Social Perception in the Infant Brain and Its Link to Social Behavior

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Abstract

■ The current longitudinal study (n = 98) utilized a developmental cognitive neuroscience approach to examine whether and how variability in social perception is linked to social behavior in early human development. Cortical responses to processing dynamic faces were investigated using functional near-infrared spectroscopy at 7 months. Individual differences in sociability were measured using the Early Childhood Behavior Questionnaire at 18 months. Confirming previous work with infants and adults, functional near-infrared spectroscopy results show that viewing changing faces recruited superior temporal cortices in 7-month-old infants, adding to the view that this brain system is specialized in social perception from early in ontogeny. Our longitudinal results show that greater engagement of the right superior temporal cortex at 7 months predicts higher levels of sociability at 18 months. This suggests that early variability in social perception is linked to later differences in overtly displayed social behavior, providing novel longitudinal evidence for a social brain–behavior association. ■

INTRODUCTION

Extending the standard two (dorsal and ventral) visual pathway model (Goodale & Milner, 1992), a third visual pathway specialized for social perception has recently been identified (Pitcher & Ungerleider, 2021). This third pathway is located at the lateral surface of the brain, in between the ventral and dorsal pathways, processes dynamic social information, and projects into the superior temporal sulcus. Much has been learned about the developmental emergence of this third pathway in the human brain during infancy. Prior neuroimaging work with human infants using functional near-infrared spectroscopy (fNIRS) shows that superior temporal cortical regions become specialized in dynamic social perception during the first year of postnatal development (Frijia et al., 2021; Farroni et al., 2013; Lloyd-Fox et al., 2009). Cortical specialization for social perception in superior temporal cortex during infancy can be seen across cultures and demographics. Cross-cultural research extends the original work conducted with European infants in the United Kingdom to the rural Gambia and poor urban Bangladesh (Perdue et al., 2019: Lloyd-Fox et al., 2017), pointing to the universal importance of social-perceptual brain system in early human ontogeny.

With respect to the developmental emergence of this brain pathway, already newborn infants have been shown to engage posterior superior temporal regions when viewing facial actions (Farroni et al., 2013). Importantly, this study also demonstrates that the engagement of posterior superior temporal regions during social perception increases with infant age (in hours), thus suggesting that early experience and face-to-face engagement play a role in the specialization of this cortical system involved in social perception. Moreover, the existing neuroimaging work with infants suggests that posterior superior temporal brain regions are also involved in infants' processing of dynamic social information such as eye gaze, body motion, and voices (Lisboa, Queirós, et al., 2020; Grossmann, Cross, Ticini, & Daum, 2013; Lloyd-Fox, Blasi, Mercure, Elwell, & Johnson, 2012; Grossmann, Oberecker, Koch, & Friederici, 2010; Grossmann et al., 2008). Recent fNIRS work with 7-month-old infants provides direct support for infants' superior temporal cortex being specifically engaged when processing dynamic social information (Lisboa, Miguel, et al., 2020). In this study, only when viewing dynamic upright point-light walkers approaching (looming) but not when viewing inverted or nondynamic (rigid) point-light walker did infants engage their right superior temporal cortex. This study further showed that infants responded to point-light walkers that dynamically changed by looming and thereby moving from the periphery to the center of the screen, which likely required infants to utilize information from an expanded visual field. The response properties observed in studies with infants are similar to what is known from adults (Pitcher & Ungerleider, 2021). In aggregate, this attests to the notion that beginning in infancy, this brain system undergirds the perception of dynamic social information, coming from multiple sources (Grossmann, 2015, 2021). Preferential responding to changing faces in bilateral superior temporal cortex using fNIRS has also been reported in

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3-year-old children, suggesting that this brain system emerges during infancy and continues to play a role in social perception beyond infancy (Richardson et al., 2021).

Furthermore, from an individual differences perspective, there is evidence indicating that reduced engagement of superior temporal cortex seen during social perception in infancy may be linked to neurodevelopmental disorders such as autism spectrum disorder (ASD). Specifically, infants 4–6 months of age with an increased genetic risk for ASD (defined as having an older sibling diagnosed with ASD) show less selective responses during social perception in superior temporal cortex than infants with a low genetic risk (Lloyd-Fox et al., 2013). This suggests that early-developing individual variability in the third pathway for social perception exists and might represent an early risk marker of atypical neurodevelopment associated with ASD. However, it is currently unknown whether beyond these specific risk groups, variability in social perception reflected in superior temporal cortex responses in infancy is more generally predictive of observable individual differences in social behavior. Therefore, the main goal of the current study was to investigate the possibility that variability in social perceptual brain processes longitudinally predict individual differences in social behavior.

