewarding themselves only than to both monkeys receiving

the reward. Interestingly, the preference to dispense juice to another over dispensing no juice disappeared when the conspecific was replaced with a non-social control (a depository bottle). In a follow-up study, researchers found that oxytocin increased the tendency to dispense juice to the other monkey versus juice to no one, but OT also increased the number of self-relevant choices (Chang, Barter, Ebitz, Watson, & Platt, 2012). The authors caution, however, about interpretation of the self over self and other preference as indicating any spite; rather, monkeys may simply have learned over social experience that when another monkey receives food, they tend to receive less for themselves.

Human neural evidence. A recent meta-analysis of fMRI research on vicarious reward examined 25 recent studies, and found, across paradigms, both reward circuitry and mentalizing regions were active (Morelli, Sachet, & Zaki, 2014). These paradigms spanned a wide array of modalities, including watching others receive money, praise, and physical touch. The authors then compared vicarious rewards to a meta-analysis of personal reward, although the included personal studies were non-social in nature. Both vicarious and personal reward resulted in increased OFC and amygdala activation, but personal reward resulted in greater NAcc activity, whereas vicarious reward more strongly activated STS and dMPFC. Thus, OFC may represent general value, whereas social cognitive regions are more active when considering the rewards experienced by others. Further, diminished striatal activation to vicarious reward suggests that it may be less, or at least differentially rewarding, than personal reward. Given that personal social rewards, however, appear to engage social cognitive regions, future research should contrast vicarious reward to positive

social evaluation, cooperative games, SID paradigms, and other types of social reward. Such comparison may reveal reduced or even eliminated differences in social cognitive regions.

Whereas the meta-analysis grouped together all extant vicarious reward studies, a more fine-grained analysis indicates several important dimensions on which to classify and understand the effects of vicarious reward. Importantly, the effects of vicarious reward are modulated by who is receiving the reward. Increased similarity to the recipient increases reward circuitry activation (Mobbs et al., 2009), as does feelings of liking toward the recipient (Braams et al., 2013). Conversely, reward circuitry activity decreases when seeing a disliked individual receive an award (Braams et al., 2013), and increases when seeing misfortune befall a higher status individual (Takahashi et al., 2009).

Several other contextual variables also affect how vicarious reward activates reward circuitry. For example, charitable donations have been linked to VS activity (Moll et al., 2006), and this activation is greater when donations are voluntary (Harbaugh, Mayr, & Burghart, 2007) and observed (Izuma et al., 2010a). Such findings suggest that important components of altruism may be both subjective feelings of reward from donation and the additional components of social reputation. Sensitivity to vicarious reward is also affected by priming. Although the meta-analysis indicated that striatal response to vicarious reward is consistently reduced compared to personal reward, interdependence priming (i.e., listening to a short story with plural pronouns versus first-person pronouns) creates equivalence between the two reward types (Varnum, Shi, Chen, Qui, & Han, 2014). Participants, however,

were winning money for a friend; it is unclear if interdependence priming affects response to strangers' rewards, but this an important direction for future research, especially considering cross-cultural differences in interdependence (Markus & Kitayama, 1991).

Ultimately, in comparison to personal reward, vicarious reward is understudied. For example, do the differential classifications of personal reward (e.g., non-social versus social; observational vs. interactive) have similar analogues vicariously? Additionally, do the separate components of traditional reward literature (e.g., wanting, liking, learning) map onto vicarious rewards? Recent research has also begun to probe the neural mechanisms of not just watching others receive rewards, but of vicarious learning (Burke et al., 2010). Before making a choice, participants observed a confederate make a choice and receive a reward or punishment. DLPFC was sensitive to observational action prediction error (e.g., whether the confederate makes a choice you expect) and VMPFC tracks observational outcome error (e.g., whether the confederate receives a predicted outcome). Consistent with prior literature, VS tracked prediction errors for outcomes that the individual participant experience, but showed decreased activation for the confederate receiving rewards. Overall, vicarious reward activates many of the same neural regions as personal reward (e.g., mOFC), although vicarious activation is weaker in VS. Various reward also engages the social cognitive network, suggesting that important components of processing social rewards extend beyond the canonical reward network.

Cultural Reward

Behavioral manifestation. The previously reviewed types of reward (observational, interactive, evaluative, and vicarious) have fairly robust literatures in both humans and animals, and, especially in the case of evaluative and vicarious reward, have been discussed and reviewed as single constructs. The next category of social reward is more nebulous, and is rooted in the behavioral observation that following social norms, especially norms such as fairness, appear to be motivating for humans (cf. Tomasello & Vaish, 2013). At a young age, children will not only follow, but enforce social norms using generic language, which indicates that children identify with their group and are motivated to follow its rules (Schmidt & Tomasello, 2012). Similarly, adults rate core values (e.g., following tradition) as more important and rewarding than tangible rewards (e.g., food; Brosch et al., 2011). Evolutionarily, such intrinsic reward associated with following social norms would be advantageous, making this type of reward an important target for study.

