



Published in final edited form as:

*Dev Sci.* 2018 May ; 21(3): e12581. doi:10.1111/desc.12581.

## Let's chat: Developmental neural bases of social motivation during real-time peer interaction

Katherine Rice Warnell<sup>1,\*</sup>, Eleonora Sadikova<sup>2</sup>, Elizabeth Redcay<sup>2,3</sup>

<sup>1</sup>Department of Psychology, Texas State University, San Marcos, TX 78666

<sup>2</sup>Department of Psychology, University of Maryland, College Park, MD 20742

<sup>3</sup>Neuroscience and Cognitive Science Program, University of Maryland, College Park, MD 20742

### 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 improve, social networks grow, and social brain networks specialize. To assess interactive social motivation, the current study used a novel fMRI paradigm in which children believed they were chatting with a peer. 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 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 brain systems support real-time social interaction in middle childhood. An interactive approach to understanding social reward has implications for clinical disorders, 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) 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

\*Corresponding author Katherine Rice Warnell, Department of Psychology, Texas State University, San Marcos, TX 78666, Tel.: 512-245-5564, warnell@txstate.edu.

continues into adulthood (Baumeister & Leary, 1995). Furthermore, diminished social motivation is theorized to be core to many clinical disorders, such as autism, social anxiety, and depression, which are most acute in real-world contexts (see Schilbach, 2016 for review). Thus, mapping the neurobiological bases of social motivation in naturalistic, interactive contexts 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, a network that includes ventral tegmental area, substantia nigra, amygdala, orbitofrontal cortex (OFC), medial prefrontal cortex (MPFC), insula, anterior cingulate cortex, and ventral striatum (VS; reviewed in Haber & Knutson, 2010). In particular, VS is often considered a 'hub' of reward processing, given its connections to other dopaminergic regions (Sesack & Grace, 2010; Kohls et al., 2012). Mounting evidence suggests that this reward circuitry may index a 'common currency' across both monetary and social rewards (Izuma, Saito, & Sadato, 2008; Lin, Rangel, & Adolphs, 2011; Montague & Berns, 2002). Importantly, however, 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). Although many social reward paradigms use non-interactive rewards (e.g., photographs), the real-world roles of social cognitive and reward circuitry may be best captured by more naturalistic studies (Schilbach et al., 2013).

Recent adult neuroimaging literature has begun to examine naturalistic social motivation (e.g., Cox et al., 2015; Izuma, 2012; Pfeiffer et al., 2014), but the important developmental period of middle childhood (ages 8-12) remains underexplored. This age range is characterized by rapid behavioral social development, as peers become increasingly salient (Sroufe, Egeland, & Carlson, 1999). Additionally, middle childhood represents a time of significant structural (Mills et al., 2014; Uematsu et al., 2012; Urošević, Collins, Muetzel, Lim, & Luciana, 2012) and functional (Carter & Pelfrey, 2006; Gweon, Dodell-Feder, Bedny, & Saxe, 2012; Forbes et al., 2010) development in two neural networks likely to underlie social motivation: the social cognitive network and the reward network. Understanding of how these networks support distinct components of real-world social motivation, however, is limited.

A set of developmental studies have investigated the neural correlates of social reward, but have predominately focused on one component—peer evaluation from computer-generated social partners which participants believe to be real. For example, in the Chatroom task (Guyer et al., 2008; 2009; 2012; 2014) children rate the desirability of social partners based on photographs and are told that they are similarly evaluated by the peers. During the scan session, participants predict and learn how they were perceived by each peer. VS activation was increased for positive versus negative peer feedback (Guyer et al., 2012), with age-related increases in VS activation when anticipating evaluation (Guyer et al., 2009). A similar paradigm by Gunther Moor and colleagues (2010) also found increased reward circuitry activation when anticipating and receiving positive feedback, with age-related VS increases during anticipation but not receipt. Finally, both VS and MPFC have been implicated in learning about the probabilities of particular peers providing positive feedback (Jones et al., 2014). Although these paradigms indicate an important role for reward circuitry

in social evaluation, they do not examine social motivation during real-time engagement, which may be when the desire to engage is most salient and clinically-relevant (Kohls et al., 2012).

A more recent study of social evaluation (Jarcho et al., 2016) did examine real-time peer feedback. In a novel paradigm, children believed they were chatting with peers who were either predictably nice, predictably mean, or unpredictable. The study found that children who were socially reticent in early childhood showed differential neural responses to unpredictable peers in middle childhood, but the main effects of anticipation and receipt of social reward were not reported. Further, as with previous paradigms whose focus was on social evaluation, peer responses were only positive or negative. Given that VS may also encode negative outcomes (Bissonette et al., 2013), a contrast involving a neutral social stimulus may better isolate the motivation to socially engage. Importantly, to be neutral, these neutral social responses should be non-contingent or non-engaged, while being free of the negative connotations of social exclusion (e.g., Bolling et al., 2011; Masten et al., 2009).

One set of studies that has examined non-evaluative and contingent social interaction is research on joint attention. In such studies a participant responds to or directs another's gaze (e.g., Koike et al., 2016; Oberwelland et al., 2016; Schilbach et al., 2010). These paradigms frequently recruit reward circuitry in addition to activating social cognitive regions (Gordon et al., 2013; Pfeiffer et al., 2014; Redcay et al., 2010; Schilbach et al., 2010; but see Caruana et al., 2015; Redcay et al., 2012). These paradigms are limited, however, by the fact they frequently confound contingency (e.g., receiving a response to a gaze shift) and social context (e.g., the presence of a social actor). One possibility is that the contingency of these social interactions drives their reward value. Another possibility is that perceiving a social partner is what makes interaction rewarding. Finally, the effects of contingency and social context may interact, such that the reward system is most sensitive to social contingencies. Given substantial evidence that both contingency (e.g., Stefani & Moghaddam, 2006; Yin, Knowlton, & Balleine, 2006) and social context (e.g., Aharon et al., 2001; Cloutier, Heatherton, Whalen, & Kelley, 2008; O'Doherty et al., 2003) involve reward systems, disambiguating children's desire to receive feedback from effects of social context will yield insight into social reward.

A second limitation of most existing studies of real-time interaction is that they analyze a joint attention event as a single trial, failing to separate out one's social bid from the partner's response. Substantial literature using non-interactive social stimuli has found distinct brain bases for anticipating versus receiving social reward (Social Incentive Delay paradigm; Spreckelmeyer et al., 2009; Rademacher et al., 2010), but it is unclear how these constructs map onto real-time interaction. 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 clinical disorders (cf. Kohls et al., 2012; Mundy & Newell, 2007).

Thus, three key gaps remain in the developmental social motivation literature. First, most extant paradigms contrast positive versus negative evaluation. Given evidence that VS is sensitive to negative outcomes (Bissonette et al., 2013), contrasting social engagement with neutral social non-engagement could better isolate social motivation. Second, most studies that have examined engagement per se have confounded social context with contingency, which may be differentially rewarding processes. Finally, social interaction has multiple phases that may differentially involve reward and social cognitive systems, but many interactive paradigms collapse across phases. Closing these three gaps in an interactive, naturalistic, and developmentally-salient context will offer new insight into social motivation.

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. The current paradigm's use of reciprocal sharing about real-world interests was designed to increase children's attention and interest in a naturalistic setting, especially as sharing self-relevant information is a cornerstone of 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"). In order to separate effects of social context and contingency, we also included a non-social computer control that responded contingently. 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. Further, to assess the intrinsic reward of mutual social engagement, social engagement (i.e., contingent agreement) was contrasted with non-engagement instead of disagreement. On peer non-engagement trials, children believed the social partner wanted to chat, but had to complete another task. On computer non-engagement trials, the child believed the computer had become disconnected. This design allowed us to separately test the effects of contingency (i.e., engaged vs. non-engaged replies) and social context (i.e., peer vs. computer).