The current study conducted a preregistered reanalysis (https://osf.io/jwd37) of existing fNIRS data from 7-month-old infants (Grossmann, Missana, & Krol, 2018) by computing a contrast between dynamic face processing and inanimate object processing in superior temporal brain regions in both hemispheres. The previously published study also included an eyetracking task administered at 7 months of age, which always followed the fNIRS measurement (Grossmann et al., 2018). On the basis of prior work reviewed above (Frijia et al., 2021; Farroni et al., 2013; Lloyd-Fox et al., 2009), our prediction was that dynamic face processing recruits superior temporal cortices. We then longitudinally assessed whether variability in infants' brain responses during social perception (dynamic face processing) at 7 months of age predict social behavior, especially sociability levels, at 18 months of age. Sociability was defined as observed behaviors indicative of seeking and taking pleasure in interactions with others (Putnam, Gartstein, & Rothbart, 2006). On the basis of prior work on ASD risk reviewed above (Lloyd-Fox et al., 2013), our prediction was that superior temporal cortex responses longitudinally predict sociability levels, with greater responses being positively predictive of heightened levels of sociability.

METHODS

Participants

Ninety-eight 7-month-old infants (M_{age} = 214 days) of European descent (49 girls) participated in this study. This study represents a preregistered reanalysis (https://osf.io/jwd37) of existing fNIRS data from 7-month-old infants (Grossmann et al., 2018). The preregistration follows the preregistration template from AsPredicted.org and consists of a preregistered hypothesis, a dependent variable, conditions, and multiple regression model assessing whether superior temporal cortex responses at 7 months predict sociability levels at 18 months, exclusion criteria and sample size, but did not undergo peer review and did not specify the exact details of the analysis parameters. No formal power analysis was conducted, but the existing sample of 98 participants is exceptionally large for an infant neuroimaging study and was deemed to be sufficient for the preregistered reanalysis (https://osf.io/jwd37). All infants resided in Leipzig, a metropolitan German city of about 600,000 people. All infants were born at standard birth weight (> 2500 g) and gestational age (> 38 weeks). No medical issues regarding development were reported at the time of testing, and there was no reported history of ASD or other neurodevelopmental disorder in any of the parents or older siblings of the infants. Parents provided written informed consent and were compensated with travel money, a toy for the infant, and a printed photograph of their infant in the fNIRS cap. All procedures were approved by the Leipzig University Medical School Ethics Committee and were conducted in accordance with the Declaration of Helsinki.

fNIRS

Infants were presented with photographs of five White female participants expressing happiness, anger, fear, and neutrality. These actresses were chosen from a validated and published stimulus set (FACES Collection; Ebner, Riediger, & Lindenberger, 2010) and had expressions with average recognition accuracies at or above 93.25% (see Ebner et al., 2010, for details). Using Adobe Photoshop CS5, faces were placed inside an oval in the center of a gray background. Baseline images consisted of photographs of five inanimate objects (vegetables) provided by Otsuka and colleagues (Otsuka et al., 2007), placed centrally within the same gray background. These stimuli have been successfully used as baseline images in infant fNIRS studies concerned with face processing (Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011; Nakato et al., 2009; Otsuka et al., 2007). The visual angles of the facial and baseline stimuli were around 15.7° × 21.7° and 16.8° × 16.8°, respectively.

The experimental fNIRS paradigm consisted of blocks of three randomized trials each of happiness, anger, and fear (Grossmann et al., 2018). Each block began with an attention-getter to orient infants to the center of the screen (a video clip of a shaking rattle accompanied by sound; see Krol, Monakhov, Lai, Ebstein, & Grossmann, 2015). At the beginning of each trial, a brief 150-msec bell sound (about 600 Hz) occurred to maintain infant attention. Trial presentation was pseudorandomized such that each infant viewed every possible actress–emotion combination, no actress expressed the same emotion

consecutively, and no emotional expression was repeated more than twice in a row. Similar pseudorandomization parameters were used for the baseline stimuli such that no image served as baseline twice in a row, and every possible baseline–emotion combination was presented.

Baseline and face stimuli were presented in the following fashion to create dynamically changing visual stimulation: The baseline consisted of 6 sec of the same photograph of an inanimate object (different kinds of vegetables) changing from its original size (500 msec) to a slightly larger size (~1° increase in visual angle; 700 msec) at least five times. The face presentation consisted of 6 sec of the same actress changing from a neutral expression (500 msec) to one of three emotional expressions (700 msec) five times (emotional expressions used were angry, fearful, and happy faces; see https://doi.org/10.1371/journal.pbio.2005281.g005 for details). Note that the stimulus presentation protocol used in the current study employs pseudodynamically changing stimuli rather than naturally moving faces, which limits the ecological validity of the stimuli and comparability to prior work (Pitcher & Ungerleider, 2021).