One of the difficulties of studying cultural reward, however, is that it overlaps with many other reward-relevant constructs. First, the behavioral and neural bases for several related concepts, including empathy (e.g., Rameson, Morelli, & Lieberman, 2012), morality (e.g., Tomasello & Vaish, 2013), and altruism (e.g., Penner, Dovidio, Piliavin, & Schroeder, 2005), have been extensively interrogated, and are outside the scope of this review. Rather, this section focuses on how the construct of cultural reward has been operationalized in the literature. Second, in addition to overlapping with a variety of other constructs such as empathy, one of the reasons that cultural reward is difficult to define is that it overlaps with evaluative reward (receiving

others' good opinions) and vicarious reward (seeing others rewarded). This review suggests that what may set cultural reward apart is that it is most salient in the context of a group, rather than a dyad, and may relate to more high-level representations of social norms (e.g., fairness more abstractly compared to the more immediate reward of seeing the smile of a charity recipient). As demonstrated in the following sections, however, more research needs to be done to determine if this claim is justified.

Animal evidence. Translating the concept of social norms to animal research is difficult, but behavioral research does suggest that outcome equality is desirable for animals. For example, across species, animals show inequality aversion and will reject unfair allocation (e.g., monkeys: Brosnan & De Waal, 2003; dogs: Range, Horn, Viranyi, & Huber, 2009). For example, dogs show increased stress and refusal when another animal has been rewarded for a behavior and they have not. Thus, context alters the rewarding value of stimuli (e.g., vicarious reward). In a recent review, Brosnan and de Waal (2014) argue that this evolutionarily-conserved inequality aversion is foundational for the emergence of cooperative behavior—seen when in addition to refusing unequal rewards, chimpanzees and humans attempt to equalize outcomes. A separate line of behavioral research has examined prosocial behavior in animals (reviewed in Cronin, 2012), finding that contextual factors (such as relationship with the recipient and type of reward) play a large role. Higher-order non-human primates also show cultural learning consistent with the idea of social norms (e.g., in tool use; Whiten, Horner, & de Waal, 2005), but despite the role of reward in learning, these processes have not been interrogated within a reward framework and their neural circuitry is unexamined.

Human neural evidence

Inequality aversion. Equality is a strong social value and the neural correlates of inequality aversion have been relatively well-studied in humans. Even if the amount of money earned is controlled, VS is activated more for fair versus unfair monetary offers (Tabibnia, Satpute, & Lieberman, 2008), and both VS and VMPFC track equitable outcomes (Tricomi, Rangel, Camerer, & O'Doherty, 2010). Specifically, vicarious reward leads to greater reward circuitry activation when the participant received an unequal share of the initial reward. Such findings suggest that inequality aversion is not only present when the participant is receiving less reward. For example, VMPFC is more active when watching others' selfish versus unselfish actions but only when such behaviors are couched in the context of donation (Cooper, Kreps, Wiebe, Pirkel, & Knutson, 2010). Additionally, individuals differ in their prosociality and inequality aversion tendencies. In a study of individuals classified as either prosocial or individualist, based on a behavioral monetary-allocation paradigm, Haruno & Frith (2010) found increased amygdala activation in prosocial, but not individualistic, participants in response to unequal allocation.

Such studies, however, have focused on the observation of inequality, rather than action. Supporting the rewarding value of fairness, individuals will actively punish individuals who take advantage of the economic system, and punishing such individuals has been linked to VS activation (de Quervain, Fischbacher, Treyer, & Schellhammer, 2004; Singer et al., 2006). Similarly, cooperation, as reviewed in the section on interactive reward, activates OFC and VS (e.g., Rilling et al., 2002), as does altruism, as reviewed on the section on vicarious reward (e.g., Moll et al., 2006).

In a recent study, Zaki and Mitchell (2014) found that acting equitably activated OFC similarly, regardless of whether it was self-serving or generous equity. The authors argued that such findings suggest an intrinsic reward value to equality. The neurobiological processes underlying these responses are unknown, but there is some evidence that decreasing serotonin leads to increased rejection of unfair outcomes (Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008). Finally, a promising future direction involves the role of reward circuitry in learning about the equitable tendencies of social partners over time. Participants first played Cyberball with confederates (which created expectations about following social norms such as fair play), and then played an investment game with the same partners (Fareri, Chang, & Delgado, 2012). Ventral striatum activity during the investment game related to prediction error in terms of the partners' decisions, suggesting an important role for the regions in short- and long-term learning about social partners.

