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Infant Behavior and Development

journal homepage: www.elsevier.com/locate/inbede

Processing third-party social interactions in the human infant brain

Katrina Farris^{a,1}, Caroline M. Kelsey^{a,1}, Kathleen M. Krol^a, Maleen Thiele^b, Robert Hepach^c, Daniel B. Haun^b, Tobias Grossmann^{a,*}

^a Department of Psychology, University of Virginia, Charlottesville, VA, USA

^b Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

^c Department of Psychology, Oxford University, Oxford, UK

ARTICLE INFO

Keywords:

Social interaction
Social cognition
Infancy
Brain
Development

ABSTRACT

The understanding of developing social brain functions during infancy relies on research that has focused on studying how infants engage in first-person social interactions or view individual agents and their actions. Behavioral research suggests that observing and learning from third-party social interactions plays a foundational role in early social and moral development. However, the brain systems involved in observing third-party social interactions during infancy are unknown. The current study tested the hypothesis that brain systems in prefrontal and temporal cortex, previously identified in adults and children, begin to specialize in third-party social interaction processing during infancy. Infants ($N = 62$), ranging from 6 to 13 months in age, had their brain responses measured using functional near-infrared spectroscopy (fNIRS) while viewing third-party social interactions and two control conditions, infants viewing two individual actions and infants viewing inverted social interactions. The results show that infants preferentially engage brain regions localized within the dorsomedial prefrontal cortex when viewing third-party social interactions. These findings suggest that brain systems processing third-party social interaction begin to develop early in human ontogeny and may thus play a foundational role in supporting the interpretation of and learning from social interactions.

1. Introduction

Humans are intensely social beings who live in complex cooperative groups (Tomasello, 2014). One major challenge for the human brain is to develop perceptual and cognitive processes that enable us to effectively navigate this complex social environment (Adolphs, 1999; Frith & Frith, 2006). Much research has been dedicated to delineating the brain processes involved in social perception and its early development, showing that a network of brain regions, commonly referred to as the social brain, is preferentially employed when infants engage in first-person social interactions or view individual agents and their actions (Grossmann, 2015).

However, to date, little is known about the early development of the brain processes involved in observing and interpreting social interactions between agents in third-party contexts. Interpreting and learning from third-party social interactions is thought to play a foundational role in social, cognitive, and moral development (Akhtar, 2005; Rogoff, Paradise, Arauz, Correa-Chávez, & Angelillo,

* Correspondence to: Department of Psychology, University of Virginia, PO BOX 400400, Charlottesville, VA 22904, USA.

E-mail address: grossmann@virginia.edu (T. Grossmann).

¹ These authors contributed equally

<https://doi.org/10.1016/j.infbeh.2022.101727>

Received 29 September 2021; Received in revised form 25 May 2022; Accepted 25 May 2022

Available online 3 June 2022

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2003; Tomasello, 2019; Wynn & Bloom, 2014). Existing behavioral work shows that sensitive responding to third-party social interactions emerges during infancy and thus represents an early-developing feature of human social cognition (Augusti, Melinder, & Gredeback, 2010; Beier & Spelke, 2012; Gredeback & Melinder, 2010; Hamlin, Wynn, & Bloom, 2007; Powell & Spelke, 2013, 2018). Research using functional magnetic resonance imaging (fMRI) with adults shows that key brain regions implicated in social perception and mentalizing (Amodio & Frith, 2006; Frith & Frith, 2006; Pelphrey & Morris, 2006), namely, the superior temporal sulcus (STS) and the dorsomedial prefrontal cortex (dmPFC) are involved in representing and interpreting third-party social interactions (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Isik, Koldewyn, Beeler, & Kanwisher, 2017; Walbrin, Downing, & Koldewyn, 2018). For example, Isik et al. (2017) described the existence of a specialized brain system involved in processing social interactions. In this study, a specific region within the posterior STS was found to be preferentially engaged when adult participants viewed social interactions between two human agents but not when viewing pairs of human agents not interacting with each other, physical interactions between two inanimate objects, and individual (non-human) agents performing goal-directed actions, which activated different parts of the STS. Isik et al. (2017) also showed that this specific region distinguishes between prosocial (helping) and antisocial (hindering) interactions between agents, demonstrating its functional relevance in interpreting the kind of social interaction observed (see Walbrin et al., 2018, for similar results). In addition to specific responses in temporal cortex, there is evidence to show that adults also engage parts of prefrontal cortex when processing third-party social interactions (Centelles et al., 2011; Sapey-Triomphe et al., 2017). Specifically, during social interaction processing adults employ dmPFC (Centelles et al., 2011; Sapey-Triomphe et al., 2017), which is thought to be involved in attributing emotional and mental states to others (Amodio & Frith, 2006). The overall pattern of results in these studies suggests that these brain regions might underpin social-cognitive abilities enabling a complex understanding of the social environment including third-party interactions.

Humans are not the only primates with a keen interest in observing third-party social interactions. Recent work has identified brain regions in the rhesus macaque cortex that selectively respond to movies of other monkeys' social interactions (Sliwa & Freiwald, 2017). In this study, adult monkeys showed specialized responses to social interactions in the frontal and parietal cortex but, different than in human adults (Isik et al., 2017), temporal cortex responses in monkeys did not distinguish between social interactions and interactions between inanimate objects, thus suggesting that the specialization of the pSTS involvement in social interaction processing might be human-specific. Irrespective of the issue of species-specificity, based on the existing work reviewed above, a specific cortical brain system appears to exist that processes social interactions in the human adult brain, encompassing regions within the pSTS and dmPFC.