Infant fNIRS data were recorded using a NIRScout system and NIRStar acquisition software (NIRx). A custom-built elastic cap (EasyCap) contained 32 optodes (16 sources, 16 detectors) placed at an approximately 2.5-cm distance. This arrangement comprised 49 channels (source–detector pairs) placed over frontal and temporal cortices of both hemispheres. Data were recorded at a sampling rate of 6.25 Hz. Near-infrared light was emitted at two wavelengths (760 nm and 850 nm) with a power of 20 mW/wavelength. The system automatically adjusted light intensity to provide optimal gain. ROIs were selected to analyze responses within superior temporal cortices in

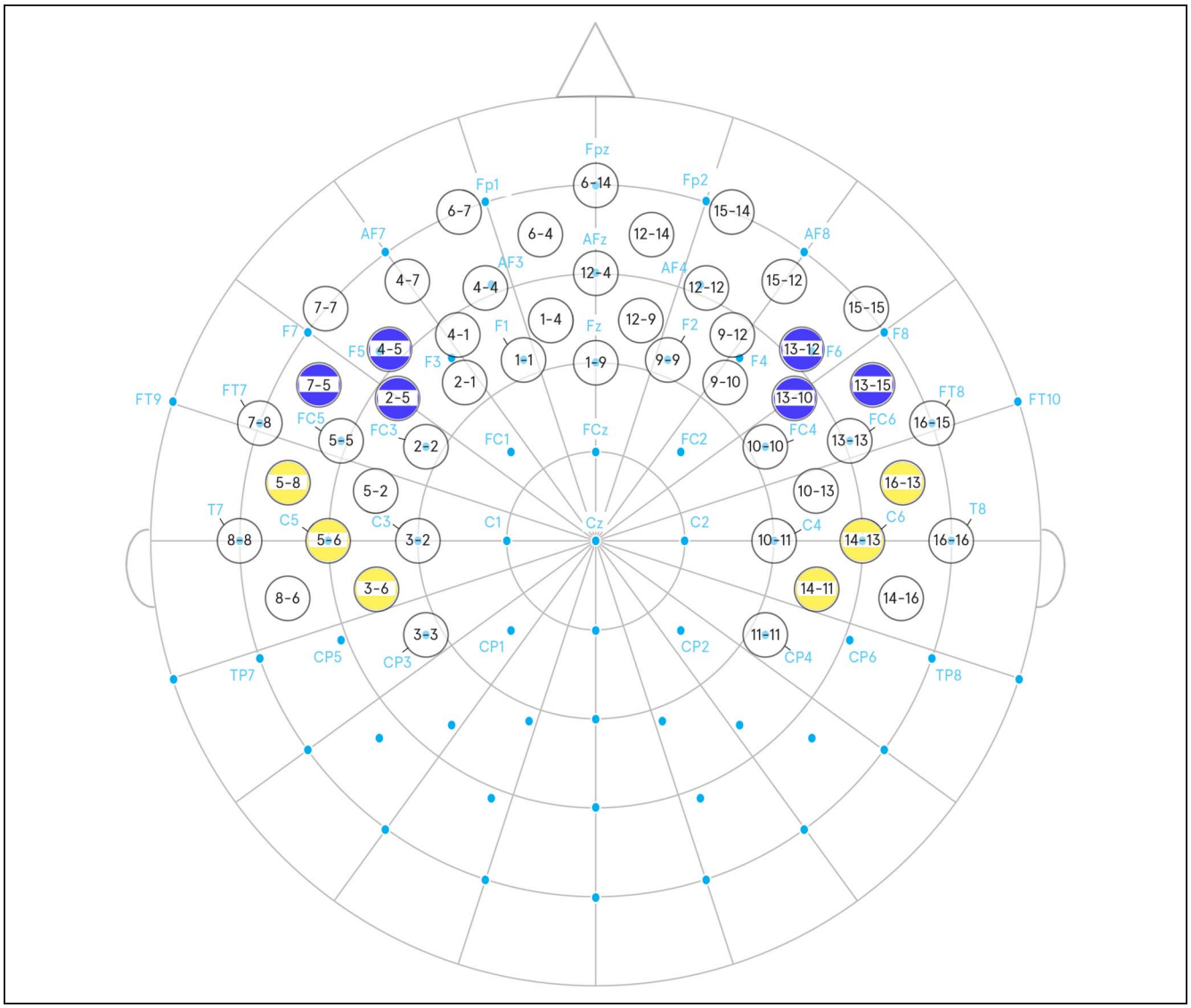

Figure 1. This shows the fNIRS channels included in the ROIs in the left and the right hemisphere with reference to the 10–10 EEG electrode placement (nose pointing up) for the superior temporal cortex ROI highlighted in yellow and for the inferior frontal cortex ROI highlighted in blue.