Social norms. Although inequality aversion may be one of the most salient and evolutionarily-conserved examples of cultural reward, human social norms span a far greater set of domains. To test the value of social norms outside of equality contexts, researchers had participants read sentences about other 'core values' (e.g., respecting tradition) or about tangibly rewarding activities (e.g., eating an apple). Results indicated some dissociation in activated regions, with increased OFC to tangible rewards and increased MPFC and caudate activation in response to core values (Brosch et al., 2011). Interestingly, although mOFC tracked participant's individual ratings of tangible rewards, precuneus tracked subjective evaluations of social norm rewards, suggesting that social cognitive regions may play stronger

evaluative roles in cultural reward processing. Further, social observers may modulate the effect of social norm following on reward circuitry. Specifically, in a paradigm where participants indicated whether or not they followed social norms (e.g., being punctual for appointments) in the presence or absence of observers, caudate activation was modulated by (Izuma, Saito, & Sadato, 2010b). Additionally, self-relevant judgments showed typical effects in MPFC, consistent with previous literature (e.g., Tamir & Mitchell, 2012).

In addition to merely reflecting upon social norms, acting in accordance with such norms appears to activate reward circuitry. For example, when making moral decisions, VS and OFC are both active, with VS representing the expected value of various outcomes (e.g., the number of lives saved; Shenhav & Greene, 2010). Additionally, VS response to the expected value of these outcomes is correlated with individual's specific moral choices.

Ultimately, consistent with the reviewed evidence, Rilling and Sanfey (2011) suggest that a broad neural network is involved in social norms. For example, dACC is responsive to social norm violations and VLPFC represents the potential punishment for norm violations, consistent with the previously reviewed social exclusion literature. dMPFC may track trustworthiness and social strategy, consistent with the role of mentalizing regions in social reward. Subcortical regions are also crucial, as amygdala tracks inequality and VS processes the reward value of these social behaviors.

Previous studies, however, have investigated the reward value of already present social norms, which may have developed their rewarding value over a long

evolutionary history. Future work should investigate whether following more arbitrary rules and conventions is also rewarding. Several studies have examined whether conformity itself is rewarding. For example, Klucharev and colleagues (2009) found that disagreeing with group norms about facial attractiveness triggered a response in VS consistent with models of prediction error (i.e., deactivation), and that greater levels of prediction error were related to increased behavioral correction (i.e., alignment back to group norms). Subsequent studies have found similar reward circuitry involved in conformity (e.g., Zaki, Schirmer, & Mitchell), and this effect may be greater when the participant learns that his or her preference matches that of an expert (Campbell-Meiklejohn, Bach, Roepstorff, Dolan & Frith, 2010).

Affiliative Reward

Behavioral manifestation. The previous five types of reward (observational, interactive, evaluative, affiliative, and cultural) were categorized based principally on *how* social reward was operationalized (e.g., viewing an attractive face versus learning that you were considered trustworthy by a peer). The final type of reward considered is more focused on *who*. Behavioral evidence indicates that certain types of human bonds are especially salient, and lead to the kind of approach behaviors, learning, and subjective feelings typically associated with reward. In particular, the attachment system appears to contain elements of reward. Briefly, as first explained by Bowlby (1969/1982) children are evolutionarily programmed to seek proximity to a specific caregiver, since, when the species evolved, this was an adaptive strategy to avoid predation. Bowlby drew heavily on ethology, which suggests there may be phylogenetically conserved neurobiological mechanisms underlying attachment.

Further, attachment bonds persist with caregivers throughout development and individuals can also be attached to romantic partners (Ainsworth, 1985). Although attachment is a specific system, with its own predictors and outcomes, other types of human social bonds also have special reward value, including the parent-child relationship and close friends. Throughout the lifespan, individuals seek out these relationships and delight in them, although they can also lead to some of the most profound feelings of depression, punishment, and exclusion.

Animal evidence. The neurochemical bases of affiliative reward have been extensively investigated in the contexts of maternal care and mating (see Numan & Young, 2015 for a complete review of both systems). Broadly, in both behavioral systems, dopamine and neuropeptides play important roles. Dopamenergic circuitry in NAcc has been linked to parental care in rats (Champagne et al., 2004), with dopamine antagonists linked to diminished maternal care (Brynes, Rigerio, & Bridges, 2002). Expression of oxytocin, a neuropeptide, has been linked to both uterine contraction and lactation (reviewed in Young et al., 1997), and increasing oxytocin has been linked to increased maternal behaviors across several species (including both sheep and rats; reviewed in Leng, Meddle, & Douglas, 2008).