Research has also begun to investigate the development of social interaction processing brain systems in childhood (6–12 years), demonstrating that neural responses in pSTS, while being enhanced when observing third-party social interactions across the ages studied, become increasingly more specialized and localized over development continuing into adolescence (Sapey-Triomphe et al., 2017; Walbrin, Mihai, Landsiedel, & Koldewyn, 2020). Yet, the development of the brain system underpinning social interaction processing has thus far not been examined in human infancy.

Human infants preferentially orient to individual agents as seen in their behavioral (attentional) responses to faces, moving bodies, and voices from birth (Farroni et al., 2005; Farroni, Csibra, Simion, & Johnson, 2002; Simion, Regolin, & Bulf, 2008; Vouloumanos, Hauser, Werker, & Martin, 2010). Over the first year of postnatal life, these responses become more finely tuned to their social environment through experience (Grossmann, 2015; Leppanen & Nelson, 2009). Much less is known about third-party social interaction processing in infancy, but there now is an emerging body of behavioral research suggesting that infants display a sensitivity for viewing social interactions. By 6 months of age, infants begin to frequently shift their gaze between human agents when watching videos of two agents facing each other, engaging in mutual gaze and conversing, but not when viewing two people standing back-to-back, averting their gaze while talking (Augusti et al., 2010). Gaze shift patterns in infants progressively increased from 6 to 11 months of age. Similarly, starting at 9 months of age, infants more frequently shift their gaze between human agents when viewing still images of social interactions (face-to-face) than when viewing images depicting social disengagement (back-to-back) (Handl, Mahlberg, Norling, & Gredeback, 2013).

Most recently, additional evidence for infants' sensitivity to third-party social interactions comes from a study with 6-month-old infants examining differential looking times for two images, presented side-by-side each featuring two bodies in different spatial relations (Goupil, Papeo, & Hochmann, 2022). This multi-experiment study showed that infants (a) discriminated between face-to-face and back-to-back body dyads only in an upright orientation, but not when inverted, and (b) processed face-to-face dyads with higher efficiency when compared to back-to-back dyads. Moreover, this study reported that looking times for dyads displaying one body facing another without reciprocation were comparable to looking times for face-to-face dyads, and differed from looking times to back-to-back dyads, indexing unspecific detection of the presence of a relation. Critically, this study further showed that 6-month-old infants' discrimination was specific to the relation between two bodies as it was not seen when infants viewed body-object pairs. Goupil and colleagues' (2022) study, therefore, provides evidence that, by 6 months of age, infants display a sensitivity to the relative positioning of bodies in a scene, which is likely foundational for effectively processing third-party social interactions. Yet, it is not until 10 months of age that infants can discriminate between a) videos showing face-to-face mutual gaze interactions and videos of two human agents interacting back-to-back and b) social interaction and disengagement from silent videos, using habituation measures (Beier and Spelke, 2012). This study also found that it is not until 10 months of age that infants are able to form expectations about the presence of a social partner (behind an occluder) on the basis of observing social interactive cues in a third-party context.

Another line of behavioral research with preverbal infants using animated schematic agents with human eyes found that by 4.5 months of age infants prefer third-party imitators and that by 7 months of age infants expect group members to imitate each other or act alike (Powell & Spelke, 2013, 2018). Furthermore, by around 6 months of age infants distinguish between helping and hindering behaviors based on observing interactions between animated geometric shapes with human eyes, which is reflected in looking and

touching preferences directed at the helping agent by around 6 months of age (Hamlin et al., 2007). This suggests that synchronized or coordinated action when observing third-parties may serve as an early cue guiding infants' detection of and preference for affiliative third-party social interactions. Moreover, these studies further add to the behavioral evidence supporting the notion that humans' processing and sensitive responses to social interactions develop early in ontogeny (Hamlin et al., 2007; Powell & Spelke, 2013, 2018).

The existing behavioral work presented above suggests that infants develop a sensitivity to third-party, face-to-face interactions during the second half of the first year of life. However, until recently it remained unclear when exactly during infancy a behavioral preference for observing human social interactions emerges. A recent study (Thiele, Hepach, Michel, & Haun, 2021) more closely examined the developmental emergence of infants' preference for social interactions by measuring looking time using eye tracking in a visual-paired preference procedure, comparing a group of younger infants (7–8.5 months) to a group of older infants (9.5–11 months). In this study, infants were simultaneously presented with two video clips, one social interaction (face-to-face) stimulus, and one non-interactive (back-to-back) control stimulus. The social interaction stimulus showed two women turning toward each other to be face-to-face and then engaging in different kinds of synchronized social interactions. The control stimulus showed the same two women facing away from each other to be back-to-back, performing the same synchronized actions individually. This study showed that older infants preferentially looked at the social interaction stimuli, whereas younger infants did not show such a preference, indicating that a preference for watching social interaction emerges after 9 months. In the same study, this finding was replicated and extended in the second experiment in a different sample of infants (Thiele et al., 2021), showing that the preference for watching social interactions increases linearly from 7 to 13 months of age and may thus develop more continuously as experience with watching others interact increases.

The current study's main goal was to close the gap between the existing work primarily with adults demonstrating a specialized brain system involved in social interaction processing and the behavioral competencies shown by infants in detecting and using information from observing third-party social interactions. We tested the hypothesis that the brain systems localized in the dmPFC and STS begin to specialize in third-party social interaction processing during infancy. To this end, we measured infants' brain responses in these specific regions when viewing third-party social interactions and compared this to two control conditions, infants viewing two individual actions and infants viewing inverted social interactions using functional near-infrared spectroscopy (fNIRS) in a group of human infants, ranging from 6 to 13 months in age. In addition, we measured brain responses from regions in the ventromedial prefrontal cortex (vmPFC) to assess whether infants engage brain processes previously shown to be involved in first-person face-to-face social interactions (Grossmann et al., 2008; Grossmann, 2015, 2017).