both hemispheres. In each hemisphere, three fNIRS channels were chosen to best capture responses from the superior temporal cortex using Kabdebon and colleagues' anatomical correlations of the infant 10–10 system (Kabdebon et al., 2014) and using nirsLAB software (NIRx), which estimates the projection of designated channels onto Montreal Neurological Institute space (see Figure 1 for channel locations included in the two ROIs). In addition, using the same approach, three fNIRS channels were chosen to capture responses from inferior frontal cortex as a control region (see Figure 1 for channel locations included in the two ROIs). Note that this approach is limited and only provides an approximate anatomical mapping based on landmarks and EEG placement methods. For an exact anatomical mapping of the fNIRS channels, it would require a co-registration approach (Lloyd-Fox et al., 2014).

Infants were seated on a parent's lap in a quiet, dimly lit room, facing a 52 × 32 cm monitor at approximately 60 cm. A camera attached to the bottom of the presentation screen recorded infant behavior for online and offline tracking of attention to each trial. The fNIRS paradigm was designed and presented in Presentation software (Neurobehavioral Systems). Videos from each session were manually coded for infant looking duration on each trial. Trials were only included if infants attended to the screen at least four of the 6 sec for which both baseline and face stimuli were presented and were visually inspected for motion artifacts. Trials with motion artifacts were removed from further analyses. Using the MATLAB (The MathWorks)-based software Nilab2 (NIRx), data were filtered with a 0.2-Hz low-pass filter to remove fluctuations because of infant heart rate and a high-pass filter of 0.083 Hz (12 sec) to remove changes too slow to be related to experimental stimuli (i.e., fluctuations because of drift). Measurements were converted into oxygenated hemoglobin (oxy-Hb) and deoxygenated hemoglobin absorption using the modified Beer–Lambert law. Boxcar functions corresponding to the four stimulus conditions were convolved with a standard hemodynamic response function based on the stimulus length parameter (Boynton, Engel, Glover, & Heeger, 1996). The average concentration changes of oxy-Hb in response to each face stimulus condition were extracted for each channel, for each individual infant.

Within each of the two ROIs (right superior temporal cortex and left superior temporal cortex), brain responses to dynamic face stimuli for each individual infant were computed by averaging across the three emotional expressions. Note that during the prestimulus baseline, inanimate objects were presented and responses to the dynamic face stimuli were baseline corrected.

Sociability

Individual differences in sociability—defined as behaviors indicative of seeking and taking pleasure in interactions with others—was measured using the sociability scale taken from the commonly used and validated Early Childhood Behavior Questionnaire (ECBQ) (Putnam et al., 2006). Children's sociability levels were determined on the basis of eight items asking parents to report on the frequency of specific observed behaviors on a 7-point, Likert-style scale ranging from "never" to "always" (see Table 1). Individual sociability scores were determined by computing the mean average of responses. To normalize scores, a *z*-transformation was applied.

Table 1. The Eight Items Taken from the ECBQ Used to Determine the Sociability Score in the Current Study

Sociability Scale (8 items)
When a familiar child came to your home, how often did your child
21. engage in an activity with the child?
22. seek out the company of the child?
When visiting the home of a familiar adult, such as a relative or friend, how often did your child
40. want to interact with the adult?
When visiting the home of a familiar child, how often did your child
84. engage in an activity with the child?
85. seek out the company of the child?
When a familiar adult, such as a relative or friend, visited your home, how often did your child
172. want to interact with the adult?
When around large gatherings of familiar adults or children, how often did your child
199. want to be involved in a group activity?
200. enjoy playing with a number of different people?

RESULTS

The current study reanalyzed existing fNIRS data from 7-month-old infants (Grossmann et al., 2018) by computing a contrast between dynamic face processing and inanimate object processing used as a baseline presented with the same frequency (50%) as the dynamically changing faces (Grossmann et al., 2018) in superior temporal brain regions in both hemispheres. From the full sample of 98 7-month-old infants, 82 infants were included in this analysis because they provided the fNIRS data required for this analysis (n = 16 failed to provide sufficient, artifact-free fNIRS data and were therefore not included). This analysis using one-sample t tests, comparing brain responses during face processing to brain responses during object processing (zero, represents the baseline condition), revealed that infants showed significant activation in superior temporal brain regions in the right hemisphere, $t(81) = 4.073$; $p = .00010$; Cohen's $d = 0.450$, and in the left hemisphere, $t(81) = 3.359$; $p = .001194$; Cohen's $d = 0.371$ (see Figure 2). This is in line with our