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 no one (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, regions of the brain's reward circuitry—specifically VS—would be more active to the peer. Additionally, given evidence that social reward (reviewed in Ruff & Fehr, 2014) and social interaction (e.g., Coricelli & Nagel, 2009; Kampe, Frith, & Frith, 2003; Redcay et al., 2010; Rice & Redcay, 2016; Rilling et al., 2004) both engage the social cognitive network, we also hypothesized that the peer conditions would increase activation in regions associated with social processing (e.g., aSTS, dMPFC, TPJ; Saxe, 2009; 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, we conducted a set of exploratory analyses investigating age-related changes in the social cognitive network. Specifically, given evidence for functional specialization in this network during middle childhood (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. All children were recruited from a database of local families and were full-term, native English speakers. As assessed via parent report, no children had history of neurological or psychiatric disorders, first-degree relatives with autism or schizophrenia, nor any MRI contraindications. Behavioral data from all 26 children were analyzed. Data from two children were excluded from fMRI analyses due to excessive motion, yielding a final fMRI sample of 24 children (10 males, mean 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 learned that they would answer “Yes” or “No” to a statement about their likes or hobbies (e.g., “I play soccer”), which would start the conversation with the peer. The peer would see the child’s start of the exchange, and would be able to send his or her own answer 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”; Supplemental Figure 1A). Crucially, children believed that the peer was always able to see the child’s own answer. Thus, each time the child shared an answer, he or she was initiating a social bid that the peer would either respond to or not respond to.

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 the Yes-No question that the computer would randomly pick either “Yes” or “No” (Supplemental Figure 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 an answer, resulting in the word “Disconnected”.

After verifying participant comprehension, the experimenter took a photograph of the child (ostensibly to be sent to the chat partner), and showed children two photos of age- and gender-matched peers (smiling, direct gaze photos from the NIMH Child Emotional Faces Pictures Set; Egger et al., 2011; Supplemental Figure 1C). 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 feedback from desirable peers is more salient (cf. Guyer et al., 2009).

**Stimuli characteristics.**—In order to select the stimuli for the current study, we conducted a pilot behavioral study on a separate sample of typical children ( $n=12$ ) aged 7-12. Each child was presented with 168 self-relevant statements (e.g., “I like French fries”; “I play soccer”), and had a 2s response window in which to press a key indicating either “Yes” or “No”. The answer choices and response window matched those in the main neuroimaging experiment. The role of piloting was to select the self-relevant sentences that children were able to respond to within 2s, thus excluding difficult or ambiguous items. Out of the 168 piloted items, we excluded the 53 items that had the lowest response rates with the 2s window.

We next selected eight items to be Disagreement items. In order to increase the chat’s realism, we programmed the peer to disagree with the child on eight total items. For those items, the peer would respond with “That’s not what I picked,” regardless of the child’s selection. To make this disagreement plausible, we selected piloted items on which roughly 50% of children answered “Yes” and 50% answered “No.” In the main fMRI experiment, neural data were not analyzed for disagreement trials, given the low frequency of these items. After selecting the Disagreement items, the final set of 96 self-relevant statements were chosen such that average reaction time, response rate, and answer (i.e., “yes” versus “no”) were 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 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 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. Given that Initiation and Reply were yoked (i.e., a Peer Initiation could not proceed a Computer Reply), Initiation and Reply pairs were counted together as one trial for spacing and ordering. This model was tested for colinearity using AFNI’s 3dDeconvolve (Cox, 1996; <http://afni.nimh.nih.gov/>), ensuring that all beta values of interest were estimable.



A 2-6s jittered fixation cross, distributed exponentially and centered around 3.5s, was present between the Initiation and Reply portions and 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 peer's photo along with a message (e.g., "That was fun!"); Supplemental Figure 1D).

Each participant saw all 96 self-relevant statements (e.g., "I play soccer") that were chosen after piloting. What differed was the reply type (e.g., Peer Engagement) that followed the participant's response to the statement. To ensure that the same statements were not always paired with the same reply type, we created four stimuli sets, which differed in terms of which self-relevant item was assigned to which reply type. We randomly assigned participants to one of these sets. Within each run, the timing and order of the trial types was predetermined. Based on these constraints, self-relevant items were randomly assigned within the runs. The participant's stimuli set and run order were predetermined to represent all possibilities over the course of the study and—based on our behavioral pilot data—to match children's average response time and response rates across conditions (i.e., Peer versus Computer).

**Post-test questionnaire.**—The experimenter verbally administered children a 5-point Likert scale post-test questionnaire, 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. To assess belief in the live illusion, children were asked their general impressions of the experiment and whether they felt there was anything more to the study than they were told. This procedure was designed to prevent priming particular answers (Bargh & Chartrand, 2000) and is consistent with similar developmental studies (Jarcho et al., 2016). No children expressed any suspicion. As a follow-up, children were asked to describe the peer, rate whether the peer wanted to be friends, and were asked explicit questions about the peer's actions. All children generated several adjectives to describe the peer and did not express any doubts about the chat. Afterwards, children and parents were debriefed.

### 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 was four runs of the experiment (T2\*-weighted gradient echo-planar images; 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 one 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. Finally, data were spatially smoothed with a 5mm full-width half-maximum (fwhm) Gaussian kernel, a size selected given our interest in the subcortical structures linked to reward processing. Finally, functional data were intensity normalized so each voxel had a mean of 100.

Time points with excessive motion—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 at least three usable runs.

## Data Analysis

General linear models were constructed in order to estimate the response parameters for both Initiation and Reply. 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 using AFNI's BLOCK 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 time points with excessive motion were also included as regressors.

For Initiation, we analyzed Peer Initiation versus Computer Initiation. For Reply, 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 their interaction. 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 first thresholded at  $p < .001$  and then cluster corrected at  $p < .05$ . ( $k=19$ ,  $513\text{mm}^3$  using the updated version of AFNI's 3dClusSim, cf. Eklund, Nichols, & Knutsson, 2016). Cluster correction was calculated for the group mask and used first nearest-neighbor clustering.

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, we selected two VS ROIs: 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), which identified anatomically-based regions of VS with distinct patterns of functional connectivity and have been used in other studies of VS activation (e.g., Kelly et al., 2009; Kolla et al., in press; Padmanabhan et al., 2013). 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). Within each bilateral ROI, we extracted individual participant beta values and then analyzed effects across the group.

Finally, we were interested in conducting a set of exploratory analyses examining age-related changes in the social cognitive network (specifically dMPFC, TPJ, and aSTS; Saxe, 2009), given evidence this network undergoes functional specialization in middle childhood (Gweon et al., 2012). Nodes of the social cognitive network, however, are difficult to anatomically define, and therefore, we functionally-defined our ROIs by selecting clusters of the social cognitive network that showed a significant group effect during the Reply period. Specifically, we examined the thresholded group map for the Peer Reply > Computer Reply contrast and selected the relevant clusters (dMPFC, right TPJ, and bilateral aSTS; no left TPJ cluster was significant). We identified two left aSTS peaks, but 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](http://www.neurosynth.org)) as showing the stronger association with the terms “social cognitive” and “theory of mind.” After finalizing our ROIs, we then extracted each individual’s beta value for each cluster for Peer Reply > Computer Reply. We then correlated these extracted beta values with age. We also conducted follow-up analyses examining the correlation between age and beta values for the four reply types (e.g., Peer Engagement). 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, 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 scores lower than 3. 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 ranged from 3-5, with an average score of 4.19 (SD=.75). Additionally, children’s positive feelings toward the peer were higher after the experiment than at the beginning of the study (mean pre-test=3.69, mean post-test=4.23,  $t(25)=4.24$ ,  $p<.001$ ).