2. Material and methods

A total of 62 infants (*Mage* = 8.91 months; *SD* = 2.00; Median age = 8.35 months; 30 females, 32 males) were included in the final sample used for analysis. To test age-related changes, infants less than 9 months were placed in the younger group (*n* = 35; *Mage* = 7.39 months; *SD* = 0.71 ranging in age from 6.0 months to 8.8 months) and infants 9 months and older were placed in the older group (*n* = 27; *Mage* = 10.89 months; *SD* = 1.22; ranging from 9.1 months to 13.0 months). This age group split was performed a priori based on prior behavioral work indicating that only older infants display a clear preference for social interaction when contrasting face-to-face to back-to-back synchronized actions (Thiele et al., 2021).

All participants were born at term, with normal birth weight (>2500 g), and did not have any hearing or visual impairments. Ten additional infants were tested but excluded from the present analyses because 1) they failed to reach our pre-determined looking criterion at least 60% of the trial for at least three trials per condition (*n* = 7) or 2) they were identified as statistical outliers based on their fNIRS data (*n* = 3) (see *Data Analysis* for details). Note that this attrition rate is similar to previous infant fNIRS studies, employing three or more experimental conditions (Filippetti, Lloyd-Fox, Longo, Farroni, & Johnson, 2014; Lloyd-Fox, Széplaki-Köllöd, Yin, & Csibra, 2015; Southgate, Begus, Lloyd-Fox, Gangi, & Hamilton, 2014). Participants were recruited from a large database of infants and children in a mid-sized college town in the Mid-Atlantic region of the US. All parents gave informed consent for their infants to participate and infants received a small toy for their participation. All procedures were approved by the authors' Institutional Review Board.

2.1. Stimuli

Stimuli were adapted from a previous behavioral study (Thiele et al., 2021). For the social interaction condition, video stimuli showed two women initially facing forward for 2 s before they turned towards one another (face-to-face; starting at 3 s) and engaged in one of three social interactions, playing an interactive clapping game, leaning towards one another, or touching their hands (from 3 to 12 s). The stimuli used in the current study were not normed or rated in terms of valence or arousal. However, controls were put in place for visual features of the study. In terms of luminance, stimuli were matched across the three conditions. Also, the actresses were filmed in front of a green screen to ensure that the background color (which covered a big perceptual area of the stimuli) was identical in all videos (see Thiele et al., 2021 or <https://osf.io/czv8r/> for more information regarding stimulus creation and for example stimuli). For the individual actions condition, video stimuli showed two women facing forward before they turned away from one another, performing the identical actions as in the social interaction condition individually while standing back-to-back. For the inverted social interaction condition, video stimuli from the social interaction condition were presented upside down (inverted in their orientation), which served as a perceptual control. Inversion of moving bodies effectively disrupts body third-party social interaction processing in 6-month-old infants and adults (Goupil et al., 2022; Papeo, Stein, & Soto-Faraco, 2017), thereby demonstrating that infants and adults process third-party interactions configurally. Note that physical contact between the two actresses was present in both the social

interaction and the inverted social interaction condition but not the individual action condition. All actresses wore white t-shirts and were visible from the waist up.

Five different inanimate objects (vegetables) were used as the baseline images (see Fig. 1). These baseline images have been used in previously published fNIRS studies examining face processing in infancy. A shaking rattle video clip (from Tobii software, Sweden) and accompanying audio (three tones ranging from 109 Hz to 262 Hz) were presented after three experimental trials. This was used to regain infants' attention and orient them to the center of the screen. The videos were 1920 pixels wide and 1080 pixels high.

2.2. Procedure

Infants sat on their parents' laps in a quiet, dimly lit room, at a distance of approximately 60 cm from the screen (23-inch monitor). A small plastic teething ring was available for each infant to hold during the study to increase attentiveness to the stimuli and decrease bodily movements during the experiment (Altwater-Mackensen & Grossmann, 2015; Kelsey, Krol, Kret, & Grossmann, 2019; Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015).

The experimental paradigm was designed similarly to a block design and presented using the Presentation software package (Neurobehavioral Systems, USA). Each experimental trial lasted 12 s. Each experimental trial was preceded by a brief bell sound (about 150 ms at 600 Hz) and a dynamic non-social baseline which was presented for at least six seconds but typically longer as the presentation of the next experimental trial was controlled manually by the experimenter to ensure infant attentiveness to the screen (see Grossmann, Missana, & Krol, 2018). The non-social baseline period also ensured the hemodynamic response relaxed and returned to baseline. The sequence of the presentation was pseudo-randomized so that no more than two trials of the same experimental condition would appear in a row. The entire experimental session took approximately 12 min.

2.3. Data acquisition

Infants' fNIRS data were recorded using a NIRx Nirxcout system and NirStar acquisition software. The fNIRS method quantifies concentration changes of oxygenated hemoglobin (oxy-Hb) and deoxygenated hemoglobin (deoxy-Hb) in the cerebral cortex (see Lloyd-Fox, Blasi, & Elwell, 2010). The NIRx Nirxcout system used 16 source-detector pairs (at approximately 2.5 cm distance), arranged in a total of 49 channels, and placed in an elastic cap (Easycap) located over frontal and temporal cortices in both hemispheres (see Grossmann et al., 2018). At the beginning of the appointment, head size measurements took place for each infant and a cap was selected to fit that individual infant. A series of Easycaps (one for every 2 cm increment from 38 cm to 56 cm) were used. If the infant's head circumference fell in-between the sizes, the authors would use the larger cap (e.g., 45 cm head circumference was fitted with a 46 cm cap) to allow for better probe placement on the head. The cap was placed with reference to anatomical landmarks- nasion, vertex, and inion -standardly used for EEG cap placement. Data were recorded at a sampling rate of 3.91 Hz at 760 nm and 850 nm with a power of 25 mW/wavelength. The fNIRS system automatically adjusted light intensity in order to provide optimal gain.