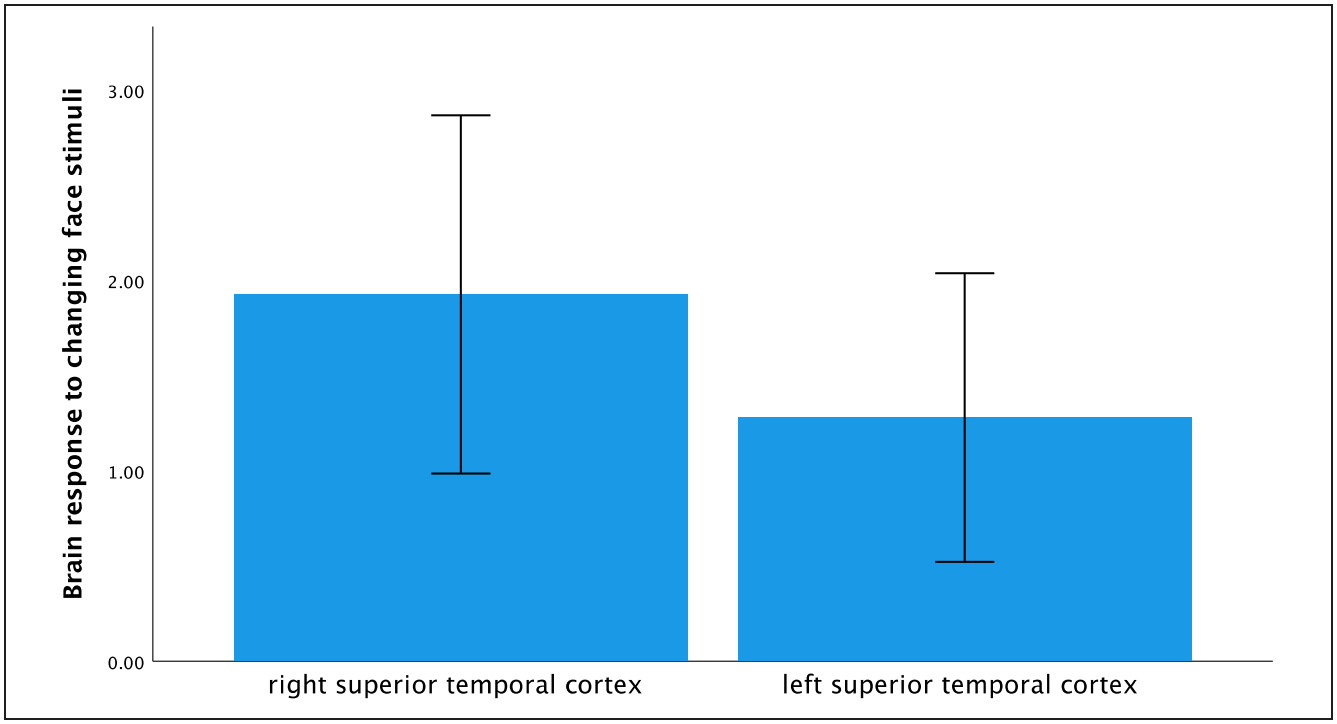

Figure 2. This shows the mean brain response (in millimolar) in the superior temporal cortex and the 95% CI for the right and the left hemisphere.

prediction that dynamic face processing recruits superior temporal cortex in both hemispheres.

We then longitudinally assessed whether infants' brain responses during social perception at 7 months of age predict sociability levels at 18 months of age by entering infants' brain responses in superior temporal cortices (left and right hemispheres) at 7 months as predictor (independent) variables into a multiple linear regression model in