For 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,  $t(25)=8.75$ ,  $p<.001$ ). That is, children preferred answering self-relevant questions when they believed they were chatting with the peer. Children also reported paying more attention to the peer (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 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 were more affected by engagement status than the ratings for the Computer.

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—as with children’s preference for Peer Engagement over Non-engagement—Peer Disagreement was also preferred to Peer Non-engagement ( $t(25)=-4.12, p<.001$ ). This preference for Disagreement over Non-engagement was not seen in the Computer trials. For both Peer and Computer, Engagement was preferred to Disagreement (Peer:  $t(25)=6.91, p<.001$ ; Computer:  $t(25)=2.96, p<.01$ ).

Finally, although there were significant differences on post-test ratings, children answered 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). In addition to whole-brain analyses, we also conducted analyses using participants’ individually-extracted beta values from two anatomically-defined striatal ROIs: NAcc and ventral caudate. NAcc (mean Peer=.083; mean Computer=.052;  $t(23)=2.16, p=.042$ ) was more active when sharing with a peer, with a marginal effect in ventral caudate (mean Peer=.13; mean Computer=.089;  $t(23)=2.02, p=.055$ ). Finally, given that no whole-brain effects emerged for Initiation, we examined a set of social brain ROIs functionally defined using Peer Reply > Computer Reply. Specifically, we examined dMPFC, right TPJ, and bilateral aSTS (no significant left TPJ cluster emerged). For all four regions, there was no significant effect of sharing with a peer versus the computer ( $t<1$ ).

**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]; Figure 3; Supplemental Table 1; Supplemental Figure 2). Receiving a reply from a peer resulted in significantly higher activation in many regions, including bilateral NAcc, vMPFC, 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 > Computer-Non engagement]) did not reveal any significant clusters.

We also conducted additional whole-brain 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 social cognitive regions. Similarly, the comparison of Peer Engagement to Computer Engagement 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 the Computer replies, differential Engagement was indexed only by a cluster in left superior frontal gyrus.

In order to further test the effects of social context and contingency on VS activity, we next examined interactions between partner type and reply type in the two anatomically-defined 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), as well as evidence for an interaction ( $F(1,23)=7.23$ ,  $p=.013$ ), and a marginal effect of engagement type ( $F(1,23)=3.69$ ,  $p=.067$ ). 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 ( $t(23)=1.91$ ,  $p=.069$ ).

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 was dependent on partner type, but the ventral caudate was equally responsive to differences in Engagement across social and nonsocial 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 ( $t(23)=2.34$ ,  $p=.028$ ). An exploratory three-way repeated measures ANOVA, however, revealed that the pattern of activation for ventral caudate across conditions was not significantly different than the pattern of results for NAcc ( $F(1,23)=1.10$ ,  $p=.31$ ).

Comparing across Reply and Initiation within the anatomical VS ROIs, 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 by extracting

participants' beta values from 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 & Pelfrey, 2008; Gweon et al., 2012), we conducted additional exploratory ROI analyses examining the relation between age and response to Peer vs. Computer replies in this network. Specifically, we first examined all the clusters identified by the whole-brain Peer Reply > Computer Reply comparison, and identified those significant clusters corresponding to dMPFC, right TPJ, and bilateral aSTS (there was no significant left TPJ cluster). These particular regions were chosen given their role of social cognition (e.g., Saxe, 2009). For each individual, we extracted their contrast beta values within each cluster for this main effect of partner type and then examined the correlation between these beta values and age. The difference between Peer and Computer trials increased with age for dMPFC, right TPJ, and left aSTS (Figure 5). Post-hoc analyses revealed that this effect was driven by age-related increases to both Peer Engagement and Peer Non-Engagement in all three regions, with no significant difference between peer reply types and no significant age-related changes in response to either Computer reply type. 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 (Supplemental Figure 3). 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 ( $ps>.05$ ).

## 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 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 vs. non-engagement) and social context (i.e., peer vs. computer) would contribute to reward system activation, they would show a significant interaction such that VS would be more sensitive to contingency in a social context.

Broadly, our hypotheses were supported. Consistent with behavioral ratings indicating that children preferred interacting with the peer, fMRI data indicated increased VS recruitment for the peer versus computer both when initiating interaction and when receiving replies. Peer replies also increased activation in social cognitive regions, including right TPJ and dMPFC. Further, within these social cognitive regions, the difference between peer and computer activation increased with age, with older children showing greater response to engaged and non-engaged peer replies. Finally, in addition to behavioral and neural evidence for main effects of partner type and engagement type, there was also an interaction between contingency and social context. Specifically, for both behavioral ratings and VS activation, the effect of engagement type was greater for the social than non-social condition.

### **Social Interaction is Rewarding**

The current paradigm provides converging behavioral and neural evidence 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 for than reply period. One possible explanation for this reduced effect during initiation is that the rewarding nature of self-disclosure minimized between-condition differences, an explanation supported by 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 the choice to approach a partner, and future paradigms should employ designs in which children choose whether and when to approach peers.

In addition to the brain and behavioral evidence attesting to the rewarding nature of interaction, both levels of analysis also indicate a significant interaction between contingency and social context. A main effect of contingency emerged, indicating that contingent replies were more rewarding than their non-contingent counterparts, and behavior and neural indices of reward were larger when this contingency was embedded in a social context. Further attesting to the power of social contingency, children 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 explain the uniquely rewarding nature of interaction that begins early in development (cf. Murray & Trevarthen, 1985).

Beyond general effects of social context and contingency on reward processing, the current study also provides preliminary evidence that individual regions of the reward network may show differential responses to social reward. For example, although both NAcc and ventral caudate revealed significant main effects of social context (i.e., Peer vs. Computer), ventral caudate also showed a main effect of contingency, whereas NAcc was modulated by contingency only in social contexts. This social sensitivity is consistent with the role of NAcc in varied social behaviors (Báez-Mendoza & Shultz, 2013; Bhanji & Delgado, 2014).

Thus, although the social reward literature often discusses VS regions interchangeably, future research should incorporate greater precision (cf. Pfeifer & Allen, 2016).

In addition to analyses of VS, post-hoc examinations of bilateral amygdala indicated that the region was sensitive to engagement and social context, producing the greatest response to engaged replies from a peer. Previous 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). Developmental studies of peer evaluation, however, have not consistently found amygdala activation (Gunther Moor et al., 2010; Guyer et al., 2009), although atypical amygdala activity has been linked to social anxiety (Guyer et al., 2008) and social reticence (Jarcho et al., 2016). Thus, 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) 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; but see Spunt et al., 2015). Recent models of amygdala function have suggested that these processes may overlap in the structure's role in assessing 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 replies were contingent, suggesting that the region may be most sensitive to social contexts that elicit a reciprocal response. Ultimately, social motivation and social cognition are likely overlapping and mutually informative systems.

The pattern of results within medial prefrontal regions (i.e., vMPFC and OFC) also speaks to the respective roles of social motivation and social cognitive systems. In particular, the current paradigm identified one region of MPFC that was sensitive to contingency (OFC) and another that was sensitive to social context (vMPFC). Previous studies have consistently implicated vMPFC/OFC in tracking task-independent subjective reward (see Levy & Glimcher, 2012 for review). Although the observed activation patterns are consistent with children's reported enjoyment of both the peer condition and contingent replies, this explanation does not account for why separate regions appear to respond to contingency versus social context. One possibility is that certain subregions of medial prefrontal cortex are more sensitive to social rewards (Wallis, 2012). Future research should continue to probe the role of medial prefrontal regions in tracking reward value, especially in interactive social contexts.