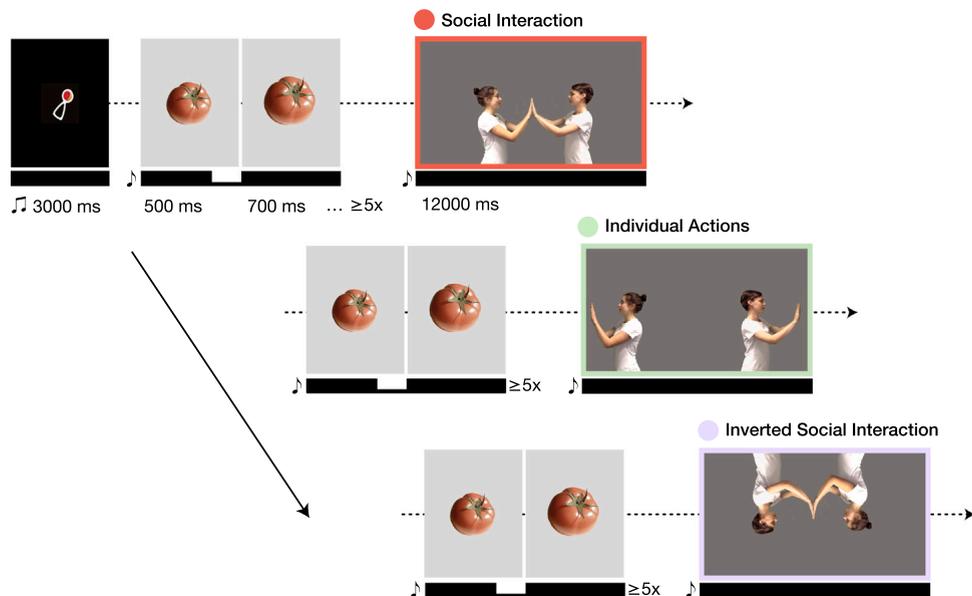


Fig. 1. fNIRS paradigm. Infants viewed 12-second video clips of two actresses in three conditions: Social Interaction, Individual Actions, and Inverted Social Interaction. Presentation blocks began with a 3-second attention-getter. All trials were preceded by at least six seconds of dynamically presented baseline (inanimate vegetable) stimuli. A single bell tone preceded both baseline and condition onset to maintain infant attention. Colored borders are shown to aid the reader in assessing the graphs below but were not presented to the infants. Stimulus duration is represented in milliseconds (ms).

2.4. Data analysis

Infants' attention to the screen during the fNIRS measurement was coded offline from video. Trials were only included if the infant looked to the screen for more than 60% of the full trial length (12 s). For infants to be included in our data analysis, they had to contribute at least 3 trials with adequate attentiveness per condition. The final sample included 62 infants that on average contributed data for a total of 23.5 trials, $SD = 7.13$ (M trials [social interaction condition] = 8.44, $SD = 2.59$; M trials [inverted social interaction condition] = 7.34, $SD = 2.52$; M trials [individual actions condition] = 7.74, $SD = 2.80$). The fNIRS data were analyzed using Homer2 adapting and extending recently published work with infants (Behrendt, Firk, Nelson, & Perdue, 2018). First, channels with very high or low optical intensity readings were excluded from further analyses (using the function `enPruneChannels`; $dRange = [1e^{-03}, 1e^{+07}]$, $SNR_{thres} = 0$, $SD_{range} = [0, .45]$). Then, the raw intensity data were converted to optical density (OD) changes. After this, a series of motion detection and correction algorithms were applied (`hmrMotionCorrectWavelet` $iqr = 0.5$; `hmrMotionCorrectPCAR` $nSV = 0.97$, $maxIter = 10$). Next, a band-pass filter (third-order Butterworth) was applied using a 0.2 Hz low-pass filter (to remove fast fluctuations related to heart rate) and a high-pass filter of 0.042 Hz (to remove changes that were too slow and related to drift). OD data were then converted to concentration changes using the modified Beer–Lambert law (Cope & Delpy, 1988; Delpy et al., 1988). Oxy-Hb and deoxy-Hb concentration changes were calculated by averaging the hemodynamic response across a 3- to 9-second time window. The time window was chosen to capture the delayed rise of the hemodynamic function in response to stimulus onset, which is typically a few seconds delayed (see also Fig. 2). Finally, two rounds of outlier detection and removal (based on being ± 3 SD above the mean for a given condition and channel) were applied to identify and remove any remaining artifacts not previously caught