Dopamine and oxytocin also play important roles in mating and pair-bonding. Dopamine release, especially in NAcc, has also been linked to mating behaviors in rats (Becker, Rudick, & Jenkins, 2001). Much of the pair-bonding research has come from examining monogamous versus non-monogamous species, specifically two species of voles. Discussion of the role of neuropeptides in pair bonding has been extensively reviewed elsewhere (e.g., Ross & Young, 2009), and the consensus is that

pair bonding voles express greater oxytocin (OT) in NAcc and greater vasopressin in AVP in VTA and ventral pallidum (Lim & Young, 2006). Additionally, as with maternal behaviors, inhibiting the expression of these neuropeptides reduces mating and mate preferences (Bielsky & Young, 2006). In a recent review, Coan (2008) suggest that the dopaminergic reward system interacts with neuropeptides to connect reward value with specific partner preference.

A recent review examined the common and distinct neurochemical mechanism of maternal behavior and pair-bonding (Numan & Young, 2015). The authors suggest additional roles for the olfactory bulbs and amygdala in recognizing conspecifics in both systems, but that there may be particular regions more linked to maternal than pair bonding (i.e., medial preoptic area), as well as dissociations in terms of the roles of specific dopamine receptors. Overall, however, the authors conclude that the systems build off of similar neural circuitry involving dopamine and oxytocin expression in NAcc, which promotes increased plasticity in the connection between NAcc and ventral pallidum and fosters the repeated activation of this reward circuitry that promotes social attraction. Further, these neurochemical processes have downstream effects that increase amygdala-ventral pallidum connectivity, which allows for the pairing of relevant social information (encoded by the amygdala) with reward network activation.

Research on non-human primates have not examined this neural circuitry in detail, although there is some evidence that opioids play a role in both maternal behavior and grooming (Martel et al., 1993), with increased oxytocin expression after social grooming (Crockford et al., 2013). Additionally, this oxytocin increases

happens after grooming with bond-partners, even outside of sexual or genetic relationships. Thus, similar neural mechanism may underlie pair bonds as other types of social affiliation, but this area is understudied. In an extensive review of ‘friendship’ in animals, Brent and colleagues (2014) concluded that friendship is adaptive across species and that oxytocin and dopamine likely play roles in supporting the formation and maintenance of friendship bonds, perhaps building on the neural circuitry involved in phylogenically-prior maternal care systems.

In sum, affiliative reward appears to rely on neural processes (e.g., vasopressin; olfactory bulbs) that are less involved in other types of social reward. Importantly, the previously reviewed social reward paradigms can intersect with these affiliative systems (e.g., a paradigm in which rats re place conditioned with their pups versus adult rats, or in which chimpanzees view photos of bond-mates versus non-bonded individuals), and such intersections represent a promising direction for future research.

Human neural evidence. Despite the wealth of animal literature on the neural bases of affiliative reward, linking this research to human behavior is complex, both due to neurophysiological differences between species and due to the fact that humans have representational capacities not possessed by other animals. New reviews, however, have begun to unite the two literatures (Bora, Yucel, & Allen, 2009; Coan, 2008). Across human neuroimaging studies interrogating various affiliative bonds (e.g., romantic love, parent-child relationships, friendships), growing evidence suggests an important role for reward circuitry, similar to the analogous regions implicated in animal studies. Importantly, however, reward circuitry is not the

primary component of these behaviors—rather, emotional, social cognitive, and cognitive control networks all play important role. Finally, given the nature of human research, the neurochemical parallels to animal research are murky, and, in the case of things like pheromones, animal research may be of limited value in understanding human relationships (cf. Coan, 2008).

Romantic love has primarily been investigated via paradigms in which participants view pictures of their beloved. For both early stage and longer-term romantic love, love has been linked to VTA activation (e.g., Aron et al., 2005; Xu et al., 2010), with increased activation in early stage love related to the duration of the relationship (Xu et al., 2012). The control images for those studies were other individuals that participants were close to (e.g., friend or sibling), but researchers have directly compared the neural bases of looking at pictures of a romantic partner versus a child (Bartels & Zeki, 2004).