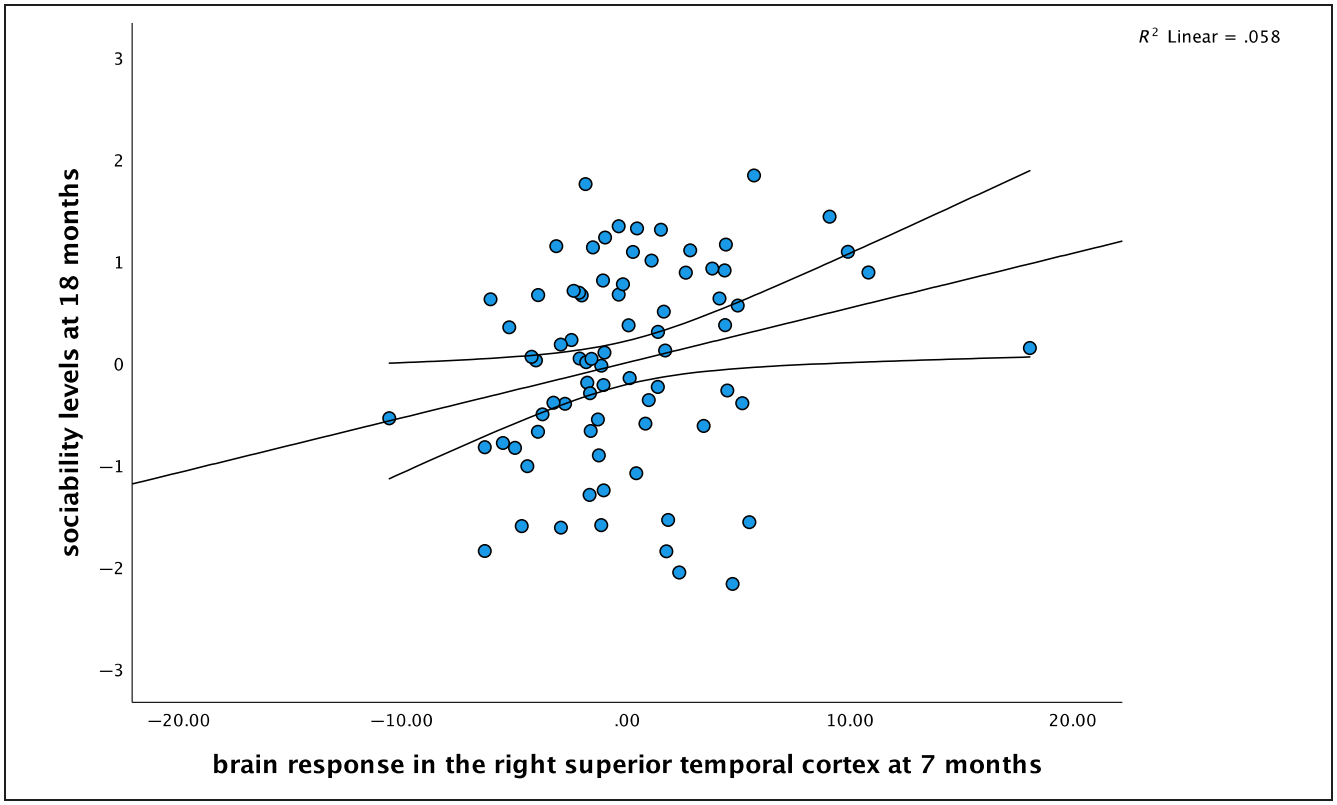

Figure 3. Partial regressions plot showing brain response in the right superior temporal cortex at 7 months (oxy-Hb in millimolar) and sociability levels (z score) at 18 months.