Although this study's design was successful in separating social non-engagement from social exclusion, future studies should investigate how varied ratios of agreement to disagreement affect reward processing (e.g., Jarcho et al., 2016; Jones et al., 2014). One possibility is that non-engagement becomes more desirable than disagreement when the peer frequently disagrees with the child. Additionally, the current study's self-report measures of perceived reward failed to produce much variability, precluding investigation into brain-behavior relations. For example, almost all participants (88%) rated their enjoyment of chatting with the peer as a 4 or 5 out of 5. Thus, future studies of peer relations may be especially fruitful if they contain detailed self-report measures and examine how children simultaneously learn about multiple social partners, especially given the role of VS in real-



time social learning (e.g., Jarcho et al., 2015; Jones et al., 2011; 2014, but see Behrens et al., 2008).

### **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) also supported 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. One possible explanation is that the social cognitive network is involved when processing any socially-relevant information, perhaps due to cognitive elaboration about what the social partner thought of the child's answer or due to anticipated future interaction. 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 demands (Rice, Moraczewski, & Redcay, 2016).

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 the initiation period, perhaps because self-disclosure was socially salient regardless of context, or because the social cognitive system was less engaged when the child wasn't receiving a peer's message. 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 modulate links within and between reward and social cognitive networks.

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

Exploratory analyses indicated that 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 that middle childhood corresponds to functional specialization of similar regions during social tasks, such as mental state reasoning (Gweon et al., 2012) and perceiving biological motion (Carter & Peltrey, 2008). Although previous research has not found dMPFC specialization (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 find similar changes in reward regions. This finding is somewhat surprising given evidence that adolescence is a time of hyperactivity in reward circuitry (see Galván, 2010 for a review)

and that previous studies have found age-related increases in VS activity when anticipating peer evaluation (Guyer et al., 2009; Gunther Moor et al., 2010). Interestingly, however, such age-related effects did not emerge for receipt of positive evaluation (Gunther Moor et al., 2010). Thus, it is possible that VS sensitivity to unpredictable peer responses increases with age, but that this current study's lack of social rejection obscured this effect. Another possible reason for the lack of age-related changes is that such changes rely on hormonal processes (e.g., Blakemore, Burnett, & Dahl, 2010; de Macks et al., 2011; Galván 2013) 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 more sociocultural (e.g., increased social network complexity, increased social autonomy). The current study's sample size, however, requires that these findings be replicated in larger samples, ideally in longitudinal studies with 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; Liu et al., 2011), such framing may be less applicable to dynamic interaction. 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 temporal structure. Indeed, these ostensible outcomes—such as a smile—help shape that interaction and thus may also serve as anticipatory cues about other rewards to come. Future studies should employ paradigms with multiple embedded and dynamic phases. 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 for real-world social behaviors.

Overall, the current study provides behavioral and neural evidence that social cognitive and social motivational systems support on-going peer interaction in middle childhood. These systems, however, may specialize at different rates and be sensitive to different components of interaction. Ultimately, real-world social interaction contains many components not assessed in this study—including multimodal sensory perception, volitional control, and the emergent properties of 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 and atypical development, 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.

### **Supplementary Material**

Refer to Web version on PubMed Central for supplementary material.

## Acknowledgements:

We thank Katherine Calabrese and Liat Hotz for assistance with stimuli creation, Laura Anderson, Dustin Moraczewski, and Kayla Velnoskey for assistance with data collection and analysis, and the Maryland Neuroimaging Center and staff for project assistance.

**Funding:** This research was partially supported by an NSF graduate fellowship to K.R. and a UMD Research and Scholarship Award to E.R.

## References

- Adolphs R (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences*, 1191, 42–61. [PubMed: 20392275]
- Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, & Breiter HC (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, 32, 537–551. [PubMed: 11709163]
- Báez-Mendoza R, & Schultz W (2013). The role of the striatum in social behavior. *Frontiers in Neuroscience*, 7.
- Bargh JA, & Chartrand TL (2000). The mind in the middle. *Handbook of research methods in social and personality psychology*, 253–285.
- Baumeister RF, & Leary MR (1995). The need to belong: desire for interpersonal attachments as a fundamental human motivation. *Psychological Bulletin*, 117(3), 497. [PubMed: 7777651]
- Baxter MG, & Murray EA (2002). The amygdala and reward. *Nature Reviews Neuroscience*, 3, 563–573. [PubMed: 12094212]
- Behrens TE, Hunt LT, Woolrich MW, & Rushworth MF (2008). Associative learning of social value. *Nature*, 456(7219), 245–249. [PubMed: 19005555]
- Bhanji JP, & Delgado MR (2014). The social brain and reward: social information processing in the human striatum. *Wiley Interdisciplinary Reviews: Cognitive Science*, 5(1), 61–73. [PubMed: 24436728]
- Bigelow AE (1998). Infants' sensitivity to familiar imperfect contingencies in social interaction. *Infant Behavior and Development*, 21(1), 149–162.
- Bissonette GB, Burton AC, Gentry RN, Goldstein BL, Hearn TN, Barnett BR, ... & Roesch MR (2013). Separate populations of neurons in ventral striatum encode value and motivation. *PLoS One*, 8(5), e64673. [PubMed: 23724077]
- Blakemore SJ, Burnett S, & Dahl RE (2010). The role of puberty in the developing adolescent brain. *Human Brain Mapping*, 31(6), 926–933. [PubMed: 20496383]
- Bolling DZ, Pitskel NB, Deen B, Crowley MJ, Mayes LC, & Pelphrey KA (2011). Development of neural systems for processing social exclusion from childhood to adolescence. *Developmental Science*, 14(6), 1431–1444. [PubMed: 22010901]
- Brainard DH (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436. [PubMed: 9176952]
- Buhrmester D, & Prager K (1995). Patterns and functions of self-disclosure during childhood and adolescence In Rotenberg KJ (Ed.), *Disclosure processes in children and adolescents* (pp. 10–56). Cambridge: Cambridge University Press.
- Carter EJ, & Pelphrey KA (2006). School-aged children exhibit domain-specific responses to biological motion. *Social Neuroscience*, 1(3-4), 396–411. [PubMed: 18174911]
- Carskadon MA, & Acebo C (1993). A self-administered rating scale for pubertal development. *Journal of Adolescent Health*, 14(3), 190–195. [PubMed: 8323929]
- Caruana N, Brock J, & Woolgar A (2015). A frontotemporoparietal network common to initiating and responding to joint attention bids. *Neuroimage*, 108, 34–46. [PubMed: 25534111]
- Chevallier C, Kohls G, Troiani V, Brodtkin ES, & Schultz RT (2012). The social motivation theory of autism. *Trends in Cognitive Sciences*, 16(4), 231–239. [PubMed: 22425667]
- Cloutier J, Heatherton TF, Whalen PJ, & Kelley WM (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. *Journal of Cognitive Neuroscience*, 20(6), 941–951. [PubMed: 18211242]