Importantly, however, these paradigms may not capture important components of romantic attachment, as aspects of the attachment system are likely to be more active during times of threat (Bowlby 1969/1982). Although affiliative reward extends beyond attachment, understanding attachment is important, given its role as a core, evolutionarily-conserved system. In paradigms involving electric shock, researchers have found that the presence (either physical or via photo) of a romantic attachment figure increases activation in structures that have been broadly implicated in affect regulation (e.g., VAcc and dLPFC; Coan, Schaefer, & Davidson, 2006; Eisenberger et al., 2011), but no differences in classic reward circuitry. Such paradigms suggest that although aspects of affiliative bonds are rewarding, they also

serve important functions in affect and stress regulation beyond dopaminergic reward circuitry.

A separate line of research has investigated maternal bonds, specifically examining maternal response to stimuli of their infants (for a comparison to animal literature, see Lonstein, Levy, & Fleming, 2015). In a recent review of this literature, Kim and colleagues (2016) find that post-partum changes in reward circuitry may support infant bonding. Supporting this view, increased maternal VS response to the audio-recorded cries of her own infant is related to maternal sensitivity (Kim et al., 2011). Further mother's attachment style predicts her neural response to her infant's face, with more securely attached mothers demonstrating increased VS activation and increased levels of oxytocin (Strathearn, Fonagy, Amico, & Montague, 2009). Additionally, mothers of children classified as securely attached showed diminished amygdala activity in response to their child's cries (Laurent and Ablow, 2012). These findings suggest important neural mechanisms underlying the intergenerational transmission of attachment patterns.

The work with mothers, however, focuses on the neural mechanisms of caregiving rather than attachment. In one of the few studies of social reward in infancy, researchers showed 12-month-old infants pictures of their mother's versus a stranger's smile and used fNIRS to demonstrate increased OFC activity in response to their own mother's smile (Minagawa-Kawai et al., 2009). In a paradigm with older children and adolescents, viewing a photograph of their mother versus a stranger produced stronger amygdala activity, with higher activity related to stronger attachment (Tottenham et al., 2012). In a more attachment-relevant study, children

were exposed to threatening words in the scanner, and, similar to adults, VLPFC activity was reduced when the caregiver was present (Conner et al., 2012). Future work should continue to probe the real-time correlates of attachment in humans, and determine if the neural bases that sustain those bonds during times of threat different from those that are most active during times of safety.

Outside of family-based affiliative reward, friendships also engage reward circuitry. For example, in a social interaction task, participants were more likely to approach photographs of friends versus photograph of famous people and liked objects, and this approach behavior was related to VMPFC and NAcc activation (Guroglu et al., 2008). Further, as evidenced by the vicarious reward literature, viewing a friend versus stranger receive a reward increases VS activity (Fareri et al., 2012). Friendships, however, remain an under-investigated facet of affiliative reward and have primarily been used as control stimuli in attachment studies.

Finally, given recent news media coverage of OT as a ‘love drug’, a brief note is warranted about the effects of intranasally administered OT on human behavior. In general, OT appears to differentially affect social behavior, such as reducing amygdala response more to social than non-social threats (Kirsch et al., 2005), and produces increased trust, eye gaze, and other social behaviors (reviewed in Bartz, Zaki, Bolger, & Ochsner, 2011). Such findings have lead to a push to use OT for treatment in social disabilities such as autism (Guastella & Hickie, 2015), but in a cautionary review of extant OT literature, Insel (2010) warns that if differences are found in the type and distribution of receptors, OT administration alone is unlikely to address a compounding lifetime of deficits.

Future Directions

Integrating Across Types of Social Reward

Across studies, social reward reliably activates the reward network, but the extent to which other networks (e.g., mentalizing, cognitive control) are engaged appears to vary with paradigms. Pinpointing the precise cognitive and neural mechanisms underlying different types of social reward, however, is complicated by the wide array of current paradigms that vary across a wide array of dimensions. More stringent, taxonomically-motivated research will parse common and distinct components of social reward. For example, recent studies have begun to examine observational reward for different social partners (e.g., Bartels & Zeki, 2004), or how relation to the recipient affects neural activation to vicarious reward (e.g., Fareri et al., 2012). Other domains include whether there is an interactive context, how tangible the reward is, and whether there is a component of social learning. The goal of this review is not to describe a definitive set of dimensions on which to categorize social reward, but rather to highlight the gaps in the literature that hinder this type of categorization. When a researcher studies altruism, for example, it would be helpful to characterize exactly how that paradigm is classified across a set of dimensions. The goal of this classification is two-fold: first, in order to ensure that these are well motivated choices (e.g., why is the study with strangers instead of family members? Why is it about observing altruism rather than acting altruistically?); and second, to properly understand how this study intersects with literature.