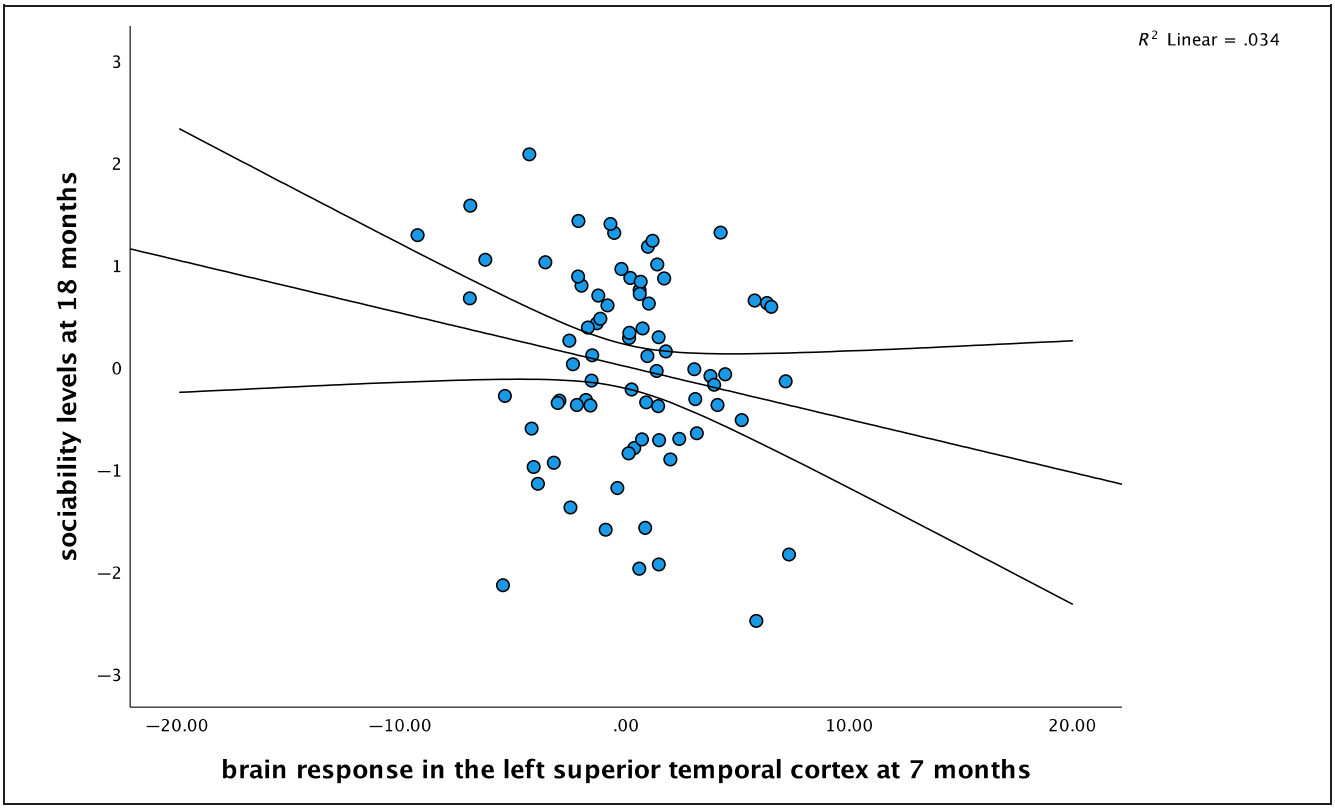

Figure 4. Partial regressions plot showing brain response in the left superior temporal cortex at 7 months (oxy-Hb in millimolar) and sociability levels (z score) at 18 months.

IBM SPSS Statistics (Version 28) and using sociability levels at 18 months as the outcome (dependent) variable. From the full sample of 98 seven-month-old infants, 77 infants were included in this analysis ($n = 16$ failed to provide sufficient, artifact-free fNIRS data and $n = 5$ failed to complete the ECBQ). This analysis revealed a significant effect for the multiple linear regression model, $F(2, 75) = 3.648$, $p = .031$, adjusted $R^2 = .064$. Specifically, the regression showed that superior temporal brain response in the right hemisphere ($\beta = 0.238$, $t = 2.156$, $p = .034$, $R^2 = .058$), but not in the left hemisphere ($\beta = -0.178$, $t = -1.613$, $p = .111$, $R^2 = .034$), predicted sociability levels (see Figures 3 and 4). Confirming our prediction, greater responses in the right superior temporal cortex at 7 months were associated with higher levels of sociability at 18 months. As an additional exploratory analysis, we repeated the longitudinal regression analysis by including maternal engagement (Grossmann et al., 2018) as an additional (control) predictor variable into the model, assessing whether infants' brain responses during social perception at 7 months of age predict sociability levels at 18 months of age. This further strengthened the effect of the multiple linear regression model, $F(2, 75) = 4.304$, $p = .008$, adjusted $R^2 = .120$. Specifically, the regression showed that superior temporal brain response in the right hemisphere ($\beta = 0.329$, $t = 2.989$, $p = .004$), but neither superior temporal brain response in the left hemisphere ($\beta = -0.215$, $t = -1.940$, $p = .056$) nor maternal engagement ($\beta = 0.047$, $t = 0.422$, $p = .674$) predicted sociability levels. This additional exploratory analysis further strengthens our findings and rules out maternal engagement as a potential covariate.

In an additional analysis, we assessed whether infants' brain responses at 7 months of age in a control region predict sociability levels at 18 months of age by entering infants' brain responses in the inferior frontal cortex (left and right hemisphere) at 7 months as predictor variables into a multiple linear regression model and using sociability levels at 18 months as the outcome variable. This analysis did not show a significant effect for the multiple linear regression model, $F(2, 75) = 0.549$, $p = .580$, adjusted $R^2 = -.012$. Specifically, the regression revealed that neither the inferior frontal brain response in the right hemisphere ($\beta = 0.118$, $t = 0.950$, $p = .345$) nor the inferior frontal brain response in the left hemisphere ($\beta = 0.005$, $t = 0.042$, $p = .967$) predicted sociability levels. This indicates that the effect was specific to the superior temporal cortex.

To ascertain the robustness of the obtained effect and its region specificity, we conducted additional analyses (not preregistered). First, we carried out a repeated-measures general linear model with brain region (superior temporal cortex vs. inferior frontal cortex) and hemisphere (left vs. right hemisphere) as within-subject

factors, and maternal engagement and sociability as between-subjects factors. This analysis revealed a three-way interaction between brain region, hemisphere, and sociability, $F(1, 71) = 8.660$, $p = .004$, $\eta^2 = .109$. Second, including all predictor variables at 7 months (superior temporal cortex in the right and the left hemisphere; inferior frontal cortex responses in the right and the left hemisphere; maternal engagement) in one multiple linear regression model, using sociability levels at 18 months as the outcome variable, revealed a significant effect for the overall multiple linear regression model, $F(5, 73) = 3.173$, $p = .012$, adjusted $R^2 = .130$. Critically, this analysis confirmed that only superior temporal brain responses in the right hemisphere at 7 months were positively associated with infants' sociability levels at 18 months ($\beta = 0.317$, $t = 2.784$, $p = .007$), ascertaining the regional and hemispheric specificity of the obtained longitudinally predictive effect.