- Collins NL, & Miller LC (1994). Self-disclosure and liking: a meta-analytic review. *Psychological Bulletin*, 116(3), 457. [PubMed: 7809308]
- Coricelli G, & Nagel R (2009). Neural correlates of depth of strategic reasoning in medial prefrontal cortex. *Proceedings of the National Academy of Sciences*, 106(23), 9163–9168.
- Cox A, Kohls G, Naples AJ, Mukerji CE, Coffman MC, Rutherford HJ, ... & McPartland JC (2015). Diminished social reward anticipation in the broad autism phenotype as revealed by event-related brain potentials. *Social Cognitive and Affective Neuroscience*, 10, 1357–1364. [PubMed: 25752905]
- Cox RW (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical research*, 29(3), 162–173. [PubMed: 8812068]
- Decety J, & Sommerville JA (2003). Shared representations between self and other: a social cognitive neuroscience view. *Trends in Cognitive Sciences*, 7(12), 527–533. [PubMed: 14643368]
- de Macks ZAO, Moor BG, Overgaauw S, Güro lu B, Dahl RE, & Crone EA (2011). Testosterone levels correspond with increased ventral striatum activation in response to monetary rewards in adolescents. *Developmental Cognitive Neuroscience*, 1(4), 506–516. [PubMed: 22436568]
- Di Martino A, Scheres A, Margulies DS, Kelly AMC, Uddin LQ, Shehzad Z, ... & Milham MP (2008). Functional connectivity of human striatum: a resting state FMRI study. *Cerebral Cortex*, 18(12), 2735–2747. [PubMed: 18400794]
- Dichter GS, Richey JA, Rittenberg AM, Sabatino A, & Bodfish JW (2012). Reward circuitry function in autism during face anticipation and outcomes. *Journal of Autism and Developmental Disorders*, 42(2), 147–160. [PubMed: 22187105]
- Egger HL, Pine DS, Nelson E, Leibenluft E, Ernst M, Towbin KE, & Angold A (2011). The NIMH Child Emotional Faces Picture Set (NIHM-ChEFS): a new set of children's facial emotion stimuli. *International Journal of Methods in Psychiatric Research*, 20(3), 145–156. [PubMed: 22547297]
- Eklund A, Nichols T, & Knutsson H (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false positive rates. *Proceedings of the National Academy of Sciences*, 113, 7900–7905.
- Farroni T, Johnson MH, Menon E, Zulian L, Faraguna D, & Csibra G (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences of the United States of America*, 102(47), 17245–17250. [PubMed: 16284255]
- Forbes EE, Hariri AR, Martin SL, Silk JS, Moyles DL, Fisher PM, Brown SM, Ryan ND, Birmaher B, Axelson DA, & Dahl RE (2009). Altered striatal activation predicting real-world positive affect in adolescent major depressive disorder. *The American Journal of Psychiatry*, 166(1), 64–73. [PubMed: 19047324]
- Galván A (2013). The teenage brain sensitivity to rewards. *Current Directions in Psychological Science*, 22(2), 88–93.
- Gordon I, Eilbott JA, Feldman R, Pelphrey KA, & Vander Wyk BC (2013). Social, reward, and attention brain networks are involved when online bids for joint attention are met with congruent versus incongruent responses. *Social Neuroscience*, 8(6), 544–554. [PubMed: 24044427]
- Gunther Moor B, van Leijenhorst L, Rombouts SA, Crone EA, & Van der Molen MW (2010). Do you like me? Neural correlates of social evaluation and developmental trajectories. *Social Neuroscience*, 5(5-6), 461–482. [PubMed: 20721813]
- Guyer AE, Benson B, Choate VR, Bar-Haim Y, Perez-Edgar K, Jarcho JM, ... & Nelson EE (2014). Lasting associations between early-childhood temperament and late-adolescent reward-circuitry response to peer feedback. *Development and Psychopathology*, 26(01), 229–243. [PubMed: 24444176]
- Guyer AE, Choate VR, Pine DS, & Nelson EE (2012). Neural circuitry underlying affective response to peer feedback in adolescence. *Social Cognitive and Affective Neuroscience*, 7(1), 81–92. [PubMed: 21828112]
- Guyer AE, Lau JY, McClure-Tone EB, Parrish J, Shiffrin ND, Reynolds RC, ... & Ernst M (2008). Amygdala and ventrolateral prefrontal cortex function during anticipated peer evaluation in pediatric social anxiety. *Archives of general psychiatry*, 65(11), 1303–1312. [PubMed: 18981342]

- Guyer AE, McClure-Tone EB, Shiffrin ND, Pine DS, & Nelson EE (2009). Probing the neural correlates of anticipated peer evaluation in adolescence. *Child Development*, 80(4), 1000–1015. [PubMed: 19630890]
- Gweon H, Dodell-Feder D, Bedny M, & Saxe R (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child Development*, 83(6), 1853–1868. [PubMed: 22849953]
- Haber SN, & Knutson B (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*, 35(1), 4–26. [PubMed: 19812543]
- Hoogendam JM, Kahn RS, Hillegers MH, van Buuren M, & Vink M (2013). Different developmental trajectories for anticipation and receipt of reward during adolescence. *Developmental Cognitive Neuroscience*, 6, 113–124. [PubMed: 24055865]
- Izuma K, Saito DN, & Sadato N (2008). Processing of social and monetary rewards in the human striatum. *Neuron*, 58(2), 284–294. [PubMed: 18439412]
- Izuma K, Saito DN, & Sadato N (2010). Processing of the incentive for social approval in the ventral striatum during charitable donation. *Journal of Cognitive Neuroscience*, 22(4), 621–631. [PubMed: 19320552]
- Izuma K (2012). The social neuroscience of reputation. *Neuroscience Research*, 72(4), 283–288. [PubMed: 22285602]
- Jarcho JM, Romer AL, Shechner T, Galvan A, Guyer AE, Leibenluft E, ... & Nelson EE (2015). Forgetting the best when predicting the worst: Preliminary observations on neural circuit function in adolescent social anxiety. *Developmental Cognitive Neuroscience*, 13, 21–31. [PubMed: 25933410]
- Jarcho JM, Davis MM, Shechner T, Degnan KA, Henderson HA, Stoddard J, ... & Nelson EE (2016). Early-childhood social reticence predicts brain function in preadolescent youths during distinct forms of peer evaluation. *Psychological science*, 27(6), 821–835. [PubMed: 27150109]
- Jones RM, Somerville LH, Li J, Ruberry EJ, Libby V, Glover G, ... & Casey BJ (2011). Behavioral and neural properties of social reinforcement learning. *The Journal of Neuroscience*, 31(37), 13039–13045. [PubMed: 21917787]
- Jones RM, Somerville LH, Li J, Ruberry EJ, Powers A, Mehta N, ... & Casey BJ (2014). Adolescent-specific patterns of behavior and neural activity during social reinforcement learning. *Cognitive, Affective, & Behavioral Neuroscience*, 14(2), 683–697.
- Kampe KK, Frith CD, & Frith U (2003). “Hey John”: signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. *Journal of Neuroscience*, 23, 5258–5263. [PubMed: 12832550]
- Kelly C, de Zubicaray G, Di Martino A, Copland DA, Reiss PT, Klein DF, ... & McMahon K (2009). L-dopa modulates functional connectivity in striatal cognitive and motor networks: a double-blind placebo-controlled study. *The Journal of Neuroscience*, 29(22), 7364–7378. [PubMed: 19494158]
- Knutson B, & Cooper JC (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, 18(4), 411–417. [PubMed: 16003117]
- Kohls G, Chevallier C, Troiani V, & Schultz RT (2012). Social ‘wanting’ dysfunction in autism: neurobiological underpinnings and treatment implications. *Journal of Neurodevelopmental Disorders*, 4(10), 1–20. [PubMed: 22958445]
- Koike T, Tanabe HC, Okazaki S, Nakagawa E, Sasaki AT, Shimada K, ... & Sadato N (2016). Neural substrates of shared attention as social memory: A hyperscanning functional magnetic resonance imaging study. *NeuroImage*, 125, 401–412. [PubMed: 26514295]
- Kolla NJ, Dunlop K, Downar J, Links P, Bagby RM, Wilson AA, ... & Meyer JH (in press). Association of Ventral Striatum Monoamine Oxidase-A Binding and Functional Connectivity in Antisocial Personality Disorder with High Impulsivity: A Positron Emission Tomography and Functional Magnetic Resonance Imaging Study. *European Neuropsychopharmacology*.
- Levy DJ, & Glimcher PW (2012). The root of all value: a neural common currency for choice. *Current Opinion in Neurobiology*, 22(6), 1027–1038. [PubMed: 22766486]
- Lin A, Adolphs R, & Rangel A (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, 7(3), 274–281. [PubMed: 21427193]