Across this review, few studies are referenced in multiple sections. Rather, separate lines of research have targeted different facets of social reward, with the

neuroeconomic literature that employs dictator games rarely interacting with studies on peer approval in adolescents. Further, in social reward studies with multiple types of reward, the other reward is almost always non-social (e.g., Brosch et al., 2011; Kohls et al., 2012). As evidence to the importance of considering social reward more broadly, social vs. non-social reward comparisons have generally indicated diminished activation to social reward (e.g., Dichter et al., 2012). Such studies have predominately examined observational reward, however, which may be less rewarding than interactive or evaluative reward (cf. Kohls et al., 2012). Thus, definitive claims about the relative value of social versus monetary rewards await comparison across a broader spectrum of social rewards (especially given behavioral evidence for the salience of social rewards; Handgraaf et al., 2013; Heyman & Ariley, 2004).

Ultimately, one of the best ways to understand social reward will be to employ multiple paradigms in a single sample. This approach has been useful for understanding the processes underlying biological motion and theory of mind (Deen, Koldewyn, Kanwisher, & Saxe, in press). For example, researchers could directly test the claim that interactive context (versus observation alone) increases the saliency of social feedback (cf. Schilbach et al., 2013), or that peer versus adult feedback is most salient in adolescence. Further, not all social interaction paradigms have revealed activation in reward circuitry (e.g., Redcay et al. 2012; Rice & Redcay, under review). Future studies could vary the interaction along different components (e.g., contingency, participant volition) to isolate the aspects of social interaction that are most rewarding. More titrated exploration of human reward, especially in the context

of interactive reward, should be paired with increased reference to the animal literature, which primarily investigates interaction (Garipey, Chang, & Plat, 2013).

Multimodal Approaches

Many of the reviewed studies rely on reverse inference (cf. Poldrack, 2011) to illustrate how a particular social construct is rewarding. That is, researchers begin the paper by highlighting a few regions involved in reward processing (typically VS and OFC), and conclude that their social paradigm was rewarding due to activation in these regions. Such claims, however, can be risky, especially given the role of VS in a host of processes, including prediction error. The next decade of social reward research should move away from picking a specific behavior and determining if that behavior is rewarding via assaying VS activation, and instead explore the broader cognitive and neural mechanisms that give rise to subjective and implicit reward.

Approaches focused on the complex neural network underlying reward are especially promising (Bullmore & Sporns, 2009). Both task-based and rest-based functional connectivity approaches will provide increased insight into the neural networks of reward. Further, resting-state functional connectivity may allow for an exploration of reward circuitry during much younger ages than are currently studied. For example, a recent paper suggests that the functional connectivity of VS undergoes age-related changes (Fareri et al., 2015). Novel paradigms have experimented with free-viewing paradigms, often utilizing movies with complex social content (Hasson, Malach, & Heeger, 2010), and more targeted investigations should examine whether particular types of social stimuli alter VS activity as compared to traditional rest.

Neuroimaging paradigms should also be integrated with other assays, including physiological measures and eye-tracking. For example, cortisol may play a role in social exclusion (Blackhard, Eckel, & Tice, 2007; although see Zoller, Maroof, Weik, & Deinzer, 2010), and the HPA axis has been implicated in affiliative behaviors (Polan & Hofer, 2008; Suomi, 2008). In terms of eye-tracking, social attention plays a large role in social behavior, and indeed some of the earliest measures of social reward examine infant preferential looking. Studies of response to social reward, however, have not typically measured social attention, which can be captured on a much finer timescale than BOLD. Similarly, although using ERP to study subcortical regions is difficult, ERP also has higher temporal resolution and is more conducive to studying clinical and developmental populations. Indeed, several ERP studies have found responsivity to social reward is affected by autism or autistic-like traits (e.g., Cox et al., 2015; Stavropoulos & Carver, 2014b). Ultimately, a multimodal approach will best illuminate the cognitive and neural mechanisms of social reward.

Beyond a diversification of methods, behavioral and neural reward studies should be in closer contact. For example, although there is an extensive body of literature suggesting that aspects of social interaction are motivating to humans, such literature is not typically couched in a framework that directly assesses reward value (e.g., conditioning behavior) and instead often focus on measuring constructs such as preference or discrimination, which may not necessarily measure reward value. Additionally, the variables leading to a relation between neural activation and behaviorally experienced reward are unclear. Although VS and OFC are sometimes

reported to track subjective experience of reward value, this is certainly not the case across all studies.

Finally, researchers should be mindful of the coarseness of the BOLD signal. Claims for a ‘common currency’ for social and non-social reward have permeated the literature due to the fact that the same general regions are active for both paradigms. More detailed single cell recordings from monkeys, however, have found that largely separate neuronal populations respond to social vs. non-social rewards (Klein & Platt, 2013). As animal researchers begin to more fully explore the cellular bases of social reward, human researchers should be cautious about claiming that an identical circuitry underlies different types of reward.