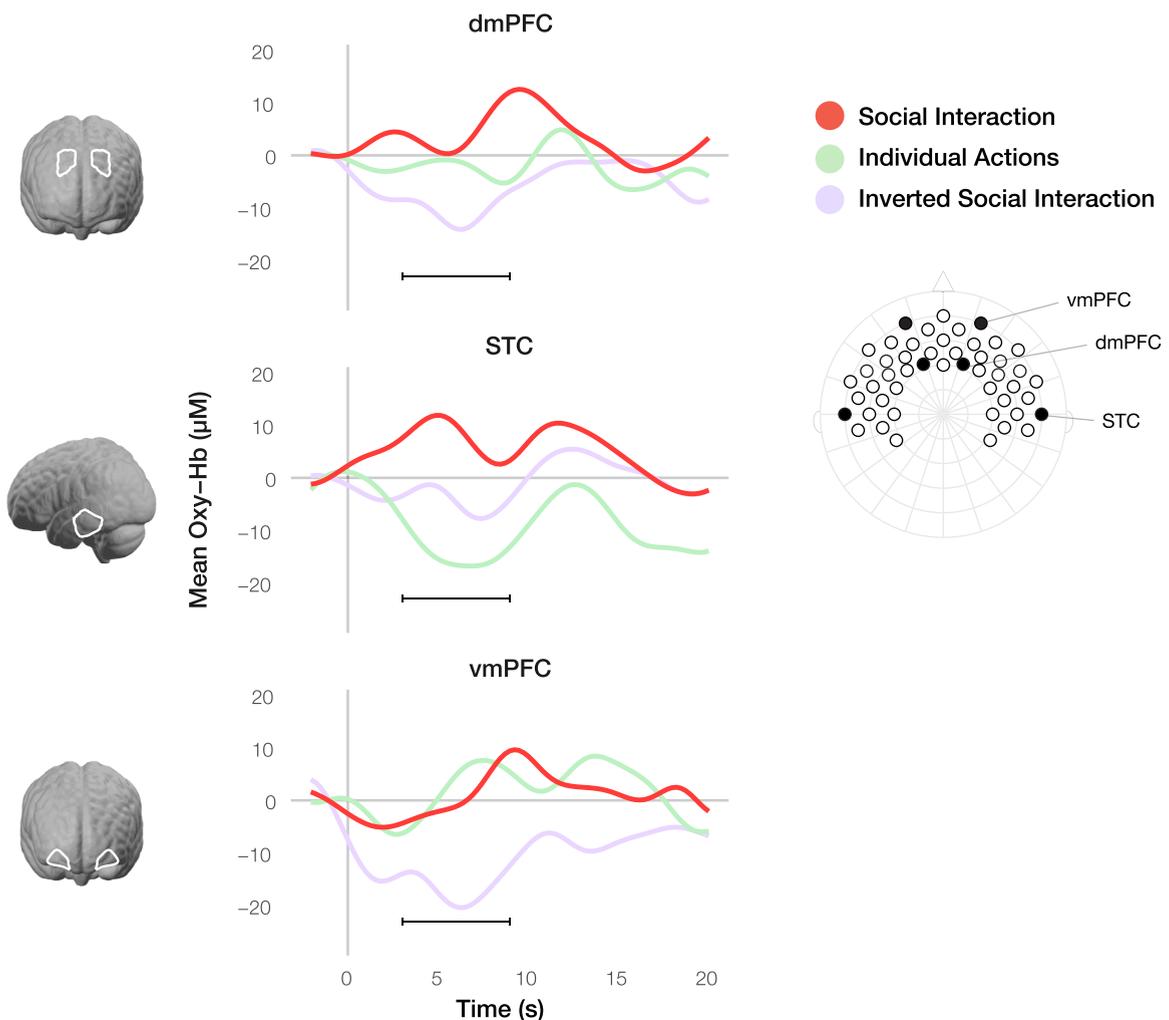


Fig. 2. Infant brain response to viewing third-party social interactions. Plotted are the group-averaged oxygenated hemoglobin (oxy-Hb) responses within dorsomedial prefrontal cortex (dmPFC; $N = 55$), superior temporal cortex (STC; $N = 50$), and ventromedial prefrontal cortex (vmPFC; $N = 52$) while viewing Social Interaction, Individual Actions, and an Inverted Social Interaction. The analyzed time window of 3–9 s is indicated by a black line. The 49-channel cap template is illustrated on the right with analyzed channels colored in black. Channels have been projected onto the cortical surface using MNI brain space for reference.

through the automatic channel exclusion. Note that we did not remove all data for any given infant but rather removed the participant's data for the given channel that did not reach this criterion.

Regions of interest were selected (see Figs. 2 and 3) to examine responses in the superior temporal cortex (STC), the dorsomedial prefrontal cortex (dmPFC), and the ventromedial prefrontal cortex (vmPFC) in both hemispheres. These regions were selected based on previously published information regarding the cortical projection of the 10–20 EEG system (Kabdebon et al., 2014) and carried out by selecting the corresponding fNIRS channels. The channels selected for the STC corresponded with the T7 and T8 electrode positions of the 10–20 EEG system review. The channels selected for the dmPFC corresponded with the F1 and F2 electrode positions of the 10–20 EEG system. The channels selected for the vmPFC corresponded with the Fp1 and Fp2 electrode positions of the 10–20 EEG system. In addition, we provide information on how the current fNIRS channel layout maps onto infant brain structure (see Supplementary Figure 1). Based on this mapping, we acknowledge that our fNIRS channel layout, though adequately suited to measure responses from dmPFC, vmPFC, and anterior regions of STS and middle temporal gyrus, might not be optimally suited to capture responses from the more posterior regions of the STS reported as specialized in social interaction processing in adults (see Isik et al., 2017). However, it should be noted that prior work also shows that neural responses to social interaction extend to anterior STS and middle temporal gyrus (Centelles et al., 2011; Sapey-Triomphe et al., 2017; Walbrin et al., 2020).