In a follow-up analysis further assessing the reliability of the obtained effect, we performed a half-split by randomly assigning half of the participating infants to one group and the other half to another group and repeated the multiple regression analysis, including all predictor variables at 7 months in one linear regression model, using sociability levels at 18 months as the outcome variable, for each of the two groups. This analysis confirmed that, across these two groups, superior temporal brain responses in the right hemisphere at 7 months were positively associated with infants' sociability levels at 18 months. However, only for one of the groups, this positive association effect reached statistical significance (Group 1: $\beta = 0.386$, $t = 2.240$, $p = .032$; Group 2: $\beta = 0.325$, $t = 1.788$, $p = .084$).

DISCUSSION

The current longitudinal study examined the brain bases of processing dynamic faces at 7 months using fNIRS and individual differences in sociability at 18 months using parent report. Our fNIRS results show that, as conceptualized in a recently proposed model (Pitcher & Ungerleider, 2021), viewing dynamic facial movement recruited superior temporal cortices. However, it should be mentioned that the current study employs pseudodynamically changing stimuli rather than naturally moving faces, which limits the ecological validity of the stimuli and the comparability to prior work used toward formulating the proposed model (Pitcher & Ungerleider, 2021). Regardless of this issue, the obtained results provide further support for the notion that the brain systems involved in social perception emerge early in human development (Grossmann, 2015, 2021; Richardson et al., 2021; Farroni et al., 2013; Lloyd-Fox et al., 2009). Moreover, our longitudinal analysis revealed that greater engagement of the right superior temporal cortex at 7 months predicted higher levels of sociability at 18 months. This suggests that early variability in social perception is linked to later differences in overtly displayed social behavior.

Our finding that reduced engagement of the right superior temporal cortex at 7 months predicted lower levels of sociability at 18 months is in line with prior work showing that reduced responsivity in superior temporal cortex seen during social perception in infancy is linked to ASD, commonly characterized by reduced sociability (Lloyd-Fox et al., 2013). The current longitudinal study goes beyond previous cross-sectional work by showing that variability in social perception reflected in superior temporal cortex responses in infancy is predictive of individual differences in social behavior observable in toddlerhood.

It is interesting to note that our data show that only superior temporal brain responses in the right hemisphere, but not in the left hemisphere, were predictive of sociability in toddlerhood. This lateralization effect is in line with a host of neuroimaging studies with infants, showing that during the second half of the first year, infants' temporal cortex responses to social stimuli become increasingly lateralized to the right hemisphere (see Grossmann, 2015, for a review). This is also in agreement with much prior neuroimaging work with adults, suggesting a predominance of the right hemisphere in visual social perception (Pelphrey & Morris, 2006; Allison, Puce, & McCarthy, 2000). In conjunction with prior work, the current results thus suggest that increased specialization and lateralization in social perceptual brain systems links to greater levels of overtly displayed sociability during early human development. Our findings further show that the longitudinal predictive effect was specific to the superior temporal brain region as it was not seen in the inferior frontal cortex, chosen as a control region. This provides additional support for the notion that there is a specific link between social perceptual processes localized in the right superior temporal cortex and the development of sociability in toddlerhood. It is worth noting that future research on this question would benefit from taking advantage of wearable high-density diffuse optical tomography to more precisely map brain responses in superior temporal cortex during social perception in human infants (see Frijia et al., 2021).

Considering that greater sociability among toddlers was characterized by higher levels of behaviors indicative of seeking and taking pleasure in interactions with others, the current findings suggest that social perception is linked to social motivation and reward. To observe such a link early in human ontogeny provides developmental support for theories assigning a critical role to motivational processes in human social cognition (Anderson, 2016; Braver et al., 2014; Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). In this context, it is important to acknowledge that the current study design only included a measure of social motivation in toddlerhood (at 18 months) but not in infancy (at 7 months). It is therefore not possible to examine whether this link is already present in infancy. Future research would hence benefit from including measures of social motivation and

investigate its relation to social perception during infancy (Hepach, Vaish, & Tomasello, 2013).

The current study pursued a developmental cognitive neuroscience approach to further our understanding of how variability in brain function is linked to social behavior during early human development. The obtained evidence attests that social perception in infancy relies on superior temporal brain regions processing dynamic social information. Critically, our results show that variability in social perception during infancy is linked to differences in overtly displayed social behavior in toddlerhood. These findings provide novel insights into how brain and behavioral process are linked in the service of human social functioning using a longitudinal approach.

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Data Availability Statement

Data are available upon reasonable request through the following OSF link: https://osf.io/6b7yw/.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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