Social Reward Across Development

Although behavioral evidence suggests early ontogenetic emergence of social reward, human neuroimaging studies of social reward are almost exclusively conducted with adults. Studying developmental dissociations in social reward (e.g., in their trajectory) may illuminate underlying categories of reward. Several open questions are especially important.

First, do certain types of social reward emerge earlier in development than others? For example, neonates show orientation toward the faces of conspecifics, but sensitivity to social norms emerges around age three (Vaish & Tomasello, 2013). Sensitivity to social feedback may also interact with contextual factors, such as whether or not the reward is coming from an attachment figure. Longitudinal research may be an especially useful technique for assessing whether different components of social reward are ontogenetically related or develop via separate mechanisms. For

example, do infants who orient more quickly to social stimuli show greater inequality aversion or sensitivity to social norm violations with age? Given the role of social feedback in shaping behaviors, there may be a direct causal link between sensitivity to social learning and later social behaviors. Although task-based fMRI is not well-suited to examine the ontogeny of social reward, several of the methodologies reviewed in the previous section, including eye-tracking, resting state fMRI in sleeping infants, ERP, and fNIRS may provide greater insight into the neural components of social reward in the first years of life.

Second, after initial emergence, how does sensitivity to social reward change with age? Much of the extant developmental research on social reward has examined response to peer evaluation (see section on evaluative reward). Behavioral evidence suggests that late childhood and adolescence are times of special sensitivity to peer feedback (Caouette & Guyer, 2014), and this is consistent with findings from studies of peer exclusion (e.g., Guyer et al., 2012; Jankowski et al., 2014). This sensitivity, however, is not limited to traditional reward circuitry. For example, sensitivity to social exclusion in VLPFC and VAcc increased with through adolescence (Bolling et al., 2011a). In spite of this evidence, no research has directly contrasted response to different types of reward in different age group. For example, perhaps sensitivity to evaluative reward peaks in adolescence, but vicarious reward sensitivity shows a different developmental pattern. Additionally, social reward is a lifespan construct, but has rarely been investigated in older adults. Suggestively, the only fMRI study comparing older and younger adults on a SID paradigm found increased NAcc activity to social reward in older adults. Future longitudinal studies spanning a wider

array of age groups across multiple tasks will help illuminate developmental trajectories.

Third, how do developmental changes in response to social reward both stem from and predict individual differences? For example, early temperament predicts response to peer feedback in adolescence (Guyer et al., 2014). Studies of non-social reward have extensively investigated constructs such as impulsivity (Plichta & Scheres, 2014) and substance abuse (Bjork, Smith, Gang, & Hommer, 2011), but such work is still relatively sparse with regards to social reward paradigms. Such age-related analyses should also consider the role of gender, both of which may affect response to social reward in adolescence (Guyer et al., 2012) and adulthood (Sprecklemeyer et al., 2009). Pubertal status is also an understudied contributor to social reward responsivity, with some evidence that it can play a role (Guyer et al., 2009). In part, clarifying what exactly is meant by social reward will enable more precise investigation of its antecedents and predictors across the lifespan.

Social Reward & Psychopathology

A growing body of research has begun to examine the relations between social reward processing and psychopathology, arguing that social (vs. non-social) rewards may give unique insight into disorders characterized by social dysfunction (Caouette & Guyer, 2014). Although the goal of this paper is not to fully review this literature, a few points bear mentioning. The first is that, similar to developmental research, psychopathology research provides a promising mechanism to parse different components of social reward. The second is that direct comparison of psychopathologies may be an especially fruitful line of research.

One of the most well-studied disorders in terms of social reward is autism spectrum disorder (ASD), a disorder characterized by extensive social and communicative impairments. In a recent review, Chevallier and colleagues (2012) argue that autism is characterized by behavioral impairments in social orientation, wanting and liking social interaction, and maintaining social relationships. Motivated by this literature, the past decade has seen increased research examining the neural bases of social reward in ASD. Such research, however, has found contradictory patterns of results: some studies have found increased amygdala activation in ASD (Dichter et al., 2012), others have found decreased amygdala and VS activation (Kohls et al., 2013; Scott-Van Zeeland, 2010), and still others have found no VS or amygdala differences (Delmonte et al., 2012). One suggestion is that observational paradigms of static photos may underestimate reward response in typical individuals, creating a false equivalency to autism (Kohls et al., 2012). Pinpointing the exact reason for these discrepancies, however, is difficult, as these ASD paradigms have differed across several dimensions, including the nature of the reward stimuli (e.g., neutral faces vs. smiling faces; whether stimuli were used in terms of social learning or in an incentive delay paradigm; whether stimuli were a known figure or a stranger) and the age group studied (e.g., children versus adults).