3. Results

For the dorsomedial prefrontal cortex (dmPFC), we conducted a repeated measures ANOVA with hemisphere (left, right) and condition (social interaction, two individual actions, and inverted social interaction) as within-subject factors and age (younger than 9 months, older than 9 months) as a between-subjects factor. Our analysis revealed a main effect of condition, $F(2, 106) = 3.77, p = .026$ [$p = .045$ FDR-adjusted], $\eta^2 = .066$ (see Fig. 2). Follow-up analysis showed that viewing social interactions evoked significantly greater brain responses ($M = 7.36 \mu\text{M}, SE = 4.36$) than viewing two individual actions ($M = -4.28 \mu\text{M}, SE = 3.61$), $p = .032$ [$p = .048$ FDR-adjusted], Cohen's $d = 0.32$, and viewing inverted social interactions ($M = -6.86 \mu\text{M}, SE = 5.04$), $p = .036$ [$p = .047$ FDR-adjusted], Cohen's $d = 0.33$ (see Fig. 3). Moreover, there was no significant difference in brain response found between viewing two individual actions and viewing inverted social interactions, $p = .57$. There were no other significant main effects or interaction effects, all p -values > 0.11 . Please see Supplementary Figure 4 for distributions of oxy-Hb concentration change separated by ROI and experimental condition.

For the superior temporal cortex (STC), we conducted a repeated measures ANOVA with hemisphere (left, right) and condition (social interaction, two individual actions, and inverted social interaction) as within-subject factors and age (younger than 9 months, older than 9 months) as a between-subjects factor. Our analysis revealed a main effect of condition, $F(2, 96) = 4.45, p = .014$ [$p = .034$ FDR-adjusted], $\eta^2 = .085$ (see Fig. 2 and Supplementary Figure 2 for oxy-Hb waveforms). Follow-up analysis showed that viewing social interactions evoked significantly greater brain responses ($M = 2.54 \mu\text{M}, SE = 5.75$) than viewing two individual actions ($M = -15.03 \mu\text{M}, SE = 5.35$), $p = .026$ [$p = .052$ FDR-adjusted], Cohen's $d = 0.29$ (see Fig. 3). In addition, viewing inverted social interactions evoked significantly greater brain responses ($M = -0.10 \mu\text{M}, SE = 5.08$) than viewing two individual actions, $p = .010$

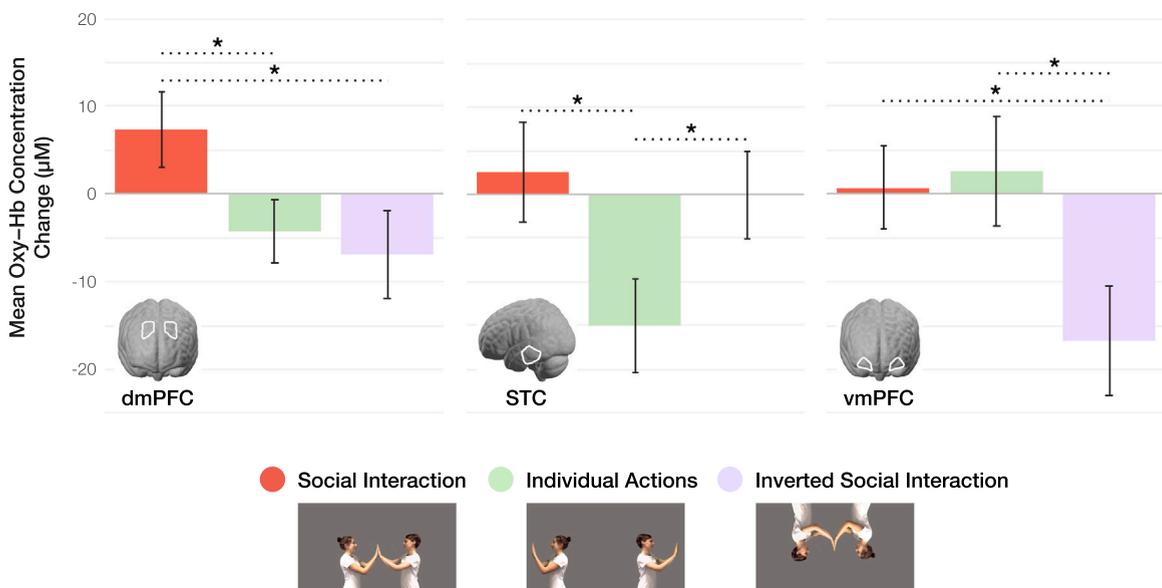


Fig. 3. Infants display enhanced brain response to third-party social interactions. Plotted is the average concentration change of oxygenated hemoglobin (oxy-Hb) in response to the three presented conditions in the dorsomedial prefrontal cortex (dmPFC; $N = 55$), superior temporal cortex (STC; $N = 50$), and ventromedial prefrontal cortex (vmPFC; $N = 52$). Both dmPFC and STC show an enhanced brain response to the upright Social Interaction stimuli. Error bars represent ± 1 standard error of the mean; * $p < .05$.

[$p = .040$ FDR-adjusted], Cohen's $d = 0.37$ (see Fig. 3). However, there was no significant difference between viewing social interactions and viewing inverted social interactions, $p = .64$. Furthermore, there was an age by hemisphere interaction, $F(1, 48) = 4.15$, $p = .047$, $\eta^2 = .080$, such that older infants ($p = .036$, $\eta^2 = .212$), but not younger infants ($p = .60$), showed a significantly greater response in the left hemisphere ($M = 7.76 \mu\text{M}$, $SE = 6.39$) compared to the right hemisphere ($M = -18.56 \mu\text{M}$, $SE = 7.44$), note that we did not consider this further as the interaction did not involve the experimental conditions (see Supplementary Figure 3 for brain responses illustrated separately by hemisphere). There were no other significant main effects or interaction effects, all p -values > 0.18 .