- Liu X, Hairston J, Schrier M, & Fan J (2011). Common and distinct networks underlying reward valence and processing stages: a meta-analysis of functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews*, 35(5), 1219–1236. [PubMed: 21185861]
- Masten CL, Eisenberger NI, Borofsky LA, McNealy K, Pfeifer JH, & Dapretto M (2011). Subgenual anterior cingulate responses to peer rejection: a marker of adolescents' risk for depression. *Development and psychopathology*, 23(01), 283–292. [PubMed: 21262054]
- Mills KL, Lalonde F, Clasen LS, Giedd JN, & Blakemore SJ (2014). Developmental changes in the structure of the social brain in late childhood and adolescence. *Social Cognitive and Affective Neuroscience*, 9(1), 123–131. [PubMed: 23051898]
- Montague PR, & Berns GS (2002). Neural economics and the biological substrates of valuation. *Neuron*, 36(2), 265–284. [PubMed: 12383781]
- Muhle-Karbe PS, & Krebs RM (2012). On the influence of reward on action-effect binding. *Frontiers in Psychology*, 3, 59–65. [PubMed: 22403563]
- Mundy P, & Newell L (2007). Attention, joint attention, and social cognition. *Current directions in psychological science*, 16(5), 269–274. [PubMed: 19343102]
- Murray EA (2007). The amygdala, reward and emotion. *Trends in Cognitive Sciences*, 11(11), 489–497. [PubMed: 17988930]
- Murray L, & Trevarthen C (1985). Emotional regulation of interactions between two-month-olds and their mothers In Field TM & Fox NA (Eds.), *Social perception in infants* (pp. 177–197). Norwood, NJ: Ablex.
- Oberwilling E, Schilbach L, Barisic I, Krall SC, Vogeley K, Fink GR, ... & Schulte-Rüther M (2016). Look into my eyes: Investigating joint attention using interactive eye-tracking and fMRI in a developmental sample. *NeuroImage*, 130, 248–260. [PubMed: 26892856]
- O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, & Dolan RJ (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, 41(2), 147–155. [PubMed: 12459213]
- Padmanabhan A, Lynn A, Foran W, Luna B, & O'Hearn K (2013). Age related changes in striatal resting state functional connectivity in autism. *Frontiers in Human Neuroscience*, 7, 226–241. [PubMed: 23785321]
- Pessoa L (2010). Emotion and cognition and the amygdala: from “what is it?” to “what’s to be done?” *Neuropsychologia*, 48(12), 3416–3429. [PubMed: 20619280]
- Pfeifer JH, & Allen NB (2016). The audacity of specificity: Moving adolescent developmental neuroscience towards more powerful scientific paradigms and translatable models. *Developmental Cognitive Neuroscience*, 17, 131–137. [PubMed: 26754460]
- Pfeifer JH, Lieberman MD, & Dapretto M (2007). “I know you are but what am I!?”: neural bases of self-and social knowledge retrieval in children and adults. *Journal of Cognitive Neuroscience*, 19(8), 1323–1337. [PubMed: 17651006]
- Pfeiffer UJ, Schilbach L, Timmermans B, Kuzmanovic B, Georgescu AL, Bente G, & Vogeley K (2014). Why we interact: on the functional role of the striatum in the subjective experience of social interaction. *Neuroimage*, 101, 124–137. [PubMed: 24996121]
- Rademacher L, Krach S, Kohls G, Irmak A, Gründer G, & Spreckelmeyer KN (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *Neuroimage*, 49(4), 3276–3285. [PubMed: 19913621]
- Redcay E, Dodell-Feder D, Pearrow MJ, Mavros PL, Kleiner M, Gabrieli JD, & Saxe R (2010). Live face-to-face interaction during fMRI: a new tool for social cognitive neuroscience. *Neuroimage*, 50(4), 1639–1647. [PubMed: 20096792]
- Redcay E, Dodell-Feder D, Mavros PL, Kleiner M, Pearrow MJ, Triantafyllou C, ... & Saxe R (2012). Atypical brain activation patterns during a face-to-face joint attention game in adults with autism spectrum disorder. *Human Brain Mapping*, 34(10), 2511–2532 [PubMed: 22505330]
- Rekers Y, Haun DB, & Tomasello M (2011). Children, but not chimpanzees, prefer to collaborate. *Current Biology*, 21(20), 1756–1758. [PubMed: 22000101]
- Rice K, Moraczewski D, & Redcay E (in press). Perceived live interaction modulates the developing social brain. *Social Cognitive and Affective Neuroscience*.