A systematic study of social reward in ASD may uncover the types of social reward that are most affected by the disorder. One argument is that although individuals with autism *like* social rewards once obtained, they do not *want* social reward; that is, the biggest impairments in ASD are in social motivation (Kohls et al., 2012). Again, however, this possibility has primarily been explored in observational,

incentive delay paradigms. More naturalistic paradigms may reveal different results. For example, individual with autism show blunted neural response to social exclusion (Bolling et al., 2011b), indicating that social reward dysfunction in ASD is complicated beyond a simple lack of social approach. Recent research has also begun to examine the effects of intranasally administered oxytocin on ASD, although findings have been mixed (reviewed in Guastella & Hickey, 2015).

In addition to autism, several other disorders have been linked to atypicalities in social motivation or processing social rewards, including depression (e.g., Davey, Allen, Harrison, & Yicel, 2011; Monk et al., 2008), and social anxiety (e.g., Cremeres et al., 2014; Guyer et al., 2008). Atypical amygdala activation has been implicated across a variety of disorders, including hyperactivity in response to positive feedback in major depressive disorder (Davey et al., 2011) and social anxiety (Guyer et al., 2008). Further, patterns of functional connectivity also appear to be heightened across several disorders in response to social evaluations, including increased NAcc-MPFC connectivity in social anhedonia (Healey, Morgan, Musselman, Olino, & Forbes, 2014) and increased amygdala-prefrontal connectivity in social anxiety (Guyer et al., 2008). Even disorders without an explicit social diagnostic component may show atypical social reward responses; for example, children with ADHD are behaviorally hyperresponsive to social versus non-social reward (Kohls, Herpertz-Dahlmann, & Konrad, 2009). Almost all of this work, however, has been in the realms of observational and evaluative reward. As with social reward in general, multimodal approaches that span a variety of types of social reward may offer the best insight into psychopathology.

In an especially promising approach, researchers have begun to compare social reward response across different psychopathologies. For example, Richey and colleagues (2014) compared response to a social incentive delay paradigm in both typical adults, adults with social anxiety, and adults with ASD. Results indicated amygdala hypoactivation in ASD vs. social anxiety during social reward anticipation and outcome, and that amygdala activation was related to anxiety severity. Further, VS hypoactivation was seen to social stimuli in both disorders, but was unique to ASD for the control, non-social rewards. Given frequent comorbidities in disorders (e.g., social anxiety is very common in individuals with ASD; White et al., 2009), understanding reward dysfunction across a variety of developmental profiles will provide the best insight into typical and atypical development.

Conclusions

The study of social reward spans disciplines and methodologies. Falling under the umbrella term of ‘social reward’ are studies targeting the neural response to social acceptance in adolescence, the cellular mechanisms underlying social conditioning in rodents, and the ontogenetic emergence of cooperation. The goal of this review was begin the synthesis of this diverse literature into a taxonomy based not on level of analysis, but on the type of social reward. The categories proposed are not intended to be exclusive or to necessarily map onto core, evolutionarily-conserved biological mechanisms. For example, observation of social reward is a necessary component of all social reward, and observation outside of the context of interaction rarely happens without additional interaction. Considering observation as its own taxonomic category, however, assists in understanding discrepancies in findings across different

types of social reward studies (e.g., sensitivity to social reward may be diminished in an observation-only context). Future research should continue to investigate commonalities and differences between these proposed categories, reclassifying reward types as needed.

The diverse set of social reward studies are unified by the fact they involve more than reward. From the potential roles of oxytocin in binding reward to social information to the involvement of mentalizing regions when considering one's social reputation, embedding reward in a social context involves more than reward circuitry. Whether the social context changes the nature of that circuitry remains an open question. Several studies and reviews have argued for a 'common currency' in which modality-independent value is signaled by striatal and frontal regions, in which any differential activation in to social vs. monetary rewards is simply due to their discrepant value. Recent work with non-human primates, however, suggests that at a cellular level, social and non-social rewards are differentially encoded. Further, more fine-grained analyses of connectivity may reveal that although BOLD activation in, say, VS, is present across multiple reward types, the functional fingerprint of that region is quantitatively different. Certainly, social rewards are not processed by a wholly different system than other reward types, but claims of a fully common currency await more precise investigation. Continued research employing a variety of methods from a diverse set of theoretical perspectives will continue to illuminate a core facet of human and animal behavior—the rewarding nature of social interaction.

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