For the ventromedial prefrontal cortex (vmPFC), we conducted a repeated measures ANOVA with hemisphere (left, right) and condition (social interaction, two individual actions, and inverted social interaction) as within-subject factors and age (younger than 9 months, older than 9 months) as a between-subjects factor. Our analysis revealed a main effect of condition, $F(2, 100) = 5.33$, $p = .006$ [$p = .072$ FDR-adjusted], $\eta^2 = .096$ (see Fig. 2). Follow-up analysis showed that viewing social interactions ($M = .518 \mu\text{M}$, $SE = 4.81$) and viewing two individual actions ($M = 3.06 \mu\text{M}$, $SE = 6.29$) evoked significantly greater brain responses than viewing inverted social interactions ($M = -17.92 \mu\text{M}$, $SE = 5.94$); $p = .008$ [$p = .018$ FDR-adjusted], Cohen's $d = 0.44$ and $p = .012$ [$p = .018$ FDR-adjusted], Cohen's $d = 0.43$, respectively (see Fig. 3). Moreover, there was no significant difference in brain response found between viewing social interactions and two individual actions, $p = .681$. There was a significant interaction between condition and age $F(2, 100) = 4.51$, $p = .013$, $\eta^2 = .083$. Descriptive statistics (see Table 1) showed that within the younger age group (< 9 months), there were no significant differences in responses between conditions, all p 's > 0.327 . Within the older age group (> 9 months), a different pattern was obtained whereby older infants displayed greater responses to both upright presented conditions (see Table 1). Specifically, among older infants, viewing inverted social interactions resulted in significantly lower brain responses ($M = -33.25 \mu\text{M}$, $SE = 8.41$) than in both upright conditions, the individual action condition ($M = 8.58 \mu\text{M}$, $SE = 10.35$), $p = .006$, and the social interaction condition ($M = -1.70 \mu\text{M}$, $SE = 8.41$), $p = .024$. Please see Supplementary Figure 4 for distributions of oxy-Hb concentration change separated by ROI and experimental condition.

All results reported above are based on the analysis of infants' oxy-Hb responses. We did not obtain any main or interaction effects of the condition when assessing infants' deoxy-Hb responses in the same brain regions (see Supplementary Figure 5). The absence of deoxy-Hb effects is common in infant fNIRS studies (Cristia et al., 2013). Moreover, oxy-Hb is more sensitive and reliable than deoxy-Hb (Dravida, Noah, Zhang, & Hirsch, 2018) and strongly correlates with fMRI responses (Strangman, Culver, Thompson, & Boas, 2002).

4. Discussion

The current study examined the hypothesis that the brain basis for processing social interactions begins to specialize during infancy. Infants' brain responses were measured using fNIRS when viewing third-party social interactions compared to two control conditions. The results show that in infants ranging from 6 to 13 months in age, social interaction processing preferentially engages dmPFC and, with less specificity, also the STC and vmPFC. These findings suggest that these brain regions may begin to become specialized in third-party social interaction processing early in human ontogeny and might thus play a foundational role in interpreting and learning from third-party social interactions.

Specifically, the responses within the dmPFC region were enhanced when processing social interactions compared to two individual actions and inverted social interactions, providing evidence for the functional specificity of the response within this brain region. This finding concerning dmPFC involvement during social interaction processing in infants is in agreement with prior fMRI work with adults and children (Centelles et al., 2011; Walbrin et al., 2018, 2020), indexing selective responding when viewing social interactions rather than processing general social information about individual agents. Recent fNIRS work with 11-month-old infants implicates the dmPFC in social evaluation and impression formation linked to person preferences in first-party social interactions (Krol & Grossmann, 2020). It is thus possible that dmPFC involvement during third-party synchronized face-to-face action observation reflects processes associated with impression formation or social evaluation. This is particularly relevant considering work with preverbal infants showing that synchronized (imitative) action serves as a cue to affiliation and social group membership (Powell & Spelke, 2013, 2018).

There was also an interaction between the experimentally manipulated viewing condition and the age of the infant for brain responses measured from vmPFC. Specifically, there were no significant differences found in responses across conditions for younger infants (< 9 months of age). However, older infants (> 9 months of age) displayed an enhancement when viewing upright (compared to inverted) social interactions. These findings are inconsistent with previous research on infants that implicates the vmPFC in

Table 1

Infants' vmPFC responses by age group. This shows the descriptive statistics: Means and Standard Errors (SE), obtained for brain responses within ventromedial prefrontal cortex (vmPFC) separated by age group (younger than [$<$] and older [$>$] than 9 months of age).

Age	Condition	Mean	SE
< 9 months	Social Interaction	2.732	6.541
	Individual Actions	-2.465	8.545
	Inverted Interaction	-2.600	8.070
> 9 months	Social Interaction	-1.695	7.066
	Individual Actions	8.583	9.230
	Inverted Interaction	-33.247	8.716

processing first-person, face-to-face social interactions involving eye contact (Grossmann et al., 2008; Grossmann, 2015, 2017; Urakawa, Takamoto, Ishikawa, Ono, & Nishijo, 2015). For future research, it would thus be critical to directly examine this possibility by assessing the overlap (or distinctiveness) of vmPFC responses to social interaction for self (first-party) and others (third-party) throughout infancy. Furthermore, the finding that, when compared to responses to inverted social interactions, older infants showed enhanced vmPFC responses to individual actions and a lesser degree to social interactions, is difficult to interpret. One possible interpretation of the observed effect might have to do with the fact that prior work demonstrated that towards the end of the first year, infants' brain systems involved in face and body processing become specialized for upright faces and bodies (see Grossmann, 2015). Enhanced vmPFC responses to upright presented faces and bodies as seen among the group of older infants in the current study may thus represent increased specialization for face and body stimuli presented in their canonical orientation.