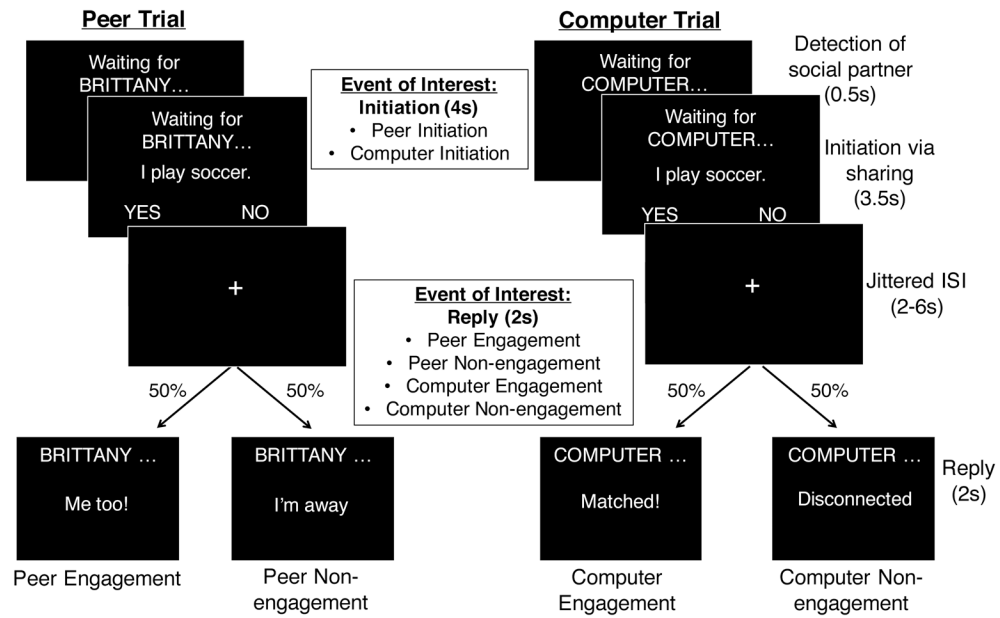


- Rice K, & Redcay E (2016). Interaction matters: A perceived social partner alters the neural processing of human speech. *NeuroImage*, 129, 480–488. [PubMed: 26608245]
- Rice K, Viscomi B, Riggins T, & Redcay E (2014). Amygdala volume linked to individual differences in mental state inference in early childhood and adulthood. *Developmental Cognitive Neuroscience*, 8, 153–163. [PubMed: 24139023]
- Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, & Cohen JD (2004). The neural correlates of theory of mind within interpersonal interactions. *Neuroimage*, 22(4), 1694–1703. [PubMed: 15275925]
- Ruff CC, & Fehr E (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*, 15(8), 549–562. [PubMed: 24986556]
- Saxe R (2009). Theory of mind (neural basis) In Banks W (Ed.), *Encyclopedia of consciousness* (pp. 401–409). Oxford: Elsevier.
- Schilbach L (2016). Towards a second-person neuropsychiatry. *Phil. Trans. R. Soc. B*, 371(1686), 20150081. [PubMed: 26644599]
- Schilbach L, Timmermans B, Reddy V, Costall A, Bente G, Schlicht T, & Vogeley K (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, 36(04), 393–414. [PubMed: 23883742]
- Schilbach L, Wilms M, Eickhoff SB, Romanzetti S, Tepest R, Bente G, ... & Vogeley K (2010). Minds made for sharing: initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience*, 22(12), 2702–2715. [PubMed: 19929761]
- Schurz M, Radua J, Aichhorn M, Richlan F, & Perner J (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience & Biobehavioral Reviews*, 42, 9–34. [PubMed: 24486722]
- Sesack SR, & Grace AA (2010). Cortico-basal ganglia reward network: microcircuitry. *Neuropsychopharmacology*, 35(1), 27–47. [PubMed: 19675534]
- Shaw P, Lawrence EJ, Radbourne C, Bramham J, Polkey CE, & David AS (2004). The impact of early and late damage to the human amygdala on 'theory of mind' reasoning. *Brain*, 127(7), 1535–1548. [PubMed: 15155523]
- Sprecher S, Treger S, Wondra JD, Hilaire N, & Wallpe K (2013). Taking turns: Reciprocal self-disclosure promotes liking in initial interactions. *Journal of Experimental Social Psychology*, 49(5), 860–866.
- Spreckelmeyer KN, Krach S, Kohls G, Rademacher L, Irmak A, Konrad K, ... & Gründer G (2009). Anticipation of monetary and social reward differently activates mesolimbic brain structures in men and women. *Social Cognitive and Affective Neuroscience*, 4(2), 158–165. [PubMed: 19174537]
- Spunt RP, Elison JT, Dufour N, Hurlemann R, Saxe R, & Adolphs R (2015). Amygdala lesions do not compromise the cortical network for false-belief reasoning. *Proceedings of the National Academy of Sciences*, 112(15), 4827–4832.
- Sroufe LA, Egeland B, & Carlson EA (1999). One social world: The integrated development of parent-child and peer relationships In Collins WA & Laursen B (Eds.), *Relationships as developmental contexts* (pp. 241–262), Mahwah, NJ: Erlbaum.
- Stefani MR, & Moghaddam B (2006). Rule learning and reward contingency are associated with dissociable patterns of dopamine activation in the rat prefrontal cortex, nucleus accumbens, and dorsal striatum. *The Journal of Neuroscience*, 26(34), 8810–8818. [PubMed: 16928870]
- Tabibnia G, Satpute AB, & Lieberman MD (2008). The sunny side of fairness preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychological Science*, 19(4), 339–347. [PubMed: 18399886]
- Tamir DI, & Mitchell JP (2012). Disclosing information about the self is intrinsically rewarding. *Proceedings of the National Academy of Sciences*, 109 (21), 8038–8043.
- Tomasello M (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Trezza V, Damsteegt R, Manduca A, Petrosino S, Van Kerkhof LW, Pasterkamp RJ, ... & Vanderschuren LJ (2012). Endocannabinoids in amygdala and nucleus accumbens mediate social play reward in adolescent rats. *The Journal of Neuroscience*, 32(43), 14899–14908. [PubMed: 23100412]

- Uematsu A, Matsui M, Tanaka C, Takahashi T, Noguchi K, Suzuki M, & Nishijo H (2012). Developmental trajectories of amygdala and hippocampus from infancy to early adulthood in healthy individuals. *PloS one*, 7(10), e46970. [PubMed: 23056545]
- Urošević S, Collins P, Muetzel R, Lim K, & Luciana M (2012). Longitudinal changes in behavioral approach system sensitivity and brain structures involved in reward processing during adolescence. *Developmental Psychology*, 48(5), 1488–1500. [PubMed: 22390662]
- Van Overwalle F (2009). Social cognition and the brain: a meta-analysis. *Human Brain Mapping*, 30(3), 829–858. [PubMed: 18381770]
- Vouloumanos A, Hauser MD, Werker JF, & Martin A (2010). The tuning of human neonates' preference for speech. *Child Development*, 81(2), 517–527. [PubMed: 20438457]
- Wallis JD (2012). Cross-species studies of orbitofrontal cortex and value-based decision-making. *Nature Neuroscience*, 15, 13–19.
- Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, & Wager TD (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature methods*, 8(8), 665–670. [PubMed: 21706013]
- Yin HH, Knowlton BJ, & Balleine BW (2006). Inactivation of dorsolateral striatum enhances sensitivity to changes in the action–outcome contingency in instrumental conditioning. *Behavioural Brain Research*, 166(2), 189–196. [PubMed: 16153716]

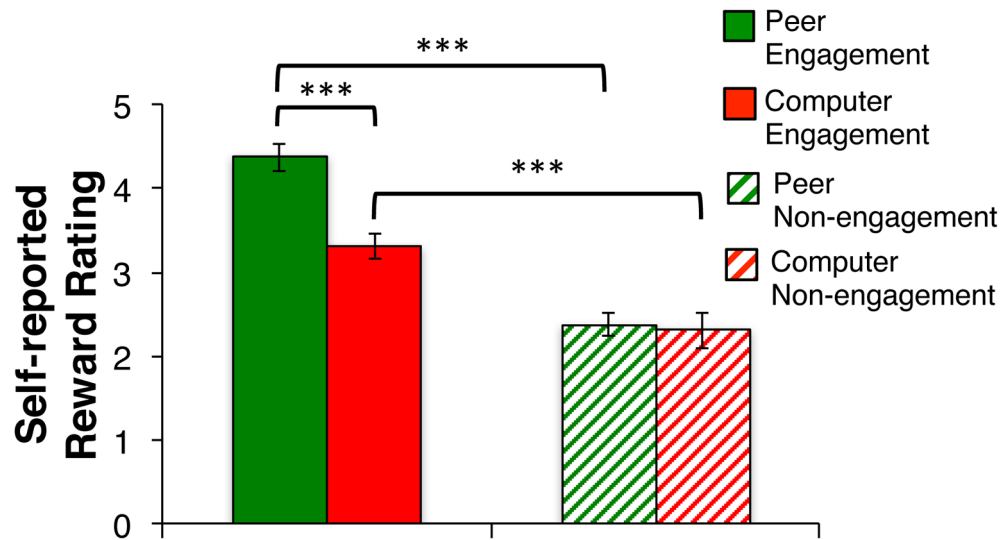
### Research Highlights

- A novel fMRI paradigm investigated social motivation when children aged 8-12 believed they were chatting with a peer and with a computer, both of which gave contingent and non-contingent replies
- Brain regions associated with reward processing and social cognition were more active when interacting with the peer versus computer
- Neural response to the peer increased with age in social cognitive regions, but not reward regions
- Reward circuitry was modulated by main effects of social context (peer vs. computer) and reply contingency as well as their interaction (i.e., social contingency)