More generally, the current findings suggesting medial prefrontal involvement (dmPFC and vmPFC) during social interaction processing in infants support the view that medial prefrontal cortex plays a role in social cognition and may do so earlier in human development than previously thought (Amodio & Frith, 2006; Blakemore, 2008; Grossmann, 2013, 2015; Singer, 2006). This observation is in line with the notion that active engagement with the social world as evident in prefrontal involvement during social information processing in young infants may represent a precondition for social learning and development rather than an outcome of prolonged social experience (see Grossmann, 2015).

Our results further showed that similar to previous work using fMRI with adults (Isik et al., 2017), responses within the STC region were significantly enhanced when processing social interactions compared to when infants were viewing two individual actions simultaneously. This provides further support for the early developmental specialization of the brain system involved in social interaction processing and suggests that this brain system encompasses regions within the medial frontal and posterior superior temporal cortices. However, it should be mentioned that although the overall pattern of results is principally congruent with Isik et al.'s (2017) findings with adults, namely, the STC response to social interactions was greater in magnitude than in both control conditions, there was no statistically significant difference between the STC response to social and inverted social interactions. Different from previous neuroimaging work with adults, we included an inverted social interaction condition as a perceptual control (Goupil et al., 2022; Papeo et al., 2017), which contains identical visual information only differing in orientation. Considering that previous work on social interaction processing did not employ such a perceptual control, it is not possible to compare between studies. Nonetheless, the patterns in the current data suggest that dmPFC shows the clearest evidence for specificity in processing upright social interactions as it is significantly enhanced when compared to both control conditions, whereas STC responses might be less specifically tuned to social interactions presented in its canonically experienced orientation.

The difference in the selectivity for social interaction processing between dmPFC and STC might have to do with the current fNIRS channel layout, which though adequately suited to measure responses from dmPFC and anterior regions of the STC, due to our system's pre-specified geometry might not have been able to capture responses from the more posterior regions of the STS reported as specialized in social interaction processing in adults (see Isik et al., 2017). It is also conceivable that the social interaction and inverted social interaction are more salient than the individual actions due to perceptual aspects of the stimuli. In the former case, actors are centered on the screen and in the latter case, for individual actions, actors are oriented and located in the periphery. In light of prior behavioral work showing infants' early-developing preference for synchronized (imitative) actions (Powell & Spelke, 2013, 2018), another possibility is that infants' STC responses reflect their sensitivity to synchronized face-to-face action regardless of body orientation. Yet another possibility is that infants' detection of physical contact (touch) between two bodies, which was present in both the social interaction and the inverted social interaction condition but not the individual action condition, may account for the response pattern obtained in STC. Regardless, the finding that superior temporal regions in infants would show less specific response patterns to third-party social interactions is in general agreement with prior work showing protracted specialization and localization of social interaction specific responses in posterior STS during childhood (Walbrin et al., 2020).

This notion of protracted development of temporal cortex specialization to third-party social interaction in human development is further supported by the observation that this specific brain system might be unique to humans and as it is not evident in other primates (Sliwa & Freiwald, 2017). More research with human infants ideally using additional non-synchronized, social interaction stimuli without direct physical contact (e.g., eye contact) and higher resolution fNIRS imaging including the more posterior region of the STS (Frijia et al., 2021) is needed to better characterize and accurately map the development of responses to social interactions.

Contrary to what has been reported measuring behavioral attentional preferences through eyetracking using the same social interaction stimuli as in the current study (Thiele et al., 2021), infant brain responses to social interaction in dmPFC and STC did not differ as a function of age. This difference across studies with infants from a similar age range tentatively suggests that brain sensitivity for social interaction might precede behavioral (attentional) preferences. Obtaining this developmental difference between neuroimaging and behavioral results is in line with previous fNIRS work with infants revealing evidence for medial prefrontal brain systems specializing in joint attention (Grossmann & Johnson, 2010; Grossmann, Lloyd-Fox, & Johnson, 2013) well before the assumed '9-month-revolution' in social cognitive development linked to the emergence of overt joint attention behaviors (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Tomasello, 1999). Another possibility is that our fNIRS setup (see Methods) did not permit us to map responses from more posterior parts of the superior temporal cortex that are selectively engaged during third-party interaction processing in children and adults (Isik et al., 2017; Walbrin et al., 2018, 2020). Therefore, the development of behavioral preferences for social interaction during infancy might be more clearly linked to brain responses in these more posterior temporal regions. Yet another possibility is that the developmental change observed in prior behavioral work (Thiele et al., 2021) is linked to the developmental differences we obtained in infants' vmPFC responses when observing social interactions. More specifically, our PFC findings suggest that before 9 months, infants use both vmPFC and dmPFC when processing third-party social interactions, whereas after 9 months infants more selectively recruit dmPFC when processing social interactions. This developmental change in more selective

recruitment of dmPFC during social interaction processing might be linked to the developmental effect seen in prior behavioral work (Thiele et al., 2021). Future studies should combine high-resolution neuroimaging and behavioral (eye tracking) measurements in the same sample of infants to directly examine the potential link between brain and behavioral development.

5. Conclusion

Observing and learning from third-party social interactions is seen across cultures and plays a vital role in social, cognitive, and moral development during infancy and beyond. In conclusion, the current study points to the early developmental emergence of the brain systems localized in medial prefrontal and temporal cortex involved in processing others' social interactions in infancy. This supports the notion that sensitive responding to third-party social interactions represents an early-developing feature of the human social-cognitive make-up and may play a foundational role in guiding infants' learning from and about others.

Declaration of Competing Interest

None.

Acknowledgements

This research was supported by the National Science Foundation (USA) #2017229 awarded to Tobias Grossmann.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.infbeh.2022.101727](https://doi.org/10.1016/j.infbeh.2022.101727).

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