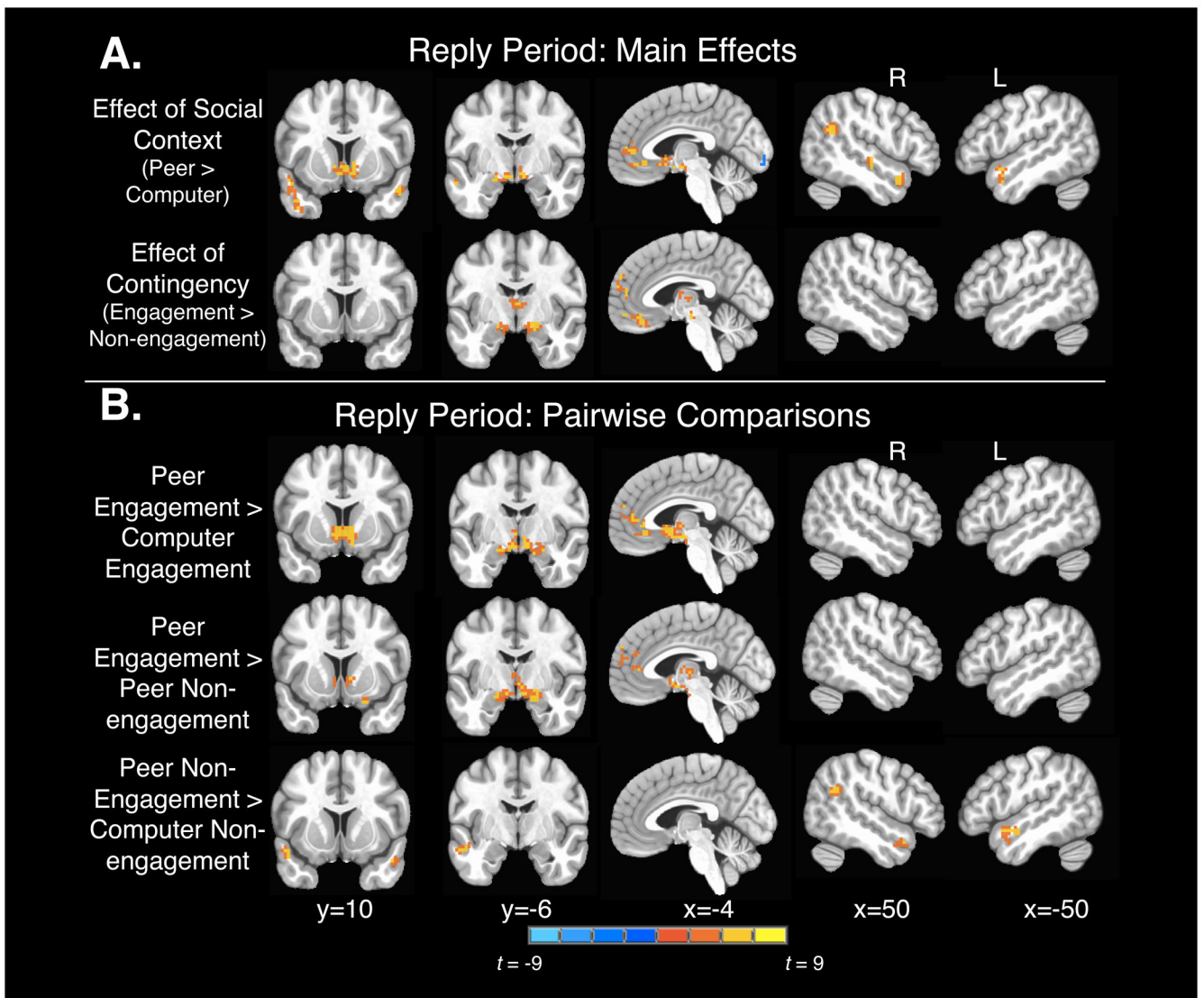


**Figure 1.**

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."



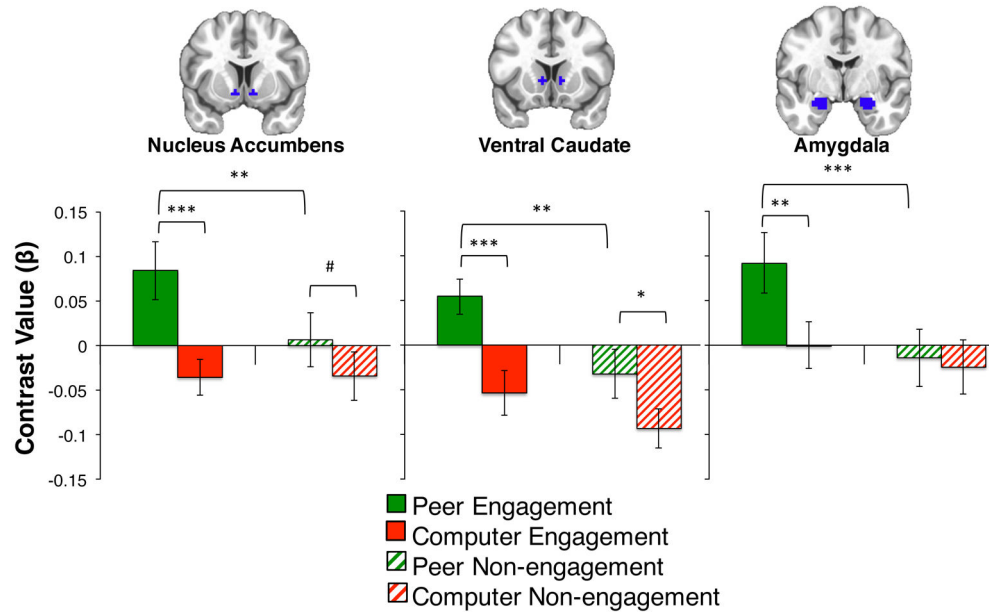
**Figure 2.** Effects of contingency and social context on subjective reward value. On a 1 to 5 Likert scale, children rated how they felt when receiving different types of replies from both peer and computer partners. Both contingency (i.e., engagement) and social context (i.e., peer) produced higher ratings of reward, with a significant interaction between the two terms. \*\*\*,  $p < .001$ .



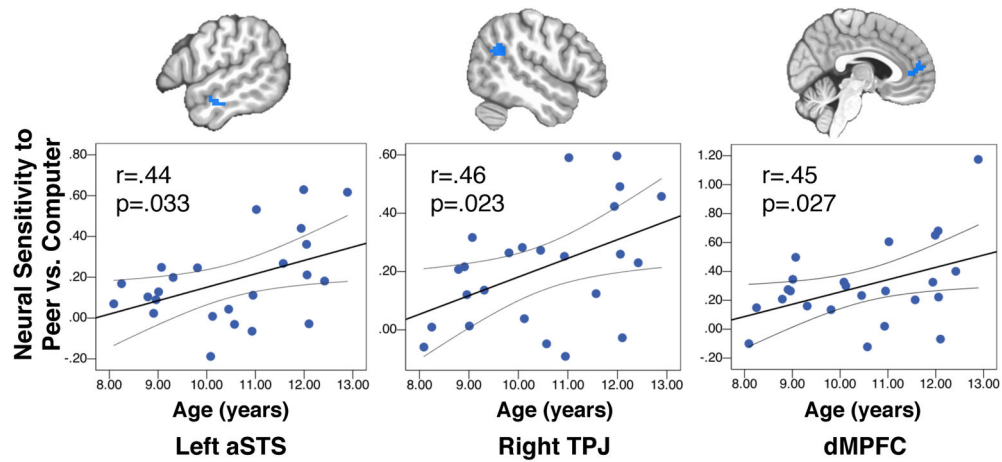
**Figure 3.**

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, vMPFC) 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).





**Figure 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  $\pm 1$  standard error. Results of 2x2 repeated-measures ANOVA are reported in the text.



**Figure 5.**

Age-related changes in sensitivity to social interaction. For Reply-period clusters identified by the whole-brain Peer>Computer comparison, we identified three significant activation clusters in social cognitive regions (i.e., left aSTS, right TPJ, dMPFC) and extracted each individual's contrast value for each cluster. The difference between Peer and Computer trials increased with age, and post-hoc analyses indicated this was driven by increased response to both Peer Engagement (e.g., “Me too”) and Peer Non-engagement (e.g., “I’m away”). Neither the anatomically- nor functionally-defined reward regions (i.e., ventral striatum) showed age related effects (Supplemental Figure 3).